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**Social Structure and Mating System of Gunnison's
Prairie Dogs, *Cynomys Gunnisoni***

A Dissertation Presented

by

Jennifer Laura Verdolin

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Ecology and Evolution

Stony Brook University

May 2008

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Abstract of the Dissertation

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Social animals often show considerable intraspecific variation in their social structure, both within and between populations. This variation provides the opportunity to investigate the evolution and maintenance of animal grouping patterns and cooperation by providing insight into the adaptive value of social plasticity and the proximate mechanisms underlying different social strategies. I investigated the ecological determinants of Gunnison's prairie dog social structure and mating system in two colonies in northern Arizona. I tested whether Gunnison's prairie dog social structure was resource-based or whether male mating strategies drive the organizational patterns observed. To do so, I experimentally changed the dispersion and abundance of resources to analyze whether and how space use and social organization of Gunnison's prairie dog responded to these changes. I collected genetic data to describe patterns of relatedness among individuals within social groups, and to determine what factors influence male reproductive success and female mate choice.

In these populations of Gunnison's prairie dogs, group size was predicted by territory size and density of food available. The spatial overlap of adults within territories was positively correlated with spatial patchiness of food resources. There

was a lack of sexual dimorphism in body mass and skull morphology between males and females. Contrary to predictions of typical mammalian male mating strategies, adult females ranged significantly further than males during the mating period. Food manipulations demonstrate that Gunnison's prairie dog adults responded to changes in food dispersion by changing territory size and modifying home ranges. Results of the genetic data indicate that Gunnison's prairie dog social groups are not composed of close kin and that relatedness is not correlated with space-use in these populations. Lastly, outcomes of paternity analysis showed that resident males do not consistently have a higher frequency of siring the offspring in their territories. Results from this study support critical components of the resource dispersion hypothesis and strongly suggest that patterns of space use and group membership in Gunnison's prairie dogs are the result of individual responses to resource abundance and distribution.

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Acknowledgements

This dissertation could not have been completed without the support, encouragement and assistance of many people. I first wish to thank my committee, for without their intellectual guidance and enthusiasm this project would still be the seed of an idea. I am grateful to my advisor, Dr. Charles Janson, for his guidance and invaluable contribution to my personal and professional development. As my graduate advisor he has been a source of inspiration and an admirable individual. I am grateful for the opportunity to have been his student. I thank Dr. John True for his encouragement, support and methodological advice for the genetics portion of this dissertation. I also appreciate being allowed to use his lab supplies and space, which greatly facilitated the results presented in this dissertation. I would like to thank Dr. Patricia Wright for serving on my committee. She has inspired me to achieve greatness and I greatly value her contribution towards this manuscript. I would also like to thank my outside committee member, Dr. Kenneth Armitage, whose thoughtful critique and advice greatly improved this dissertation work. He also generously gave of his time and was a constant source of encouragement and enthusiasm.

For unbelievable field support, veterinary services, and friendship, a heartfelt thank you to Dr. David Washabau. This project could not have been completed without many people dedicating their time and effort, including Bill and Theresa Emig, Carolyn Parker, Perry Crompton, Kristen Hoss, Jessica Hagan and many others. Financial support for this work was provided by grants from the American Museum of Natural History, Sigma Xi and the American Society of Mammalogists. Charitable donations of microchips were made by Schlering-Plough and sunflower seeds were kindly provided by Western Organics, Inc. For generously allowing me use of tomahawk traps I thank Norris Dodd.

Vegetation data were analyzed in the FERTL Lab housed in the Department of Ecology and Evolution, Stony Brook University and I want to especially thank Mike Doall for always taking the time to assist me in learning the nuances of novel software. I thank the City of Flagstaff, Arizona Game and Fish Department and the

Arizona State Land Trust Department for all necessary permits and for allowing me to conduct my research on their property.

The Department of Ecology and Evolution has been an amazing department to belong to for so many reasons. Beyond the intellectually stimulating environment, there are many people that were a source of friendship and support. Most especially I want to thank Shu-dan Yeh, Ramona Walls, Melissa Mark, and Chris Jensen for their friendship and encouragement. To Martha Nolan and Iris Roth a warm and heartfelt thank you, not only for logistical support, but for kindness, friendship, and an endless supply of smiles.

Thanks to my friends and family for always believing me and encouraging me to follow my dreams. A special thank you to Dr. Constantine Slobodchikoff, whose own work inspired me and who provided me with many resources necessary to pursue and complete this work. He has been a constant mentor and friend, always there championing me and prairie dogs.

Lastly, I want to thank the prairie dogs that were the subjects of this study. There were many, but a few stand out. First there was Christmas, for her endless trust in my ability to trap, mark and otherwise manhandle her without causing injury. Christmas's daughter Tinsel was especially fun to watch and I hope wherever she moved to she is enjoying herself. Antonio was perhaps the most handsome prairie dog and I am happy I had the chance to admire him so closely for so long. Last but not least, Wiggles, my little paralyzed prairie dog. Life is tough enough and she showed me that under incredible adversity, to persevere is to live fully.

We patronize the animals for their incompleteness, for their tragic fate of having taken form so far below ourselves. And therein we err. For the animal shall not be measured by man. In a world older and more complete than ours, they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear. They are not brethren, they are not underlings; they are nations caught within ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth. –Henry Beston

Chapter One: Introduction

The evolution and maintenance of animal grouping patterns and social behavior is typically examined in the context of costs and benefits conferred to individuals (Alexander 1974; Bertram 1978; Pulliam & Caraco 1984). For birds, primates and other mammals, increased reproductive success, enhanced foraging and reduced predation risk have often been cited as ultimate factors affecting the evolution of social behavior (Hamilton 1971; Alexander 1974; Wrangham 1983). Alternatively, increased predation rates, feeding competition and infanticide may act to depress such benefits of group living (Janson 1992). All of these factors can be influenced by resource abundance and distribution (e.g., see reviews by Bradbury and Vehrencamp 1976; Alexander 1974; Lott 1991; Janson 1992; Janson and van Schaik 2000). Lott (1991) lists 28 different species of vertebrates, ranging from fish to mammals, whose social assemblages vary from solitary to group-living depending on environmental circumstances, with patterns of association between males and females

within social groups encompassing a broad range of possibilities, including monogamy, polygyny, polyandry, and multiple-male-multiple female groups.

From this observed pattern of variation, the socio-ecological model emerged as a mechanism that could integrate group level characteristics of social systems with individual behavioral decisions and strategies (Crook 1970, Emlen & Oring 1977). A fundamental assumption of the socio-ecological model is that males and females are expected to respond to different selection pressures. Female distribution is predicted to follow the distribution of resources and predation risk, whereas male distribution will be determined by the spatial and temporal availability of females. Therefore, variation in grouping patterns may reflect variation in male mammalian mating strategies as well as variation in ecological conditions.

Initial attempts to predict the relationship between the distribution of females with resources and correlated patterns of male distribution were developed by the polygyny-threshold model. The polygyny-threshold model suggests that as critical resources become more patchily distributed, thereby less easily defensible by single individuals or pairs, polygyny will emerge because only a few individuals will have very high-quality territories (Verner 1964; Orians 1969). In other words, the polygyny threshold is the point at which an unmated female will increase her fitness by mating with an already mated male (Verner and Wilson 1966). As such, this mechanism requires male territoriality to be present within a system, as well as differential territory quality among the individuals that hold them (Wittenberger 1976, 1979; Emlen and Oring 1977).

In their seminal paper Emlen and Oring (1977) expanded on the polygyny threshold model to include mammalian mating systems and introduced the environmental potential for polygyny (EPP), which sought to provide a context for understanding sexual selection and its role in mating systems. Similar to the polygyny threshold model, the thrust of their argument rests on the ability of a proportion of the population to monopolize access to mates and effectively prevent access by others. Emlen and Oring (1977) suggest that the intensity of intrasexual competition reflects the efficiency of select individuals to control access to mates. While mate access can be constrained through direct physical intervention (e.g. territorial defense, herding of mates), controlling access to resources is an indirect and common occurrence. It is in the monopolization of resources that environmental variability plays a key role by promoting or constraining the ability of individuals to control access to such resources. Essentially, the EPP emphasizes the control of mates in terms of costs and benefits, determined by the economic defensibility of resources (Brown 1964) and the energetic costs of doing so, typically reflected in the degree of parental care (Verner and Wilson 1966; Orians 1969, Trivers 1972).

Within this theoretical framework several predictions emerged. Polygyny should be present where there is economic defensibility of resources or mates, biased operational sex-ratios favoring males, sexual dimorphism as a consequence of increased male-male competition and a lack of bi-parental care skewing the potential reproductive rate in favor of males (Emlen & Oring 1977; Clutton-Brock & Vincent 1991). A lack of bi-parental care can occur whenever the advantage of both parents caring for offspring is less than two times as beneficial (Maynard Smith 1977). In the

absence of bi-parental care, the possible ‘evolutionary stable strategies’, or ESSs, that emerge from Maynard Smith’s model are either desertion by the male or female depending on the relative investment by either sex. Generally, sequential polygyny will arise when the initial high investment by females exceeds that of males. Males then benefit by deserting the female and seeking additional mating opportunities (Maynard Smith 1977).

Other mating regimes are expected to emerge when one or more of the conditions for polygyny are absent. Monogamy should occur when the temporal distribution of resources, including females, is more evenly distributed in space and time. For example, if females are the limiting sex but breeding occurs synchronously, then males will not be able to effectively control access to females, resulting in a monogamous mating system. Polyandry is fundamentally polygyny in reverse. If the conditions of polygyny are present but favor females, polyandry will emerge (Emlen and Oring 1977). A multimale-multifemale mating system is predicted to evolve when single males are unable to defend a group of females and cooperatively defending females with another male overrides the cost of sharing access to those females (Clutton-Brock 1989). It should be noted, however, that multimale-multifemale systems can evolve if the cost of excluding other males exceeds the benefit of sole access to the females. Dominance hierarchies among males within groups may form as a mechanism to reduce male-male aggression and to influence a given individual male’s reproductive success within the group (Brown 1987; Johnstone and Cant 1999; Johnstone et al. 1999).

Lastly, a lek mating system can arise when female home ranges are sufficiently large and females sufficiently mobile, that males searching for mates may do better to wait in a favorable location for females to pass by than to move in search of receptive females. These favorable locations will attract many males, which may allow females to be choosier when selecting a mate in a lek system (Bradbury and Gibson 1983). Many studies have provided empirical support for the theoretical framework of the polygyny-threshold model (Jarman 1974; Davies 1991; Nunn 1999; Dunbar 2000).

All of these strategies are influenced by the operational sex-ratio (OSR), which is defined as the number of receptive females available per sexually active male (Emlen and Oring 1977). Consequently, the OSR is often used to indicate the potential for male monopolization of females. Where females are the limiting sex, it is predicted that there will be greater opportunities for intrasexual selection on males, leading to differential reproductive success among males. Simultaneously, female choice is limited. On the other hand, even with a relatively low OSR, females may reduce intrasexual selection by breeding synchronously, effectively limiting any given male's ability to control access to females (Schwagmeyer and Brown 1983, Grant et al. 1995). Recently, Shuster and Wade (2003) have proposed an alternative method for assessing the opportunity for sexual selection on males. By calculating the mean spatial/temporal crowding of females, a direct estimate of the degree to which males may be able to secure multiple mates may be obtained.

A fundamental assumption of these models is that the observed social structure reflects the genetic mating system, making it difficult to distinguish the

selection pressures shaping each one. This confusion was caused, in part, by considering mating and social systems to be population-level properties rather than the consequences of individual strategies and by a lack of genetic data on true mating success. However, the more recent emergence of extensive studies of mating success has demonstrated that the social system and mating system of a species can be quite distinct (e.g., Davies 1991, see Lott 1991 for review). Much of the empirical work challenging early models is due to significant advances in molecular techniques that have begun to highlight instances where observed patterns of social behavior and aggregation do not accurately reflect the underlying mating system. Among mammals, such incongruence, in varying degrees, has been documented in red foxes (*Vulpes vulpes*) (Zabel & Taggart 1989), feral asses (*Equus africanus*) (Moehlman 1998), the Alpine marmot (*Marmota marmota*) (Goossens et al. 1998), Belding's ground squirrel (*Spermophilus beldingi*) (Hanken and Sherman 1981), Gunnison's prairie dogs (*Cynomys gunnisoni*) (Travis et al. 1995), meadow voles (*Microtus pennsylvanicus*) (Boonstra et al. 1993), shrews (*Sorex araneus*) (Tegelstrom et al. 1991, Stockley et al. 1993), bears (*Ursus americanus*) (Shenk and Kovacs 1995) and the agile antechinus (*Antechinus agilis*) (Kraaijeveld-Smit et al. 2002).

In species for which the social structure is incongruent with the mating system, it becomes important to consider what factors are influencing mating patterns and social organization independently. One alternative to the 'male-mating strategies' socio-ecological model is the 'resource dispersion hypothesis' (RDH). The RDH hypothesizes that the abundance and distribution pattern of critical resources may provide an alternative underlying mechanism for the evolution of group formation

(Macdonald 1983, 1984; Slobodchikoff 1984; Carr and Macdonald 1986; Slobodchikoff and Schulz 1988; Bacon et al. 1991a,b; DaSilva et al. 1993; Woodroffe and Macdonald 2000) that is independent of mating strategies. Two of the unique features that differentiate the RDH from the earlier models are 1) shared territorial defense is the primary benefit to group living and 2) no other benefits or external forces are necessary to explain group formation and maintenance.

The RDH has been criticized as an untestable hypothesis because of a lack of well-defined predictions (von Shantz 1984). As a result, its application as a mechanism for the evolution of group living has been limited. More recently, theoretical work has focused on identifying the RDH predictions, thus creating a framework for examining animal grouping patterns (Bacon et al. 1991a,b; Johnson et al. 2002). There are two characteristics of resources that are suggested to play a role in grouping behavior: (1) their abundance or richness and (2) their distribution or dispersion in space and time. The RDH broadly predicts that the abundance of resources constrains group size, while the spatial dispersion, or patchiness, of those resources directly influences territory and home range size. In addition, temporal fluctuations in resource abundance and distribution may create stochastic changes in the environment that could affect aggregation patterns and spatial organization of individuals (Maher and Lott 2000; Johnson et al. 2002). Under the RDH, the expectation is that as resources become more variable in space and time, or more heterogeneous, territory size would increase because of the need to defend larger areas that consistently contain enough food patches to satisfy even a single animal. In addition, such food patches may be productive enough, once located, to support

several individuals, so the defense of a larger territory may favor larger group sizes. Although many species demonstrate correlation patterns consistent with the RDH, many of these correlations may be due to the costs associated with competition among group members for resources. To differentiate between social aggregation patterns driven by male mating strategies and those driven by resources, more rigorous experimental studies are necessary to test the RDH in natural populations. In principle, if resources are exerting a greater influence on aggregation patterns, variation should be the result of the changes in the grouping behavior of both males and females, independent of any particular mating strategies.

Although limited, there have been some experimental studies testing the RDH. For example, by manipulating food dispersion, Sánchez-Prieto et al. (2004) found that group size increased in Iberian red deer when food was more clumped. In addition, though not specifically testing RDH, Davies and Hartley (1996) demonstrated that territory size increased with increasing food patchiness in dunnocks. Both of these studies suggest that resource dispersion plays a significant role in grouping patterns and may provide a mechanism for group formation and explain social patterns.

Given that groups form according to RDH, mating relationships within groups are likely to be determined by social status and individual preferences, both of which constrain the ability to control mates. Essentially, the mating decisions will occur within the context of the social paradigm, limiting the occurrence of individual strategies that conflict with group living, such as differential defense of resources or females by males. However, it is possible that, similar to the female-defense or resource defense polygyny models, social status within a group, in the form of

dominance among males, may still result in some males exerting control over females thereby limiting female mate choice.

The occurrence of multiple paternity can provide a framework for evaluating how individual mating strategies within a social context may be limited. For instance, although the social and mating systems may be dissimilar, the social context may still exert a strong influence on the occurrence of extra-pair copulations (EPCs). In territorial species, a male may be able to monopolize access to females through male-male competition, herding of females, or mate guarding. As additional males are added to a group, however, the ability of a single male to monopolize mating access may be compromised (Goossens et al. 1998; Cohan et al. 2006). Thus, EPCs may be more common in social groups that contain multiple males.

In contrast to males, females may be motivated to seek out EPCs regardless of how many males are present. The two primary assumptions underlying EPCs by females are that a female's choice of social mate is constrained in some way and that a male of better quality is available (Jennions and Petrie 2000). If both of these conditions are met, then the probability that a female will actively seek EPCs will increase. Although it has been established that extra-pair paternities (EPPs) occur over a broad range of species (see Griffith et al. 2002; Carling et al. 2003; Cohan et al. 2006), determining the potential selective advantage for females in seeking EPCs has been more challenging. Because it is predicted that female strategies are driven primarily by access to resources, it has been suggested that, once a basic level of resources is secured, females may mate multiply to gain additional benefits, direct or indirect. Direct benefits may include increased access to resources, such as food, or

parental care, while indirect benefits may include increased fitness of offspring through such mechanisms as higher male quality, genetic compatibility, increased genetic diversity of offspring and genetic hedge-betting (Reynolds 1996; Jennions and Petrie 2000).

Two main hypotheses have been proposed to address the potential indirect genetic benefits that females may acquire by mating multiply. First, the 'good genes' model proposes that females may choose additional mates on the basis of phenotypic traits that reflect the quality of a male. In principle, this should apply to all the males that a female mates with. Support for this model has been mixed (see Griffith et al. 2002), indicating that other processes may be influencing the occurrence of EPPs in any given system. Second, genetic compatibility has been suggested as an alternative to the 'good genes' model and predicts that females will choose extra-pair mates that enhance the genetic diversity of their offspring (Tregenza and Wendell 2000, 2002; Blomqvist et al. 2002; Mays and Hill 2004). Females may mate with males that are genetically dissimilar to themselves to increase offspring heterozygosity, which may reduce inbreeding depression, improve offspring survival and enhance competitive abilities (Brown 1997; Coltman et al. 1998; Amos et al. 2001; Hansson et al. 2001; Foerster et al. 2003).

Kinship structure can also have a profound influence on the degree and nature of social and mating patterns by influencing group size (Giraldeau and Caraco 2000), the level of cooperation (Hamilton 1964a,b), dispersal and inbreeding avoidance (Shields 1982) and the degree of reproductive skew (Vehrecomp 1983). Although genetic relatedness is not a prerequisite for social groups, kinship may influence the

degree of aggression and membership in a group (Giraldeau and Caraco 2000). Evidence indicates that as relatedness between individuals increases, aggression between them decreases (Brown and Brown 1993, Reeve and Nonacs 1997). Kin-related groups may also determine when and which other individuals join a group, thereby regulating group size (Giraldeau and Caraco 2000).

The connection between cooperation and kinship was first proposed by Hamilton (1964a,b). Hamilton suggested that the costs and benefits of social interactions are mediated by inclusive fitness through close genetic relatedness. Later, theoretical arguments focused on how sociality evolves under the constraints imposed by intersexual and intergenerational conflicts of interest in maximizing inclusive fitness (Trivers 1972, Alexander 1974). More recently, it has been suggested that high levels of cooperation within groups may be favored by factors other than kin selection, such as a mutualistic benefits and group augmentation (Cockburn 1998; Clutton-Brock 2002). Indeed, there are many species in which unrelated cooperative groups form and where the individual fitness of all group members is enhanced (Cockburn 1998; Clutton-Brock 2002), suggesting that kin selection is not the only evolutionary mechanism that results in cooperative behavior.

Because many species exhibit between- and within-population variation in sociality, kinship structure and mating strategies, ground-dwelling squirrels have been, and continue to be, an excellent study system for investigating the evolution of sociality, mating systems, and kin selection (Armitage 1981, Hoogland 1981, Michener 1983). By focusing on the intraspecific variation present in Gunnison's prairie dogs (*Cynomys gunnisoni*), this study will contribute new information on the

social dynamics of prairie dogs and highlight potentially important differences between mating strategies and social strategies. Gunnison's prairie dog populations show significant variation in group size and composition among territories, including single male-single female, single male-multifemale, single female-multimale and multimale-multifemale groups. They have high levels of multiple paternity regardless of group size and sex ratio on a territory; over 60% of pups born to any given female are not sired by the resident male or males on her territory (Travis et al. 1995, 1996; Haynie et al. 2003). These data suggest that for Gunnison's prairie dogs, the mechanisms driving the social structure and mating system may not be closely related. Despite the prevalence of variation in group composition and the relatively high frequency of multiple paternity, Gunnison's prairie dog males have often been characterized as pursuing a female defense strategy (Fitzgerald & Lechleitner 1974; Rayor 1988; Hoogland 1999). Overall, this pattern differs markedly from the social system reported for other ground squirrels. Typically, other ground squirrels, such as Columbian ground squirrels (*Spermophilus columbiana*), yellow-bellied marmots (*Marmota flaviventris*), Belding's ground squirrels (*Spermophilus beldingi*), California ground squirrels (*Spermophilus beecheyi*), and black-tailed prairie dogs (*Cynomys ludovicianus*) are characterized as resource-based polygynous mating systems with male-biased dispersal, leading to matrilineal social units forming the core social unit (Holekamp 1984; Hoogland 1981, 1995; Wigget and Boag, 1992).

This dissertation investigated whether male mating strategies, resources (as predicted by the RDH), or kinship drive the social organization patterns observed in Gunnison's prairie dogs.

In Chapter Two, I re-examined the social structure of Gunnison's prairie dogs observed in two populations near Flagstaff, Arizona, within the framework of the predictions put forth by the socio-ecological and RDH models.

In Chapter Three, I experimentally tested if and how Gunnison's prairie dog space-use and social organization responded to changes in the dispersion and abundance of resources through a series of food manipulations.

In Chapter Four, I evaluated the mating system of the Gunnison's prairie dog, using six microsatellites, to determine whether the reproductive success of resident males is greater than non-residents.

In Chapter Five I evaluated the role of kinship in group composition and stability. The primary goals of this chapter were to 1) determine if males and females within a group were more closely related to each other than to non-group members, 2) explore the relationship between group size and relatedness, and 3) assess what impact resource availability might have on kinship patterns.

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*If all the beasts were gone, men would
die from a great loneliness of spirit, for whatever
happens to the beasts, also happens to the man-Chief Seattle*

Chapter Two

***Resources, not male mating strategies, a determinant of social structure in Gunnison's prairie dogs (*Cynomys gunnisoni*)**

*Published in Behaviour 144:1361-1382

Abstract

Previous studies of Gunnison's prairie dogs, *Cynomys gunnisoni*, have reached different conclusions about the factors influencing sociality in this species. In this study I tested whether Gunnison's prairie dog social structure was resource-based or whether male mating strategies drive the organizational patterns observed. Group size, where the term group refers to individuals occupying the same territory, was predicted by territory size and density of food available. The spatial overlap of adults within territories was positively correlated with spatial patchiness of food resources. All group members participated in territory defense, although adult males engaged in significantly more intergroup aggressive interactions. There was no significant difference in adult male and female home range size. The number of female home

ranges that any given male home range overlapped was not correlated with male body mass, male home range size, or territory size. Contrary to predictions of typical mammalian male mating strategies, adult females ranged significantly further than males during the mating period. Body mass of males and nonreproductive females was similar, whereas that of reproductive females was smaller. In addition, males and females did not differ in size, based on skull length and skull width. Results from this study strongly suggest that patterns of space use and social structure in Gunnison's prairie dogs are the result of individual responses to resource abundance and distribution and are not due to male mating strategies, such as resource defense or female defense polygyny.

Introduction

Social animals often show considerable intraspecific variation in their social structure, both within and between populations. A general principle, first described by Crook (1965), is that individuals in a population tend to aggregate more as the dispersion of their food becomes more clumped (patchy) in space or time. This general correlation has been supported in a broad array of organisms from larval amphibians to primates (reviewed in Lott 1991). The emergence of the socio-ecological model from this principle sought to integrate group level characteristics of

social systems with individual behavioral decisions and strategies (Crook 1970, Emlen & Oring 1977).

A fundamental assumption of the socio-ecological model is that males and females are expected to respond to different selection pressures. Female distribution is predicted to follow the distribution of resources and predation risk, whereas male distribution will be determined by the spatial and temporal availability of females. Previous studies provide empirical support for this prediction (Jarman 1974; Davies 1991; Nunn 1999; Dunbar 2000).

In addition, the model assumes that, where females are the limiting sex, males should compete for access to females, thereby influencing the opportunity for sexual selection to operate in a population (Emlen & Oring 1977; Clutton-Brock 1989). An underlying assumption of the socio-ecological model is that the distribution of males and females represents not only the social system but also reflects the mating system. As a result, descriptions of social structure have often incorporated mating system patterns, so that it has not been easy to distinguish the selection pressures shaping each one. This confusion was also caused, in part, by considering mating systems to be a population-level property rather than the consequence of individual strategies (but see Vehrencamp & Bradbury 1984).

From the socio-ecological model, broad classifications of possible social and mating systems were developed. Extensive studies of mating success have demonstrated that the social structure and the realized mating system of a species can be quite distinct (e.g., Davies 1991, see Lott 1991 for review), suggesting that broadly categorizing populations solely on the basis of observable patterns of association

between males and females may not reflect the true mating system. Subsequent reviews have proposed that social and mating systems are better understood in the context of individual fitness enhancing strategies (Vehrencamp & Bradbury 1984; Davies 1991). This approach may be particularly useful when there is considerable variation in the distribution and association patterns within a species.

Gunnison's prairie dogs, *Cynomys gunnisoni*, are large, diurnal, highly social ground squirrels, whose range is limited to the grasslands of the Colorado Plateau (Hall & Kelson 1959). This species serves as an excellent model system for evaluating social and mating strategies. Within each colony, individuals occupy territories that are persistent in space and time (Rayor 1988; Travis and Slobodchikoff 1993). Individuals mate annually, shortly after emergence from hibernation, with little opportunity for individuals to assess resources. In this species, dispersal by both males and females typically occurs towards the end of the active season prior to the onset of hibernation (Robinson 1989). Both males and females communally defend territories over the entire active season and correlational evidence suggests that the social structure associated with a territory varies with the availability and distribution of food resources (Slobodchikoff 1984; Travis & Slobodchikoff 1993; Travis et al. 1995).

Gunnison's prairie dog populations show variation in their group size and composition among territories, including single male-single female, single male-multiple female, single female-multiple male and multiple male-multiple female groups, with high levels of multiple paternity regardless of group size and sex ratio on a territory (Travis & Slobodchikoff 1993; Travis et al. 1995, 1996). Over 60% of pups

born to any given female are not sired by the resident male/males on her territory (Travis et al. 1995, 1996; Haynie et al. 2003). These data suggest that for Gunnison's prairie dogs, the mechanisms driving the social structure and mating system may not be closely related. Despite the prevalence of variation in group composition and the relatively high frequency of multiple paternity, Gunnison's prairie dog males have often been characterized as pursuing a female defense strategy (Fitzgerald & Lechleitner 1974; Rayor 1988; Hoogland 1999).

To resolve some of these seemingly contradictory observations, I re-examined the social structure of Gunnison's prairie dogs in the framework of the predictions put forth by the socio-ecological model. I propose that social structure, and its relationship to mating systems, as applied to Gunnison's prairie dogs, can be examined from two discrete perspectives. Specifically, social groups may form with both males and females focusing on resource defense, while mating opportunities are secondary and constrained by individual-level and group agonism. Conversely, male mating strategies and competition may dictate the mating and social structures, with female mating strategies and resource use being partly or largely constrained by males, either through female or resource defense polygyny. These two perspectives represent endpoints along a continuum of possible variation in social and mating systems within the broader clade of ground squirrels. For example, though yellow-bellied marmots (*Marmota flaviventris*), black-tailed prairie dogs (*Cynomys ludovicianus*), and Belding's ground squirrels (*Spermophilus beldingi*), are reportedly resource-based polygynous (Hoogland 1981; Armitage 1981; Sherman and Morton 1984;), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) have

been characterized as having a scramble competition polygynous mating system (Schwagmeyer & Wootner 1986; Schwagmeyer 1988). Such alternatives, that do not easily fit the resource defense or female defense model, should also be evaluated. In this study I tested the following nine predictions. If the social system is largely resource-based, I expect:

- 1) Female distribution should vary with the abundance and/or distribution of food.
- 2) Both male and female intruders onto a territory should be aggressed against equally by territorial residents of either sex.
- 3) The number of males per group should increase with territory size and/or quality, rather than with the number of females
- 4) Females should mate with males both on and off their home territories, if they can gain access to males on other territories.

If, instead, male sexual competition is the main determinant of the social structure, either through resource or female defense polygyny, I expect that:

- 5) The number of males per group should increase with the number of females, rather than with territory size or quality.
- 6) Males should have larger home ranges than females, particularly during the mating season.
- 7) Male home ranges should be equivalent to territory area, thereby overlapping the home ranges of females that occupy a given territory.
- 8) Larger males in better condition should have access to better quality territories, containing more females.

9) There should be sexual dimorphism in body size, reflecting male-biased aggression as a strategy to increase mating success.

Methods

Study area

Two colonies of Gunnison's prairie dogs were studied in northern Arizona from May 2003 to August 2005. The first study site, designated Humane Society (HS), was established in May 2003. The second study site, designated Country Club (CC), was established in August 2003. Experimental manipulations of resource abundance and distribution were conducted from June 1, 2004-August 1, 2004 and April 1, 2005- May 6, 2005. Data from these time periods are excluded from this contribution. In addition, because food addition could impact measures of body mass, data for analyses on the correlation between adult body mass and territory size, as well as comparisons among adult males, nonbreeding females and breeding females in body mass use data prior to any resource manipulations.

Both colonies were located within the city limits of Flagstaff, Arizona. Within each study site two 1 ha plots were created. At HS, the locations of the plots (HS I and HS II) were separated by a distance of 0.2 km and a road, within the 42.5 ha colony. The location of each plot was selected on the basis of two factors: 1) plots were maximally distant from each other, and 2) plots were located in areas of greatest prairie dog activity. With the exception of one individual who moved in August 2004 from HS I to HS II, individuals in different plots did not physically interact with one

another, or occupy the same area at any time during this study. During the winter in 2004, extensive flooding at HS resulted in mortality of all prairie dogs at HS II, therefore data from this plot were unavailable in 2005.

At CC, the two plots (CC I and CC II) were separated by a distance of 0.2 km and a road. Within the approximately 45 ha colony, the location of each plot was selected based on the same criteria as for HS. With the exception of two individuals known to have moved from CC I to the boundary of CC II, individuals from the two plots did not physically interact with one another, or occupy the same area at any time during this study. For each plot, at both HS and CC, a 100 m X 100 m letter/number grid system consisting of 100 100m² quadrats was established using surveyor stakes. The location of each stake, the halfway point between each stake, and the center point of each 100m² quadrat was recorded using a Garmin Etrex Global Positioning System.

Trapping and marking

Prairie dogs were live-trapped with Tomahawk live traps (50 cm x 18 cm x 18 cm and 48 cm x 15 cm x 15 cm), baited with sunflower seeds. Traps were placed at active burrows where fresh scat was visible or individual prairie dogs had been observed. Active burrows were defined as burrows with fresh scat within 0.5 m of the entrance (Biggins et al. 1993) and a lack of debris obstructing the entrance. Approximately 250 traps were placed on each 1 ha plot. Each trapped animal was placed in a specially designed sleeve, weighed to the nearest 10g with an Ohaus scale, sex-determined, and DNA samples (hair) collected. Each animal was permanently marked using AVID® or Home Again® individually packaged, sterile microchips.

Once injected, individuals were scanned to test the microchip and marked with a unique number/symbol using Lady Clairol® black hair dye for identification related to behavioral observations. The hair dye was used as directed and trapping was conducted throughout the study period to trap unmarked individuals, to re-apply markings on previously trapped individuals and collect data on body mass as the season progressed.

Vegetation and burrow survey

The abundance and distribution of food plants was obtained through monthly sampling of all plots from April-August each year. For each plot, 100 nested quadrat samples were taken by placing a 1m X 1m wooden sampling square at random in each 100m² quadrat. Random pairs of numbers, using the number of paces between two surveyor stakes, represented the combined across and down locations sampled in each quadrat and were generated in Excel. A digital image using a Hewlett Packard® 812 Photosmart digital camera set at four megapixels was taken of each sample. I used Shalaway & Slobodchikoff (1988) to identify food plant species for Gunnison's prairie dogs along with my personal behavioral observations during the course of this study. Percent cover of food resources were estimated for all plots, and all territories within each plot, using Optimas® 3.0 in the Functional Ecology Research and Training Laboratory (FERTL) at the Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York.

Relative available biomass for each plot was estimated using the average dry weight of 100cm² food plant samples collected from fifteen randomly selected 100m² quadrats in each plot during August every year. Samples were immediately placed in

a flower press and later oven dried for 24 hours. Total relative biomass per territory was estimated by multiplying the percent cover from digital samples taken on a given territory by the average dry weight of 100cm² samples. Territory food patchiness was calculated as the variance to mean ratio of biomass/m².

Burrow distribution was recorded using a Garmin® Etrex Global Positioning System in April after emergence from hibernation, in June after the emergence of juveniles, and prior to winter immergence in August. Burrows were classified as being active or inactive. All active burrows were flagged and numbered.

Behavioral data

Behavioral observations were made for a minimum of 10 days per month for 3h/ day from May-August 15, 2003 at HS plots. With the exception of days when trapping occurred, observations were made at least every other day at each plot from March 7-August 15, 2004 and March 3 -August 8, 2005, for a total of 825 hours of observation. For each plot, observations were made alternately in the morning from 0700-1000 and afternoon from 1500-1800, during the times when prairie dogs were most active (Longhurst 1944; Hoogland 1981). Data collected for this study do not encompass the entire active period of Gunnison's prairie dogs in Flagstaff, AZ, as individuals were observed active through early December. Natural terrain features, such as rock formations, hills and trees were used for observations. Observations were made using Nikon 8-24x25 zoom binoculars.

The term social group refers to individuals that are mutually tolerant of each other, as indicated by behaviors such as greet-kisses (King 1955) and co-feeding, while territory refers to the area occupied and defended by members of a social

group. Animals that were consistently chased out of an area were considered as not belonging to that territory. Individuals that were trapped once and not seen throughout the study were not included as members of any social group.

Because group territorial boundaries are relatively stable and are shared by all occupants of the territory, little confusion arises about assigning group membership. To obtain data on the composition of social groups within each study plot, behavioral observations included focal sampling, scan sampling and all occurrences sampling (Altmann 1974). Focal samples were conducted for 5 min. During the focal sample, the location of the focal animal and all occurrences of social interactions were recorded. Four such focal samples were taken in sequence, then every 30 min., a scan sample was used to record the location of each above ground animal within the study plot. Locations were recorded based on the proximity (to the nearest 0.5m) of an individual to either a surveyor stake or a flagged burrow and matched with corresponding coordinates obtained with the Garmin® Etrex Global Positioning System. Observations were removed from the estimation of home ranges and territory area in only two cases. First, data from agonistic interactions that resulted in a chase were excluded. Second, during the mating season, isolated excursions by individuals to other parts of the colony were excluded. Including either observation would have greatly inflated home ranges and territory area. Home ranges were estimated by using all location points for an individual, except as noted, whereas location points from all individuals within a social group were used to estimate territory area.

Home range and territory measurements

Home range was defined as the area routinely used by an individual within a group, while the territory was defined as the area occupied by all members of a particular group. In theory, these two could be equivalent, but are referred to distinctly. All home ranges and territory areas were estimated using the fixed kernel density estimator (ArcView 3.2a; ESRI 2000). When using the fixed kernel approach with a level of smoothing selected by least squares cross-validation (LSCV), results are less biased and more appropriate for non-normal distributions (Worton 1995; Seaman & Powell 1996). As opposed to the adaptive kernel, the fixed kernel approach is more stable for probability contours exceeding 80%. Seaman et al. (1999) suggest that contours greater than 85% do not provide meaningful biological information and are less reliable. Therefore, I used only the 85% contour probabilities for all individual home ranges, territory areas, spatial overlap of individual home ranges, and all statistical comparisons (Figures 1). There was no relationship between territory size and sampling effort (whole model: $r^2=0.03$, $F_{1,19}=0.68$, $P=0.42$). X-tools (Arcview 3.2a; ESRI 2000) was used to estimate the area of overlap of individual home ranges. The proportion of the total home range that any one individual overlapped with another individual was estimated by taking the area overlapped divided by the home range of an individual (Figure 2). Proportions were arcsine transformed for analysis (Sokal and Rohlf 1995).

Juveniles appeared aboveground between June 5-June 11 in all years and adult females continued lactation aboveground for 7-10 days. Given an average gestation of 29.3 days combined with the duration of lactation averaging 38.6 days in this species (Hoogland 1995, 1997), the majority of the mating at these study sites took place

from the last week of March to the middle of April. Data from April-May 2004 were analyzed separately by month to determine if there were differences in the ranging patterns of males and females during the mating and non-mating period of the reproductive season. To estimate ranging distances, successive distances were calculated for independent location points for each individual. Location points were considered independent if they occurred at least 2 hours apart.

Dimorphism measurements

To test for evidence of sexual dimorphism in body size I measured the maximum length and maximum width at the zygomatic arch of Gunnison prairie dog skulls from specimens housed at the American Museum of Natural History. Data were taken from 42 skulls (Females, N=22; Males, N=21) from three geographic regions including Arizona, Colorado, and New Mexico. I took measurements using a handheld caliper and all measurements were to the nearest 0.1mm.

Statistical analysis

All analyses were initially conducted on age-sex classes separately. While yearling females and males are capable of reproducing (Hoogland 1999) and participate in territorial defense (Rayor 1988; Hoogland 1999), in the absence of paternity data, categorizing reproductive yearlings as adults would result in a bias towards females since parous yearling females are easily identifiable, but reproductive yearling males are not. Individuals known to be juveniles in each year were classified as yearlings in the following year. It is not possible to reliably distinguish between adults and yearlings by weight (Tileston & Lechleitner 1966), thus all males and females of unknown age were classified as adults.

Because aboveground vegetation was recorded monthly and used to calculate territory food patchiness, there could be a complex correlation structure among the sequential sampling periods for a given colony, requiring the use of repeated-measures analysis of variance (ANOVA). However, repeated-measures ANOVA is not required when sequential data points within a category share a common covariance structure across categories (SAS Institute 2000). A test for sphericity was used to test this assumption for patchiness of food within colonies across months. The results were not significant across colonies for each year (2003: $X^2=1.61$, $df=2$, $p<0.46$; 2004: $X^2=3.70$, $df=4$, $p<0.59$; 2005: $X^2=0.56$, $df=4$, $p<0.76$), allowing acceptance of the null hypothesis that different months shared the same covariance structures across time. This criterion then allowed me to use univariate analyses for the reproductive (April-May) and non-reproductive (June-August) sample periods.

Average values for each period were used to test the effect of spatial patchiness of food on the spatial overlap of individual home ranges.

Biomass/m² and territory size were log transformed to reduce heteroscedasticity (Sokal and Rohlf 1995). Arcsine transformation was performed on proportions of active/inactive burrows and percent overlap of individual home ranges (Sokal and Rohlf 1995). For within and between group aggressive interactions, chi-square analysis was used to determine if encounters depended on age-sex class. For each possible age-sex class dyad an expected rate of aggressive encounters was calculated based on the relative proportion of each age/sex class in each group.

Since the relevant assumptions for ANCOVA were not met, I ran a Poisson regression using the generalized linear model to determine whether the raw number of individuals in each age-sex class responded to log biomass/m², territory size, patchiness, and the proportion of active burrows. I also conducted Poisson regression analyses to determine if the number of adult females that a given male overlapped within a territory was a function of his body mass or home range size. I tested for overdispersion (variance exceeding the mean) using the deviance/df and Pearson Chi-square/df and for all tests this value was less than 1. Year, site, and interactions terms are not reported, except where significant. I performed an ANOVA to test for differences in ranging distance, home range size, and spatial overlap among age-sex classes. When analyzing spatial overlap, data were insufficient to include all territories across years. Linear regression was used to test for correlations between pairs of any continuous-scaled variables, such as body mass and log territory size.

Statistical analyses were performed using JMP 4.0® and Statistica® software, and all P values reported are two-tailed.

Results

Territory size, group size and food abundance

Regardless of year or time period, larger territories had a higher total available biomass of food (whole model: 2003: $r^2=0.63$, $F_{1,6}=10.14$, $P<0.02$; 2004: $r^2=0.28$, $F_{1,18}=7.18$, $P<0.01$; 2005: $r^2=0.77$, $F_{1,12}=39.38$, $P<0.001$). This was primarily due to larger territory size, although log mean biomass/m² increased with log territory size in 2004 (whole model: $r^2=0.29$, $F_{1,18}=7.18$, $P<0.01$). Lastly, there was no significant relationship between patchiness and territory size (whole model, $r^2=0.02$, $F_{1,39}=0.69$, $P=0.41$).

All age-sex classes responded to territory size in similar ways. The Poisson GLM revealed that log territory size was a significant predictor of the number of individuals in a territory for adult males (Wald statistic=14.95, N=41, $P<0.0001$), adult females (Wald statistic=8.43, N=41, $P<0.003$), yearling females: Wald statistic=6.47, N=20, $P<0.01$), and for yearling males (Wald statistic=5.97, N=20, $P<0.01$). Patchiness of food resources, log biomass/m², and the proportion of active burrows were not significant predictors of the number of individuals in any age-sex class. However, when age-sex classes were combined the multiple regression

indicated that group size was positively correlated with both log territory size and log biomass/m² (whole model: $r^2=0.61$, $F_{2,38}=29.64$, $P<0.0001$).

Because food experiments were conducted at the end of 2004 and the beginning of 2005, potentially affecting body mass, only measurements from individuals trapped and weighed after emergence from hibernation in March 2004 were used in this analysis.

At emergence from hibernation, there was a significant positive correlation between adult male body mass and log territory size (whole model: $r^2=0.46$, $F_{1,18}=14.50$, $P<0.001$), while for adult females the relationship was not significant (whole model: $r^2=0.02$, $F_{1,31}=0.58$, $P=0.45$).

Home range size, home range overlap and ranging behavior

Among the 41 territories observed over the course of this study, there was variation in the numbers of individuals in each age-sex class (Figure 3). Despite fewer males than females per territory, on average, there was no significant difference in home range size between adult males and adult females (ANOVA: $r^2=0.02$, $F_{1,121}=3.03$, $P=0.08$), or between male and female yearlings (ANOVA: $r^2=0.00002$, $F_{1,44}=0.001$, $P=0.97$). However, adult home ranges were significantly larger than yearling home ranges (ANOVA: $r^2=0.06$, $F_{1,167}=11.68$, $P<0.008$, mean \pm SE = $681.43\text{m}^2 \pm 32.19$ and $471.57\text{m}^2 \pm 52.29$, respectively).

The average home range overlap of adults within a territory was positively correlated with patchiness of food resources (whole model, $r^2=0.55$, $F_{1,21}=25.98$, $P<0.0001$; Figure 4). There was no relationship between food patchiness and the average yearling home range overlap within a territory (whole model: $r^2=0.003$,

$F_{1,17}=0.06$, $P=0.81$). The density of individuals within a territory was not correlated with mean home range overlap (whole model: $r^2=0.004$, $F_{1,24}=0.18$, $P=0.73$) or food patchiness (whole model: $r^2=0.003$, $F_{1,39}=0.37$, $P=0.54$). There was no significant difference in home range overlap between adult male-male dyads and between adult female-female dyads (ANOVA: $r^2=0.01$, $F_{1,113}=1.93$, $P=0.57$). These dyads were combined and compared to adult male-female dyads. Adult male-female dyads had greater home range overlap than same-sex dyads (ANOVA: $r^2=0.02$, $F_{1,206}=5.12$, $P<0.02$, mean \pm SE= $39.78\pm 3.97\text{m}^2$ and $28.17\pm 3.14\text{m}^2$, respectively). The Poisson GLM indicated that the number of females that an adult male overlapped was not explained by either adult male home range size (Wald statistic=0.015, $N=14$, $P=0.90$), adult male body mass at emergence from hibernation (Wald statistic=0.001, $N=14$, $P=0.97$) or territory size (Wald statistic=0.02, $N=34$, $P=0.53$).

Adult females ranged significantly greater distances during April, when mating took place, compared to May, the period of gestation (Kologmov-Smirnov, $N=120$, $D=0.23$, $P<0.04$, mean \pm SE= $24.02\pm 1.79\text{m}$ and $16.09\pm 1.60\text{m}$, respectively). There was no significant difference in adult male ranging behavior in April compared to May (Kologmov-Smirnov, $N=173$, $D=0.09$, $P=0.92$, mean \pm SE= $18.38\pm 1.04\text{m}$ and $17.33\pm 1.50\text{m}$, respectively) Adult females ranged, on average, farther than adult males in April (Kologmov-Smirnov, $N=197$, $D=0.21$, $P<0.03$, mean \pm SE= $24.02\pm 1.79\text{m}$ and $18.38\pm 1.04\text{m}$, respectively), and there was no significant difference between adult male and female ranging behavior in May (Kologmov-Smirnov, $N=96$, $D=0.11$, $P=0.92$, mean \pm SE= $17.33\pm 1.50\text{m}$ and $16.09\pm 1.60\text{m}$, respectively). Of the 40 occasions that females were recorded in the company of a male at or near a burrow

entrance during the mating period, 65% involved females leaving their territory and visiting males at other territories.

Intragroup and intergroup agonism

Given the proportion of each age-sex class in a group, there was no age-sex class bias in the frequency of initiating intragroup aggressive interactions (Adult male $X^2= 0.45$, Adult female $X^2= 0.20$, Yearling male $X^2= 2.62$, Yearling female $X^2= 2.78$, all NS). In territories that contained multiple males, the occurrence of within-group male-male aggression was extremely low, with only five observations in 2004. Data from this time period were used to estimate a rate of aggression between males. Dividing the number of occurrences by the hours of observation yielded a rate of 0.016 aggressive interactions/hour. Adult males were never observed actively interfering with female movement across territory boundaries. Both males and females within groups were observed cooperatively defending the territory boundary beyond their individual home ranges against all age/sex classes. While all age-sex classes participated in such defense, adult males engaged in significantly more intergroup aggressive interactions than expected, given their relative proportion in the group ($X^2= 12.58$, $df=1$, $P<0.001$). Adult males more frequently targeted adult male intruders more than any other age-sex class ($X^2= 39.42$, $df=1$, $P<0.001$) and yearling males were more aggressive towards adult male intruders than any other age-sex class ($X^2= 12.94$, $df=1$, $P<0.01$). Both adult and yearling males were also aggressive towards yearling and adult female intruders. Regardless of age/sex-class or body mass, group members successfully evicted intruders and intruding males or females were never observed usurping or evicting a group member.

Sexual dimorphism

There were no significant differences among males and females in the morphological characteristics measured. There was no significant difference in the maximum length of adult male and female skulls (ANOVA: $r^2 = 0.04$, $F_{1,40} = 1.91$, $P=0.17$, mean \pm SE = 56.35mm \pm 0.72 and 55.00mm \pm 0.65, respectively) and no significant difference in the width at the zygomatic arch (ANOVA: $r^2 = 0.008$, $F_{1,40} = 0.35$, $P=0.555$, mean \pm SE = 39.38mm \pm 0.72 and 38.79mm \pm 0.66, respectively). There were significant differences in the body mass of males, females that had produced a litter and nonbreeding females, using measurements taken from individuals at the end of July 2003, approximately six weeks after lactation by breeding females had ceased. Only data from 2003 were used since food experiments, conducted in 2004 and 2005, could have influenced body mass values. The Tukey-Kramer multiple comparisons test revealed that there was no difference between males and nonbreeding females, while both groups had a significantly higher body mass than females that had produced a litter earlier in the season (ANOVA: $r^2 = 0.66$, $F_{2,49} = 47.53$, Bonferroni adjusted $P < 0.0003$, mean \pm SE = 955.00g \pm 49.91, 1041.25g \pm 22.78, and 726.52g \pm 23.27, respectively).

Discussion

Consistent with a resource based social system, the results of this study supported the following observational conclusions: 1) The number of females and

males varied with territory quality and 2) adult home range overlap varied with food patchiness and 3) all age-sex classes participated in territory defense. In addition, contrary to the predictions that social systems might be driven by male sexual competition, I found that: 1) females ranged further than males during the mating period, 2) males did not have larger home ranges than females, 3) male home ranges were smaller than the territory size, 4) larger males did not have home ranges that overlapped more females, 5) adult males on larger territories did not overlap more females and 6) there was no apparent sexual dimorphism in body size.

Previous studies have reached different conclusions about the social organization of Gunnison's prairie dogs and the selective pressures driving this system. The results of this study suggest that resource abundance drives patterns of social organization in this population. Contrary to the predictions of the socio-ecological model, both males and females responded to food availability in similar ways. For all age-sex classes, the number of individuals was influenced by total available biomass of food, as reflected in territory size and the density of food available. In addition, the degree of spatial overlap for adults, but not yearlings, within territories was strongly correlated with patchiness of food resources.

If the social organization of Gunnison's prairie dogs was being driven by male mating strategies, either through female defense or resource defense polygyny, then it is predicted that male home ranges would be equivalent to territory size and overlap the home ranges of many females within a territory (Emlen & Oring 1977). In this study, as in others (Rayor 1988), there was no difference in the home range size of adult males and females. It could still be possible that, in territories containing

multiple adult males, a larger, perhaps dominant male, would overlap more females in that territory. However, there was no relationship between male body mass and the number of female home ranges overlapped in territories that contained multiple adult males. This pattern implies a lack of dominance hierarchies among males within Gunnison's social groups, particularly since the rate of aggression among males within territories was so low that it would not allow for the maintenance of any such hierarchies even if they existed.

In female defense mating systems, males are predicted to directly control female movement patterns. Gunnison's prairie dog males in these populations were never observed interfering with resident female movement across territory boundaries. During the month when mating occurred, females were often observed "visiting" other territories. These visits were sometimes brief, lasting one day, sometimes extended, lasting 2-3 days, and on several occasions, females permanently moved to a different territory. These observations were supported by the findings that females ranged further during this time period. This result sheds some light on the high levels of extra-group paternity found in previous studies (Travis et al. 1995, 1996; Haynie et al. 2003), in that it appears females actively seek copulations with nonresident males. On this basis, scramble competition polygyny can also be rejected, since it would be expected that males would actively search for females (Schwagmeyer & Woontner 1986; Schwagmeyer 1988).

A resource defense mating system predicts that males control access to resources that are important to females (Emlen & Oring 1977; Davies 1991). Though at emergence from hibernation heavier males did occupy better quality territories, it is

not clear that this was the result of competitive ability. Rather, results suggest that better quality territories result in heavier males. While I found that adult males do engage in significantly more aggressive interactions against intruders than any other age-sex class, results from this study also support previous findings that there is cooperative defense of the territory by all age-sex classes against all age-sex classes (Rayor 1988). In either resource defense or female defense polygyny, females are not expected to assist males in territorial defense (Orians 1969; Downhower & Armitage 1971). Female Gunnison's prairie dogs engaged in aggressive interactions with both male and female intruders and efforts to evict intruders extended beyond individual female home ranges.

As male competition for females increases, it is predicted that the variance in male reproductive success correspondingly increases (Emlen & Oring 1977). As a result, there is often a correlation between polygyny and sexual dimorphism as a consequence of increased sexual selection on males (for review see: Clutton-Brock et al. 1977; Alexander et al. 1979; Shine 1989). Male Gunnison's prairie dogs are morphologically similar to females, with the primary observed difference being that males have a higher body mass than females (Hoogland 2003). This mass difference has led to the conclusion that there is significant sexual dimorphism between males and females (Hoogland 2003). However, there was no difference between average male and female skull length or width at the zygomatic arch, despite a relatively large and geographically extensive sample. This similarity of male and female skull size, coupled with the result that the body mass of non-reproductive females was not different from adult male body mass, suggests that there is no dimorphism in skeletal

tissues between sexes as a consequence of sexual selection. Rather the differences in body mass appear to be merely a byproduct of the high reproductive effort of females, which may be due to a reduction in foraging effort or the high energetic demand of lactation. More extensive trapping data support the patterns observed in this study and suggest that lactating females frequently plateau in their weight gain or lose body mass during lactation (Slobodchikoff unpubl. data).

In this study, two ecological factors influenced overall group size and spatial overlap of adults in Gunnison's prairie dogs: the abundance and the spatial dispersion of food resources. These factors are consistent with predictions put forth by the resource dispersion hypothesis (Bradbury & Vehrencamp 1976; Macdonald 1983; Kruuk & Macdonald 1985; Carr & Macdonald 1986; Johnson et al. 2002), but not with predictions of typical mammalian male mating strategies. Both male and female Gunnison's prairie dogs have similar energetic requirements if they are to survive overwinter hibernation. Consequently, the primary purpose of territories appears to be to provide group members with sufficient resources, while constraining the absolute group size possible within a territory as a function of the abundance of those resources. Both adult males and females appear to settle spatially within territory boundaries so as to limit within-group feeding competition, while cooperatively defending territories from intruders.

Gunnison's prairie dogs are seasonal breeders and there is evidence that the estrous period for any given female is very brief. However, unless females are also highly synchronous in their estrous period, it is not clear whether a narrow estrous period of a single day (Hoogland 1998) would limit or enhance a male's ability to

monopolize access to females directly. Although previous studies have revealed high levels of copulations with nonresident males, in the absence of detailed male mating success, it is not possible to conclude that resident males do not gain some reproductive advantage.

Results from this investigation, though not conclusive, strongly suggest that male Gunnison's prairie dogs in this region do not exhibit a female defense strategy and potentially not even a resource defense mating strategy. If Gunnison's prairie dog social organization is driven by ecological factors for both adult males and females, as suggested, then experimental manipulations and rigorous testing of the predictions of the resource dispersion hypothesis should support this conclusion. Ultimately, whether males pursue a resource defense strategy may be determined by male reproductive success. Paternity analysis from these populations will provide the necessary insight to distinguish among these male strategies. If males are pursuing a resource defense strategy, then it is predicted that the resident male would contribute to a higher number of offspring in his territory than any other individual male. Lastly, I suggest that because the patterns observed in this study are consistent with other populations of Gunnison's prairie dogs (e.g. roaming females, no difference in male and female home ranges, groups containing multiple adult males), the interpretations presented here may be more general and applicable to this species in other regions.

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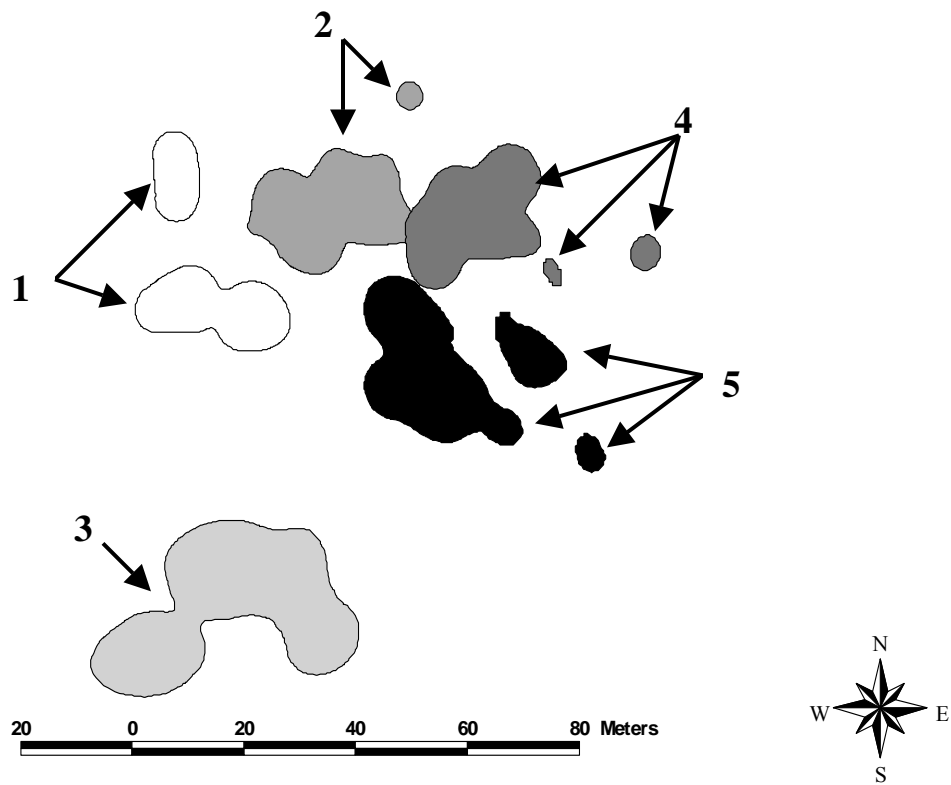


Figure 1. Gunnison's prairie dog territories on HS II in Flagstaff, Arizona during 2004 that were estimated using 85% contour probabilities in ArcView 3.2. Though territories appear discontinuous, these areas were traversed, but individuals were recorded in these locations less than 15% of the time.

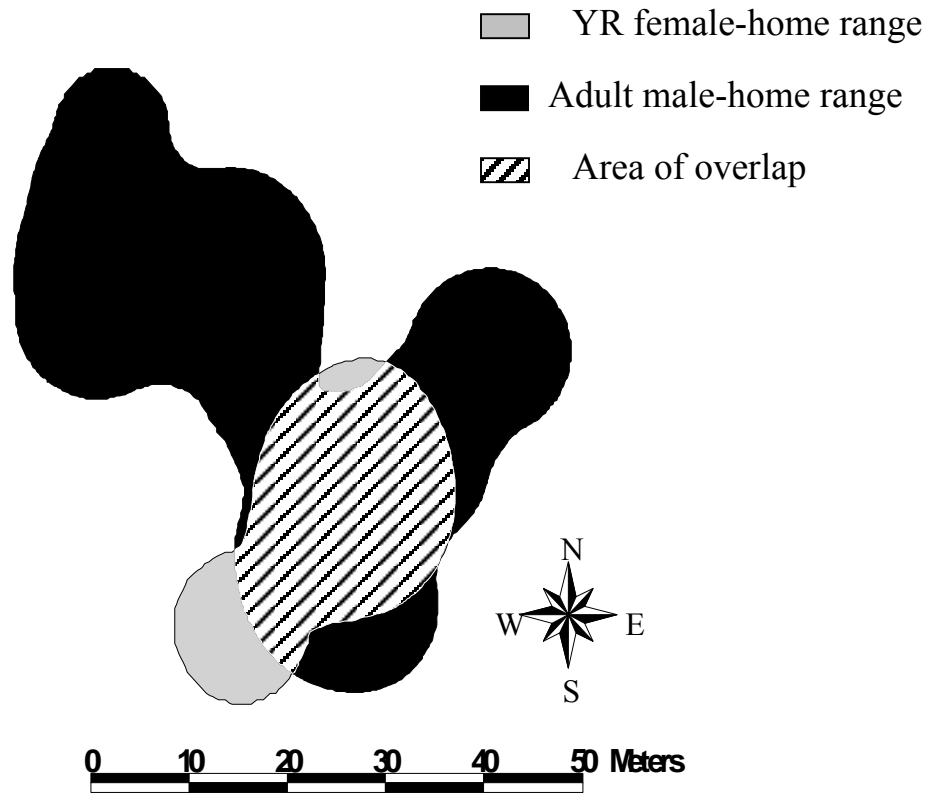


Figure 2. By merging the home ranges of two individuals, the adult male had a home range of 1494.37 m², while the yearling (YR) female had a home range of 533.74 m². The estimated area of spatial overlap between them was 425.20 m², representing 28.44% of the male's home range and 79.62% of the yearling female's home range.

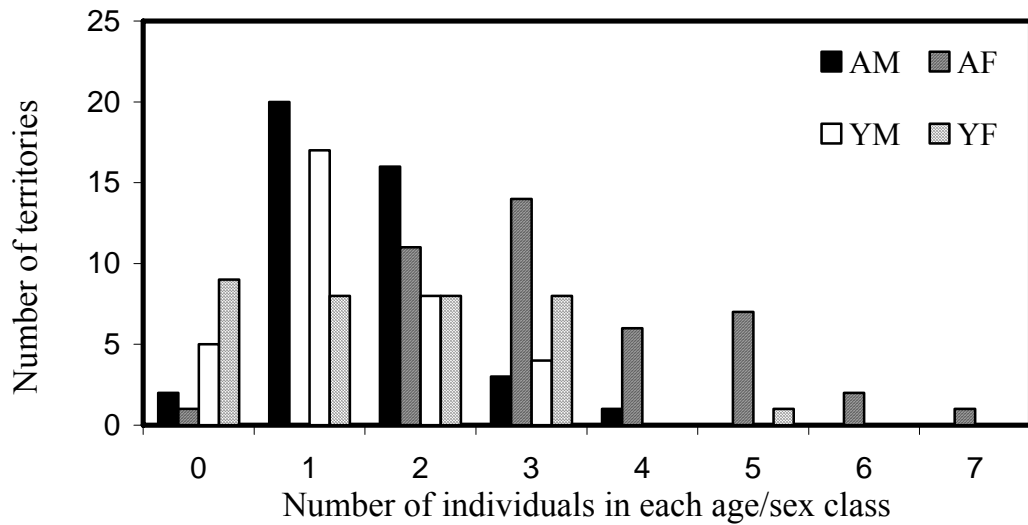


Figure 3. Frequency of occurrence of the number of individuals comprising each age-sex class in the territories observed during this study in Flagstaff, Arizona. AM=adult male, AF=adult female, YM=yearling male, and YF=yearling female. Group sizes ranged from 2-14 individuals, with mean group size = 7.21 ± 0.44 (SE), where $n=41$.

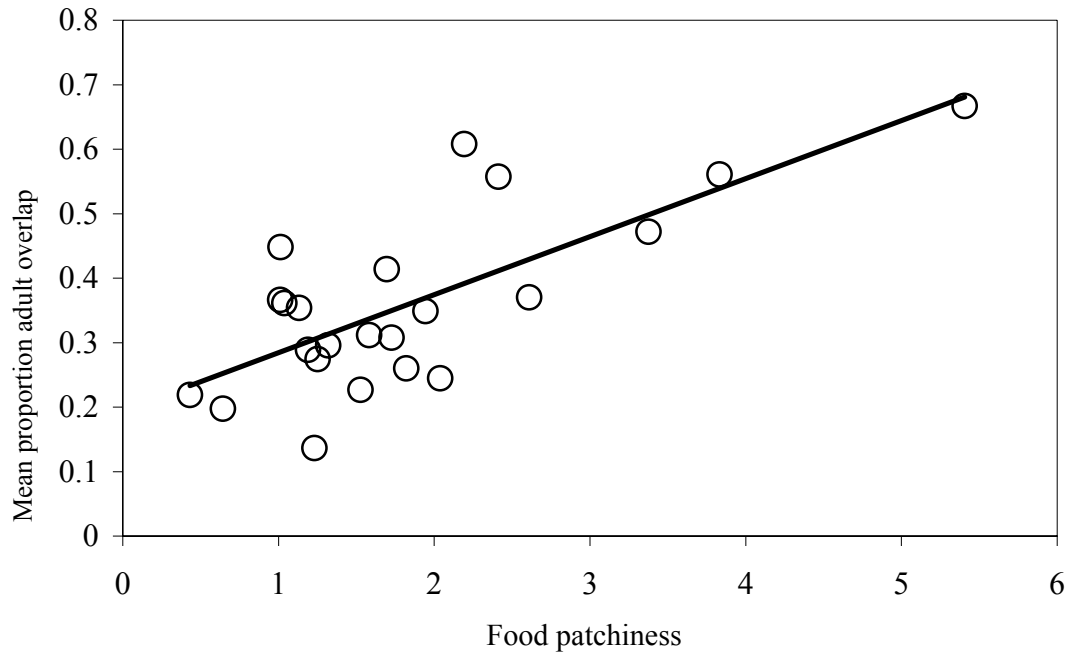


Figure 4. The effect of food patchiness on the mean proportion of adult home range overlap (non-transformed), where patchiness is measured as the variance to mean ratio of biomass/m². Linear regression: $\hat{y}=0.19+0.10(x)$; $r^2=0.55$, $F_{1,21}=25.98$, $P<0.0001$.

I went to the woods because I wished to live deliberately, to front only the essential facts of life, and see if I could not learn what it had to teach, and not, when I came to die, discover that I had not lived.-Henry David Thoreau

Chapter Three

Gunnison's prairie dog (*Cynomys gunnisoni*) responses to changes in resource distribution and abundance: An experimental test of the resource dispersion hypothesis.

Abstract

Few studies have experimentally tested the Resource Dispersion Hypothesis (RDH). In this study I tested whether space use and social organization of Gunnison's prairie dog responded to changes in the dispersion and abundance of resources. Food manipulations were carried out during the reproductive and non-reproductive seasons across two years. Gunnison's prairie dog adults responded to the experiments by decreasing territory size as food became patchier in space and time. Both males and females modified their home ranges, with no detectable difference between sexes, either prior to or during the experiments. As food became patchier in space and time, the spatial overlap of adults increased, whereas it decreased as food became more evenly dispersed. The average size of a group, defined as those individuals occupying the same territory, did not change significantly as a result of the experiments. Where changes in the composition and size of groups did occur, there was no indication that

such changes were sex-specific. Results from this study support critical components of the RDH and strongly suggest that patterns of space use and social structure in Gunnison's prairie dogs are the result of individual responses to resource abundance and distribution.

Introduction

A general principle, first described by Crook (1965), is that individuals in a population tend to aggregate more as the dispersion of their food becomes more clumped (patchy) in space. This broad correlation has been verified in an extensive array of organisms (birds: Myers et al. 1981; Stouffer et al 1988; Gunnison's prairie dogs, *Cynomys gunnisoni*: Travis & Slobodchikoff 1993; European badgers, *Meles meles*: Kruuk & Parish 1982, 1987; brown hyenas, *Hyena brunnea*: Owens & Owens 1996; primates: Yamagiwa & Hill 1998; see Lott 1991 for review). Many of these correlations are likely due to the costs associated with competition among group members for resources balanced against the benefit of exploiting a clumped resource (Waser 1977, 1988; Janson 1992; van Schaik and Janson 2000).

An extension of this general pattern, the 'resource dispersion hypothesis' (RDH) states that the abundance and distribution pattern of critical resources may provide a distinct underlying mechanism for the evolution of groups (Macdonald 1983, 1984; Slobodchikoff 1984; Carr and Macdonald 1986; Slobodchikoff and

Schultz 1988; Bacon et al. 1991a,b; DaSilva et al. 1993; Woodroffe and Macdonald 2000). The RDH differs from Crook's hypothesis in that it is limited to territorial animals, while Crook suggested that territoriality could act as an impediment to sociality (Crook 1965). Although the RDH is also similar Brown's (1982) model of optimal group size, two unique assumptions differentiate the RDH from this and other models. First, the RDH assumes shared territorial defense as the primary benefit to group living. Second, no other benefits or external forces are assumed necessary to explain group formation and maintenance.

The RDH can also be thought of as an alternative hypothesis to grouping patterns that reflect more typical male mammalian mating strategies. Much of the research on mating systems has centered on the prediction that males and females respond to different selection pressures. Female distribution is predicted to follow the distribution of resources and predation risk, whereas male distribution will be determined by the spatial and temporal availability of females rather than of resources (Emlen and Oring 1977). Thus, it is possible that females only follow RDH, whereas males follow individual mating strategies, but are not involved in resource defense against other groups (Waser 1977; Packer 1990). Alternatively, if resources are the dominant influence on aggregation patterns, variation should be the result of the changes in the grouping behavior of both males and females, independent of any particular mating strategies.

The RDH has been criticized as an untestable hypothesis because of a lack of well-defined predictions (von Shantz 1984). As a result, its application as a mechanism for the evolution of group living has been limited. More recently,

theoretical work has focused on identifying the RDH predictions, thus creating a framework for examining animal grouping patterns (Bacon et al. 1991a,b; Johnson et al. 2002). There are two characteristics of resources that are suggested to play a role in grouping behavior: (1) their abundance or richness and (2) their distribution or dispersion in space and time. Like other models, the RDH broadly predicts that the abundance of resources constrains group size, but in contrast to other models, RDH predicts that the spatial dispersion, or patchiness, of those resources directly influences territory and home range size. In addition, temporal fluctuations in resource abundance and distribution may create stochastic changes in the environment that could affect aggregation patterns and spatial organization of individuals (Maher and Lott 2000; Johnson et al. 2002). Under the RDH, the expectation is that as resources become more variable in space and time (more heterogeneous), territory size would increase because of the need to defend larger areas that consistently contain enough food patches to satisfy even a single animal. In addition, such food patches may be productive enough, once located, to support several individuals, so the defense of a larger territory may favor larger group sizes.

Although many species show patterns of correlations consistent with the RDH, more rigorous experimental studies are scarce due to practical difficulties in testing the RDH in natural populations. Though not specifically testing RDH, some experimental evidence does exist to suggest that resource abundance and distribution may exert a strong influence on aggregation patterns. For example, by manipulating food abundance and dispersion simultaneously, Sánchez-Prieto et al. (2004) found that group size increased in Iberian red deer when food was patchier and denser. In

addition, Davies and Hartley (1996) demonstrated that territory size increased with increasing food patchiness in dunnocks. Though neither study system meets the assumptions for testing the RDH, both studies indicate that behavioral flexibility in response to changing environmental conditions may be common.

Gunnison's prairie dog (*Cynomys gunnisoni*) provides an excellent model system for experimentally testing the RDH and satisfies the assumptions associated with this model in the following ways. First, all individuals within a territory have access to all parts of the territory, and both males and females communally defend territories larger than individual home ranges (Rayor 1988; Verdolin 2007). Second, food resources are heterogeneous and individuals respond to this variation (Slobodchikoff 1984; Travis & Slobodchikoff 1993). Last, there is observational and experimental evidence suggesting that the social structure associated with a territory varies with the availability and distribution of food resources (Slobodchikoff 1984; Travis & Slobodchikoff. 1993; Travis et al. 1995).

In this study, I explored the effect of resource abundance and dispersion on Gunnison's prairie dog social organization and space use through a series of food manipulations designed to test the following predictions of the RDH (see Johnson et al. 2002):

- (1) Group size is correlated with resource abundance.
- (2) Resource dispersion directly affects group size and territory size such that as resources (a) become more evenly distributed, territory size and group size decrease, b) become increasingly

spatially patchy, group size and territory size increase, (c) become temporally heterogeneous, group size and territory size increase.

In addition, I predicted that, under the RDH:

- (3) Resource dispersion should influence the spatial overlap of adult home ranges within a territory such that as resources (a) become more evenly distributed, spatial overlap remains the same or decreases, (b) become increasingly spatially patchy, spatial overlap increases, (c) as resources become temporally heterogeneous, spatial overlap increases.
- (4) Both males and females respond to changes in resource abundance and dispersion similarly.
- (5) The response of individuals to changes in resource abundance and dispersion follows the same pattern during the reproductive and non-reproductive seasons.

Methods

Study area

Two colonies of Gunnison's prairie dogs were studied in northern Arizona from May 2003 to August 2005. The first study site, Humane Society (HS), was established in May 2003. The second study site, Country Club (CC) was established in August 2003. Experimental manipulations of resource abundance and distribution

were conducted from June 1, 2004-August 1, 2004 and April 1, 2005- May 6, 2005. Data from 2003 are excluded from the current analysis.

Both colonies were located within the city limits of Flagstaff, Arizona. Within each study site two 1 ha plots were created. At HS, the location of the plots (HS I and HS II) were separated by a distance of 0.2 km and a road, within the 42.5 ha colony. The location of each plot was selected on the basis of two factors: 1) plots were maximally distant from each other, and 2) plots were located in areas of greatest prairie dog activity. With the exception of one individual who moved in August 2004 from HS I to HS II, individuals in different plots did not physically interact with one another, or occupy the same area at any time during this study. During the winter in 2004, extensive flooding at HS resulted in mortality of all prairie dogs at HS II, therefore data from this plot were unavailable in 2005.

At CC, the two plots (CC I and CC II) were separated by a distance of 0.2 km and a road. Within the approximately 45 ha colony, the location of each plot was selected based on the same criteria as for HS. With the exception of two individuals known to have moved from CC I to the boundary of CC II, individuals from the two plots did not physically interact with one another, or occupy the same area at any time during this study. For each one-hectare plot, a 10m X 10m letter/number grid system consisting of 100m² quadrants was established using surveyor stakes. The location of each stake, the halfway point between each stake, and the center point of each 100m² quadrant was recorded using a Garmin Etrex Global Positioning System.

Trapping and marking

Prairie dogs were live-trapped with Tomahawk live traps (50 cm x 18 cm x 18 cm and 48 cm x 15 cm x 15 cm), baited with sunflower seeds. Each trapped animal was placed in a specially designed sleeve, weighed with an Ohaus scale, sexed, and DNA samples (hair) collected. Each animal was permanently marked using AVID or Home Again individually packaged, sterile microchips. Once injected, individuals were scanned to test the microchip and marked with a unique number/symbol using Lady Clairol black hair dye for identification related to behavioral observations. The hair dye was used as directed and trapping was conducted throughout the study period to trap unmarked individuals and to re-apply markings on previously trapped individuals.

Vegetation and burrow survey

The abundance and distribution of food plants was obtained by monthly sampling of all plots from April-August each year. For each plot, a 1m² wooden sampling square was placed at random in each 100m² quadrant. This measure is comparable to previous studies measuring food distribution in Gunnison's prairie dogs. Random pairs of numbers, using the number of paces between two surveyor stakes, represented the horizontal and vertical locations to be sampled and were generated in Excel (Microsoft 2000). A digital image using a Hewlett Packard 812 Photosmart digital camera set at 4 megapixels was taken of each sample, for a total of 100 vegetation samples per month, per plot. Food plant species were determined by using the data of Shalaway and Slobodchikoff (1988) on the dietary preferences of Gunnison's prairie dogs together with behavioral observations made during this study. Percent cover was calculated for all plots, and all territories within each plot, using

Optimas 3.0. Relative available biomass for each plot was estimated using the average dry weight of 100cm² food plant samples collected from fifteen randomly selected 100m² quadrants each year. Total relative biomass per territory was calculated by multiplying the percent cover from digital samples taken on a given territory by the average dry weight of edible plant material per 100cm² sample. Territory food patchiness during the non-experimental portion of the study was calculated as the variance to mean ratio of biomass/m². Territory food patchiness during the experiments was calculated as the variance to mean ratio of biomass/m², with the daily amount of sunflower seeds distributed to each territory incorporated in the mean biomass/ m². Changes in patchiness were calculated as the difference in patchiness prior to and during the experiments. In 2005, just prior to the onset of the experiments, there was little aboveground vegetation cover. Individuals were observed foraging on roots and were likely living off of post-hibernation fat reserves. Due to the lack of aboveground biomass in March and widespread snow cover, data to estimate pre-treatment patchiness were unavailable. Instead, I assigned a pre-treatment patchiness to all territories of 1, corresponding to a random distribution.

Behavioral data

Only data from 2004 and 2005 are reported in this study. With the exception of days when trapping occurred, observations were made at least every other day at each plot from March 7-August 15, 2004 and March 3 -August 8, 2005, for a total of 825 hours of observation.

For each plot, observations were made alternately in the morning from 0700-1000 and afternoon from 1500-1800, during the times when prairie dogs were most

active (Longhurst 1944; Hoogland 1981). Data collected for this study do not encompass the entire active season of Gunnison's prairie dogs in Flagstaff, AZ, as individuals were active through early December. However, individuals were observed intensely beginning with emergence from hibernation, during and after the reproductive season (March-May), and after juvenile emergence (June-August). Observations were conducted from vehicle rooftops as well as natural terrain features, such as rock formations, hills and trees. Observations were made using Nikon 8-(24x25) zoom binoculars.

I refrain from applying terminology previously used to refer to Gunnison's prairie dog(s) social groups, namely coterie or clan. Here, the term social group refers to individuals that are mutually tolerant of each other, as indicated by behaviors such as greet-kisses (King 1955) and co-feeding, while communal territory refers to the area occupied and defended by members of a social group. Because group territorial boundaries are relatively stable and are shared by all occupants of the territory, little confusion arises about assigning group membership. Behavioral observations included focal sampling, scan sampling and all occurrences sampling (Altmann 1974). Focal samples were conducted for five minutes. Active individuals were chosen at random for observation, with the qualification that no individual was observed more than once in a daily time block. During the focal sample, all occurrences of social interactions were recorded, along with the identities of all individuals the focal animal interacted with. Four such focal samples were taken in sequence, then every 30 minutes, a scan sample was used to record the location of each animal above ground within the study plot. Locations were recorded based on

the proximity of an individual to either a surveyor stake or a flagged burrow and matched with corresponding coordinates obtained with the Garmin Etrex Global Positioning System. Trap locations were combined with behavioral observations to increase sample sizes for calculating home ranges and territories. Observations were removed from the calculation of home ranges and territory area in only two cases. First, data from agonistic interactions that resulted in a chase were excluded. Second, during the month of April, when mating took place, isolated excursions by individuals to other parts of the colony were excluded. Including either observation would have greatly inflated home ranges and territory area. Animals that were consistently chased out of an area were considered as not belonging to that territory. Individuals that were trapped once and not seen throughout the study were not included as members of any territory or social group.

Home range and territory measurements

Home range was defined as the area used by an individual. As stated above, communal territory was defined as the area occupied and defended by individuals that exhibited friendly and tolerant interactions. In theory, home range could be equivalent to communal territory, but is referred to distinctly. All home ranges and territory areas were calculated using the fixed kernel density estimator (ArcView 3.2a; ESRI 2000). When using the fixed kernel approach with a level of smoothing selected by least squares cross-validation (LSCV), results are less biased and more appropriate for non-normal distributions (Worton 1995; Seaman & Powell 1996). As opposed to the adaptive kernel, the fixed kernel approach is more stable for probability contours exceeding 80%. Seaman et al. (1999) suggest that contours greater than 85% do not

provide meaningful biological information and are less reliable. Therefore, I used only the 85% contour probabilities for all individual home ranges, territory areas, spatial overlap of individual home ranges, and all statistical comparisons. There was no relationship between territory size and sampling effort (whole model: $r^2=0.03$, $F_{1,18}=0.68$, $P=0.42$). X-tools (Arcview 3.2a; ESRI 2000) was used to calculate the area of overlap of individual home ranges. The proportion of the total home range that any one target individual overlapped with another individual was calculated by taking the area overlapped divided by the home range of the target individual. Proportions were arcsine transformed for analysis. Changes in home range overlap were calculated as the difference between the proportion of overlap between two individuals prior to the experiments and the proportion of overlap during the experiments.

Experimental Design

Food manipulation experiments were conducted by imposing a spatiotemporally even treatment, a spatially patchy treatment or a spatiotemporally heterogeneous treatment in 2004 to the study plots. In 2005 the experiments were repeated using only the even and heterogeneous treatments. The food source used was sunflower seeds, a high energy, naturally occurring food source. Prairie dogs within each plot were supplemented with 70% of their daily energetic requirements. The average weight of a sunflower seed used in this study was 0.065 ± 0.003 g, $N=15$ (unhusked) and 0.040 ± 0.002 g, $N=15$ (husked). The estimated energetic requirements for an adult prairie dog weighing an average of 836.8 ± 26.15 g ($N=36$) is 660.22 ± 4.71 kJ/day (Nagy et al.1999). Thus, the estimated daily food intake per

adult prairie dog, based on 16.9 kJ/g of dry matter for granivores, was 39.06 ± 3.59 g, yielding a value of 44.0g of unhusked sunflower seeds/individual in order to supplement 70% of the daily energetic requirement.

Post-reproductive season experiments

Food manipulations during the non-reproductive season began June 3, 2004 and continued until August 1, 2004. This time period encompassed the start of juvenile emergence (early June) and the start of the monsoon season (mid-July). One of the four plots, selected at random among the four, served as the control. Each of remaining three plots received one of the treatments, according to a fixed rule. The plot with the highest natural food patchiness received the even treatment, the plot with the least patchiness relative to the other experimental plots received the patchy treatment and the experimental plot with an intermediate patchiness received the heterogeneous treatment (Table 1).

To obtain an even distribution, the total amount of sunflower seeds was divided by 100, such that each 10x10m quadrant received equal portions every day. To achieve a higher spatial patchiness, ten 10x10m quadrants were selected using a random number generator in Excel. The total amount of sunflower seeds to be distributed daily was then divided by 10 and each selected quadrant received that amount daily throughout the duration of the experiment. Because resources can vary temporally as well spatially, the plot with the intermediate patchiness value (relative to the others) was given a heterogeneous treatment. Again ten 10x10m quadrants were selected at random and the total amount of sunflower seeds to be distributed daily was then divided by 10. Each selected quadrant received that amount for two

weeks. After two weeks an additional set of ten quadrants were selected at random and food was distributed in the new set of quadrants for two weeks. This process was repeated four times throughout the experiment. Territories did not necessarily receive equal amounts of food because the size of a territory and the fraction of its area included in the hectare plot affected how much food it received, in addition to the random choice of locations to receive supplements. However, the variation in food added per territory was similar for all three experimental treatments (Bartlett's test, $P=0.27$).

Reproductive season experiments

Extensive flooding during the winter of 2004 resulted in 100% mortality of all individuals on HS II, eliminating this plot from the study in 2005. Food manipulations during the mating portion of the reproductive period began April 2, 2005 and continued until May 11, 2005. The CCII remained the control plot, while HS I received the even treatment and CC I received the heterogeneous treatment (Table 1). The procedures were identical to the post-reproductive season experiments. Though territories did not receive equal amounts of food, the variation in food added per territory was similar for all three experimental treatments (Bartlett's test, $P=0.14$).

Statistical analysis

Previous results indicated that yearlings and adults had different home range sizes and that yearling home range overlaps did not correlate with differences in food patchiness (Verdolin 2007), thus all analyses of home range and food patchiness were conducted on adults. Because it is not possible to reliably distinguish between adults and yearlings by weight (Tileston and Lechleitner 1966), all males and females of

unknown age were classified as adults. Previous results also indicated that territory size predicted the number of individuals in a group, regardless of age and sex (Verdolin 2007), therefore analyses of group size includes both male and female adults and yearlings.

Aboveground vegetation was recorded monthly and analyzed to calculate territory food patchiness. Due to the monthly sampling regime, there could have been complex correlation structure among the sequential sampling periods for a given colony, requiring the use of repeated-measures ANOVA. However, repeated-measures ANOVA is not required when sequential data points within a category share a common covariance structure across categories (SAS Institute 2000). A test for sphericity was used to test this assumption for patchiness of food within colonies across months. The results were not significant for each colony in each year (2004: $X^2=3.70$, $df=4$, $P=0.59$; 2005: $X^2=0.56$, $df=4$, $P=0.76$). Therefore, I accepted the null hypothesis that different months shared the same covariance structures across time. This criterion then allowed me to use univariate analyses for the reproductive (April-May) and post-reproductive (June-August) experimental periods.

Because the relevant assumptions for ANCOVA were not met, I ran a Poisson regression using the generalized linear model to determine whether the raw number of intrusions into a territory depended on group size. I ran analysis of variance (ANOVA) to test for differences in home range overlaps and territory size. Linear regression was used to test for correlations between pairs of any continuous-scaled variables, such as patchiness and log territory size. Multiple regression analysis was used to test for correlations among territory size, biomass/m² and group size, as well

as the number of individuals in each sex class and the changes in the number of males and females. Wilcoxon paired signed-rank tests were used to test for changes in group size. A paired t-test was used to compare the difference in territory sizes at two-week intervals in 2004, and test for differences among changes in home ranges between adult males and females in response to the experiments.

Average food patchiness for each period was used to test the effect of patchiness of food on the spatial overlap of individual home ranges. Biomass/m² and territory size were log transformed to reduce heteroscedasticity. Arcsine transformation was performed on the proportion overlap of individual home ranges. Year, site, and interaction terms are not reported, except where significant. Statistical analyses were performed using JMP 4.0 and Statistica software, and all P values reported are two-tailed.

Results

Post-reproductive season

Prior to beginning the food manipulation experiments in 2004, log territory size was a significant predictor of group size (whole model: $r^2=0.61$, $F_{1,18}=28.36$, $P<0.0001$). Log mean food biomass/m² increased with log territory size (whole model: $r^2=0.29$, $F_{1,18}=7.18$, $P<0.01$) and the log food biomass/individual increased with log territory size (whole model: $r^2=0.42$, $F_{1,18}=12.82$, $P<0.0002$). In addition, the per capita number of intrusions did not depend on group size ($W=0.04$, $P=0.85$, $N=20$). While group sizes changed on most territories during the experiment (Table

2), mean group size per treatment plot did not change significantly (Wilcoxon paired signed rank test: $W=4$, $P=0.92$). Multiple regression results indicated that while treatment type did not strongly affect group size after the experiments, the positive relationship between group size and territory size remained significant (whole model: $r^2=0.47$, $F_{4,15}=3.45$, $P<0.03$).

There was a significant treatment effect on the change in territory size (ANOVA: $r^2=0.59$, $F_{3,16}=7.65$, $P<0.002$). Territories on plots receiving the patchy and heterogeneous food treatments decreased in size, while territories on the even plot increased in size to about the same extent as those on the control plot (Figure 1). Prior to the experiments there was no significant relationship between food patchiness and territory size (whole model: $r^2=0.05$, $F_{1,18}=1.02$, $P=0.33$). However, the change in food patchiness was significantly correlated with the changes in territory size during the experiment (whole model: $r^2=0.45$, $F_{1,18}=14.74$, $P<0.001$). Changes in territory size on the even plot followed a similar pattern to the control plot. A comparison of territory sizes measured at two week intervals, beginning two weeks after the start of the experiments, showed that the territories on the even plot expanded significantly more than those on the control plot (t-test: $t_7=-2.909$, $P<0.02$). This difference in expansion pattern was no longer significant after the monsoon season began (paired t-test: $t_7=-2.232$, $P=0.06$), suggesting that the effects of the experiments were diluted as the summer progressed, as natural foods became more common and palatable.

The mean adult home range overlap for territories on plots receiving the patchy and heterogeneous food treatments increased, while the mean home range overlap for territories on the even plot decreased and was more similar to that of the

control plot (Figure 2; ANOVA: $r^2=0.59$, $F_{3,16}=7.65$, $P<0.002$). The difference in territory patchiness was significantly correlated with the change in mean adult home range overlaps (whole model: $r^2=0.38$, $F_{1,11}=6.23$, $P<0.03$).

Adult males and females did not differ in their responses to the experiment. The starting number of males and females did not explain changes in either the number of males added or lost to a group (whole model: $r^2=0.06$, $F_{2,17}=0.55$, $P=0.67$) or the number of females added or lost to a group (whole model: $r^2=0.22$, $F_{2,17}=2.45$, $P=0.12$). Prior to the experiments there was no significant difference between adult male and female home range sizes (ANOVA: $r^2=0.001$, $F_{1,68}=0.11$, $P=0.74$). Both males and females altered their home ranges in response to the experiment and data were pooled, as there were no sex differences across treatments. Neither average total home range size, nor changes in home range size, differed between males and females after the experiment (respectively, ANOVA: $r^2=0.01$, $F_{1,48}=0.59$, $P=0.44$; paired t-test: $t_{35}=0.47$, $P=0.64$).

Reproductive season

As in 2004, log territory size was a significant predictor of group size prior to the experiments (whole model: $r^2=0.38$, $F_{1,12}=6.76$, $P<0.02$). Food biomass was not analyzed in 2005, as measurements of biomass were not feasible in March, prior to the experimental treatment (see Methods). Although group sizes changed, both increasing and decreasing (Table 3), mean group size did not change significantly (Wilcoxon paired signed rank test: $W=24$, $P=0.10$). One territory on CC1 contributed heavily to the changes in group size. Shortly after the experiments began, five individuals left this territory, with four individuals, two males and two females,

settling just 30-40 meters north of their original territory and one individual moving 50-60 meters east to a territory outside of the plot. However, removing this territory from the analysis did not yield different results ($W=16$, $P=0.10$). Unlike in 2004, after the experiment, the relationship between group size and territory size was no longer significant, even when controlling for treatment type (whole model: $r^2=0.23$, $F_{3,10}=1.01$, $P=0.43$).

However, as with experiments conducted during the non-reproductive season (2004), there was a significant treatment effect on the difference in territory size (ANOVA: $r^2=0.45$, $F_{2,11}=4.12$, $P<0.05$), with territories on plots receiving the heterogeneous treatment decreasing in size, while territories on the even plot increased in size (Figure 3). Territory expansion occurred principally by individuals incorporating previously unutilized and undefended portions of the plots. The change in food patchiness was again strongly correlated with the average change in territory size during the experiment (whole model: $r^2=0.42$, $F_{1,12}=8.09$, $P<0.02$).

Consistent with the results from the non-reproductive season (2004), there was a significant treatment effect on the change in adult home range overlaps (ANOVA: $r^2=0.46$, $F_{2,11}=3.93$, $P<0.05$). The mean adult home range overlap on the heterogeneous treatment plot increased, while mean adult home range overlap on the even plot decreased (Figure 4). The change in mean adult home range overlaps within territories was correlated with the changes in territory food patchiness (whole model: $r^2=0.35$, $F_{1,12}=5.31$, $P<0.04$).

As in 2004, males and females did not differ in their responses to the experiments. The starting number of males and females did not explain changes in the

number of males added or lost to a group (whole model: $r^2=0.45$, $F_{2,11}=3.67$, $P=0.07$). Similarly, the starting number of males and females did not explain changes in the number of females added or lost to a group (whole model: $r^2=0.14$, $F_{2,11}=0.73$, $P=0.77$). Like 2004, there was no significant difference between adult male and female home range sizes prior to the experiments (ANOVA: $r^2=0.02$, $F_{1,32}=0.56$, $P=0.46$). There was no significant difference between adult males and females in the degree to which home range sizes changed during the experiment (paired t-test: $t_{27}=0.04$, $P=0.96$), nor was there any overall difference in adult male and female home range size after the experiment (ANOVA: $r^2=0.007$, $F_{1,43}=0.33$, $P=0.57$).

Discussion

Overall, results of this study indicate that food dispersion exerts a strong effect on the spatial aggregation patterns and territory size of Gunnison's prairie dogs. Male and female adult Gunnison's prairie dogs showed indistinguishable and significant changes in territory size and spatial overlap in response to experimental changes in food abundance and dispersion, and did so whether or not it was the mating season. These experimental results support some key components of the RDH as a potential mechanism for the evolution of group living in this species, while forcing a reassessment of some of the detailed predictions of RDH.

By increasing the average carrying capacity of all territories across experimental plots through increasing food abundance, I could evaluate what effect changes in the distribution of food had on each territory. Unexpectedly, territories on

the plots that received patchy and heterogeneous treatments contracted around the resource patches added, while territories on the plot receiving the even treatment expanded to encompass additional areas where food was being added. While the presence of a significant effect is concordant with the RDH, the outcome was opposite to currently published predictions.

Theoretical studies have emphasized the trade-offs associated with territorial defense. As territories become larger, additional defense costs should be incurred, offsetting the potential to gain additional resources (Brown 1964). The expectation is that individuals will be spatially conservative and minimize the area over which they must forage to meet their metabolic needs (Brown 1964; Charnov et al. 1976; Gill and Wolf 1975). However, results of this study suggest that Gunnison's prairie dogs seek to maximize their energy gain by expanding their ranging and territory size when additional energy makes it beneficial to do so. The ability to expand territory size without incurring excessive additional defense costs might be associated with vacant marginal space that was previously not being utilized. On both the control and even plots, such space for expansion was available and territories expanded by individuals incorporating previously unused and undefended areas. Although contrary to the predictions of the RDH, similar responses to changes in resource dispersion have been observed in other species when population sizes were low or below carrying capacity (red fox: Baker et al. 2000; badger: Revilla and Palomares 2002; arctic fox: Eide et al. 2004).

Of particular interest, and importance in supporting the RDH as a mechanism to explain group formation, was the effect of the treatments on adult home range

overlaps. Not surprisingly, because territory size decreased as food patchiness increased, adult home range overlaps correspondingly increased. Therefore, within a territory it appears that individuals become more spatially tolerant of group members as food becomes increasingly patchy. Within the RDH framework, greater spatial overlap in home ranges, and the resulting closer proximity of individuals to each other, may facilitate a higher frequency of social interactions among individuals, providing the potential for the evolution of increased sociality.

Although resource distribution affected both territory size and home range overlap, the changes in abundance and dispersion did not significantly alter group size. Previous results indicated a strong correlation between territory size and group size that was linked, not to patchiness, but to total available food biomass and density (Verdolin 2007). The experiments conducted in this study, emphasizing the effect of resource dispersion, decoupled this relationship by altering territory size in response to the dispersion of food. This decoupling supports the RDH because it is explicitly predicted that territory size will be influenced by the dispersion of resources (Johnson et al. 2001; 2002). In contrast, group sizes were not strongly affected by increasing abundance or dispersion. The short duration of the experiments may have left little opportunity for population responses to yield significant differences in group size. Given the experimental design, all territories within a given treatment plot were stochastically similar. Because there should have been little incentive for individuals to switch territories, it would have been unlikely to detect significant changes in group size.

For the RDH to apply as a general mechanism, both males and females should respond similarly to changes in resource distribution. If not, RDH might be useful only for one sex, and it might be difficult to distinguish the RDH from other hypotheses that stress male mating strategies as a determinant of social structure. This assumption is rarely emphasized, but is critically important to establishing the RDH as an independent general model for group formation. Results from this study indicate that males and females responded similarly to the experiments across the reproductive and non-reproductive season. Changes in the demography of groups as a result of the experiments were not related to the original composition of the group. In addition, changes in home range size were not sex-specific, indicating that both adult males and females adjusted home ranges in similar ways in response to the food manipulations.

Another key element of the RDH is that there are intrinsic advantages to group living other than benefits more typically assumed for mammalian social groups (eg. reduced predation risk, access to mates). The RDH is unique in that it requires no additional external force or benefit to explain group living, beyond shared territorial defense in response to patterns of abundance and distribution of resources. Prior to the 2004 experiments, Gunnison's prairie dogs living in larger groups lived on larger territories and had a higher food biomass available per individual. With individuals on larger territories having access to greater resources, coupled with no evidence that the per-capita rate of intrusions depends on group size, these results provide support in favor of the communal defense assumption of RDH and indicate a potential synergistic benefit associated with living in a larger group.

Unlike in black-tailed prairie dogs, there is little evidence to suggest that Gunnison's prairie dog social groups acquire additional benefits. For example, black-tailed prairie dogs frequently engage in allogrooming with group members (Hoogland 1995). Allogrooming can provide several benefits including the removal of ectoparasites, increased tolerance, strengthening pair bonds, food acquisition and parental care (Seyfarth and Cheney 1984; Tanaka and Takafushi 1993; De Waal 1997; Henzi and Barrett 1999). Although allogrooming occurs, its incidence in Gunnison's prairie dogs is extremely rare (pers. observ.) and unlikely to confer any significant benefit.

Infanticide is another seemingly common occurrence among black-tailed prairie dogs (Hoogland 1995), but has not been recorded in Gunnison's prairie dogs despite long-term studies. The lack of infanticide in Gunnison's prairie dogs is not surprising because none of the classical hypotheses for the existence of infanticide appear to apply. Though females could potentially benefit by eliminating the offspring of competing females, because females breed once per year, there is no real chance for males to benefit from infanticide. In addition, females of this species do not appear to regularly nest communally, decreasing the likelihood that infanticide by females would occur.

Increased protection from predators is thought to be a major benefit in many species that live in groups, including black-tailed prairie dogs. Increased vigilance could reduce predation risk for black-tailed prairie dogs living in larger groups within a colony (Hoogland 1979). For Gunnison's prairie dogs, however, such antipredatory

benefits may be largely due to overall colony size and not to group size per se (Verdolin and Slobodchikoff 2002).

Lastly, while individuals living in groups clearly have access to potential mates by proximity, behavioral observations (Verdolin 2007), coupled with high levels of extra-group paternity found in previous studies (Haynie et al. 2003; Travis et al. 1995, 1996), indicates that females actively seek copulations with males outside the territory. These data suggest that individuals of either sex may not derive clear benefits of territorial defense via enhanced access to mates. However, a comparison of male mating success (resident males versus nonresident males) will ultimately be the only way to address this issue. Genetic analyses of the reproductive success of individuals from these populations are in progress and perhaps will reveal if access to mates is an additional driving force shaping Gunnison's prairie dog social group formation and maintenance.

If none of the classical benefits for sociality apply, what factors might favor larger group sizes in Gunnison's prairie dogs? They are obligate hibernators, though hibernation is interrupted by cyclic periods of activity (Bakko and Nahorniak 1986). As the season progresses, individuals need to acquire adequate resources to meet their daily requirements and obtain additional resources if they are to survive overwinter hibernation. Therefore, the primary purpose of territories in this species may be to secure sufficient resources and reduce individual defense costs, while constraining the absolute group size possible within a territory by the intensity of competition for those resources. Optimal group size will then be determined by the fitness maximum,

the net difference between reproductive output and mortality, that results from access to resources and the costs of group defense as territory size increases (Figure 5).

Overall, this study provides strong empirical support for the RDH as an explanation of group living in Gunnison's prairie dog. Adult males and females responded to the experiments by adjusting territory size and spatial overlap during both seasons. These changes occurred as both adult males and females modified their home ranges, and there were no consistent differences between adult male and female home ranges, both prior to and during the experiments. Although significant group size changes were not observed, there was no indication that alterations in the composition of groups were sex-specific. However, the contraction of territories on the patchy and heterogeneous experimental plots, suggests that an extension to the current predictions of the RDH is needed to allow for the possibility that, under condition of superabundant patchy or heterogeneous food availability, individuals will minimize energetic costs and risks associated with territorial defense.

The RDH has been previously claimed not to be a testable hypothesis, because it has been used *ad hoc* to explain grouping patterns for which no reasonable alternative appears to exist. Results of the current investigation suggest that the RDH is a practical, feasible, and testable hypothesis. While it may not be possible to conduct such experimental manipulations for all species, this study demonstrates that the RDH is no longer limited to purely descriptive conclusions and may be applicable to a broader array of species.

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Table 1. Experimental design for the post-reproductive season in 2004 and the reproductive season in 2005.

Plot	2004 Experiments	2005 Experiments
CCI	Patchy	Heterogeneous
CCII	Control	Control
HSI	Heterogeneous	Even
HSII	Even	-----

Table 2. Changes in territory size (TS), group size (GS), and mean adult home range size (HRS) for each territory by experimental treatment in 2004. With the exception of group size, reported values are in m².

Plot	Treatment 2004	Territory	TS	GS	HRS
CCII	Control	1	634.86	1	490.44
		2	953.38	0	337.97
		3	-26.24	-2	-204.13
		4	706.59	1	346.87
CCI	Patchy	1	326.28	-2	946.02
		2	-676.21	-1	235.00
		3	-702.5	-4	804.82
		4	-162.83	-3	151.39
		5	94.14	1	583.60
		6	-477.47	0	394.79
HSI	Heterogeneous	1	-560.77	1	194.62
		2	6.03	1	-52.71
		3	146.71	0	642.49
		4	-480.08	3	-297.21
		5	-207.7	0	67.41
HSII	Even	1	700.74	0	102.40
		2	465.84	3	375.99
		3	126.01	-1	-79.40
		4	388.16	1	-100.89
		5	806.39	1	-106.26

Table 3. Changes in territory size (TS), group size (GS), and mean adult home range size (HRS) for each territory during experimental treatment in 2005. With the exception of group size, reported values are in m². The (-) symbol indicates a lack of data for this territory as it did not exist prior to the experiments. Territory numbers do not correspond to those listed in Table 2a.

Plot	Treatment 2005	Territory	TS	GS	HRS
CCII	Control	1	-397.16	-2	366.408
		2	340.87	0	605.87
		3	472.19	1	167.59
		4	169.87	1	208.651
		5	61.47	0	79.269
CCI	Heterogeneous	1	-240.92	0	-84.92
		2	-209.59	0	-766.77
		3	-93.96	-1	-394.22
		4	-334.10	-5	157.12
		5	-	-	-
HSI	Even	1	163.24	-2	114.25
		2	218.03	0	48.06
		3	89.34	0	589.78
		4	408.83	0	219.34

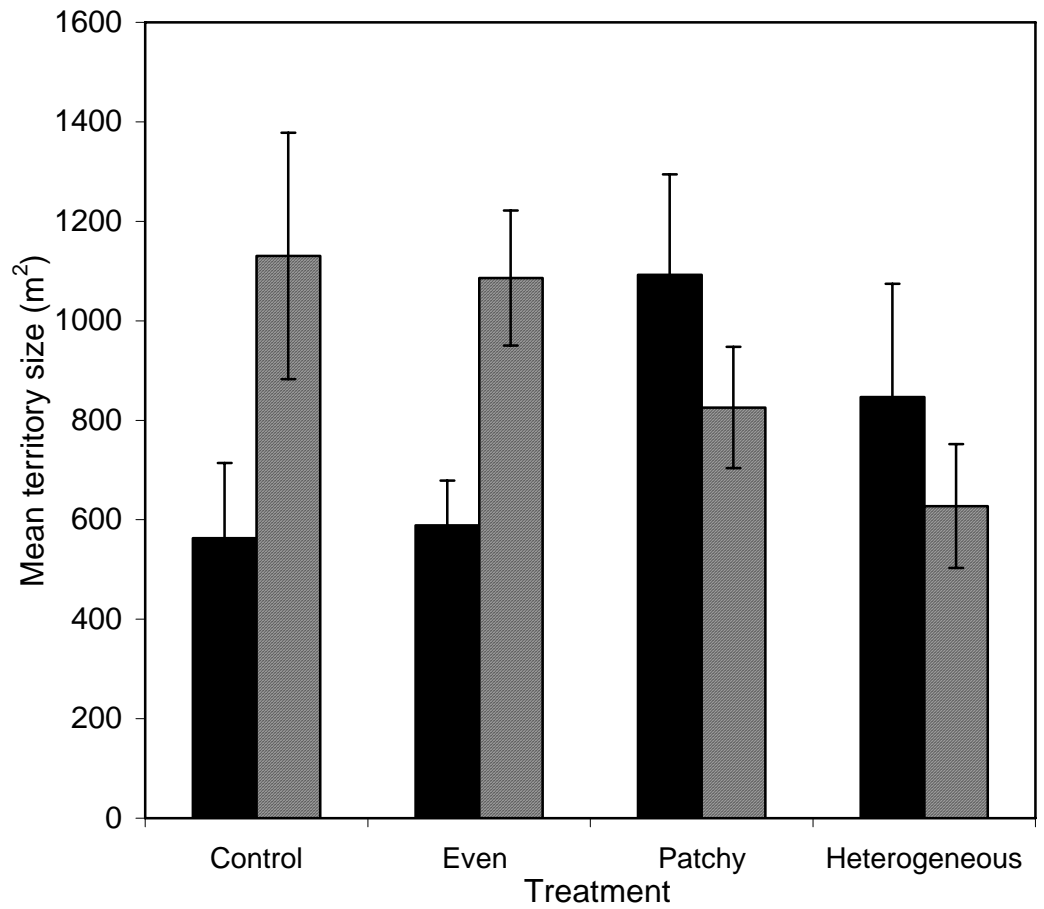


Figure 1. Mean (\pm SE) territory sizes before and after the experiments for each treatment and the control plot during the non-reproductive season in 2004. The solid bars indicate mean territory size prior to the experiments, while the hatched bars reflect the mean territory size at the end of the experiments.

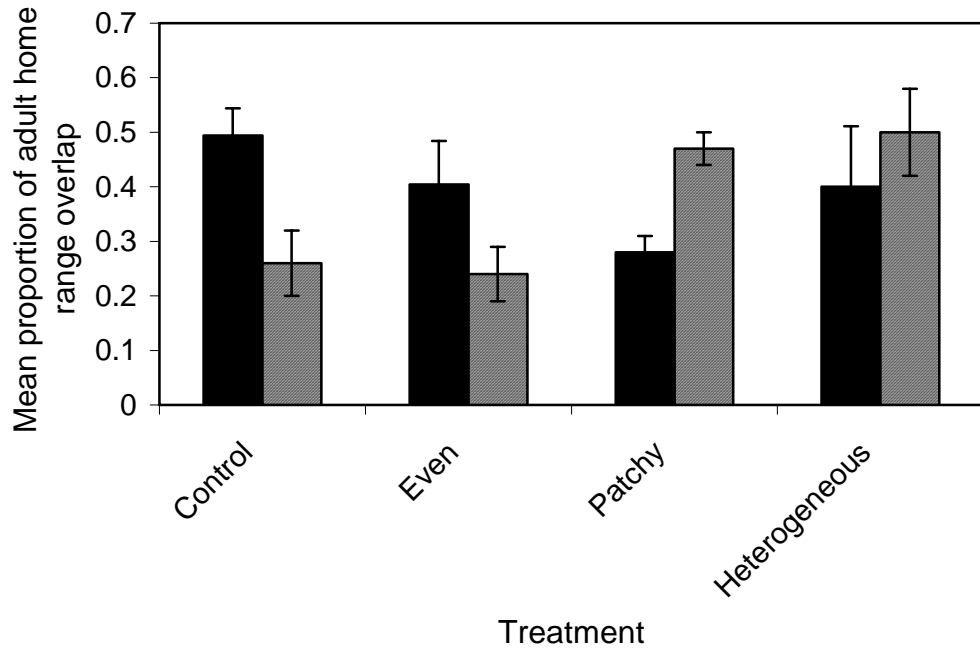


Figure 2. Mean (\pm SE) untransformed proportion of adult home range overlap before and after the experiments for each treatment and the control plot during the non-reproductive season in 2004. The solid bars indicate mean proportion of adult home range overlap prior to the experiments, while the hatched bars reflect the mean proportion of adult home range overlap at the end of the experiments.

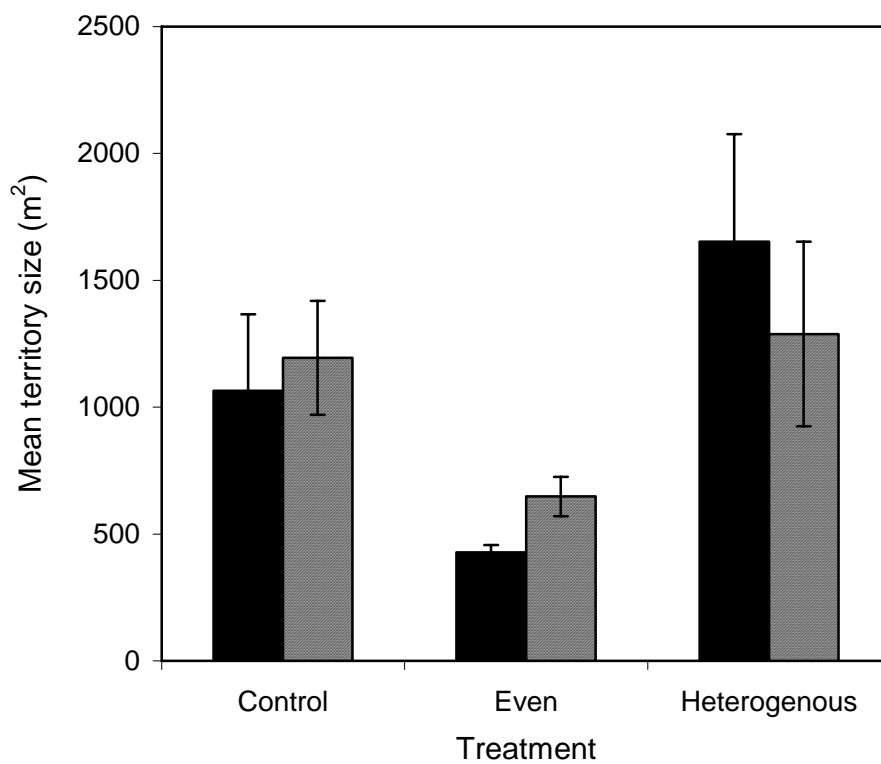


Figure 3. Mean (\pm SE) territory sizes before and after the experiments for each treatment and the control plot during the reproductive season in 2005. The solid bars indicate mean territory size prior to the experiments, while the hatched bars reflect the mean territory size at the end of the experiments.

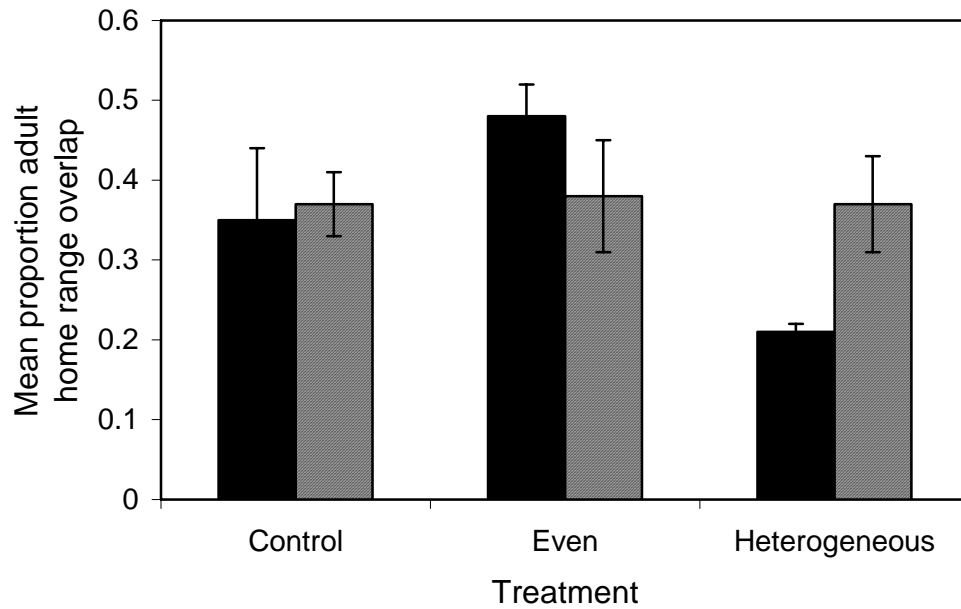


Figure 4. Mean (\pm SE) untransformed proportion of adult home range overlap before and after the experiments for each treatment and the control plot during the reproductive season in 2005. The solid bars indicate mean proportion of adult home range overlap prior to the experiments, while the hatched bars reflect the mean proportion of adult home range overlap at the end of the experiments.

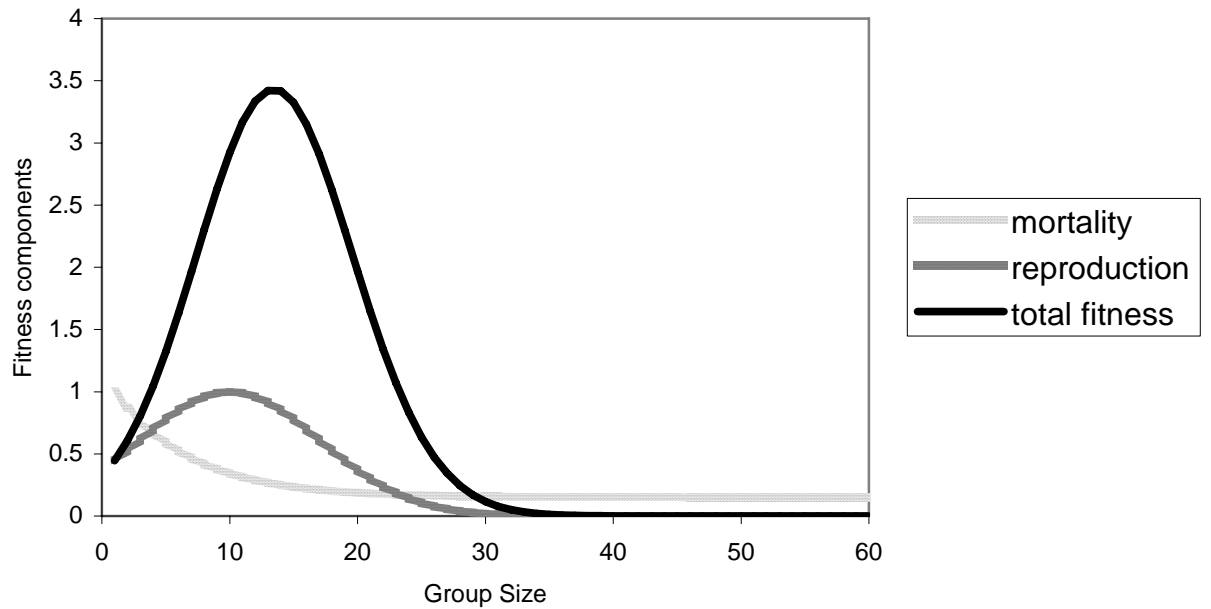


Fig. 5. Graphical model of selection on group size in an RDH system. It is assumed that in general larger groups inhabit larger territories. Reproduction at first increases with group size, because of the benefits of better group defense (lower costs, and/or better quality territories), but eventually competition among group members reduces reproductive success in larger groups. Mortality decreases in larger groups because individuals on larger territories are more likely to find sufficient food regardless of seasonal and annual variations in productivity, although unpredictable climatic events (e.g., floods) place a lower limit on mortality rates. Total fitness (taken simplistically as the reproductive rate divided by mortality, assuming constant vital rates throughout life) peak at slightly larger group sizes (and presumably territory sizes) than those that maximize reproduction alone.

It is not the strongest of the species that survives, nor the most intelligent that survives. It is the one that is the most adaptable to change.- Charles Darwin

Chapter Four

Male reproductive success in Gunnison's prairie dogs (*Cynomys gunnisoni*)

Abstract

In this study I describe patterns of paternity in Gunnison's prairie dog (*Cynomys gunnisoni*) social groups. Resident males sired the majority of offspring from their respective territories only 10.5% of the time, contrary to what is expected if males of this species were pursuing a female defense mating strategy. In addition, a single nonresident male sired equal or greater number of offspring than a single resident male 71.2% of the time. For resident males the number of other males present did not influence the number of offspring sired. Territory size was significantly correlated with offspring number and mean litter size suggesting a reproductive advantage for females that occupy larger, better quality territories. Therefore, it is possible that individual mating strategies are secondary to the social structure that emerges in response to resource availability.

Introduction

Typically, variations in male mating strategies are evaluated against the background of the polygyny-threshold model (Verner 1964; Verner and Willson 1966; Orians 1969; Wittenberger 1976) and the environmental potential for polygyny model put forth by Emlen and Oring (1977). Female strategies are rarely emphasized in these models because females are predicted to pursue resources, regardless of the male strategy Trivers (1972). In general, males are predicted to control access to females directly (female defense polygyny) or indirectly through resources (resource defense polygyny). Males may form coalitions when single males are unable to defend a group of females and the benefits of cooperatively defending females overrides the cost of sharing access to potential mates (Clutton-Brock 1989, Davies 1991).

Extensive studies of mating success have demonstrated that the social mating system and the genetic mating system of a species can be quite distinct (Birkhead et al. 1987; Davies 1991; Lott 1991), suggesting that broadly categorizing populations solely on the basis of observable patterns of association between males and females may not reflect the true mating system. Additional reviews have proposed that social and mating systems are better understood in the context of individual fitness enhancing strategies (Vehrencamp and Bradbury 1984; Davies 1991). While social and mating systems can be dissimilar, the social context may still exert a strong influence on the occurrence of extra-pair copulations (EPCs). For example, in territorial species, a male may monopolize access to females through male-male

competition, herding of females, or mate-guarding (Emlen and Oring 1977; Bradbury and Vehrencamp 1977; Hanken and Sherman 1981). As additional males are added to a group, however, the ability of a single male to monopolize mating access may be compromised (Goossens et al. 1998; Cohan et al. 2006). Thus, multiple paternity may be more common in social groups that contain multiple males.

A female may be motivated to mate multiply regardless of how many males are present and their attempts to monopolize access to her. The two primary assumptions underlying the occurrence of multiple mating by females are 1) that a female's choice of social mate is constrained in some way and 2) that a male of better genetic quality is available (Jennions and Petrie 2000). If both of these conditions are met, then females should actively seek additional mates. Although multiple paternity occurs over a broad range of species (see Griffith et al. 2002; Carling et al. 2003; Cohan et al. 2006), determining the potential selective advantage for females in seeking EPCs has been more challenging. Because it is expected that female strategies are driven primarily by access to resources, it has been suggested that, once sufficient resources are secured, females may mate multiply to gain additional direct or indirect benefits. Direct benefits may include increased access to resources such as food or nest sites, and fitness-enhancing behaviors such as feeding of offspring or 'baby-sitting', while indirect benefits may include increased fitness of offspring through such mechanisms as 'good genes' expressed in phenotypic traits, genetic compatibility, increased genetic diversity of offspring and genetic hedge-betting (Reynolds 1996; Jennions and Petrie 2000). Empirical studies have demonstrated that multiple mating by females can often be explained largely due to the genetic benefits

gained (Kempnaers et al. 1997; Richardson and Burke 2001; Foerster et al. 2003; Cohan et al. 2006).

Two main hypotheses have been proposed to address the potential genetic benefits that females may acquire by mating multiply. First, emphasizing indirect benefits, the ‘good genes’ model proposes that females may choose additional mates on the basis of phenotypic traits that reflect the quality of a male. In principle, this should apply to all the males that a female mates with. Support for this model has been mixed (see Griffith et al. 2002), indicating that other processes may be influencing the occurrence of multiple paternity in any given system. Genetic compatibility was suggested as an alternative to the ‘good genes’ model and predicts that females will choose additional mates that enhance the genetic diversity of their offspring (Tregenza and Wedell 2000, 2002; Blomqvist et al. 2002; Mays and Hill 2004). Females may mate with males that are genetically dissimilar to themselves to increase offspring heterozygosity, which may reduce inbreeding depression, improve offspring survival and enhance competitive abilities (Brown 1997; Coltman et al. 1998; Amos et al. 2001; Hansson et al. 2001; Foerster et al. 2003).

Within the ground squirrels, multiple mating by females is common in several species (Hanken and Sherman 1981; Boellstorff et al. 1994; Murie 1995; Lacey et al. 1997; Michener and McLean 1996; Schwagmeyer and Fultz 1990; Sherman 1989), including the highly social, territorial Gunnison’s prairie dog (*Cynomys gunnisoni*) (Travis et al. 1995 1996; Hoogland 1998; Haynie et al. 2003). In Gunnison’s prairie dogs, females range further than males during the brief mating season and are frequently observed in the company of nonresident males (Verdolin 2007). Previous

studies report that 60% of pups born to any given female are not sired by the resident male/s on her territory (Travis et al. 1995, 1996). Thus, not only is the frequency of multiple paternity high in this species but a large portion of offspring are sired by non-resident males. These observations and empirical results contradict what is expected if, indeed, males are pursuing a female defense polygyny strategy as previously reported (Fitzgerald & Lechleitner 1974; Rayor 1988; Hoogland 1999).

The purpose of this study was to re-examine the mating success of resident males and determine if it conforms to what one would expect if males were pursuing a female defense or resource defense mating strategy. I also evaluated whether males occupying territories that had fewer males had higher reproductive success.

Methods

Study area

Two colonies of Gunnison's prairie dogs were studied in northern Arizona from May 2003 to August 2005. The first study site, Humane Society (HS), was established in May 2003. The second study site, Country Club (CC) was established in August 2003. Experimental manipulations of resource abundance and distribution were conducted from June 1, 2004-August 1, 2004 and April 1, 2005- May 6, 2005. Because only a small percentage of the total numbers of juveniles were captured during the 2003 and 2005 seasons, these data are excluded from this study.

Both colonies were located within the city limits of Flagstaff, Arizona. Within each study site Humane Society (HS) and Country Club (CC) two 1 ha plots were

created. At both sites, the location of the plots (HS I, HS II, CC I and CCII) were separated by a distance of 0.2 km and a road. The location of each plot was selected on the basis of two factors: 1) plots were maximally distant from each other, and 2) plots were located in areas of greatest prairie dog activity. With the exception of one individual who moved in August 2004 from HS I to HS II and two individuals from CC I that moved to the boundary of CC II, individuals in different plots did not physically interact with one another, or occupy the same area at any time during this study.

For each plot, at both HS and CC, a 100 m X 100 m letter/number grid system consisting of 100 10x10m quadrats was established using surveyor stakes. The location of each stake, the halfway point between each stake, and the center point of each 10x10m quadrat was recorded using a Garmin Etrex Global Positioning System.

Trapping and marking

Prairie dogs were live-trapped with Tomahawk live traps (50 cm x 18 cm x 18 cm and 48 cm x 15 cm x 15 cm), baited with sunflower seeds. Each trapped animal was placed in a specially designed sleeve, weighed with an O'Haus scale, sexed, and DNA samples (hair) collected. Hair from all individuals was stored in coin envelopes in the field and transferred to 1.5mL sterile tubes and stored until analysis upon returning to Stony Brook University at the end of each field season. Each animal was permanently marked using AVID or Home Again individually packaged, sterile microchips. Once injected, individuals were scanned to test the microchip and marked with a unique number/symbol using Lady Clairol black hair dye for identification related to behavioral observations. The hair dye was used as directed and trapping

was conducted throughout the study period to trap unmarked individuals and to re-apply markings on previously trapped individuals.

Behavioral data

Behavior was observed for a minimum of 10 days per month for 3h/ day from May-August 15, 2003. With the exception of days when trapping occurred, observations were made at least every other day at each plot from March 7-August 15, 2004 and March 3 -August 8, 2005, for a total of 825 hours of observation. Only data from 2004 are reported in this study.

For each plot, observations were made alternately in the morning from 0700-1000 and afternoon from 1500-1800, during the times when prairie dogs were most active (Longhurst 1944; Hoogland 1981). Data collected for this study do not encompass the entire active period of Gunnison's prairie dogs in Flagstaff, AZ, as individuals were observed active through early December. However, individuals were observed intensely beginning with emergence from hibernation, during and after the reproductive season (March-May), and after juvenile emergence (June-August). Natural terrain features, such as rock formations, hills and trees were utilized for observations. Observations were made using Nikon 8-24x25 zoom binoculars.

The term social group refers to individuals that are mutually tolerant of each other, as indicated by behaviors such as greet-kisses (King 1955) and co-feeding, while territory refers to the area occupied and defended by members of a social group. Animals that were consistently chased out of an area were considered as not belonging to that territory. Individuals that were trapped once and not seen throughout the study were not included as members of any social group.

Because group territorial boundaries are relatively stable and are shared by all occupants of the territory, little confusion arises about assigning group membership. To obtain data on the composition of social groups within each study plot, behavioral observations included focal sampling, scan sampling and all occurrences sampling (Altmann 1974). Focal samples were conducted for five minutes. During the focal sample, all occurrences of social interactions were recorded, along with the identities of all individuals the focal animal interacted with. Four such focal samples were taken in sequence, then every 30 minutes, a scan sample was used to record the location of each above ground animal within the study plot. Locations were recorded based on the proximity of an individual to either a surveyor stake or a flagged burrow and matched with corresponding coordinates obtained with the Garmin Etrex Global Positioning System. Trap locations were combined with behavioral observations to increase sample sizes for calculating territory sizes. Observations were removed from the calculation of territory area in only two cases. First, data from agonistic interactions that resulted in a chase were excluded. Second, during the month of April, when mating took place, isolated excursions by individuals to other parts of the colony were excluded. Including either observation would have greatly inflated territory area.

Territory size

A territory was defined as the area occupied by all members of a particular group. Territory areas were calculated using the fixed kernel density estimator (ArcView 3.2a; ESRI 2000). When using the fixed kernel approach with a level of smoothing selected by least squares cross-validation (LSCV), results are less biased

and more appropriate for non-normal distributions (Worton 1995; Seaman & Powell 1996). As opposed to the adaptive kernel, the fixed kernel approach is more stable for probability contours exceeding 80%. Seaman et al. (1999) suggest that contours greater than 85% do not provide meaningful biological information and are less reliable. Therefore, I used only the 85% contour probabilities for all calculations of territory area and statistical analyses. There was no relationship between territory size and sampling effort (whole model: $r^2=0.03$, $F_{1,18}=0.68$, $P=0.42$).

DNA extraction and PCR amplification

DNA was extracted two independent times from each hair sample using Qiagen DNeasy tissue extraction kits utilizing a modified protocol for hair. Six microsatellite markers were used to determine allelic diversity, heterozygosities, and parental identities of offspring. The markers used were CGS-08, CGS-14, CGS-12, CGS-22, CGS-25, and CGS-26. Haynie et al. (2003) redesigned markers CGS-8, CGS-12, CGS-14, and CGS-22 that were originally published by Stevens et al. 1997. Marker CGS-25 and CGS-26 were used as originally published by Stevens et al. 1997. PCR amplification of the loci was performed using a 20- μ L volume that contained: 5- μ L of extracted genomic DNA, 2- μ L *Taq* buffer, .8- μ L 50mm $MgCl_2$, 0.4- μ L dNTP, 0.04- μ L *Taq* DNA polymerase, 1.0- μ L of each primer and 9.76- μ L water. The optimal annealing temperature during PCR amplification varied depending on the marker but the remainder of the PCR protocol was identical to that published in Stevens et al. (1997). Samples were submitted to the Genomic Analysis and Technology Core facility at the University of Arizona where multiplexed PCR

reactions amplified with compatible labeled primers were scored with the ABI PRISM® 3730 DNA Analyzer. Data were visualized using GeneScan freeware.

Marker analysis

In these populations, the numbers of alleles ranged from 3-9 per locus and were comparable to results reported by Haynie et al. (2003) (see Chapter 5). FSTAT 2.9.3 (Goudet 1995) was used to calculate expected heterozygosity, the observed heterozygosity, to test for deviations from Hardy-Weinberg, and detect linkage disequilibrium for each locus using all individuals sampled in 2004 (see Chapter 5).

When performing parentage analyses using microsatellites, genotyping errors can occur, particularly when utilizing noninvasive DNA samples (Gagneux et al. 1997). Two primary stochastic errors that may arise are, *allelic dropout*, when an individual is scored as a homozygote due to the amplification failure of an allele, and *false alleles*, where human genotyping error, mutations, or PCR artifacts result in the true allele being misgenotyped (Taberlet et al. 1996; Gagneux et al. 1997; Taberlet and Waits 1998; Broquet and Petit 2004). Allelic dropout is more likely to have an impact on kinship inference and hence, parentage assignment (Johnson and Haydon 2007). However, allelic dropout can potentially be identified due to mismatches between parents and offspring, where the offspring appears homozygous for an allele detected in only one parent. Alternatively, Mendelian inconsistencies due to false alleles may be detected when an offspring is genotyped for an allele not present in either parent (Johnson and Haydon 2007). To reduce the incidence of these potential genotyping errors, DNA was extracted twice from each sample. While time and financial constraints precluded PCR amplification and genotyping of every sample two times as recommended for noninvasive DNA samples that typically yield low

quantities of template DNA (Taberlet et al. 1996, 1998; Gagneux et al. 1997; Johnson and Haydon 2007), a subset of approximately 30% of samples were independently repeated to confirm assigned genotypes. If in the second amplification a different genotype was scored, the sample was repeated a third time. If the genotype could not be resolved, the locus was not included in the final analysis for that individual. Only 5.4% of repeated samples could not be confirmed for a given genotype.

Parentage analysis

Parentage analysis was performed using genetic exclusion, followed by submitting individuals for analysis in Cervus 1.0 (Marshall et al. 1998), which uses a maximum-likelihood approach. An LOD score is reported for each candidate parent and represents the natural log of the overall likelihood ratio (Marshall et al. 1998).

At these study sites, females and juveniles within the same territory occasionally intermingled prior to the capture of juveniles. Therefore, maternity could not always be assigned based on the burrow that a lactating female utilized. In those cases, and on the basis of behavioral observations (eg. lactating vs. nonreproductive), only those females that were determined to be potential mothers for offspring in their respective territory were submitted for analysis, thus reducing the number of candidate mothers. In addition, only females from a juvenile's natal territory were considered potential mothers. Genetic exclusion of females was used to determine maternity or reduce the number of potential mothers, by excluding any female as a potential mother if she contained a pair of alleles, neither of which was present in the juvenile. In cases where only one female remained as a possible mother, maternity was assigned to that female. If maternity could not be resolved by genetic exclusion,

the remaining potential mothers were submitted for analysis in Cervus 1.0, where the mother with the greatest likelihood score was accepted as the true mother. Any cases of suspected homozygous-homozygous mismatching between mother and offspring were excluded from further analysis. If two females were equally likely to be the mother, the offspring was removed from further analysis.

For paternity analysis, all males sampled on the plot, both yearlings and adults, were considered as potential sires. To provide a conservative estimate of the frequency of extra-territorial paternity, only resident males were initially considered as candidate sires, unless genetic exclusion eliminated a male from consideration. A resident male that was not excluded and had a positive LOD score was assigned paternity. If more than one resident could be assigned paternity, the one with the highest LOD score was accepted as the true sire. If all resident males were excluded as possible sires for a given offspring, based on allelic mismatches, then all nonresident males were considered potential sires for that offspring. In this case, the nonresident male with the highest positive LOD score was accepted as the true sire of that offspring; if no nonresident male had a positive LOD score, the infant was not assigned a sire.

Data Analysis

The frequency of multiple paternity was calculated as the proportion of all litters that were sired by more than 1 male. A chi-square was performed testing whether the frequency of paternity by residents was greater than expected given the proportion of resident males relative to all candidate males sampled. Because the relevant assumptions

of analysis of variance (ANOVA) were not met, I used a Poisson regression using the generalized linear model to determine whether the number of offspring a given male sired in his territory was correlated with the number of other males present on that territory. To estimate the total number of offspring per territory, I added the number of offspring caught per territory and the highest number of unmarked juveniles observed during scanning, once trapping was complete. From this I calculated an estimated mean litter size by dividing the total number of offspring per territory by the number of females known to be potential mothers. I used linear regression to test for a relationship between territory size and mean litter size produced in a given territory. All statistical tests were performed using JMP 4.0 (SAS Institute 2000) and Statistica. Unless otherwise stated, all tests were two-tailed and the level of significance was set to $P < 0.05$.

Results

A total of 149 juveniles from 69 litters were trapped, and of those, 113, or 75.8%, were successfully genotyped from the four study plots. Among females for which multiple offspring were trapped and successfully genotyped, 90.6% (N=32) had offspring sired by more than one male. Females, on average \pm SD, mated with 2.13 ± 0.61 males.

Study plots varied in the percentage of the total number of candidate males that successfully sired offspring, based on paternity assignments. CCI had the highest percentage of males that sired offspring (75.0%), followed by HSII (67.9%), HSI (63.2%) and CCII (54.6%). Of the males that successfully sired offspring, not all sired more than one offspring. At CCII only 33.3% sired ≥ 2 juveniles, while at the other plots higher values were observed (CCI=42.6%, HSII=53.6%, and HSI=75.0%). Among the males that sired offspring, a portion of the inferred sires were yearling males, but percentages varied across the study sites. Compared to the other plots, yearling males at CCI sired the highest proportion of juveniles (34.3%), followed by HSI (21.9%), HSII (17.65%), and at CII, no juveniles were sired by yearling males.

On 2 out of 19 territories, or 10.5%, resident males sired more offspring on their territories than expected given the total number of candidate males (Table 1) and Fisher's combined probability test indicated that the overall trend was not significant ($X^2_{.05[38]}=34.82$, $P=0.62$). On 71.2% of the territories, a single nonresident male contributed equal, or higher, numbers of offspring than any individual resident male.

The number of offspring a male sired on his territory was not significantly correlated with the number of other males present on that territory (Wald statistic=0.31, $N=26$, $P<0.58$), indicating that number of other males present has little impact on a given male's reproductive success in his respective territory. Interestingly, as log territory size increased the number of offspring produced (Figure 1) and mean litter size increased (Figure 2).

Discussion

In this study, I successfully assigned parentage to 113/149 (75.8%) juveniles from the four study populations. Territorial males in these populations sired a significantly higher number of offspring than nonresidents from their respective territories only 10.5% of the time. This value may even be an overestimate, as resident males were assigned as sires if any of them had a positive LOD score for a given infant, even when a non-resident male had a higher LOD score for the same infant. This result is consistent with previously published results for Gunnison's prairie dogs in this area (Travis et al. 1995, 1996). In addition, larger territories produced a greater number of offspring and larger mean litter sizes, which implies a potential for fitness benefits associated with occupying a larger territory.

In female defense mating systems, males are predicted to directly control female movement patterns and sire the majority of offspring. Previous results from behavioral observations concluded that resident males in these populations never interfered with resident female movement across territory boundaries, that females were often observed "visiting" other territories, and that females ranged further during the mating period than at any other time (Verdolin 2007). Similarly, if males are pursuing a resource defense strategy, then it is predicted that the resident male would contribute to a higher number of offspring in his territory than any other individual male. The results of this study present strong support that, at least the

majority of the time, a resident male does not sire more offspring on his territory than any other single nonresident.

It is possible that incomplete genotyping of all offspring biased these results by leaving a large uncertainty about the true sire and mistakenly attributing a non-resident male as the sire when the true sire was a resident. This situation is unlikely to have produced the observed relatively low siring success of resident males, for two reasons. First, I used a conservative procedure in assigning paternity to non-resident males, so that, all else being equal, the bias would favor assigning paternity to resident males. For instance, for the 37 juveniles assigned to resident males as sires, there were 7 cases (18.91%) in which a non-resident male had a substantially higher LOD score (at least 1.0 units higher) for paternity in that infant than the resident male. Second, if high variance in assigning paternity were the cause of the pattern, then there should be link between assignment of non-resident males as sires and the number of loci successfully genotyped for a given infant. In fact, the number of loci successfully genotyped for infants ascribed to resident and non-resident males did not differ (Wilcoxon two-sample test: $Z_{0.025[75,38]}=0.51$, $P=0.61$).

It has been suggested that as additional males are added to a group, the ability of a single male to monopolize mating access may be compromised (Goossens et al. 1998; Cohan et al. 2006). For example, extra-pair paternity in alpine marmots (*Marmota marmota*) increased with the number of subordinate males present (Cohan et al. 2006). Results of this study do not support this hypothesis as an explanation for multiple paternity, as there was no evidence that the number of males present on a territory influenced the number of offspring sired by a given resident male. In

addition, there is no evidence for dominance hierarchies among Gunnison's prairie dog males that occupy the same territory (Verdolin 2007). Although females routinely visited areas that contain additional males, the interpretation that they did so to gain additional mating opportunities is limited by the inability to determine if female movements into other areas was exclusively for the purposes of mating (Westneat and Stewart 2003).

Given that multiple mating is frequent in all populations of Gunnison's prairie dogs studied to date (This study; Travis et al. 1995, 1996; Haynie et al. 2003), why are females mating multiply? Hoogland (1998) suggests that female Gunnison's prairie dogs that mate multiply increase the probability of insemination, but found that the probability of parturition did not differ between females that copulated with one versus two males. Because copulation almost always occurs below ground, I was unable to accurately assess how many males a female mated with. Hoogland (1998) also reports that litter size for a given female increased with the number of males she mated with. In this study, not all offspring were successfully trapped, and though estimates of mean litter size per territory were possible by combining trapped offspring with counts of the number of unmarked offspring remaining in a given territory, I was unable to confidently determine litter size for all females.

Another possible explanation for why females are mating with multiple males may be that offspring viability is enhanced. It has been argued that for females to engage in extra-pair copulations, two criteria must be met: 1) a female's choice of social mate is constrained in some way and 2) a male of better quality is available (Slagsvold and Dale 1994; Jennions and Petrie 2000). If females were closely related

to resident males, one might expect a higher incidence of extra-pair copulations as means of avoidance of genetic incompatibility due to inbreeding (Zeh and Zeh 1996,1997; Tregenza and Wedell 2000). Evidence for this was demonstrated in several species including common shrews (Stockley et al 1993), adders (Madsen and Shine 1992; Madsen et al. 1996, 1999), and field crickets (Tregenza and Wedell 2002). However, kinship results for Gunnison's prairie dog populations in this study suggest that within territories, males and females are not more closely related than expected at random (see Chapter 5). Though increased offspring viability due to inbreeding avoidance may still explain why female Gunnison's prairie dogs mate with multiple males, it does not address why females frequently mate with non-resident males.

Lastly, it is possible that female Gunnison's prairie dogs choose to settle on good quality territories that contain sufficient resources for raising their offspring, but are mating with males that exhibit some superior phenotype, or males that are more heterozygous. Previous data from these study plots showed a clear positive relationship between territory size, group size and food abundance (Verdolin 2007). More importantly, larger territories had a higher per-capita amount of food available (see Chapter 3). Here, I found that larger territories produced a higher number of offspring, which might be expected since larger territories generally had more females. More importantly, mean litter size was larger on larger territories and may explain the potential fitness benefits for females to settle on particular territories. Though not all juveniles were accounted for, it is unlikely that there is any systematic bias that would skew trapping success in favor of larger territories.

Trivers (1972) postulated that while males seek to maximize their mating opportunities, females should select males that increase the genetic fitness of their offspring. Recent empirical data from natural populations suggest that high levels of homozygosity reduce survival in many species (Soay sheep: Coltman et al. 1999; Song sparrows: Keller 1998; Collared flycatcher: Kruuk et al. 2002). Thus, increasing offspring heterozygosity may improve offspring fitness (Brown 1997; Foerster et al. 2003). Whether females are then choosing mates based on phenotype or increasing genetic heterozygosity of their offspring remains to be explored in these populations and may ultimately elucidate what factors influence the high prevalence of multiple paternity. However, if a female were only seeking a sire of the highest quality (or genetic compatibility) for her offspring, it is not clear why she would mate with many males, as opposed to merely one male that might happen to be a non-resident.

In this study, I found that paternity results strongly suggest males are not pursuing a female defense, or even a resource defense, polygyny strategy. Resident males do not appear to have a consistent reproductive advantage with females that they co-defend territories with. In addition, mean litter size and the total number of offspring produced were both significantly correlated with territory size, supporting previous observational and experimental results demonstrating that the primary purpose of territories appears to be to provide group members with sufficient resources. Therefore, possibly individual mating strategies are secondary to the social structure that emerges in response to resource availability.

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Table 1. Results of the chi-square analysis testing whether resident males had a higher than expected frequency of paternity given the proportion of potential sires that were resident males relative to the number of candidate males sampled per territory. * denotes significance at the Bonferroni corrected P-value of 0.003.

Plot	Territory #	#Offspring Genotyped	#Offspring Sired by resident	X^2	P-value
HSII	1	4	0	0.14	0.71
HSII	2	2	0	0.36	0.55
HSII	3	3	0	0.44	0.51
HSII	4	23	8	6.36	0.01
HSII	5	2	1	1.78	0.18
CCII	1	3	3	4.54	0.03
CCII	2	7	2	0.02	0.89
CCII	4	1	0	0.06	0.80
CCI	1	10	5	5.82	0.02
CCI	2	7	1	0.16	0.69
CCI	3	5	2	7.56	0.0006*
CCI	4	6	0	0.21	0.64
CCI	5	2	1	2.88	0.09
CCI	6	5	1	0.05	0.82
HSI	1	13	7	9.65	0.002*
HSI	2	2	0	0.24	0.63
HSI	3	8	4	0.49	0.48
HSI	4	7	0	0.82	0.36
HSI	5	3	2	7.69	0.006

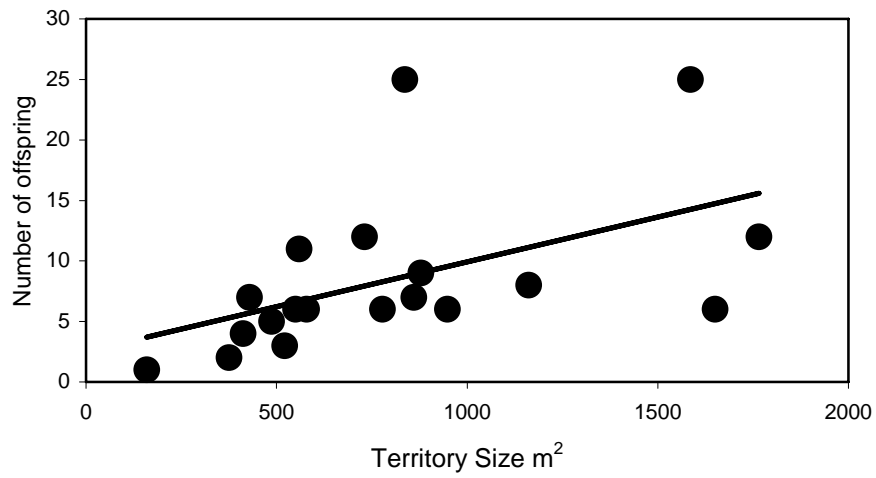


Figure 1. The relationship between territory size and the number of total offspring produced. Linear regression: $\hat{y} = -42.43 + 7.99(x)$; $r^2 = 0.39$, $F_{1,17} = 10.93$, $P < 0.0004$.

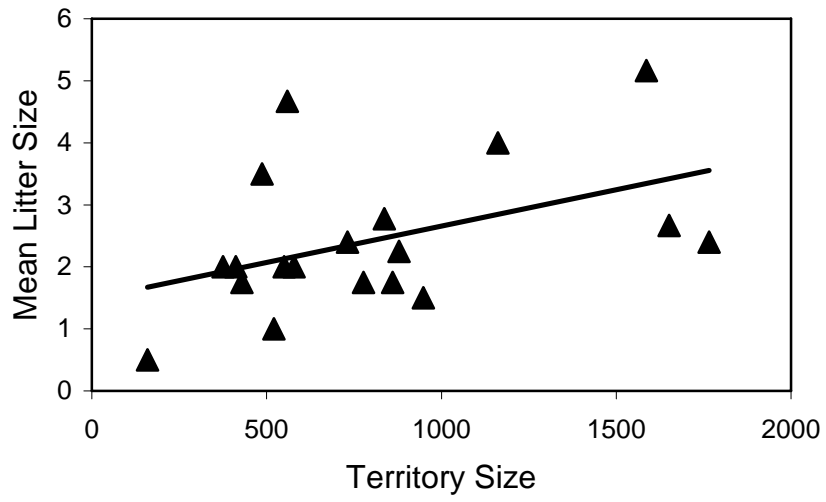


Figure 2. The relationship between territory size and mean litter size. Linear regression: $\hat{y} = -4.04 + 0.99(x)$; $r^2 = 0.24$, $F_{1,17} = 5.42$, $P < 0.03$.

*Look deep into nature, and then you will
understand everything better- Albert Einstein*

Chapter Five

Dispersal, philopatry and kinship in Gunnison's prairie dogs (*Cynomys gunnisoni*): does resource availability play a role?

Abstract

In this study I describe patterns of relatedness in Gunnison's prairie dog (*Cynomys gunnisoni*) social groups. Kin selection is often cited as a mechanism for the evolution and maintenance of social groups, and Gunnison's prairie dog females are occasionally described as being strongly philopatric. Overall, randomization tests revealed that females within groups were not more closely related to each other than expected at random. A similar pattern was found among males and between males and females, indicating that there was no sex-biased dispersal occurring in these populations. Ecological variables measured in this study, such as food abundance and food dispersion, were not correlated with relatedness. In addition, territory size and density/m² did not correlate significantly with relatedness. Though there was variability in the spatial overlap among individuals within groups, there was no indication that relatedness explained this variation. These results strongly suggest that kin selection is not maintaining social groups in these populations, but that competition for access to resources required by both males and females may explain dispersal patterns in these populations.

Introduction

A central theme of behavioral ecology lies in understanding the evolution and maintenance of animal grouping patterns and cooperation. Because living in groups can carry significant reproductive costs (e.g., reduced resource acquisition, increased infanticide, reproductive suppression), individuals living in groups must experience fitness benefits that exceed the actual fitness costs of sociality (Alexander 1974; Bertram 1978; Wasser and Barash 1983; Wrangham and Rubenstein 1986; Janson 1992; Emlen 1997; Solomon and French 1997; Armitage 2003). For birds, primates and other mammals, increased reproductive success, enhanced foraging and defense of resources, reduced predation risk, and better care of young have often been cited as ultimate factors affecting the evolution of social behavior (Hamilton 1971; Alexander 1974; Armitage 1981; Wrangham 1983).

Kinship structure can have a profound influence on the degree and nature of social interactions by affecting the level of cooperation (Hamilton 1964a,b), dispersal, inbreeding avoidance (Shields 1982) and the degree of reproductive skew (Vehrencamp 1983). Although genetic relatedness is not a prerequisite for social groups, kinship may influence the degree of aggression during periods of environmental stress and membership status in a group (Giraldeau and Caraco 2000). Evidence indicates that as relatedness increases, aggression decreases both within the group and with neighboring related groups (Brown and Brown 1993, Reeve and

Nonacs 1997). Kin-related groups may also determine when and who joins a group, thereby regulating group size (Giraldeau and Caraco 2000).

The connection between cooperation and kinship was first proposed by Hamilton (1964a,b). Hamilton suggested that the costs and benefits of social interactions are mediated by inclusive fitness through close genetic relatedness. Later, theoretical arguments focused on how sociality evolves under the constraints imposed by intersexual and intergenerational conflicts of interest in maximizing that fitness (Trivers 1972, Alexander 1974).

More recently, it has been suggested that high levels of cooperation within groups may be favored by factors in addition to kin selection (Clutton-Brock 2002). For instance, when dispersal is limited and juveniles cannot locate suitable mates, it is predicted that relatedness within groups will be higher (Dugatkin 1997). For many birds and mammals retention of young in the natal group (philopatry) is common and believed to provide the foundation for the evolution of sociality and lead to the formation of kin-structured groups (Hatchwell and Komdeur 2000). The two primary hypotheses explaining natal philopatry are the ‘ecological constraints hypothesis’ (Emlen 1984) and the ‘benefits of philopatry hypothesis’ (Stacey & Ligon 1987,1991). Both hypotheses postulate costs and benefits of staying versus dispersing. Dispersing often can carry significant costs that result in lower survival rates (Daniels and Walters 2000). However, not dispersing can lead to increased within-group competition via foraging interference, reproductive suppression, and reduced access to mates (Wasser and Barash 1983; Janson 1988; Solomon and French 1997; Armitage 2003). Thus, balancing costs and benefits, individuals may disperse

to improve the quality of their reproductive success or, as population density increases, individuals may disperse to reduce their intraspecific competition within a territory. Therefore, dispersal decisions may modify population structure, influencing the degree to which kin selection may play a role.

Frequently, dispersal decisions are sex-biased, with either males or females remaining in the natal territory. According to Greenwood (1980), dispersal is linked to mating systems (eg. resource based) and whichever sex competes for resources should be philopatric. While in some species the occurrence of philopatry may be correlated with the mating system, recent experimental studies suggest that the frequency of philopatry may instead depend on the population density and the availability of food resources and their predictability in space and time (Emlen 1982, 1995; Koenig et al. 1992; Johnson et al. 2002). This pattern suggests that parent-offspring conflicts over food resources may influence how much dispersal occurs, leading to varying degrees of relatedness among individuals in a social unit (Waser and Jones 1983). In crows (*species name*), for example, increases in food abundance increased the retention of offspring, suggesting that when times are good, dispersal from the natal territory may be reduced (Baglione et al. 2006). Similarly, resource abundance is positively correlated with dispersal for a broad array of other organisms (Zack & Ligon 1985; Stacey & Ligon 1991; Komdeur 1992; Putland & Goldizen 2001; Funston et al. 2003).

Among the social sciurids, a resourced-based polygynous mating system is common, leading to matrilineal forming the core social unit. In accordance with Greenwood's (1980) predictions for polygynous mating systems, dispersal is often

sex-biased, with females remaining in the natal territory and males dispersing more readily (Columbian ground squirrels (*Spermophilus columbiana*): Wiggett and Boag, 1992; yellow-bellied marmots (*Marmota flaviventris*): Armitage 1981, 1991, 1998, 1999; vanVuren and Armitage 1994; Belding's ground squirrels (*Spermophilus beldingi*): Holekamp 1984; (*Spermophilus townsendii*): Wiggett and Boag 1993; black-tailed prairie dogs (*Cynomys ludovicianus*): Hoogland 1995).

While Gunnison's prairie dog (*Cynomys gunnisoni*) males have often been characterized as pursuing a female-based or resource-based defense strategy (Fitzgerald & Lechleitner 1974; Rayor 1988; Hoogland 1999) and earlier studies conclude female philopatry resulting in matrilineal (Travis et al. 1996; Hoogland 1999), recent empirical and experimental evidence suggests these conclusions warrant closer examination (Verdolin 2007a, b). Like many other ground-dwelling sciurids, Gunnison's prairie dogs are large, diurnal, and highly social. Within each colony, individuals occupy territories that persist in space and time (Rayor 1988; Travis and Slobodchikoff 1993), males and females communally defend territories over the entire active season, and dispersal occurs by both sexes (Rayor 1988; Robinson 1989).

Gunnison's prairie dog populations show variation in their group size and composition among territories, including single male-single female, single male-multiple female, single female-multiple male and multiple male-multiple female groups. This variation is associated with resource abundance and distribution (Slobodchikoff 1984; Travis & Slobodchikoff 1993; Travis et al. 1995, Verdolin 2007). Within territories, spatial overlap of individuals varies and is correlated with

the distribution of resources (Verdolin 2007). A lack of sexual dimorphism and high levels of multiple paternity, regardless of group size and sex ratio on a territory, (Travis & Slobodchikoff 1993; Travis et al. 1995, 1996; Haynie et al. 2003; Verdolin 2007) suggests that resource abundance and not mating strategies are driving social patterns observed in this species. Therefore, it remains unclear what role, if any, kinship plays in the formation and stability of Gunnison's prairie dog social groups.

The purpose of this study was to characterize relatedness among members of a social group and determine if natal philopatry is a significant feature of sociality in this species. Here, natal philopatry refers to remaining in the natal territory.

Specifically, I predicted that, if males and females are both dispersing from the natal territory, then relatedness among females and among males within a group will not be significantly higher than if groups are formed at random. In contrast, if relatedness among group members is higher within groups than expected if groups formed randomly, I predicted that there would be a positive correlation between relatedness and group size, assuming group size conflicts of interest are more likely to occur among unrelated individuals (Vehrencamp 1983). Of particular interest was determining if patterns of kinship among groups varied with resource availability, territory size or density. If dispersal in this species is influenced by conflicts over resource availability, I predicted that there would be a positive correlation between resource abundance and relatedness. Lastly, I wanted to determine if variability in spacing patterns within territories was correlated with relatedness.

Methods

Study area

Two colonies of Gunnison's prairie dogs were studied in northern Arizona from May 2003 to August 2005. The first study site, Humane Society (HS), was established in May 2003. The second study site, Country Club (CC) was established in August 2003. Experimental manipulations of resource abundance and distribution were conducted from June 1, 2004-August 1, 2004 and April 1, 2005- May 6, 2005. Due to time and financial constraints, only data from 2004 was acquired for this dissertation chapter.

Both colonies were located within the city limits of Flagstaff, Arizona. Within each study site Humane Society (HS) and Country Club (CC) two 1 ha plots were created. At both sites, the location of the plots (HS I, HS II, CC I and CCII) were separated by a distance of 0.2 km and a road. The location of each plot was selected on the basis of two factors: 1) plots were maximally distant from each other, and 2) plots were located in areas of greatest prairie dog activity. With the exception of one individual who moved in August 2004 from HS I to HS II and two individuals from CC I that moved to the boundary of CC II, individuals in different plots did not physically interact with one another, or occupy the same area at any time during this study.

For each plot, at both HS and CC, a 100 m X 100 m letter/number grid system consisting of 100 10x10m quadrats was established using surveyor stakes. The location of each stake, the halfway point between each stake, and the center point of each 10x10m quadrat was recorded using a Garmin Etrex Global Positioning System.

Because food supplementation experiments were conducted beginning in June 2004, all analyses reflect group size and composition and territory and home range sizes prior to the onset of the experiments.

Trapping and marking

Prairie dogs were live-trapped with Tomahawk live traps (50 cm x 18 cm x 18 cm and 48 cm x 15 cm x 15 cm), baited with sunflower seeds. Traps were placed at active burrows or where individual prairie dogs had been observed. Active burrows were defined as burrows with fresh scat within 0.5 m of the entrance (Biggins et al. 1993) and a lack of debris obstructing the entrance. Approximately 250 traps were placed on each 1 ha plot. Each trapped animal was placed in a specially designed sleeve, weighed to the nearest 10g with an Ohaus scale, sex-determined, and DNA samples (hair) collected. Each animal was permanently marked using AVID® or Home Again® individually packaged, sterile microchips. Once injected, individuals were scanned to test the microchip and marked with a unique number/symbol using Lady Clairol® black hair dye for visual identification. The hair dye was used as directed and trapping was conducted throughout the study period to trap unmarked individuals, to re-apply markings on previously trapped individuals and collect data on body mass as the season progressed.

Vegetation survey

The abundance and distribution of food plants was obtained through monthly sampling of all plots from April-August each year. For each plot, 100 nested quadrat samples were taken by placing a 1m X 1m wooden sampling square at random in each 10x10m quadrat. Random pairs of numbers were generated in Excel and

represented the combined horizontal and vertical locations sampled in each quadrat. A digital image using a Hewlett Packard® 812 Photosmart digital camera set at four megapixels was taken of each sample square. I used Shalaway & Slobodchikoff (1988) to identify food plant species for Gunnison's prairie dogs along with my personal behavioral observations during the course of this study. Percent cover of food plants determined to be part of the diet were estimated for all plots, and all territories within each plot, using Optimas® 3.0 in the Functional Ecology Research and Training Laboratory (FERTL) at the Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York.

Aboveground biomass for each plot was estimated using the average dry weight of 100cm² food plant samples collected from fifteen randomly selected 100m² quadrats in each plot during August every year. Samples were immediately placed in a flower press and later oven dried for 24 hours. Total aboveground biomass per territory was estimated by multiplying the percent cover from digital samples taken on a given territory by the average dry weight of 100cm² samples. Territory food patchiness was calculated as the variance to mean ratio of biomass/m².

Behavioral data

Behavioral observations were made for a minimum of 10 days per month for 3h/ day from May-August 15, 2003. With the exception of days when trapping occurred, observations were made at least every other day at each plot from March 7-August 15, 2004 and March 3 -August 8, 2005, for a total of 825 hours of observation. Because food experiments were conducted from June 1, 2004-August 15, 2004 and affected home range overlaps significantly (Verdolin 2007b), behavioral data on groups and home ranges uses and data from March 3-June 1, 2004.

For each plot, observations were made every other day, alternating between 0700-1000 and 1500-1800, the times when prairie dogs were most active (Longhurst 1944; Hoogland 1981). Natural terrain features, such as rock formations, hills and trees were used to station the observer during sampling. Observations were made using Nikon 8-24x25 zoom binoculars.

The term social group refers to individuals that are mutually tolerant of each other, as indicated by behaviors such as greet-kisses (King 1955) and co-feeding, while territory refers to the area occupied and defended by members of a social group. Animals that were consistently chased out of an area were considered as not belonging to that territory. Individuals that were trapped once and not seen throughout the study were not included as members of any social group.

Because group territorial boundaries are relatively stable and are shared by all occupants of the territory (Rayor 1988; Slobodchikoff 1984), little confusion arises about assigning group membership. To obtain data on the composition of social groups within each study plot, behavioral observations included focal sampling, scan sampling and all occurrences sampling (Altmann 1974). Focal samples were conducted for 5 min. During the focal sample, the location of the focal animal and all occurrences of social interactions were recorded. Four such focal samples were taken in sequence, then every 30 min., a scan sample was used to record the location of each above ground animal within the study plot. Locations were recorded based on the proximity (to the nearest 0.5m) of an individual to either a surveyor stake or a flagged burrow and matched with corresponding coordinates obtained with the Garmin® Etrex Global Positioning System. Observations were removed from the

estimation of home ranges and territory area in only two cases. First, data from agonistic interactions that resulted in a chase were excluded. Second, during the mating season, isolated excursions by individuals to other parts of the colony were excluded. Including either observation would have greatly inflated home ranges and territory area. Home ranges were estimated by using all location points for an individual, except as noted, whereas location points from all individuals within a social group were used to estimate territory area.

Home range and territory measurements

Home range was defined as the area routinely used by an individual within a group, while the territory was defined as the area occupied by all members of a particular group. In theory, these two could be equivalent, but are referred to distinctly. All home ranges and territory areas were estimated using the fixed kernel density estimator (ArcView 3.2a; ESRI 2000). When using the fixed kernel approach with a level of smoothing selected by least squares cross-validation (LSCV), results are less biased and more appropriate for non-normal distributions (Worton 1995; Seaman & Powell 1996). As opposed to the adaptive kernel, the fixed kernel approach is more stable for probability contours exceeding 80%. Seaman et al. (1999) suggest that contours greater than 85% do not provide meaningful biological information and are less reliable. Therefore, I used only the 85% contour probabilities for all individual home ranges, territory areas, spatial overlap of individual home ranges, and all statistical comparisons. X-tools (Arcview 3.2a; ESRI 2000) was used to estimate the area of overlap of individual home ranges. The proportion of the total home range that any one focal individual overlapped with a target individual was

estimated by taking the area overlapped divided by the home range of the focal individual.

DNA extraction and PCR amplification

DNA was extracted two times independently from each sample using Qiagen DNeasy tissue extraction kits utilizing a modified protocol for hair. Six microsatellite markers were used to determine allelic diversity, heterozygosities, paternities of offspring, individual heterozygosity, and genetic similarities between females and all potential mates. The markers used were CGS-08, CGS-14, CGS-12, CGS-22, CGS-25, and CGS-26 (Table 1). Haynie et al. (2003) redesigned markers CGS-8, CGS-12, CGS-14, and CGS-22 that were originally published by Stevens et al. (1997). Marker CGS-25 and CGS-26 were used as originally published by Steven's et al. (1997). PCR amplification of the loci was performed using a 20- μ L volume that contained: 5- μ L of extracted genomic DNA, 2- μ L *Taq* buffer, .8- μ L 50mm $MgCl_2$, 0.4- μ L dNTP, 0.04- μ L *Taq* DNA polymerase, 1.0- μ L of 5' fluorescent-labeled primer, 5 μ L 0.05mg/ μ ml BSA, and 4.76- μ L water. The optimal annealing temperature during PCR amplification varied depending on the marker, but the remainder of the PCR protocol was identical to that published in Stevens et al. (1997). Samples were submitted to the Genomic Analysis and Technology Core facility at the University of Arizona where multiplexed PCR reactions amplified with compatible labeled primers were scored with the ABI PRISM® 3730 DNA Analyzer. Data were visualized using GeneScan freeware.

Statistical Analysis

FSTAT 2.9.3 (Goudet 1995) was used to calculate expected heterozygosity, the observed heterozygosity, to test for deviations from Hardy-Weinberg, and detect linkage disequilibrium for each locus using all individuals sampled in 2004 (adult, yearling and juvenile). Pairwise relatedness values were estimated using KINSHIP (Queller and Goodnight 1989). In KINSHIP the allele sharing coefficient, r , is the proportion of alleles shared by two individuals weighted by the frequency of the alleles in the population, thus providing a maximum –likelihood measure of relatedness. Pairwise values of r range from -1 to 1 , with negative values signifying that individuals share, on average, fewer alleles than randomly chosen individuals in the population.

In multiple pairwise comparisons there is a lack of independence among samples because one individual can occur in more than one comparison. Therefore randomization tests were performed using Resampling Stats (Blank et al. 1999) to determine significance. For each group, comparisons among males, among females and between males and females within and between groups were performed using two randomization procedures. First, the observed mean relatedness within a group was compared with groups that had been randomly reshuffled keeping the same number of pairwise comparisons in each group. This procedure generated a randomized distribution by repeatedly reshuffling the data 10,000 times. Second, the mean relatedness value of individuals within a group was compared to the mean relatedness values of individuals in different groups. Observed values of r were randomly reassigned into the two groups 10,000 times, and the observed difference between the two was compared to the randomized difference. In both tests, the proportion of

resulting values that were as large, or larger, than the observed value determined the p-value, with significance for each group determined by using a Bonferroni corrected p-value and Fisher's combined probabilities test. Data for each plot were analyzed separately. I calculated 95% CI for estimates of mean pairwise relatedness by resampling with replacement 10,000 times to generate a distribution for which the upper 2.5% and lower 97.5% represent the upper and lower confidence intervals (Blank et al. 1999). Outcomes were consistent for all plots using both methods of analyses, so only results from the first procedure are presented here.

I used linear regression to determine if log territory size, density, food biomass, or food dispersion was correlated with group r values among females, among males and between males and females. I ran a Poisson regression using the generalized linear model to determine whether the number of individuals in a given sex class within a group was correlated with the mean r value for that respective sex class.

Because the proportion of spatial overlap among individuals within groups was variable (among females: 0.30 ± 0.27 ; among males: 0.25 ± 0.21), a comparison of home range overlap and relatedness was made. For each group I generated a matrix of pairwise proportion of home range overlap and pairwise r values for comparison among females and among males. A Mantel test was performed for each group and Fisher's combined probabilities test was used to determine significance.

Results

In all, 134 adults and yearlings from 20 groups were used in these analyses. In these populations, the numbers of unique alleles for each of the six loci ranged from 3-9 per locus (Table 2). Observed heterozygosities did not deviate significantly from Hardy-Weinberg for all loci. In addition, there was no evidence of linkage disequilibrium among the loci. Group r values across the four plots were variable, ranging from -0.44 to 0.50 among males ($SD=\pm 0.24$), -0.26 to 0.37 ($SD=\pm 0.18$) among females, and -0.28 to 0.24 ($SD=\pm 0.14$) between males and females.

Female-female relatedness

I compared the mean relatedness of females within groups with the mean relatedness of females that had been randomly reshuffled into groups keeping the same number of pairwise comparisons in each group. Using the randomization test, I found that the mean relatedness among females within groups did not differ significantly from that of females randomly assigned to groups (Table 3) and results from the Fisher's combined probability test concurred with results using Bonferroni corrected p-values ($X^2_{.05[36]}=21.06$, $P=0.98$). Among females there was no correlation between mean female relatedness per territory and any of the territory-level variables measured in this study (Log territory size: $r^2=0.00006$, $F_{1,18}=0.001$, $P=0.97$; Biomass/m²: $r^2=0.07$, $F_{1,18}=1.24$, $P=0.28$; Patchiness: $r^2=0.0006$, $F_{1,18}=0.11$, $P=0.75$; Density of individuals/m² $r^2=0.002$, $F_{1,18}=0.04$, $P=0.84$). In addition, the relationship between relatedness and proportion of home range overlapped of females was not statistically significant ($X^2_{.05[22]}=24.02$, $P=0.35$). Lastly, the number of females within

a group was not correlated with female relatedness (Wald statistic=1.90, N=19, P=0.17).

Male-male relatedness

As with females, the mean relatedness of males within groups was compared with the mean relatedness of males that had been randomly reshuffled into groups keeping the same number of pairwise comparisons in each group. Using the randomization test, I found that mean relatedness among males within groups did not differ significantly from that of males randomly assigned to groups (Table 3) and results from the Fisher's combined probability test concurred with the findings using Bonferroni corrected p-values ($X^2_{.05[26]}=11.12$, P=0.99). Similar to the results for females, there was no correlation between mean male relatedness per territory and any of the territory-level variables measured in this study (Log territory size: $r^2=0.11$, $F_{1,18}=0.19$, P=0.19; Biomass/m²: $r^2=0.02$, $F_{1,18}=0.43$, P=0.52; Patchiness: $r^2=0.008$, $F_{1,18}=0.12$, P=0.73; Density of individuals/m² $r^2=0.02$, $F_{1,18}=0.46$, P=0.51). The relationship between relatedness and proportion of home range overlapped among males was not statistically significant ($X^2_{.5[22]}=29.84$, P=0.12). Lastly, male relatedness within groups was not correlated with the number of males present (Wald statistic=0.07, N=19, P=0.79).

Male-female relatedness

The final comparison examined the pairwise relatedness of males and females. The same procedure described above was performed. I found that mean relatedness among males and females within groups did not differ significantly from that of randomly assigned individuals (Table 3) and results from the Fisher's combined

probability test concurred with the findings using Bonferroni corrected p-values ($X^2_{.05[40]}=19.48$, $P=0.99$). As with male-male and female-female comparisons, there was no correlation between mean male-female relatedness per territory and any of the territory-level variables measured in this study (Log territory size: $r^2=0.06$, $F_{1,18}=1.11$, $P=0.30$; Biomass/m²: $r^2=0.03$, $F_{1,18}=0.51$, $P=0.48$; Patchiness: $r^2=0.02$, $F_{1,18}=0.44$, $P=0.51$; Density of individuals/m² $r^2=0.09$, $F_{1,18}=1.76$, $P=0.20$).

Discussion

The results of this study strongly suggest that kin selection is not maintaining Gunnison's prairie dog social groups or influencing spatial structure within groups in these populations. These results differ markedly from observational studies of Gunnison's prairie dogs in other areas (Hoogland 1999). Though some individuals within groups were more closely related to each other, no group had relatedness values that differed significantly from random, and none of the variables measured in this study appear to play a significant role in explaining patterns of relatedness among females or males. In addition, there was no indication that males and females differed in their patterns of relatedness within groups, suggesting that sex-biased dispersal is not occurring in these populations. Lastly, results indicate that relatedness has no bearing on the spatial structure among males and among females within groups.

These results contrast with those from other ground-dwelling sciurids, in which female philopatry and male-biased dispersal is commonplace (Armitage 1981, 1991, 1998, 1999; Holekamp 1984; Holekamp & Sherman 1989; Wiggett & Boag 1992, 1993; Hoogland 1995). Several observational studies of Gunnison's prairie dogs report male-biased dispersal and female philopatry (Fitzgerald & Lechleitner 1974; Rayer 1985, 1988; Hoogland 1996, 1999), suggesting that females form kin-structured groups in this species. In contrast, Robinson's (1989) study of Gunnison's prairie dogs in northern Arizona concluded that both males and females dispersed, but that males more frequently dispersed greater distances. Although some individuals, both males and females, within groups were related, results of this study concur with Robinson (1989), in that females belonging to the same group were rarely closely related and patterns of relatedness among females did not differ from those among males.

Why do both sexes disperse in this population of Gunnison's prairie dogs? According to Greenwood (1980), if dispersal is linked to mating systems, then the sex that competes over resources should be philopatric. Gunnison's prairie dog males have been described as pursuing a harem polygynous strategy, in which case, the expectation is that females should be philopatric and therefore closely related. Recently, however, there is strong evidence that indicates males in these populations are not pursuing such a mating strategy, and perhaps not even a resource defense strategy (Verdolin 2007). The results of this study are consistent with those findings. If male Gunnison's prairie dogs in this population are not using a female-defense mating strategy, there may be little benefit to being philopatric.

If dispersal is not linked to the individual mating strategies and there is no sex-biased dispersal in Gunnison's prairie dogs, what other factors might predict who disperses and when? Experimental studies have suggested that dispersal may be more tightly linked to population density and resource availability (Emlen 1982, 1995; Koenig et al. 1992; Johnson et al. 2002). If food abundance plays a role in Gunnison's prairie dog dispersal, then one would expect that as food availability increased, relatedness would correspondingly increase, due to greater retention of offspring. In this study, I found that there was no relationship between relatedness and food abundance or food dispersion, and that neither density nor territory size was correlated with relatedness.

Despite failing to detect kin structure within groups for either sex, the variation in spatial overlap among individuals within groups could reflect preferences for, or greater tolerance to, closely related individuals. However, it appears that relatedness is unimportant in determining spacing behavior of males and females within territories. Lastly, apparent widespread dispersal by both sexes could arise if insufficient genetic markers were used to detect relatedness among individuals, though this is unlikely since similar markers and numbers of loci were used to successfully identify parent-offspring relationships in Gunnison's prairie dogs (Haynie et al. 2003).

If neither mate defense nor food competition are obvious explanations, why else might both males and females disperse from their birth territories in this population? For both males and females, one possibility may be that dispersal is more likely if the resident male/s from the previous year is still present. Both male and

female Gunnison's prairie dogs reach sexual maturity as yearlings and successfully mate, and unlike black-tailed prairie dog males (Hoogland 1995), related Gunnison's prairie dog males do not appear to form coalitions. So, while females may disperse to avoid inbreeding, males may disperse to avoid competition with resident males for access to mates.

The lack of relatedness among individuals in groups could also reflect stochastic demographic variation in survivorship. If more females survive, then there may be greater competition among females for space and resources, leading some females to choose to disperse in search of better territories. However, neither territory size, density or food abundance and dispersion appear to play a significant role in patterns of relatedness among females, suggesting that female competition over resources is not a sufficient explanation. In addition, previous research indicates that there is little difference in the survivorship of male and female offspring (Hoogland 2001). Another possibility for why females disperse may be related to gaining access to suitable nesting burrows. Data from this study are insufficient to ascertain whether or not certain burrows are consistently used as maternity burrows from year to year, but if there are features that constitute a suitable nesting burrow, and there is some limitation to how many burrows are available, then competition for maternity burrows may place an upper limit on the number of yearling females that can remain on their natal territory. Although female Gunnison's prairie dogs have been observed nesting communally in other areas (Haynie et al. 2003), in this population, they were not seen doing so, which could increase the potential for competition over maternity burrows. While individuals of both sexes were seen utilizing common burrows, patterns of

spatial overlap and relatedness from this study suggest that kinship does not predict burrow sharing.

A possible resource necessary for both males and females is access to hibernation burrows. Unlike black-tailed prairie dogs, Gunnison's are obligate hibernators, though hibernation is interrupted by cyclic periods of activity (Bakko and Nahorniak 1986). From burrow excavations it is apparent that not all burrow structures have bedding or nesting material present (Smith 1982; Verdolin et al. 2007), but it is not clear whether only particular burrows are suitable for hibernation. Previous studies indicate that the deepest parts of burrows are more thermally stable and that hibernacula must be constructed at precise depths in order to avoid overwinter freezing (Smith 1982). The topography of certain areas may limit the number of suitable locations to construct hibernacula, and although laboratory prairie dogs have been observed sleeping together (Smith 1982), it is not certain whether individuals hibernate together. Thus, hibernacula may be a key limiting resource for both males and females.

The results of this study indicate that kin selection, for both males and females, is unimportant to maintaining social groups in these populations. Furthermore, relatedness does not influence the spatial interaction of individuals within the same group. Given that kin selection can be rejected as the basis of maintaining sociality in this species, why are Gunnison's prairie dogs territorial and social? For both males and females access to resources are critical to survival. The findings of this investigation, coupled with results from previous studies (Slobodchikoff 1984; Verdolin 2007), strongly suggest that the primary purpose of

territories in this species may be to secure sufficient resources and reduce individual defense costs. For both males and females, burrows may act as a limiting resource promoting dispersal. By examining patterns of burrow use by females associated with reproduction, some insights may be gained as to whether or not the availability of nesting sites influences female dispersal. For both males and females, determining what constitutes suitable hibernacula and developing methods to identify them above the surface may aid in discerning what role, if any, this resource has on patterns of dispersal.

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Table 1. Summary of social groups/territories found on each plot, including group size, and male to female sex-ratio (M:F) prior to experimental treatments in 2004.

Plot	Group	Group size	M:F
CC1	1	10	1:1
CC1	2	8	0.33:1
CC1	3	12	0.71:1
CC1	4	5	0.66:1
CC1	5	7	0.4:1
CC1	6	7	0.75:1
CC2	1	5	0.25:1
CC2	2	9	0.28:1
CC2	3	6	1:1
CC2	4	3	0.5:1
HS1	1	9	0.5:1
HS1	2	3	2:1
HS1	3	7	0.75:1
HS1	4	4	1:1
HS1	5	5	0.66:1
HS2	1	4	0.33:1
HS2	2	7	0.75:1
HS2	3	8	0.6:1
HS2	4	14	1:1
HS2	5	4	1:1

Table 2. Number of alleles (A) and expected (H_E) and observed (H_O) heterozygosity at each locus for prairie dogs sampled from each of the four plots: CCI ($n=133$) CCII ($n=70$), HIS ($n=131$), HSII ($n=123$).

Plot	Locus	A	H_E	H_O
CCI	GS8	6	0.73	0.76
	GS12	5	0.52	0.62
	GS14	7	0.72	0.65
	GS22	4	0.74	0.69
	GS25	5	0.56	0.55
	GS26	4	0.62	0.53
CCII	GS8	6	0.69	0.72
	GS12	9	0.77	0.74
	GS14	5	0.75	0.68
	GS22	4	0.77	0.69
	GS25	5	0.49	0.48
	GS26	4	0.63	0.65
HSI	GS8	6	0.73	0.67
	GS12	5	0.41	0.44
	GS14	6	0.71	0.62
	GS22	3	0.50	0.57
	GS25	4	0.62	0.63
	GS26	4	0.53	0.60
HSII	GS8	6	0.73	0.67
	GS12	5	0.41	0.44
	GS14	5	0.71	0.62
	GS22	4	0.50	0.57
	GS25	4	0.62	0.63
	GS26	4	0.53	0.60

Table 3. The mean r value with confidence intervals (CI) for each group among females (F-F), among males (M-M) and between males and females (M-F) with 95% CI. *Denotes significance of the randomization test using Bonferroni corrected p-values and (--) refers to groups where there were ≤ 2 individuals available.

Plot	Group	F-F	M-M	F-M
CCI	1	0.006 (-0.10-0.14)	0.14 (-0.17-0.28)	0.07 (-0.11-0.10)
	2	0.04 (-0.11-0.15)	0.03 (-0.07-0.17)	0.06 (-0.10-0.09)
	3	0.15 (-0.13-0.17)	0.03 (-0.22-0.34)	-0.21 (-0.13-0.12)
	4	0.02 (-0.07-0.11)	--	-0.07 (-0.23-0.22)
	5	-0.05 (-0.08-0.13)	0.06 (-0.15-0.26)	-0.02 (-0.11-0.10)
	6	0.04 (-0.23-0.27)	0.02 (-0.17-0.28)	-0.07 (-0.17-0.16)
CCII	1	-0.13 (-0.12-0.09)	0.005 (-0.23-0.33)	-0.07 (-0.09-0.07)
	2	0.04 (-0.11-0.08)	0.15 (-0.23-0.37)	0.01 (-0.10-0.07)
	3	0.13 (-0.28-0.24)	0.002 (-0.23-0.37)	0.02 (-0.13-0.11)
	4	--	--	0.24 (-0.32-0.30)
HSI	1	-0.05 (-0.03-0.09)	-0.23 (-0.28-0.22)	-0.06 (-0.10-0.12)
	2	--	--	0.008 (-0.48-0.43)
	3	0.38 (-0.35-0.38)	-0.01 (-0.003-0.10)	0.18 (-0.13-0.14)
	4	0.18 (-0.60-0.51)	--	-0.27 (-0.30-0.33)
	5	0.32 (-0.36-0.38)	--	-0.06 (-0.24-0.26)
HSII	1	-0.26 (-0.28-0.46)	--	0.14 (-0.31-0.12)
	2	0.28 (-0.27-0.47)	-0.07 (-0.38-0.28)	-0.11 (-0.20-0.17)
	3	0.09 (-0.12-0.28)	0.28 (-0.38-0.27)	0.02 (-0.16-0.12)
	4	0.08 (-0.03-0.18)	-0.18 (-0.28-0.19)	-0.01 (-0.12-0.08)
	5	--	--	-0.14 (-0.24-0.22)

*In every walk with nature one receives
far more than one seeks- John Muir*

Chapter Six: Conclusions

Summary

The purpose of this dissertation was to investigate if and how ecological factors influenced social organization, and whether mating strategies were distinct from observed patterns of association between males and females in Gunnison's prairie dogs (*Cynomys gunnisoni*). Observational data were complemented with experimental manipulations of food distribution that were designed to test predictions associated with the resource dispersion hypothesis (RDH). Molecular tools were used to investigate what role kinship plays in Gunnison's prairie dog social groups and to assess male reproductive success. In the past, some have concluded that Gunnison's prairie dog social organization most closely resembles what one would expect under female defense polygyny (Fitzgerald and Lechleitner 1974; Rayor 1988; Hoogland 1999), while others maintain that the social organization reflects a more flexible response to resource availability and distribution (Slobodchikoff 1984; Slobodchikoff and Schultz 1988; Travis and Slobodchikoff 1993). This dissertation represents the first study to explicitly test the predictions of the socio-ecological models and determine if male mating strategies are sufficient to explain patterns of association between males and females in this species using a combination of observational and

genetic data. This work also represents the first study designed to experimentally test the predictions of the Resource Dispersion Hypothesis (RDH) presented in Johnson et al. (2002). In addition, I investigated what role kin selection might play in maintaining cooperative behaviors among members of the same social group. In this dissertation, I have presented a comprehensive characterization of the ecological determinants of Gunnison's prairie dog social organization that has provided insights into the selection pressures on sociality in this species.

In Chapter 1, I presented a general review of the socio-ecological, kinship, and RDH models that provided the theoretical framework for this dissertation.

In Chapter 2, I presented results from a detailed observational study that was designed to test the specific predictions that emerge from the socio-ecological models and partially resolve some of the contradictory conclusions that others have reached about what factors drive the patterns of group formation and associations among males and females. I found that territory size and food availability predicted the number of males and females belonging to a given social group. Within social groups, all individuals participated in territory defense, although adult males did engage in significantly more intergroup aggressive interactions. Contrary to predictions of typical mammalian male mating strategies, there was no significant difference in adult male and female home range size and adult females ranged significantly further than males during the mating period. In addition, the number of female home ranges that any given male home range overlapped was not correlated with male body mass, male home range size, or territory size. While previous studies report significant sexual dimorphism in this species, it is possible that reproductive status was

unaccounted for when making comparisons. Indeed, when comparing body mass among adult reproductive females, adult nonreproductive females and adult males, I found that the body mass of males and nonreproductive females was similar, whereas that of reproductive females was smaller. An additional approach used to assess sexual dimorphism was comparing skull morphology between males and females. My results show that males and females did not differ in size, based on skull length and skull width. Collectively the data presented in Chapter 2 indicated that published results about the mechanisms driving social relationships in this species, namely male mating strategies, were not upheld by rigorous testing of the predictions put forth by the socio-ecological model. Instead, results were suggestive of the important role that resource availability and distribution might play in explaining this social system.

In Chapter 3, I tested the predictions of the Resource Dispersion Hypothesis (RDH) as presented in Johnson et al. (2002). I showed that both male and female Gunnison's prairie dogs responded to changes in resource distribution by modifying territory size and home range overlap. Responses were consistent during the reproductive and nonreproductive seasons. These data suggest that patterns of space use and social structure in Gunnison's prairie dogs are the result of individual responses to resource abundance and distribution. Although individuals responded, the direction of the changes was opposite in direction to that predicted by the RDH. While the RDH predicts directional changes in territory size based on changes in resource distribution, it broadly states that the direction of these changes are contingent on initial patterns of distribution, without providing *a priori* expectations. Thus, this study reflects testing of the predictions for which clear directional

hypothesis testing was permitted. Furthermore, it may be that the response of individuals does not depend on initial conditions, but rather, on patch size reaching a critical threshold that allows other individuals to utilize the patch.

In contrast to the predictions of RDH, I found that the average size of a group did not change significantly as a result of the experiments. However, as the experiments were brief, it is possible that the short time frame left little opportunity for population responses to yield significant group size changes. In addition, all territories within a given treatment plot were stochastically similar leaving little incentive for individuals to switch territories. Future experiments could impose changes in resource distribution and abundance by territory to allow for better testing of this prediction. Another constraint of testing the effect of resource abundance and distribution experimentally is the inability to manipulate only one variable. In order to achieve different states of resource distribution, resources abundance must also vary. Currently, an individual-based modeling approach is being used to determine how abundance and distribution independently and collaboratively produce results concordant with expectations of the RDH using Gunnison's prairie dogs as a model. Overall, the results of this chapter conform to RDH in the broad sense but do not uphold specific details of the model. However, this study highlights some of the limitations of the RDH model and provides the opportunity to generate more specific directional hypotheses.

In Chapter 4, I provided genetic evidence from paternity data that resident males are not achieving paternity rates consistent with a female-defense or resource-defense mating strategy. For offspring of a given female, paternity rates for individual

nonresident males were equal to or greater than individual resident males in the majority of territories. Though incomplete genotyping could have produced these results, it is unlikely because I used a conservative procedure in assigning paternity to non-resident males, so that, all else being equal, the bias would favor assigning paternity to resident males. In addition, there was no link between assignment of non-resident males as sires and the number of loci successfully genotyped for a given infant. I found that larger territories produced a higher number of offspring, which might be expected since larger territories generally had more females. More importantly, mean litter size was larger on larger territories and may explain the potential fitness benefits for females to settle on particular territories and is consistent with the assumptions of the RDH model. Although it is clear that females consistently mate with multiple males, the question of why females mate with particular males remains unanswered.

In Chapter 5, I provide evidence that, contrary to other studies of this species, kin selection does not appear to be a significant factor explaining space-use or the maintenance of social groups in Gunnison's prairie dogs from these populations. In general, females were not more closely related to females on the same territory than to females on other territories. The same pattern held for comparisons among males and between males and females. In addition, space-use among individuals within territories was not correlated with relatedness for both males and female. Ecological variables measured in this study, such as food abundance and food dispersion, were not correlated with relatedness. Other factors such as territory size and density/m² also did not correlate with relatedness. These results strongly suggest that competition

for access to resources required by both males and females may explain dispersal patterns in these populations.

Results of this study reveal the Gunnison's prairie dogs in different environments respond adaptively by altering social dynamics. While it is generally agreed that coloniality in this species is a function of reduced risk of predation, others have reached very different conclusions about what selective pressures are important in the sociality of this species. However, the relevance of these empirical inquiries extends beyond understanding aspects of prairie dog ecology and behavior. This study represents one of the first attempts to explicitly test the predictions of the RDH. In general, the RDH model has received little support and the majority of theoretical and empirical work evaluates sociality in the context of male mating strategies and kin selection. Traditionally, the RDH has been used as an *ad hoc* explanation for grouping patterns that have no reasonable alternative. Results of this study suggest that the RDH is a practical, feasible, and testable hypothesis, but requires some clarification and modification of the predictions.

Several studies have reported that Gunnison's prairie dog males are pursuing a female defense strategy (Fitzgerald & Lechleitner 1974; Rayor 1988; Hoogland 1999), while others have suggested that Gunnison's prairie dog social groups are formed and maintained as a response to patterns of resource variability (Slobodchikoff 1984; Travis & Slobodchikoff 1993; Travis et al. 1995). My results support the conclusions of these latter studies and contradict specific elements of the former. In particular, I found that the number of females and males varied with territory quality and that adult home range overlap varied with food patchiness, both

of which are consistent with Travis & Slobodchikoff (1993). Contrary to the predictions that social systems might be driven by male sexual competition as suggested by Fitzgerald & Lechleitner (1974), Rayor (1988) and Hoogland (1999), I found that females ranged further than males during the mating period, males did not have larger home ranges than females, larger males did not have home ranges that overlapped more females, and that adult males on larger territories did not overlap more females. Furthermore, Hoogland (2003) reports strong sexual dimorphism between males and females as a function of body mass. However, by not taking into account the reproductive status of females, results would be biased in favor of finding a significant difference. In this study I found that the body mass of adult males was not significantly different than that of non-reproductive adult females. In addition, I found no difference between average male and female skull length or width at the zygomatic arch, despite a relatively large and geographically extensive sample.

The results of the experimental test of the RDH model also provide experimental support for the conclusions reached by Slobodchikoff (1984), Travis & Slobodchikoff (1993) and Travis et al. (1995) and suggest that the primary purpose of territories in this species may be to secure sufficient resources and reduce individual defense costs, while constraining the absolute group size possible within a territory by the intensity of competition for those resources. Results from the paternity analysis, presented in Chapter 4, also concur with findings reported by Travis et al. (1995) and Travis et al. (1996) that, in general, the resident male/s do not gain a significant reproductive advantage with resident females.

Lastly, based solely on behavioral observations, Hoogland (1999) concluded strong male-biased dispersal and female philopatry indicating that females remained in their natal territory for life, resulting in matrilineal forming the core social unit. Preliminary genetic analysis from Travis et al. (1996) appeared to support this conclusion. A comprehensive analysis of kinship among females and males in this study revealed no significant difference in relatedness among group member than expected if the population was sampled at random. In this analysis, six microsatellite loci were used for comparison, whereas three minisatellite loci were utilized by Travis et al. (1996). The difference in the results of this study with those presented by Travis et al. (1996) is most likely the results of different resolution capabilities as a function of the number and variability of the loci.

Overall, the results of this dissertation indicate that ecological factors, namely resource abundance and distribution are the determinants of Gunnison's prairie dog social organization, with individuals demonstrating behavioral flexibility in the face of changing environmental conditions. The most significant conclusions of this study are that: 1) Male mating strategies are not driving patterns of association between males and females in these populations, 2) Individuals respond to changes in patterns of resource distribution by adjusting space-use and potentially tolerance of other individuals, 3) Resident males do not have a reproductive advantage over non-resident males, and 4) Kin selection is not maintaining social groups or fine-grained patterns of space use in these populations.

The ability to adaptively respond to changes in ecological conditions may help explain differences among social groups and populations of Gunnison's prairie dogs

and provide insights into how sociality is maintained. For example, by modifying space-use pattern towards greater spatial overlap within territories as resources become extremely abundant and patchy, a higher degree of tolerance may be expressed promoting amicable interactions among individuals. This behavioral flexibility may provide the foundation for which sociality can emerge, especially in the absence of cooperation based on kinship.

Although historically the RDH has been used as a default hypothesis to explain passive group formation when more traditional theoretical models, such as those emphasizing male mating strategies and kin selection, have not been detected, this study suggests that RDH can be viewed as an alternative hypothesis and be explicitly tested. If this were true, then under what conditions would one expect RDH to apply? RDH might be an important factor for species where there is a key limiting resource necessary for *both* males and females. For example, in this study, the availability of food is critical to both males and females, particularly for overwinter survival. In addition, the availability of hibernation burrows may act as a secondary limiting resource, further promoting cooperation and tolerance among individuals. There are indications that these conditions are important to species other than Gunnison's prairie dogs (eg. *Meles meles*: Rosalino et al. 2005) and may be an indication of when the RDH is relevant. In addition, because sex-biased dispersal may be frequently correlated with the mating system or indicate a potential underlying kinship structure, species for which there is a lack of sex-biased dispersal may be indicative of processes more congruent with the RDH. Lastly, intraspecific variation

within the same geographic area or across geographic regions may be a clear signal that environmental variability plays a significant role in social dynamics.

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