

THE EVOLUTION OF LEKKING: INSIGHTS FROM A SPECIES WITH A
FLEXIBLE MATING SYSTEM

By

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This dissertation is dedicated to my parents, Kalyani and Balkrishna Isvaran. I owe much to their love, support, and belief that I can accomplish anything I set my mind to.

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The study of intraspecific variation can provide insights into the evolution and maintenance of behavior. To identify the conditions associated with the rare and unusual mating system, lekking, I studied variation in male mating behavior of the blackbuck, *Antilope cervicapra*, an Indian antelope with a flexible mating system. Blackbuck show wide variation in the distribution of mating territories, from large solitary territories to tightly clumped, classical leks. Rather than viewing lekking as a discrete mating system, I treat leks as one extreme in a range of territory distributions, and describe the mating system of a population in terms of the distribution of mating territories (the degree of clustering and territory size). I studied factors influencing male clustering and territory size in ten blackbuck populations, nine in India and one in Texas, U.S.A. I also studied one Indian population more intensively. I found that large-scale, among-population variation in territory clustering was most strongly related to the size of female groups. In turn, female group size was best explained by habitat structure and resources.

Interestingly, I found similar patterns at a smaller spatial scale within the intensively studied population. However, my findings suggested that at finer scales, other selective factors (e.g., female choice, male competition, male harassment) are likely to shape the clustering of territories. Using a dynamic modeling approach, I found that male clustering at finer scales was favored when benefits to clustering increased nonlinearly with cluster size. Of three prominent hypothesized selective factors that I evaluated, female mating bias for larger clusters appeared most likely to satisfy the conditions favoring male clustering. Finally, I found that in addition to examining male clustering, understanding the factors leading to reduced territory sizes is essential. Models and empirical analyses of territory size suggest that a female bias for mating in the center of an aggregation (or at restricted mating sites) in combination with large cluster sizes likely favors the reduced territory sizes typically seen in classical leks. Taken together, my work suggests that multiple factors acting on different aspects of male mating behavior and at different spatial scales maintain lekking.

CHAPTER 1 GENERAL INTRODUCTION

The lek-mating system has attracted much research attention because it displays several unusual features and presents a challenge to our understanding of mating system evolution. Males fiercely defend tiny, highly clustered territories, which are devoid of resources (e.g., forage, breeding sites) attractive to females (Bradbury 1981). Females are thought to visit these territorial aggregations, called leks, for the sole purpose of mating. This form of mating system is rare and very unlike more typical mammalian and bird systems in which males attempt to monopolize access to females by defending either a group of females or resource territories that predictably attract females (Clutton-Brock 1989, Davies 1991). Indeed, fewer than 2% of birds and 1% of mammals display this mating system (Davies 1991). Lekking is also characterized by a strong potential for sexual selection. In lekking populations, most matings typically occur on leks (Höglund and Alatalo 1995), and male mating success on leks is highly skewed (Apollonio et al. 1989, Clutton-Brock et al. 1988, Gosling and Petrie 1990, Höglund and Alatalo 1995), indicating strong sexual selection. Females in many species appear to be free to move between lekking males, suggesting that female choice might play an important role in sexual selection on leks (Alatalo et al. 1992, Höglund et al. 1993). Males on leks also experience intense male-male competition with many studies detailing the high costs that lekking males experience (Apollonio et al. 1992, Höglund et al. 1993, Gosling and Petrie 1990, Nefdt 1995). Further, sexual conflict has also been recorded in many species, largely in the form of males harassing females visiting leks and interrupting courtship

(Clutton-Brock et al. 1992, Nefdt and Thirgood 1997). The potential for strong sexual selection on leks and the unusual territorial behavior of lekking males have spurred many theoretical and empirical studies. But, despite extensive efforts, the evolution of lekking remains debated. Through this dissertation, I seek to understand lekking by studying an antelope species that shows wide variation in mating behavior, both among and within populations.

Variation in mating behavior provides the opportunity to investigate the broad ecological conditions associated with lekking and to evaluate the importance of hypothesized selective factors. Studies of intraspecific or interspecific variation in lekking behavior are rare. Instead, studies of lekking typically focus on one population and comparisons of lekking and mating behavior are usually made in reviews (e.g., Clutton-Brock et al. 1993, Wiley 1991) using findings from studies that vary in the behavior patterns measured and in the methods used. Many lekking ungulates show extensive variation in mating system (topi *Damaliscus lunatus*, Gosling 1991; fallow deer *Dama dama* Thirgood et al. 1999; Uganda kob *Kobus kob* Balmford et al. 1992, Fischer and Linsenmair 1999) and allow one to explore the selective factors favoring lekking. One such species is the blackbuck (*Antilope cervicapra*). This is an endangered antelope native to the Indian subcontinent. It is a group-living grazer that is found in a wide range of habitats (semi-arid grasslands, scrub, open woodlands, marshy coastal plains; Ranjitsinh 1989). The mating system is based on the defense of mating territories by males; these territories range widely in size and dispersion (Isvaran and Jhala 2000, Mungall 1978, Prasad 1989, Ranjitsinh 1989). Within a population, males may hold a

territory in territorial aggregations of different sizes, hold solitary territories or attempt to mate with females in herds (Isvaran and Jhala 2000).

Previous studies treat lekking as a discrete mating system and compare it with other mating systems such as resource defense polygyny (Gosling 1986, Nefdt and Thirgood 1997). A preliminary study of the blackbuck mating system suggested that this classification hides much variation and may obscure patterns in mating behavior (Isvaran unpublished data). Hence, I take a different approach towards lekking. I treat leks as one extreme in a range of territory distributions that extends from solitary dispersed to highly clumped territories. Using this approach, I describe the mating system of a population in terms of the distribution of mating territories (the degree of clustering). I then examine the correlates of large-scale variation in territory-clustering among nine blackbuck populations. I also examine the correlates of small-scale spatial variation in clustering within a population. I use this comparative approach to describe the ecological, demographic, and social conditions associated with lekking and to evaluate hypotheses about lek evolution (Chapter 2).

I also use a modeling approach to evaluate the conditions that will favor the clustering of territories and to test some of the most popular hypotheses of lek evolution (Chapter 3). The main hypotheses proposed to explain lek evolution have been modeled mathematically (Bradbury et al. 1986, Gibson et al. 1990, Stillman et al. 1996), and several predictions of the alternative models are supported by available data. However, many of the predictions are shared by more than one model (Bradbury et al. 1986, Stillman et al. 1996). Further, most modeling efforts have focused on one or a few costs and/or benefits while generating hypotheses about lek evolution. Field studies of leks,

however, report that many variables that potentially affect the payoffs to lekking correlate with territory clustering (Höglund et al. 1993, Nefdt and Thirgood 1997). To incorporate such complexity, I use dynamic state variable modeling (Clark and Mangel 2000). This approach allows one to predict sequences of optimal decisions through an individual's lifetime and provides a common framework within which the effects of several potential selective forces and their interactions can be compared. The main aims of this modeling effort are (1) to evaluate the main selective factors hypothesized to favor lek evolution; (2) to examine the consequences of assumptions made about how hypothesized selective factors affect the behavior of interest; and (3) to identify the general conditions under which these factors are likely to lead to the evolution of male clustering (Chapter 3).

While studies of lekking typically focus on the extreme levels of territory clustering that lekking males display, the unusually small size of lek-territories has received much less attention both theoretically and empirically. Territory sizes vary both among and within species and do not always covary with territory clustering (Jiguet et al. 2000, Thirgood et al. 1992). Thus, understanding the factors influencing territory size may contribute to our understanding of lek evolution. Since there are few quantitative models of mating territory size, I first construct alternative spatial simulation models of territory size based on verbal explanations from the literature. I then test predictions from these models using comparative data on territorial behavior from six blackbuck populations and more detailed observations from within one lekking population (Chapter 4).

Many discussions of mating systems explain male mating behavior as a response to the dispersion of females. In particular, lekking is often associated with large female groups (Clutton-Brock et al. 1993, Höglund and Alatalo 1995). Group sizes vary widely

in blackbuck (Ranjitsinh 1989) and offer the opportunity to investigate the factors influencing grouping and thus variation in male territory clustering. The principal factors thought to favor grouping in large mammals, such as cervids, bovids, and macropods, are predator density, habitat structure, and resource abundance and distribution (Brashares and Arcese 2002, Estes 1974, Jarman 1974, Jarman and Southwell 1986). While studies have provided evidence for the effect of each of these three factors, their relative importance in influencing group size is rarely assessed simultaneously (Brashares and Arcese 2002). I examine the relative roles of the three main selective factors in maintaining group size variation both among ten blackbuck populations and within one population (Chapter 5).

This dissertation is an examination of the maintenance of lekking using a species with a flexible mating system. I hope to provide fresh insights (1) by treating lekking as part of a range of territory distributions that extends from solitary dispersed territories to large clusters; (2) by focusing on two important features of lekking, male clustering and territory size, (3) by using behavior measured at different scales (among and within populations) to formulate and test hypotheses. I show that lekking in blackbuck is most likely an outcome of multiple factors acting at different spatial scales and on different components of mating behavior. My findings suggest that diverse aspects of female behavior (dispersion in the environment, movement among leks of different sizes, mate-sampling behavior within a lek) may be some of the most important factors favoring lekking and emphasize the need for a better understanding of female behavior in relation to mating. I also show that the mating system of a population likely reflects individuals

responding flexibly to immediate conditions rather than intrinsic differences among individuals or among populations

CHAPTER 2
THE ECOLOGICAL, DEMOGRAPHIC, AND SOCIAL CORRELATES OF LEKKING
IN AN ANTELOPE WITH A FLEXIBLE MATING SYSTEM

Introduction

Mating systems in which males do not provide any parental care have usually been explained in terms of males monopolizing mates or resources attractive to females (Clutton-Brock 1989). From this perspective, the evolution of the lek-mating system is intriguing because males defend neither females nor any obvious resources. Lekking males typically defend small mating territories in aggregations. These territories are devoid of resources such as food or water, and females are thought to visit leks for the sole purpose of mating (Bradbury 1981). The lek-mating system is rare (occurring in less than 2% of birds and 1% of mammals), but it appears in a wide diversity of taxa (in at least 14 bird families, and at least 5 mammal families; Höglund and Alatalo 1995). Furthermore, many species that lek also display variation in their mating system. This is especially common among lekking ungulates. For example, in topi *Damaliscus lunatus* and fallow deer *Dama dama*, males in some populations lek while males in others show resource-defense polygyny and female-following strategies (Clutton-Brock et al. 1988, Gosling 1986, Langbein and Thirgood 1989). Furthermore, variation in male mating strategies has been reported even within populations (Gosling 1986, Thirgood et al. 1999). Such variation offers the opportunity to evaluate the factors that vary systematically with male mating strategy and identify the conditions associated with lekking, thereby providing insights into the evolution and maintenance of this mating

system. Although systematic studies of intraspecific variation are relatively rare, this approach has been used previously to understand the adaptiveness of mating systems (e.g., in dunnoek *Prunella modularis*; Davies 1985). I studied the blackbuck (*Antelope cervicapra*), an endangered Indian antelope with highly variable mating behavior, to identify the ecological, demographic, and social conditions associated with lekking.

A wide range of factors is correlated with lekking in different species (Bradbury et al. 1986, Clutton-Brock 1989, Wiley 1974). The main ecological factors that have been suggested are resources, habitat structure, and predation. Resources are thought to affect lekking by influencing female density and distribution. For example, several studies of ungulates (Gosling 1986, Deutsch 1994a, Nefdt and Thirgood 1997) have suggested that when resources are homogeneously distributed, females are more evenly and predictably distributed, and under such conditions, males defend resource territories. Conversely, when resources show unpredictable changes in distribution seasonally or annually, females are found in large groups and move erratically over large areas as they track resources. In these circumstances, the defense of resource territories that predictably attract females may be less successful than lekking (Gosling 1986, Nefdt and Thirgood 1997). Habitat structure is thought to affect mating systems in two ways, by influencing female distribution (Gosling 1986), and by constraining mating options available to males, for example if habitat suitable for mating territories is limiting (Wegge and Rolstad 1986). A third ecological factor, predation, also affects both male and female mating behavior by, for example, favoring males that aggregate or females that mate in aggregations (Gosling and Petrie 1990, Wiley 1974).

Apart from ecology, lekking is also thought to be influenced by several demographic factors, principally female density. Many studies have found that lekking is associated with relatively high population densities (Langbein and Thirgood 1989, Balmford et al. 1993a,b). Further, there are several accounts of switches in mating system following changes in density. For example, in the Uganda kob (*Kobus kobus*) and fallow deer, a decline in population density was associated with a change in mating system from lekking to resource defense (Clutton-Brock et al. 1993). Operational sex ratio (OSR) may also be associated with lekking (Apollonio 1989).

Two social factors correlate with lekking in several species: the social behavior of females (grouping and ranging), and harassment of estrous females by males. Lekking often occurs in species in which females move unpredictably in large groups and have large home ranges (Bradbury et al. 1986, Clutton-Brock et al. 1993). A popular hypothesis about the evolution of lekking in ungulates proposes that lekking is favored when there is high harassment of estrous females (Clutton-Brock et al. 1992, Nefdt 1995). Under such conditions, lekking males are thought to be more effective than males on solitary territories or in herds at repelling harassing males and monopolizing estrous females. A comparison of the mating behavior of the lekking Kafue lechwe *Kobus leche kafuensis* and its close non-lekking relative, the black lechwe *Kobus leche smithemani* found that harassment and mating disruptions were much lower in black lechwe than in Kafue lechwe herds (Nefdt and Thirgood 1997). Further, in the Kafue lechwe, although the frequency of mating initiations was similar in herds and on leks, mating sequences were more likely to be disrupted in herds than on leks (Nefdt 1995).

Overall, many ecological, demographic, and social factors have been associated with lekking, but studies do not provide a consistent picture of the conditions favoring lekking. While it is likely that these conditions vary among taxa, evidence for the role of various ecological and demographic factors is mixed even within a species (Apollonio 1989, Balmford et al. 1993b). One possible reason for the lack of clear patterns is that most studies focus on a single population and on testing specific processes (e.g., female choice) thought to maintain the lek mating system in that population. The general conditions associated with lekking are typically assessed in reviews that compile results from different single-population studies, studies that differ in the behavioral patterns measured, in the factors quantified, and in the methods used. While some studies have looked at behavioral variation within a lekking population (Apollonio et al. 1992, Clutton-Brock et al. 1988), very few have systematically examined mating system variation among populations of a species. In one such study (Langbein and Thirgood 1989), the factor that explained most of the variation in mating system among fallow deer populations was male density. Langbein and Thirgood (1989) suggested that male density is associated with increased male-male competition, which, in turn, results in increased aggregation of territories and reduction in territory size. In their study, female density and habitat type were secondarily related to mating system variation.

To identify the ecological, demographic, and social conditions associated with lekking, I studied variation both among and within populations of blackbuck. Previous studies have treated lekking as a discrete mating system and have classified populations as lekking or non-lekking. However, studies of blackbuck (Mungall 1978, Ranjitsinh 1989, Isvaran and Jhala 2000) suggest that this classification conceals much variation that

might yield insights into the conditions favoring lekking. Further, most theoretical studies model lekking as a matter of the clustering of territories, a continuous rather than a categorical approach (Bradbury 1981, Gibson et al. 1990, Stillman et al 1993). Hence, rather than classify the mating system of a population into discrete categories, I take a novel empirical approach and describe the mating system in terms of the distribution of mating territories, specifically the degree to which territories are clustered. I surveyed 10 blackbuck populations and measured the distribution of territories, and the ecological, demographic, and social factors that have been hypothesized to favor lekking. In addition to making cross-population comparisons, I also studied the correlates of territory clustering within a lekking population. In this paper, I examine the factors associated with variation in territory clustering, both among and within populations. I evaluate the correlates of extreme territory clustering (lekking) and discuss the implications of my findings in light of current hypotheses about lek evolution.

Methods

Study Organism

The blackbuck, *Antelope cervicapra*, is an antelope native to the Indian subcontinent. Although it reaches its highest densities in open plains, it is found in a wide range of habitats from grasslands to open woodlands. It is a selective grazer living in groups that range from 2 to several hundred individuals (Ranjitsinh 1989). Social groups are of three types: 1) all-male herds; 2) female herds (that contain adult females and juveniles of both sexes); and 3) mixed-sex herds (that contain adults and juveniles of both sexes). There are two annual mating peaks, from March to April and August to October (Ranjitsinh 1989). Males display to females on territories and in mixed-sex herds, but no matings have been observed in herds (Mungall 1978, Prasad 1989, this study).

Study Sites

I surveyed nine populations in India and one population in Texas, USA, during August - November 1998 and 1999 (Figure 2-1). The nine Indian populations were scattered throughout the range of the blackbuck (Figure 2-1, Table 2-1) and represented a wide range of habitat type, blackbuck density and predator density. All nine Indian populations lie in semi-arid regions and habitats range from open grasslands to thorny shrublands and forest (Table 2-1). All populations in India except Savainagar are designated protected areas managed by the Indian Forest Department. Blackbuck are native at all sites except at Vanasthali, where blackbuck were introduced about thirty years ago. I also studied a free-ranging population in natural habitat on Kyle ranch in Texas (Table 2-1). Since their introduction from zoos onto Texas ranches 70 to 80 years ago (Mungall 1978), blackbuck numbers have rapidly increased and currently rival their overall numbers in India (Mungall 1998). The Texas population thus represents a natural experiment and provides an opportunity to examine whether the correlates identified for the Indian populations hold in a population of animals introduced into a new habitat. Kyle ranch is located in a semi-arid region and is largely comprised of shrublands and forest with small grassy openings. The blackbuck population at Kyle ranch is free ranging and largely unmanaged, except for the provision of supplementary feed and occasional culling.

I studied spatial variation in territory clustering in greater detail within one of the Indian populations, Velavadar National Park, Gujarat, from January to May 2000. This area is a mosaic of grasslands, shrublands, and mudflats. It holds one of the largest blackbuck populations in India.

Among Population Variation In Mating System

Distribution of mating territories

Since most of the study areas are relatively small (1 km² to 36 km²), each site was repeatedly surveyed, and the distribution of territorial males was recorded on maps of the site. From these distributions, I identified clusters of territories. A cluster included all males that shared territory boundaries. This was inferred from observing areas used by each territorial male and interactions between neighboring males. Clusters were typically unambiguously identified. For example, at Velavadar the mean nearest neighbor distance of territorial males within a cluster was 85m (22 territories in 5 clusters) while the mean distance from a cluster to its nearest neighboring cluster was 900 m (5 clusters).

Correlates of mating system variation

I divided each study site into four to seven units (depending on the area of the site), and laid a one km line transect in each unit. At 50m intervals along these transects, habitat structure (habitat openness and habitat homogeneity) and resource abundance were measured as described below.

Habitat openness. Since blackbuck prefer open habitats (primarily grasslands; Ranjitsinh 1989, Jhala 1991), the measured habitat structure variables focused on open habitats. For the purposes of this paper, I placed habitats in two categories – open and closed habitats. Open habitats included those with less than ten percent of woody shrubs and trees more than one m high (mainly grasslands, and bare ground). Closed habitats were defined as those with more than ten percent of woody shrubs and trees more than one m high (mainly shrublands and forest). At 50 m intervals along each transect, I visually estimated the percentage of the area occupied by open and closed habitats in circular plots of 10 m radius. Habitat openness was calculated as the mean percentage of

open habitat in a plot (estimates were first averaged across plots and then across transects).

Habitat homogeneity. For each transect, I counted the number of successive sampling points with open habitat as the major habitat type; thus, each transect can be broken down into segments of varying lengths (1 to 20), where each segment consists of successive points with open habitat. These segments are an index of the size of open habitat patches through which the transect ran. A transect that did not go through any open habitat was assigned a value of zero. A transect with all 20 points falling in open habitat represented maximum homogeneity of open habitat (value of 20). The mean length of segments of open habitat was averaged across transects to obtain a measure of homogeneity of open habitat at each study site.

Resource abundance. At each sampling point along a transect, I measured grass height and visually estimated the percentage of area covered by grass in circular plots of one m radius. Grass height \times percent cover was used as an index of resource abundance.

Predator density. I obtained estimates of the number of predators (wolves) of adult blackbuck known to use each study site from Forest Department records and from information obtained from researchers working at the sites. Using these estimates, I calculated predator density (number of wolves per km²) for each site.

I used total counts or line transects to estimate (1) population density; (2) male density (number of males of all age classes per km²); (3) female density (number of females of all age classes per km²); and (4) operational sex ratio (number of females of all age classes divided by the number of males of all age classes). At seven sites, total counts (a recommended census technique for conspicuous animals that aggregate and that

are found in relatively open areas, Sutherland 1996) were used to estimate demographic parameters. During each total count, I systematically surveyed the study area (in the morning and evening hours when animals were most active), and recorded the age class and sex of every animal encountered. I conducted three to four total counts at each of the seven sites. At three sites (Point Calimere, Guindy, and Kyle ranch), total counts were difficult to conduct because of relatively dense vegetation. At these three sites, I walked six to seven 1 km strip transects. Along each transect, I recorded the age and sex of every animal encountered within 50 m (visually estimated) on either side of transects. The density of individuals was calculated as the total number of individuals sighted divided by the area sampled (the study area for total counts and the area of the strip transect for the transects).

Group size. I used total counts and transects described above to estimate group sizes. I defined a group as individuals within at least 50 m of another individual (Clutton-Brock et al. 1982, Lingle 2001). During total counts and transects, for each individual or group encountered, I recorded the number, age and sex of individuals.

Female group size. Since male mating behavior is hypothesized to be influenced by the degree to which females in particular (rather than all individuals) are aggregated in an area, I took the data on group sizes (recorded as described above), selected only groups that contained females (female groups and mixed-sex groups), and estimated the mean number of females per group.

Female ranging. I was interested in estimating the variation among study sites in the extent of female ranging since this movement is thought to influence male mating behavior by modifying female encounter rates that males experience at any one location

in a study site. For example, when females range widely over large areas males are expected to experience low female encounter rates at any given location in the study site (Deutsch 1994a). Due to the limited time that I spent at each study site I could not measure female home range sizes. Instead I used an index of female ranging, the distance moved during a sampling period. In each population, I followed ten to fifteen (mean = 13, SD = 3) female or mixed-sex groups for 30 to 60 minutes (mean = 40, SD = 7) on different days. During each group follow, I noted the location of the group at the beginning and the end of the follow and paced out the straight-line distance between the two locations. This measure (meters moved per hour) was used as an index of female ranging.

Male harassment. During the group follows described above, I recorded the number and duration of chases of females by males. I used the number of chases per female per hour as a measure of male harassment of females.

Within Population Variation In Mating System

I examined the correlates of variation in territory clustering within a primarily lekking population (Velavadar National Park), from January to April 2000. I divided the study area into approximately one km² (1.1 × 1.1 km) sampling units. The exact grid size was chosen based on the scale of the map obtained from the Forest Department. Every two weeks, I surveyed the study area three to five times on consecutive days and recorded the location and distribution of territories on maps. From these maps, I estimated the number of territorial males, and cluster sizes (number of males in a territory cluster) in each spatial unit. Along with collecting territorial data, I performed three to five total counts during morning and evening hours and estimated the number of males and females, and the OSR in each 1 km² spatial unit. I measured habitat characteristics in the

different 1 km² spatial units. In each unit, I laid two 500m transects at random. Along each transect, I measured habitat characteristics and resource abundance as described in the among-population comparison.

Analyses

Among-population variation in territory clustering

The extent of territory clustering in the different populations was estimated in two ways.

Crowding index. First, to estimate the cluster size (number of males in cluster) that the average male was found in, I used Lloyd's crowding index (Lloyd 1967):

$$\frac{\sum_i^n x(x-1)}{N}$$

where x is the number of males in a cluster, n is the number of clusters and N is the total number of territorial males. A solitary male was counted as a cluster of one and thus was assigned a crowding index of 0. The crowding index gives the mean number of territorial males the average territorial male associates with.

Standardized Clustering Index (SCI). Since the total number of territorial males differed among populations, I sought an index of territory clustering that was independent of the number of males in a population. For each population, I took the total number of territorial males as the maximum possible cluster size and then divided this number into six equal intervals of cluster sizes (six equivalent levels of clustering across populations). Thus, in a population with six territorial males, clustering levels range from one male (the lowest level) to six males (the highest level), while in a population with 60 territorial males, clustering levels range from a minimum of 1-10 males to a maximum of 50-60 males. I then calculated the mean level of clustering adopted by the average male

(example in Appendix). The Standardized Clustering Index represents a relative rather than an absolute measure of clustering; thus, a territory cluster of six in a population of six territorial males represents the same level of clustering as a cluster of 60 in a population with 60 males. I chose six levels of clustering based on the minimum territorial male population size ($n = 6$ in Vanasthali). The SCI is based on the null expectation that absolute cluster size should increase linearly with the number of territorial males in a population. Note that this expectation may be unreasonable when territorial male populations and/or study areas are very large.

I used parametric correlation analyses to explore the relationship between the extent of territory clustering (crowding index and SCI) and the various ecological, demographic, and social correlates. I also used stepwise multiple regression analyses with Standardized Clustering Index as the dependent variable to identify the factor(s) that best explain the variation among populations in the degree of clustering. The independent variables used were habitat homogeneity, resource abundance, population density, sex ratio, and female group size. To minimize problems associated with multicollinearity, if two or more variables displayed a correlation greater than 0.9, only one was randomly chosen and used in the analysis. Using this procedure, habitat openness was dropped since it was highly correlated with habitat homogeneity. Similarly, population density was used to represent both male and female density since all three variables were highly correlated. Predation, male harassment and female ranging were not included in the regression analysis since data on these factors could not be collected in all populations. Predation and ranging estimates could not be collected at Texas, and harassment at Texas and Guindy. The residuals were tested for normality (Kolmogorov-Smirnov test).

Relationships between the dependent variable and all independent variables were checked for linearity and variables were transformed appropriately to meet linearity assumptions. Since the sample size is small ($n = 9$ populations), residuals were also visually inspected for deviations from normality and linearity. The population at Guindy was dropped from both correlation and regression analyses since overall population size ($N = 40$) and the number of territorial males ($N = 2$) was so small that SCI could not be calculated.

Within-population variation in territory clustering

The clustering of territories in each one km^2 sampling unit was represented by the crowding index (at this spatial scale, SCI could not be used, since there was usually one and not more than 2 clusters per spatial unit). The relationship between the crowding index and the various factors measured (habitat openness, habitat homogeneity, resource abundance, male numbers, female numbers, and female group size) was explored using correlation analyses. To identify the factor explaining the most variation in crowding index I used stepwise multiple regression analyses. Since clusters were only seen in eight of the 14 sampling units, to avoid entering too many explanatory variables in the stepwise regression I only used variables that showed a significant correlation ($P < 0.1$) with crowding index. These variables were resource abundance, female numbers, and female group size. Similar regression analyses were conducted with the number of territorial males in each spatial unit as the dependent variable. All analyses were performed on log-transformed data.

Results

Among-Population Variation In Territory Clustering

The distribution of territories varied widely among populations (Figure 2-2). In some populations (e.g., Vanasthali, Rehekuri), most territorial males were solitary or in

small clusters of up to 5 males. In other populations, males were found in varying mixtures of small and intermediate clusters (e.g., Savainagar, Point Calimere). Yet others showed extreme clustering with most males forming a single large classical lek (e.g. Tal Chappar, Velavadar).

The crowding index, the mean number of territorial males that the average territorial male associated with, ranged from 0.3 males in Vanasthali, where males were largely on solitary dispersed territories, to 37.8 males in Tal Chappar, where most males were in a single large cluster of 50 males (Table 2-2). The crowding index reflects absolute levels of territory clustering and is affected by the total number of territorial males in a population. Thus, for example, a population with 9 territorial males where all 9 males were maximally clustered into one group will still have a lower crowding index than a population with 100 males distributed in multiple clusters, say 10 clusters of 10 each. Hence, I used a relative measure of clustering, SCI, to represent the relative degree to which territorial males in a population were clustered (Table 2-2). SCI is the level of clustering adopted by the average territorial male in a population taking into account differences among populations in the total number of males. Using this index I found that males in populations with very different numbers of territorial males and with different absolute cluster sizes still exhibited a similar level of clustering (Table 2-2). For example, territory clusters ranged from 1 to 5 males at the Kyle ranch and from 1 to 15 at Point Calimere. While absolute cluster sizes and the crowding index were very different for these two populations, the SCI was very similar (2.0 and 2.1 at Point Calimere and Kyle ranch respectively). In both populations, around 50% of territorial males adopted the lowest level of clustering (clusters of 1-2 males at the Kyle ranch and of 1-3 males at

Point Calimere) and 50% an intermediate level of clustering (a cluster of 5 in the Kyle ranch and one of 15 at Point Calimere).

Apart from establishing territories, males were also seen in mixed-sex herds and in all-male herds. Males in all-male herds rarely interact with females (Mungall 1978, Isvaran and Jhala 2000) and thus, being in an all-male herd is likely a non-reproductive tactic. However, males in mixed-sex herds often perform courtship displays (Mungall 1978) to females; hence, joining a mixed-sex herd is likely a reproductive tactic. Populations varied in the distribution of males among these three social categories (Table 2-2).

Of the ecological factors measured, only habitat structure (both habitat openness and habitat homogeneity) was correlated with SCI, the relative degree of territory clustering (Tables 2-2 and 2-3). Clustering increased with an increase in the proportion of open habitats (Pearson's $r = 0.69$, $N = 9$, $P = 0.038$) in the study area and with an increase in the size of open habitat patches ($r = 0.74$, $N = 9$, $P = 0.024$). Extreme-clustering (classical leks) was found in study sites that were largely composed of homogenous open habitats (primarily grasslands). However, in the stepwise regression analysis, these factors did not have a significant effect because of a larger effect from another factor (female group size, reported below). Clustering was not associated with resource abundance (grass volume; $r = 0.56$, $N = 9$, $P = 0.12$). I also used annual rainfall as an index of resource abundance (Maher 2000), but did not find a correlation between annual rainfall and SCI ($r = -0.42$, $N = 9$, $P = 0.26$) nor with predator density ($r = -0.02$, $N = 9$, $P = 0.95$; Table 2-3). Since for several populations I relied on information from secondary sources for predator density estimates and since such densities are difficult to estimate in

the absence of intensive sampling, the error around these estimates is uncertain.

Therefore, I also tested for the effect of predator density in a more general manner. I placed populations in Low (wolves absent) and High (wolves present) categories of predation pressure and tested for a difference in SCI between the two categories. SCI did not differ significantly between the two categories (t-test on log-transformed data: $t = 2.4$, $df = 7$, $P = 0.46$).

I found no clear relationship between SCI and any demographic factor including female density (Table 2-3, Figure 2-3). Among the social variables, there was a strong correlation between SCI and female group size ($r = 0.92$, $N = 9$, $P = 0.0005$). Clustering increased with female group size and extreme clustering (classical leks) was associated with large female groups (Figure 2-4). In the stepwise regression analysis, female group size was the only variable that entered the regression and explained a large portion of the variation in SCI ($R^2 = 0.84$, $N = 9$, $P = 0.0005$). Clustering increased with an increase in the ranging of female groups ($r = 0.74$, $N = 9$, $P = 0.033$), but showed no clear pattern with male harassment ($r = 0.18$, $N = 9$, $P = 0.67$).

The degree of territory clustering in the Kyle ranch (Texas) population matched expectations based on the relationship between clustering and group size in the Indian populations. Group sizes were relatively small at Kyle ranch and, correspondingly, the level of territory clustering was relatively low (Figure 2-4).

The main predictor of female group size was habitat structure. In a stepwise regression with female group size as the dependent variable and habitat homogeneity, resource abundance, and population density as independent variables, habitat homogeneity was the only variable that entered the regression ($R^2 = 0.72$, $N = 9$, $P =$

0.002). Since habitat homogeneity was strongly correlated with habitat openness only the former was included in the multiple regression to minimize problems associated with multicollinearity. Thus, it is not possible to distinguish between habitat openness and homogeneity as predictors of female group size.

Within-Population Variation In Territory Clustering

At Velavadar, where I studied the correlates of territory clustering within a population, cluster sizes varied from solitary territories and small clusters of two to four males to a lek of 50 males. The general distribution of territories among the one km² sampling units was correlated with female distribution. In a stepwise regression analysis with the number of territorial males in a sampling unit as the dependent variable, the number of females in a unit was the only factor that entered the analysis ($R^2 = 0.56$, $N = 14$, $P = 0.002$, Figures 2-5 and 2-6).

Territories were observed in eight of the 14 sampling units at Velavadar. Variation in territory clustering (measured as the crowding index) among these eight units was correlated with average female group size ($r = 0.93$, $N = 8$, $P = 0.001$ Figure 7), number of females observed in each unit ($r = 0.89$, $N = 8$, $P = 0.003$), and male numbers ($r = 0.72$, $N = 8$, $P = 0.042$). In a stepwise regression analysis of male territory clustering, female group size was the only variable that was included in the regression ($R^2 = 0.86$, $N = 8$, $P = 0.001$). The crowding index was not correlated with any habitat factors at Velavadar (Table 2-4). It is possible that overall grass volume did not reflect resource abundance well. However, this measure was strongly correlated with the abundance of three of the most preferred forage species suggesting that it was an appropriate measure of resource abundance (Chapter 5).

Discussion

Patterns Of Variation In Territory Clustering

A striking result of this study was the wide variation among populations in mating system, specifically in the degree to which territories were clustered. Two populations (Velavadar and Tal Chappar) displayed classical lekking, while males in one population (Vanasthali) defended large scattered territories in foraging areas used by females (resource territories). The remaining six populations displayed different degrees of intermediate clustering of territories. Population patterns of territory clustering ranged from those in which males were found in several small territory clusters to those in which males defended territories in a range of small and moderately sized clusters (two to 18 males). Further, territory sizes ranged widely from 350 m² to 100,000 m² in area as did abundance of forage on territories (Chapter 4). Due to this variation, the mating system in the majority of blackbuck populations could not be easily placed in discrete mating system categories (e.g., resource-defense territoriality and lekking). These findings show that classical lekking is one extreme pattern in a wide range of territorial behavior. Understanding extreme territory clustering (i.e., lekking) is embedded in the larger question of understanding the processes that lead to variation in territorial behavior.

Interestingly, in each population, only a limited range of territory-cluster sizes was seen. For example, at Nannaj, a major proportion of territorial males were in a cluster of 18, while the rest were either solitary or in clusters of two to four (Figure 2-2). Thus, examining a single population might lead to the conclusion that males display a limited set of territorial behavior. The wide range of territorial options adopted by male blackbuck is most apparent when looking across multiple populations.

Such variation in territory clustering is not unusual. Wide variation in clustering has been reported in groups of closely related species. For example, in grouse, spatial patterns of territories range from solitary display territories (e.g., spruce grouse, Hjorth 1970) and loosely clustered territories (e.g., blue grouse, Lewis 1985) to large leks (e.g., sage grouse, Wiley 1974). Within species, lekking and non-lekking populations have been described in many taxa including mammals, birds, amphibians, and fish (reviewed in Lott 1991, Höglund and Alatalo 1995). However, extensive intraspecific variation in territory clustering appears to be most common in lekking ungulates (Höglund and Alatalo 1995). Such variation has been described in detail in fallow deer (Clutton-Brock et al. 1988, Langbein and Thirgood 1989) and there is evidence that this variation is common in other lekking ungulates (Gosling 1986, Balmford et al. 1992).

Intermediate levels of territory clustering that are difficult to categorize may not be specific to blackbuck. For example, in the black lechwe, a sub species of the lekking Kafue lechwe antelope, males defend territories that have characteristics of both resource- and lek-territories (Thirgood et al. 1992). Territories are situated in feeding areas used by females. However, the territories are unusually small and clustered. Thirgood et al. (1992) conclude that overall these territories resemble resource- rather than lek-territories. Similarly, in the little bustard (*Tetrax tetrax*, Jiguet et al. 2000) and in the grassquit (*Volatinia jacarina*, Almeida and Macedo 2001), territories are relatively large and contain some resources, but are more clustered than expected, a lek-like feature. Terms such as ‘exploded leks’ and ‘dispersed leks,’ have been used to describe some of the intermediate clustering patterns found in many bird and insect species. Such variation has led some authors (Höglund and Alatalo 1995) to suggest that the difference between

many spatial distributions (e.g., dispersed leks versus classical leks) is continuous rather than discrete. These observations suggest that territorial mating systems are much more variable than is usually discussed in the literature. While this variation makes the placement of observed mating systems into currently recognized categories problematic, it provides the opportunity to study the conditions that influence mating system variation and that favor unusual mating systems such as lekking.

Correlates Of Territory Clustering From Among-Population Comparisons

A second striking result of this study was that female group size was the principal correlate of male territory clustering among populations (female group size explained most of the variation, 84%). In populations in which females were in small groups, males defended territories either alone or in small clusters. At the other extreme, classical leks were associated with large groups of females. While few previous studies have examined continuous variation in territory clustering, many studies report conditions associated with lekking and non-lekking mating systems. The three main conditions identified by these studies are group size, population density, and female range size (Bradbury et al. 1986, Clutton-Brock et al. 1993, Davies 1991).

Territory clustering, female group size, and population density

Several studies report an association between lekking and female group size although this relationship has not been investigated quantitatively. In a comparison of grouse mating systems, Wiley (1974) found that lekking occurred in species in which females moved in relatively large groups. Clutton-Brock et al. (1993) similarly found that ungulate species with large female group sizes displayed lekking, while those with small group sizes displayed non-lekking systems such as resource-defense territoriality. Within species, this relationship again has not been investigated systematically, but informal

comparisons across studies provide some evidence (Balmford et al. 1993a,b). Thus, the results from examining intraspecific variation in blackbuck provide strong quantitative support to previous observations concerning the relationship between female group size and mating system. The main explanation proposed for the association between large female groups and lekking is that male mating strategies, such as defense of female groups or of resources that attract females, are not economical when females occur in large unstable groups and local numbers of females are high (Clutton-Brock et al. 1993, Davies 1991). This argument, however, does not address why lekking performs better than the other mating strategies under such conditions.

Another important condition thought to influence mating system is population density. Several authors suggest that lekking occurs when population density is high. It is thought that, in high-density populations, local numbers of females are high enough so that clusters of males may attract enough females to offset the costs of clustering (Clutton-Brock et al. 1988). An association between density and lekking has been reported in most lekking ungulates, such as Uganda kob, topi, fallow deer, and sika deer (Balmford et al. 1992, Balmford et al. 1993b, Langbein and Thirgood, 1989). Surprisingly, I found no relationship between population density and territory clustering in blackbuck.

Why might female group size rather than population density be associated with territory clustering in blackbuck? Population density is thought to influence lekking through large local numbers of females. However, in blackbuck, female group size is likely a better estimate of local numbers of females than overall population density. Groups do show some overlap in home ranges, but during a given time period this

overlap is usually limited (e.g., 5 to 30% in blackbuck, Prasad 1981), and thus group sizes reflect the number of females present at a local spatial scale. Further, females in most ungulates rarely leave their daily ranges to mate and a previous study of lekking antelope found that most estrous females sample mates within their home ranges (Balmford et al. 1992). Hence, female group sizes, in effect, represent the number of estrous females available in a given area. Overall population density, on the other hand, may not always represent local distribution of females, especially in heterogeneous environments (Apollonio 1989). Indeed, I found no relationship between population density and local density (represented by group size). The lack of correlation is probably because group sizes were strongly correlated with local habitat characteristics. On the other hand, population density appeared to be less influenced by local habitat characteristics and more by management features. For example, at two forested sites with low grass abundance, Kyle ranch and Vanasthali, supplementary feeding probably maintains a high population density. Also, most protected areas in India are surrounded by varying mosaics of habitat, including forage-rich crop fields that may influence densities within protected areas.

Since population density and group size are not correlated in blackbuck (unlike many other ungulate populations, Clutton-Brock et al. 1993), this allows one to analyze whether male territorial behavior is related to the distribution of females at a local scale or at the population level. My findings suggest that male territorial behavior is relatively more influenced by local patterns in female numbers than by overall population patterns. Apollonio (1989) arrives at a similar conclusion for fallow deer. In Italy, unlike in England, fallow deer lek even when population densities are relatively moderate.

Apollonio (1989) argues that despite relatively low overall density, high environmental heterogeneity leads to areas of high local density of fallow deer, and leks are found in such areas.

Territory clustering and female ranging patterns

Apart from density, another important characteristic thought to be associated with lekking is large home range size of females (Clutton-Brock 1989, Clutton-Brock et al. 1993, Davies 1991). Among reduncine antelope and grouse, large female home range size is associated with lekking, while smaller home ranges are associated with other mating systems, such as resource-defense, solitary mating territories, or harem defense (Bradbury et al. 1986, Clutton-Brock et al. 1993). Comparing across blackbuck populations, I found a correlation between female ranging and territory clustering. The degree of territory clustering increased with an increase in female ranging. However, this correlation was not as strong as the relationship between clustering and female group size. Further, female ranging and group size were also correlated, a pattern reported before in comparisons of closely related antelope species (Clutton-Brock et al. 1993). The main hypothesis for the influence of female ranging patterns on lekking does not directly explain how this factor may influence territory clustering, but instead explains why large ranges are a prerequisite to lekking. Several authors have suggested that when females have large ranges, other more common mating strategies, such as the defense of resources consistently used by females, are no longer economical (Davies 1991, Gosling 1991, Clutton-Brock et al. 1993). When females have very large home ranges, males can only defend a small part of the resources used by females. Thus, males on resource territories may not be regularly or predictably visited by females and experience low female encounter rates (Deutsch 1994a, Nefdt and Thirgood 1997). However, while these

arguments address why resource defense may not do well, they do not explain why lekking will do better in such situations. Lekking is thus treated as a ‘default strategy’ (Deutsch 1994a).

Territory clustering and habitat features

Apart from female group size and ranging, the only other significant correlates of among-population variation in territory clustering were features of habitat structure, habitat openness and homogeneity of open habitat. Large classical leks were found at sites where large grasslands predominated. However, the correlation with habitat factors was not as strong as that with group size and statistically, the effects of habitat factors disappeared once the effect of female group size was incorporated. This suggests that these ecological variables do not act directly on male mating behavior, but influence male behavior through their effects on female group size. In blackbuck female group size is closely correlated with several habitat features (Chapter 5). Habitat features have been linked to lekking in a similar fashion in other species (Gosling 1986, Höglund and Alatalo 1995, Thirgood et al. 1999, Wiley 1974).

Conclusions from among-population comparisons

The main correlate of large-scale variation in mating system across blackbuck populations was female group size. My findings suggest that local patterns in female distribution in the environment rather than overall population density influence the clustering of male mating territories. Specifically, classical lekking (extreme territory clustering) was associated with large female groups. Studies of other lekking species describe a similar association between group size and lekking. However, several other studies also report an association between mating system and overall population density (contrary to my findings). But in most of these studies female group size and population

density are also correlated and thus their individual effects on mating system cannot be easily examined. Female ranging, a third important factor identified by previous studies, was less strongly correlated with male clustering in blackbuck.

Patterns And Correlates Of Territory Clustering From Within-Population Comparisons

My findings from within-population variation supported the findings from the comparison among populations. Furthermore, they suggest that males respond flexibly to variation in female distribution at small spatial scales. I found that the local distribution of females was a good predictor of both the number of territorial males in an area and the degree to which these males were clustered. The number of territories in a 1 km² sampling unit was positively correlated with the number of females suggesting that male mating dispersion is influenced by female dispersion. Further, the relative clustering of these territories among sampling units was correlated with both local female numbers and with female group size. The principal lek (average of 50 males, maximum of 90 males) was located in a large grassland which was regularly used by an average of 280 females distributed among large groups (mean group size = 75 animals). Smaller territory clusters on the other hand were found in areas with an average of 18 to 35 females moving in small groups (mean group size = 4 to 15 animals).

At the local spatial scale (one km²) at which the within-population study was conducted, local female numbers and group size were strongly correlated. This supports the idea presented in the among-population comparison that female group size is a good index of local female distribution.

While local female distribution may predict territorial male distribution and clustering at the spatial scale of one km², this factor is insufficient to explain territory

clustering at even finer scales. Within each sampling unit, territory clusters occupied a very small part of the area used by females. For example, in the area of highest local female numbers (280 females/ km²) males did not defend dispersed territories covering the whole area; instead they defended small territories, often less than 20 m in diameter, in a single classical lek that covered only a small portion of the area. Bradbury et al. (1989) similarly report that, in sage grouse, female density explains male dispersion only at coarse spatial scales (4 km² and higher); they invoke other selective factors, such as female choice, to explain clustering at finer scales.

In summary, patterns in small-scale variation in male territory clustering within a blackbuck population again suggest that local female distribution can explain a large part of male clustering patterns. Males appear to respond to changes in female distribution at a relatively small spatial scale, i.e., across one km² sampling units. However the extreme degree to which territories are clustered at even finer scales (i.e. within each one km² sampling unit) remains to be explained.

Evaluating Different Hypotheses Of Lek Evolution

Five major kinds of hypotheses have been proposed to explain lek evolution (reviewed in Höglund and Alatalo 1995, Clutton-Brock et al. 1993), although these are not necessarily mutually exclusive.

Hotspot hypothesis

This hypothesis argues that males establish territories in areas of maximal overlap of female ranges (Bradbury et al. 1986). The first explicit model of this process (Bradbury et al. 1986) assumed that the tendency for a female to mate at one hotspot reduced the likelihood of that female mating at other hotspots within her home range. Computer simulations predicted that the male clustering generated by this process should

increase with female home range size and decrease with female density. My findings support the first prediction, that lekking should be associated with large female home ranges, but not the second, that lekking should be associated with low female density.

Variations on the original hypothesis state that females cluster on environmental hotspots and males in turn cluster their territories in accordance with the distribution of females (Gosling and Petrie 1990). According to this version of the hotspot hypothesis, clustering is predicted to increase with local female density. This prediction is supported by the correlation between female group size and clustering across blackbuck populations.

Within a population too, at the scale of a square kilometer, territory density and territory clustering were associated with local female density. However, at finer scales (within the sampling units), the distribution of females did not explain why territorial males occupied only a small part of the area used by females.

Female-choice hypothesis

The female-choice hypothesis (Bradbury 1981) proposes that males cluster their territories because females prefer to mate with clustered males. I did not directly measure female visits or copulation rates at clusters of different sizes. However, the results from this study, that local distribution of females is associated with territory clustering, are consistent with the female-choice hypothesis. The number of estrous females in an area constrains the mating benefits to males holding territories in that area. For example, even when females in a population strongly prefer clustered males, if females in that population are scattered (represented by small female group sizes), the extent of clustering of males will be low. This is because any one location in that population has relatively few estrous females and the benefits from female preference are unlikely to offset the costs of defending a territory in a cluster. Another prediction that was

supported is that female range size should be related to clustering since female ranges should be large enough to include multiple males (so that females can exert their preference for clustered versus dispersed males) (Bradbury 1981, Balmford 1992).

Black hole hypothesis

This hypothesis is one of the most popular explanations for ungulate leks (Clutton-Brock et al. 1993). The black hole hypothesis stemmed from the observation that, in many ungulate populations, females on territories are harassed by non-territorial (usually immature) males and move at random between territories as a result of this harassment. Under such conditions, clusters may act as black holes and may retain females better than solitary territories. Strictly, the black hole process does not depend on male harassment and may act whenever females move randomly, multiple times and to the nearest territory before mating. However, male harassment is thought to be the main factor behind such female movement. Moreover, harassment avoidance has been proposed as an important benefit to female ungulates from moving to and mating on leks (Clutton-Brock et al. 1993, Nefdt and Thirgood 1997). One prediction of this hypothesis is that extreme territory clustering is associated with high harassment rates in the population (Nefdt and Thirgood 1997). One might also expect territory clustering to be associated with more male-biased sex ratios, since harassment levels likely increase with an increase in male numbers relative to female numbers. My findings did not support these predictions since neither harassment rates nor sex ratio was correlated with the level of clustering in a population. However, estimates of rates of harassment, behavioral patterns that are typically brief and variable, were based on relatively small samples (30-60 minute watches of 10 to 15 groups in each population). Therefore, while these data

suggest a lack of a strong relationship with male territory clustering, more work is needed to better estimate the relationship.

Hotshot hypothesis

This hypothesis argues that leks are formed when unpopular males cluster around popular males to intercept females visiting attractive males (Beehler and Foster 1988). No predictions have been made from this hypothesis concerning the general conditions associated with male clustering. Hence, this study cannot be used to evaluate this hypothesis.

Predation hypothesis

Predation is currently not a popular explanation for lekking, but it is evaluated in most reviews of lekking (e.g., Clutton-Brock et al. 1993) since it is an important part of the natural history of most lekking species. Predation was one of the first selective factors proposed to favor clustering (Koivisto 1965). Territorial males were thought to cluster to reduce the individual risk of predation. Females were also suggested to prefer clustered males because they may provide protection from predation while mating. Some studies of lekking ungulates show that males and females pay attention to predation risk when making decisions about territory location and mating respectively (Deutsch and Weeks 1992). In blackbuck, predator density was not associated with the relative clustering of territories. Further, one of the two populations with large classical leks has not experienced wolf predation for about five decades. Thus, in blackbuck, predation is unlikely to be the primary factor maintaining clustering.

Conclusions from evaluating hypotheses of lek evolution

My findings from among- and within- population comparisons of territory clustering provide support to one form of the hotspot hypothesis. They are also consistent

with the female-choice hypothesis although I could not directly test this hypothesis. Predictions from hypotheses based on male harassment of estrous females and predation were not supported.

General Conclusions

Territory clustering varied widely among blackbuck populations from solitary dispersed territories to large classical leks. The wide variation in territorial patterns suggests that lekking is best viewed as one extreme in an array of territory distributions. Using the wide variation in blackbuck mating system, along with a continuous approach, I evaluated the relative importance of a suite of ecological, demographic, and social conditions thought to influence lekking. The main correlate of mating system variation in blackbuck was female group size. This factor explained most of the variation in male territory clustering both among populations and, at a smaller spatial scale, within a population. Lekking, in particular, was associated with large female groups. In contrast to the results from several studies (e.g., Balmford et al. 1993b, Langbein and Thirgood 1989), I found no relationship between territory clustering and population density. My findings suggest that territorial males respond to local patterns in female distribution (represented by group size) rather than population-level patterns when making decisions regarding territory location. Furthermore, male mating behavior in the Texas population was similar to that found in Indian populations with similar female distributions. This observation taken together with the small-scale variation seen within a population suggests that male blackbuck respond in a flexible fashion to immediate conditions in female group size. Finally, while this study suggests that the distribution of females can largely explain the distribution of territorial males, both at the population level and more locally within a population, other selective factors (e.g., female choice, male competition,

male harassment) are likely to shape the sizes and clustering of territories at even finer scales.

The observed variation in territory distribution in blackbuck, along with evidence from other species (Gosling 1986, Thirgood et al. 1999), has implications for the study of mating systems and more specifically, lekking. Previous studies of the ecological correlates of lekking largely take categorical approaches and compare the conditions in lekking versus non-lekking populations. For example, Langbein and Thirgood (1989) report wide variation in territory distributions in fallow deer from solitary territories, and multiple stands to classical leks, but while analyzing mating system patterns this study collapsed the variation into two categories. I suggest that retaining and analyzing the variation yields greater insights into factors that potentially favor the clustering of territories (and thus leks). Such a continuous approach may also be preferable to a categorical approach because separating variable behavior into a few mating system categories can be a matter of judgment. It is likely that intermediate mating behavior that shares features with more than one mating system will, to an extent, be arbitrarily placed in one or another mating system category. This may obscure factors that influence mating system. An alternative may be to ignore intermediate variation. But in species, such as blackbuck and fallow deer, in which this variation is extensive, this will provide an inaccurate picture of factors influencing lekking and, more generally, mating system variation.

Table 2-1. Location, area, and major habitat types for the 9 Indian and one North American* blackbuck populations. Climatic data are 30 year averages, from 1951 to 1980 for the Indian populations (Anonymous 1999) and 1971 to 2000 for the North American population (Anonymous 2002).

Population	State	Location (lat/long)	Normal mean daily temperatures (Max.; Min) ° C	Normal mean annual precipitation (mm)	Area studied (sq. km)	Major habitat types
Tal Chappar	Rajasthan	c.27° 88'N c.74° 58'E	32.9; 17.1	421	7.2	Grassland, shrubland
Velavadar	Gujarat	21° 56'N 72° 10'E	33.6; 21.1	669	34	Grassland, shrubland, mudflats
Savainagar	Gujarat	21° 52'N 72° 01'E	33.6; 21.1	669	8	Shrubland, mudflats
Nannaj	Maharashtra	c.17° 41'N c.75° 56'E	33.8; 20.8	760	5	Grassland
Rehekuri	Maharashtra	c.19° 42'N c.75° 44'E	33.0; 18.5	584	2.2	Forest, grassland
Vanasthali	Andhra Pradesh	17° 21'N 78° 33'E	32.0; 20.2	813	1	Forest
Rollapadu	Andhra Pradesh	c.15° 52'N c.78° 18'E	34.1; 22.1	726	6.1	Grassland
Guindy	Tamil Nadu	13° 04'N 80° 17'E	32.9; 24.2	1334	4	Forest, grassland
Point Calimere	Tamil Nadu	10° 18'N 79° 51'E	32.3; 24.2	1503	12	Forest with grassy openings
Kyle ranch*	Texas	29° 63'N 98° 88'E	26.6; 14.2	823	1.4	Forest with grassy openings

Table 2-2. Estimates (mean±SE) of (1) territory clustering, (2) distribution of males among different social categories, and (3) ecological, demographic and social variables in nine blackbuck populations.

	Nannaj	Point Calimere	Rehekuri	Rollapadu	Savainagar	Tal Chappar	Texas	Vanasthali	Velavadar
Crowding index	11.1	8.2	2	2.8	4.7	39.4	2.2	0.3	37.8
Standardized Clustering Index	3.4	2	1.8	2.2	1.8	4.1	2.1	1.3	4
% males in all-male herds	25±4	48±18	55±5	37±9	42±15	13±6	38±21	36±9	35±0
% males in mixed-sex herds	32±6	18±18	9±4	36±9	25±15	30±5	17±21	52±9	36±0
% males on territories	43±5	33±0	36±3	27±1	33±0	58±1	45±0	12±1	30±0
Habitat openness (percent open habitat)	90±3	61±15	19±5	93±5	89±5	92±5	54±10	4±2	95±5
Habitat homogeneity (mean length of open habitat segments)	9±2	7±3	2±.4	15±3	10±4	15±3	3±1	1±.3	15±3
Resource abundance (mean grass volume)	257±61	104±15	687±216	592±88	64±29	135±16	5±2	1±.1	742±343
Predator density (number of adult wolves per sq. km)	0.4	0	0	1	0.5	0	-	0	0.1
Male density (per sq. km)	7±7	14±11	25±3	10±.2	12±3	31±1	28±12	77±2	8±.2
Female density (per sq. km)	146±4	35±21	44±2	27±2	20±7	48±2	42±13	71±1	17±1
OSR (all females:all males)	2.1±.2	3.3±2.2	1.9±.3	2.6±.2	1.8±.5	1.5±.1	1.7±.5	0.9±.03	2.2±.05
Mean female group size	19±3	11±5	6±1	14±2	6±2	35±4	4±1	3±.3	52±7
Ranging (meters moved per hour)	251±99	109±21	114±29	285±68	303±135	276±66	-	64±19	475±120
Harassment rates (no. of chases per female per hour)	.13±.07	.67±.42	.56±.34	.56±.41	.27±.27	.85±.38	-	0	.12±.09

Table 2-3. Results from correlation analyses on among-population variation in territory clustering. The correlation coefficients (Pearson's r), sample sizes (N number of populations), and significance values (P) from the correlation analysis between the Standardized Clustering Index and various ecological, demographic and social factors are reported. All variables were log-transformed.

Factor	r	N	P
Habitat openness	0.69	9	0.038
Habitat homogeneity	0.74	9	0.024
Resource abundance	0.56	9	0.120
Predation	-0.02	8	0.950
Female density	-0.02	9	0.964
Male density	-0.17	9	0.666
Sex ratio	0.26	9	0.493
Female group size	0.92	9	0.0005
Female ranging	0.74	8	0.033
Male harassment	0.18	8	0.674

Table 2-4. Results from correlation analyses on *within-population* variation in territory clustering. The correlation coefficients (Pearson's r) and significance values (P) from the correlation analysis between the crowding index and various ecological, demographic and social factors are reported. The study area was divided into 14 one sq. km units but only spatial units ($N = \text{eight}$) that contained at least one territorial male were included in the analysis.

Factor	r	P
Habitat openness	0.23	0.58
Habitat homogeneity	0.34	0.4
Resource abundance	0.54	0.16
Female numbers	0.89	0.003
Male numbers	0.72	0.042
Female group size	0.93	0.001



Figure 2-1. Location of the nine Indian study populations. Velavadar in western India was the intensive study site.

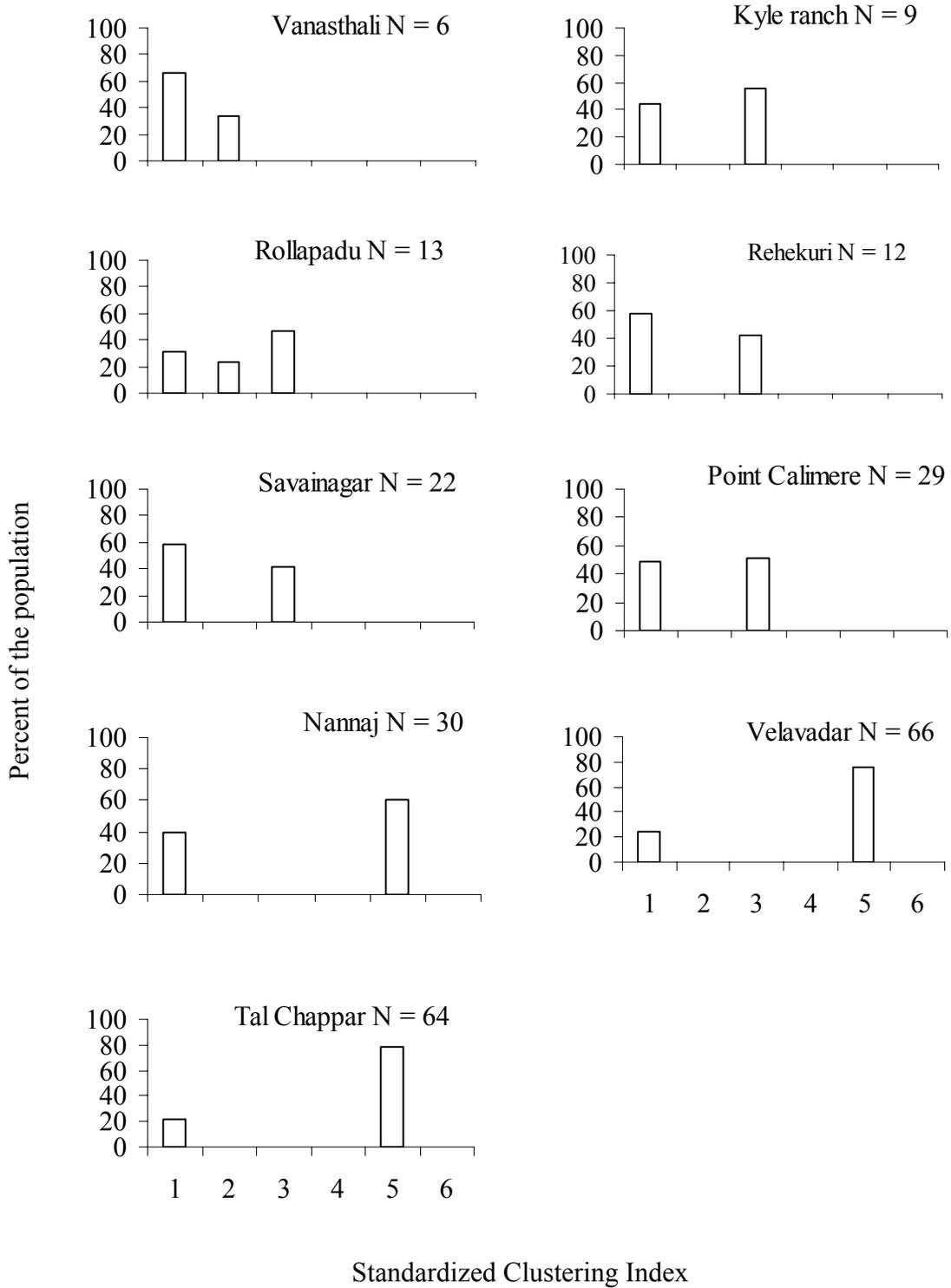


Figure 2-2. Relative frequency of territorial males in standardized clusters of different sizes in 9 blackbuck populations. N represents the number of territorial males in a population

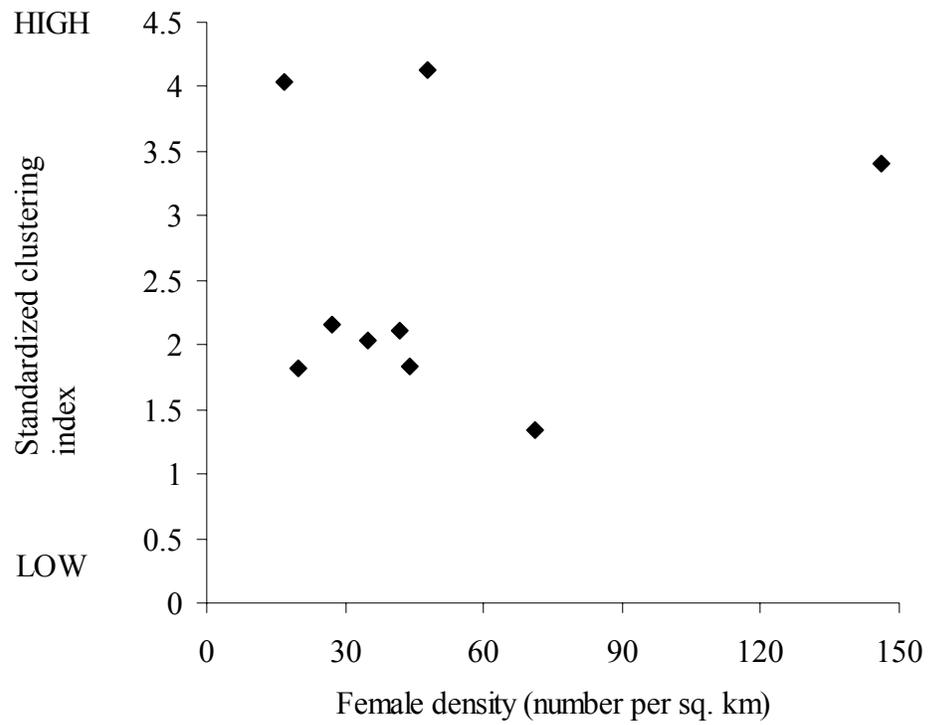


Figure 2-3. Relationship between the degree of territory clustering and female density across blackbuck populations (Pearson's $r = -0.02$, $N = 9$, $P = 0.9$). Each data point represents a population.

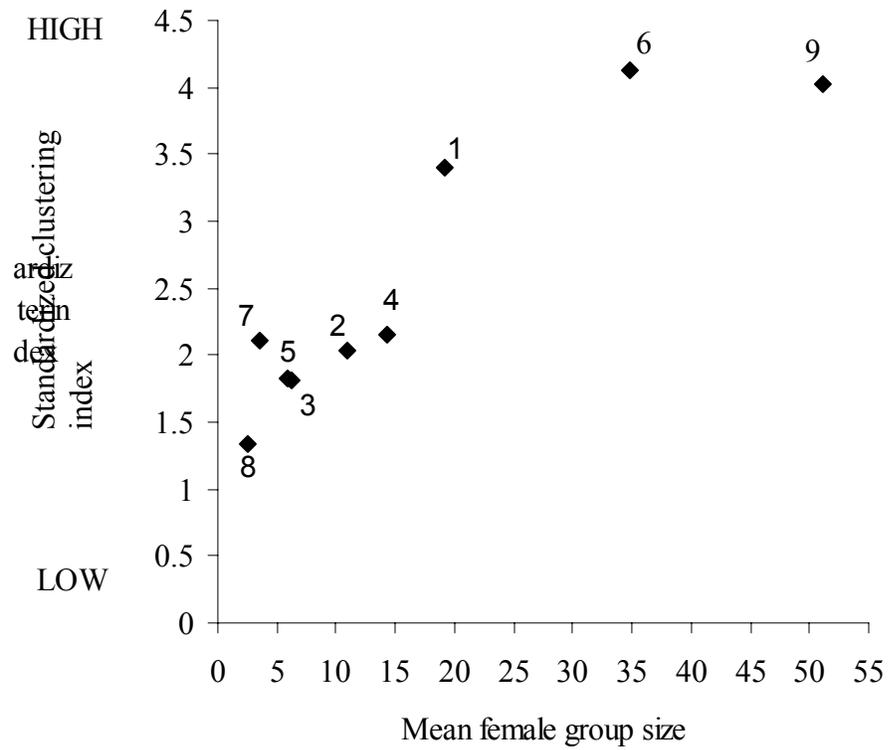


Figure 2-4. Relationship between the degree of territory clustering and female group size across blackbuck populations (Pearson's $r=0.92$, $N=9$, $P=0.0005$). Each data point represents a population (1-Nannaj, 2-Point Calimere, 3-Rehekuri, 4-Rollapadu, 5-Savainagar, 6-Tal Chappar, 7-Texas, 8-Vanasthali, 9-Velavadar).

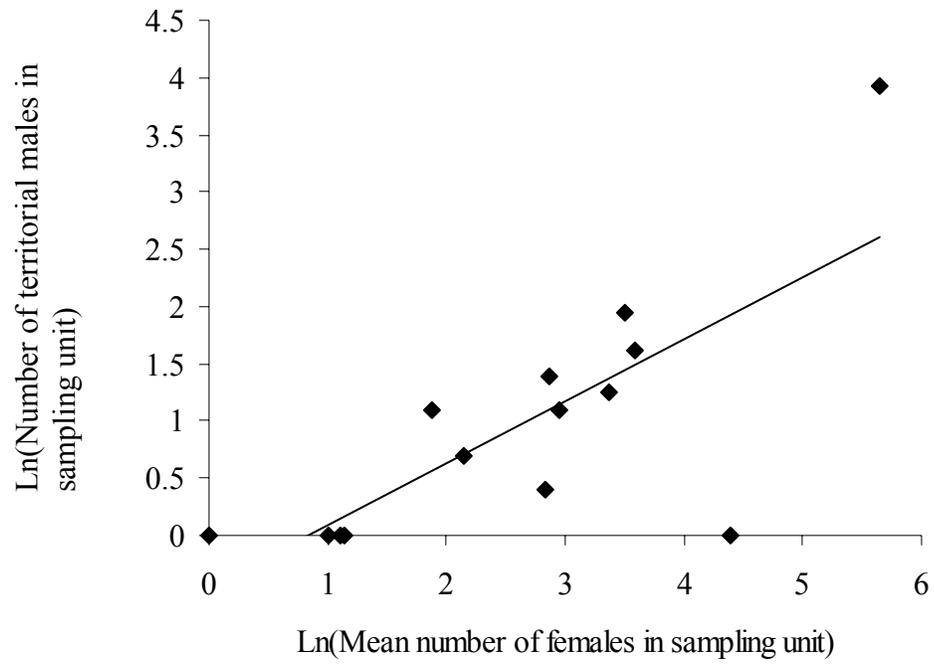


Figure 2-5. Relationship between the number of territorial males and the number of females among 1 sq. km sampling units *within* a population (Pearson's $r=0.75$, $N=14$, $P=0.002$). Each data point represents a sampling unit.

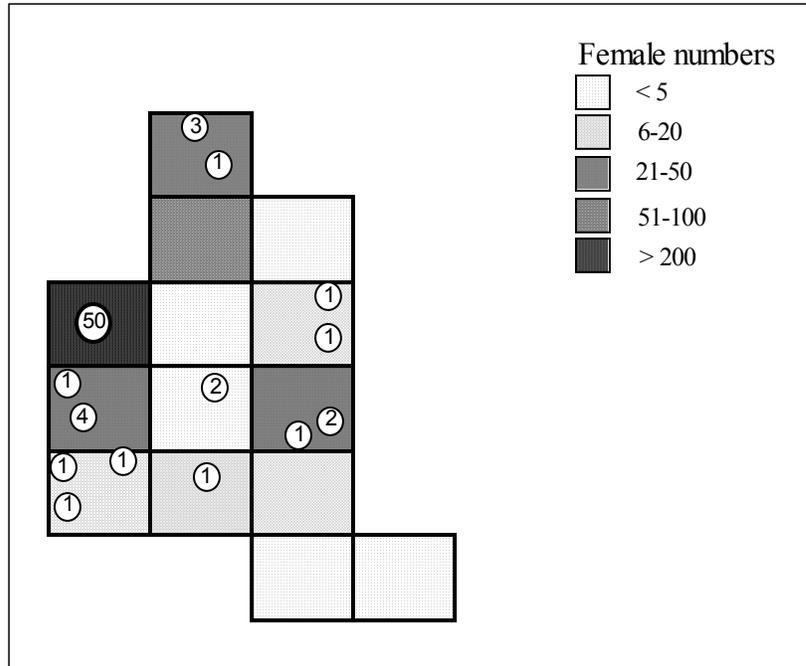


Figure 2-6. Distribution of females (average female numbers) and territory clusters across sampling units in Velavadar, Gujarat. The study area was divided into 14 one km² sampling units. Open circles represent approximate location of territory clusters and numbers within circles indicate number of territorial males in a cluster. Circles do not indicate either the area occupied by a cluster or the distance between clusters.

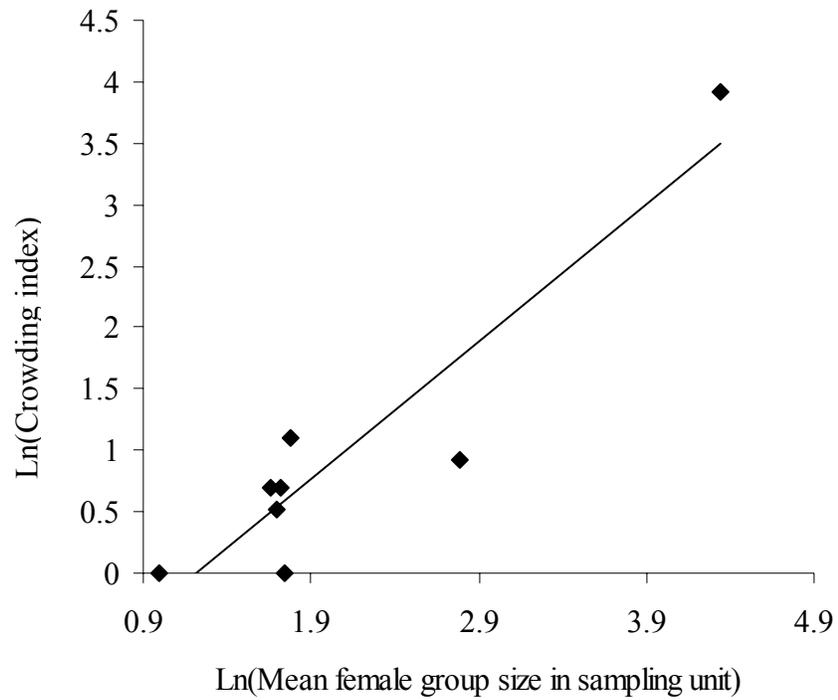


Figure 2-7. Relationship between the crowding index (degree of clustering of territorial males) and female group size among 1 sq. km sampling units *within* a population (Pearson's $r = 0.93$, $N = 8$, $P = 0.001$). Each data point represents a sampling unit.

CHAPTER 3
WHEN SHOULD MALES LEK? INSIGHTS FROM A DYNAMIC STATE
VARIABLE MODEL

Introduction

Lekking is an unusual mating system in which males typically defend small aggregated territories that are the sites of most matings; because these territories do not contain resources attractive to females and there is no paternal care, females are thought to visit leks for the sole purpose of mating (Bradbury 1981). One of the most puzzling aspects of the lek-mating system is the extreme clustering of territories. Why do competing males choose to defend clumped territories and thus incur the costs of aggression associated with such dense aggregations?

The most prominent hypotheses proposed to explain the evolution and maintenance of such extreme clustering of territories can be broadly classified into those that invoke some form of female mating bias and those that do not (Höglund et al. 1993). There are two classes of female bias hypotheses. First, leks may form because females prefer to mate with clustered males (Bradbury 1981, Gibson et al. 1990). Several reasons for a female bias for clustering have been proposed, such as that average male quality may be correlated with cluster size, costs of mate-searching and mate-sampling may decline with cluster size, and predation risk may be reduced in clusters (reviewed in Höglund and Alatalo 1995). Second, the ‘hotshot’ hypotheses propose that females seek out and try to mate with high quality males; leks are formed when less attractive males establish

territories around popular males and intercept females that are traveling to popular males (Beehler and Foster 1988).

Of the hypotheses that do not invoke any female mating bias, one group suggests that leks develop because males establish territories in areas of maximal overlap of either female ranges or resources used by females ('hotspot' models; Bradbury et al. 1986). Another hypothesis that assumes a lack of female preference is the 'black hole' model (Stillman et al. 1993). This hypothesis was motivated by observations from several lekking ungulates that estrous females on leks are harassed by immature males who intrude onto lek territories (Clutton-Brock et al. 1992, Nefdt 1995). This harassment may drive females out of territories or even out of the lek. Thus, females may be forced to move among multiple territories before mating. Based on these observations, the black hole hypothesis assumes that females move among territories at random (in response to harassment) until they eventually mate. Under such conditions, males that are close neighbors are more likely to receive females from each other's territories; thus, males in clusters have a higher mating success than those on solitary territories. Territory clustering is selected for because clusters are better able to retain estrous females than solitary territories, and larger clusters receive and retain more females than smaller ones (Clutton-Brock et al. 1992). The black hole process is not strictly related to harassment; it is applicable under any conditions that create this pattern of female movement among territories. Several other hypotheses also propose benefits to males (rather than to females) from clustering their territories (e.g., a reduction in predation risk; reviewed in Höglund and Alatalo 1995).

Most of the hypotheses described above have been modeled mathematically (Bradbury et al. 1986, Gibson et al. 1990, Stillman et al. 1996), and several predictions of the alternative models are supported by available data. However, many of the predictions (typically involving the spatial distribution of territorial males) are shared by more than one model. For example, both the hotspot and black hole models predict that territory clustering should be positively correlated with female range size (Bradbury et al. 1986, Stillman et al. 1996). Similarly, a female bias model (Bradbury 1981), as well as the black hole model (Stillman et al. 1996), predict that leks will be evenly spaced one female range diameter apart. Further, most modeling efforts have focused on one or a few costs and/or benefits while generating hypotheses about lek evolution. Field studies of leks, however, report that many variables that potentially affect the payoffs to lekking correlate with territory clustering (Höglund et al. 1993, Nefdt and Thirgood, 1997). Clearly, to understand the extreme territory clustering at leks, we need a modeling approach that can incorporate multiple costs and benefits especially those that are measured in different currencies and evaluate their relative importance (as well as interactions among them).

One such approach is dynamic state variable modeling (Clark and Mangel 2000). This modeling approach allows one to predict sequences of optimal decisions through an individual's lifetime. Multiple fitness components can be incorporated while calculating the payoffs to alternative tactics; these components can even be measured in different currencies. Dynamic modeling provides a common framework within which the effects of several potential selective forces and their interactions can be compared. More generally, the value of modeling approaches goes beyond their ability to produce testable

quantitative predictions. Models allow one to examine the consequences of assumptions made about how hypothesized selective factors affect the behavior of interest. One can also identify the general conditions under which these factors are likely to lead to the evolution of that behavior.

I used a dynamic state variable model to examine several hypothesized selective pressures leading to lekking. Like previous theoretical efforts (Gibson et al. 1990, Stillman et al. 1996), I treat lekking as a matter of the clustering of territories and evaluate the ability of multiple selective factors to produce territory clustering. I based the model on lekking ungulates since, in most lekking ungulates, there is considerable variation in mating strategies among and within populations (Höglund and Alatalo 1995). Males may establish territories in clusters of different sizes, may hold resource-based territories, and may also attempt to court and mate with females in mixed-sex herds (groups containing adults of both sexes) (Clutton-Brock et al. 1988, Gosling 1986, Langbein and Thirgood 1989). One can model this variation and ask when lekking is favored.

I assessed the ability of (1) a female mating bias for larger clusters, (2) male harassment of estrous females, and (3) a reduction in predation risk in larger clusters to produce extreme territory clustering (lekking). The decision to focus on these three factors was driven by both the theoretical treatment and the empirical support they have received. For instance, the female bias hypothesis has received much modeling attention (Bradbury 1981, Gibson et al. 1990, Kokko 1997) and is supported by data from several lekking ungulates and birds (Balmford et al. 1992, Nefdt 1995, Alatalo et al. 1992). In this model, I examined the consequences of female mating bias on male territory

clustering without regard to the causes of the bias (e.g., reduced predation risk or male harassment, increased genetic benefits).

The second factor, male harassment, is thought to play a crucial role in the black hole model, arguably the most popular hypothesis about the evolution of ungulate leks (Clutton-Brock et al. 1993, Nefdt and Thirgood 1997, Stillman et al. 1996). I could not address the black hole hypothesis directly because it involves a spatial process which dynamic modeling cannot accommodate. Instead, I modeled male harassment of estrous females, the factor proposed to be most likely to promote random female movement between territories before mating (Clutton-Brock et al. 1992, Nefdt and Thirgood 1997); this movement is the main cause of territory clustering in the black hole model. Harassment can also potentially lead to a female mating bias (for example, females may prefer to mate in larger clusters if they experience less harassment in them). However, I was interested in harassment as an alternative to female preference, and hence examined whether harassment can lead to lekking even in the absence of any female mating bias, as suggested in one form of the black hole model (Clutton-Brock et al. 1992). I also considered the effect of a third factor, predation risk, on optimal male mating strategy because this factor is thought to influence social grouping in ungulates (FitzGibbon and Lazarus 1995, Jarman 1974). Safety from predation was one of the first hypothesized benefits of lekking (Koivisto 1965), but empirical support for this hypothesis is ambiguous. However, predation risk is reportedly lower on several bird leks (Höglund and Alatalo 1995) compared with areas off leks, and some studies of lekking antelopes suggest that males and females are sensitive to predation risk while establishing

territories and making mate choice decisions, respectively (Gosling 1986, Deutsch and Weeks 1992).

To evaluate these three selective factors in a lekking ungulate system, I constructed a dynamic state variable model that predicts optimal male mating decisions. The mating options available to males were to establish a solitary territory, to join territory clusters of different sizes, or to join a mixed-sex herd. I use ‘cluster’ to mean closely-spaced territories with interacting neighbors. The basic model included the major costs and benefits associated with different mating options reported from lekking ungulates. I then modeled each selective factor of interest and compared patterns of territory clustering produced to see whether the model made testable alternative predictions. I also examined interactions between factors and performed sensitivity analyses of several variables built into the basic model, such as foraging yield, the degree of synchrony of estrus, and the energetic costs of maintaining territories in clusters of different sizes.

Methods

The Basic Model

Understanding the trade-offs associated with different strategies and determining the optimal strategy is not always intuitive. The costs and benefits of a strategy may vary with time and depend on the condition (state) of the animal (which may also vary with time). Further, the decision that an animal makes at one time affects its state and thus the decisions that are optimal in the future. Dynamic state variable modeling incorporates these features and allows one to model the sequence of decisions that an animal must make to maximize fitness. The basic approach entails defining a state variable, the alternative tactics that an individual can adopt, the costs and benefits associated with these tactics, the time period of interest, and the time intervals within this period over

which an individual makes a single decision (e.g., a day). The optimal solution is found by iterating backwards through time. In each time interval and for each state, the current reproductive increment and expected future reproduction associated with the alternative tactics are evaluated; the tactic that maximizes overall fitness (current reproduction + expected future reproductive success) is optimal. Further, in each time interval the state of the individual is modified based on the tactic chosen, i.e., the individual gains or loses condition, and the modified state influences the expected future reproductive success of the individual. The basic model thus predicts a sequence of state- and time-specific tactics that maximizes the overall fitness of the individual (Clark and Mangel 2000).

I used energy reserves as the state variable $X(t)$ and arbitrarily defined 24 energy levels. I considered a single breeding season (T) consisting of 15 time intervals, t , each of which corresponded to a day. In each time interval t , the following eight tactics were available: (1) join an all-male *bachelor herd* (a non-reproductive option), (2) join a *mixed-sex herd* (groups with adults and immatures of both sexes), (3) establish a *solitary territory*, (4) establish a territory next to one territorial male, *join 1*, (5) establish a territory next to two males, *join 2*, (6) establish a territory next to three males, *join 3*, (7) establish a territory next to four males, *join 4*, and (8) establish a territory next to five males, *join 5*. The territorial tactics represent a relative degree of territory clustering from low to high, rather than absolute levels of clustering.

Each tactic was associated with a set of costs and benefits. The cost structure was based on data from Uganda kob (*Kobus kob*; Balmford et al. 1992), Kafue lechwe (*Kobus leche kafuensis*; Nefdt and Thirgood 1997), fallow deer (*Dama dama*; Apollonio et al. 1992, Clutton-Brock et al. 1988;), topi (*Damaliscus korrigum*; Gosling and Petrie 1990),

and blackbuck (*Antelope cervicapra*; Isvaran and Jhala 2000;). I considered two kinds of costs: an energetic cost c_i associated with maintaining a particular reproductive tactic and a reduction in foraging yield y_i . Several studies have reported that fighting rates are lower on solitary territories than on leks (Apollonio et al. 1990, Nefdt and Thirgood 1997). Further, one study of the Kafue lechwe (Nefdt and Thirgood, 1997), which measured per capita male fighting rates in leks of different sizes, found that these rates were positively correlated with the numbers of males on the lek. That study also found that males on territories fought more frequently than males in mixed-sex herds. Based on these data, I assumed that the energetic cost, c_i , increased approximately linearly from tactic 2 (mixed-sex herd) to tactic 8 (join 5) (Table 3-1). This energetic (reproductive) cost was zero for tactic 1 (bachelor). Studies of lekking ungulates also report reduced foraging among territorial males compared with males in herds; further, males holding lek territories forage less than males defending solitary territories (Apollonio et al. 1989, Clutton-Brock et al. 1988, Nefdt and Thirgood 1997). Hence, I assumed that foraging yield, y_i , was highest for tactics 1 and 2 (bachelor and mixed-sex herd) and decreased linearly from tactic 2 to tactic 8 (Table 3-1). In each time interval, the energy state (x) dynamics were specified by the equation, $x' = x - c_i + y_i$, where c_i is the tactic-specific energetic cost, y_i is the tactic-specific foraging yield, x is the state variable at time t and x' is the state at $t + 1$. If $x' < 1$, the individual was assumed to die. Thus, in each time interval, depending on the tactic adopted, an individual experienced a gain in state (determined by the tactic-specific foraging yield y_i) and a loss in state (determined by the tactic-specific energetic cost c_i). For example, if in a given time interval an individual with a state of 20 energy units adopted tactic 2, *mixed-sex herd*, then the individual gained five units of energy

through foraging and lost three units of energy due to reproductive, energetic costs associated with that tactic. While all reproductive tactics were associated with both gains (through y_i) and losses (through c_i) in state, *bachelor* males never experienced any loss in state (since c_i , a reproductive cost, is zero for tactic 1).

For simplicity, I assumed that individuals had a low probability of surviving to breed in the next season and thus the expected future reproductive success at the end of the breeding season, Φ , was a small function of the state at that time: $\Phi = 0.01X(T)$. I then sought the reproductive strategy (i.e., series of state- and time-specific tactics) that maximized lifetime mating success. Specifically, I searched for the strategy that gave the maximum expected mating success from time t to the time horizon T , given an energetic state x at time t , by solving the following generalized dynamic state variable equation:

$$F(x, t, T) = \max_i [M_i + s_i F_i(x'_i, t+1, T)],$$

where M_i is the current mating success

associated with tactic i in time t , s_i is the tactic-specific probability of surviving during that time interval, and $F(x'_i, t+1, T)$ is the expected future reproductive success given x'_i , the tactic-specific state at $t+1$. Thus, in each time interval, for each state, the overall fitness associated with each of the eight tactics was first computed. This was done by calculating the current fitness (mating success M_i), modifying the state based on foraging yield and energetic costs, finding the future fitness associated with the modified state, and lastly adding the current fitness to the future fitness to yield the overall fitness. Next, the overall fitness was compared across tactics and the tactic with the highest fitness was chosen as the optimal state-specific, time-specific tactic. The model was iterated backwards through time and the above procedure was repeated for each state in each time

interval to give a series of state-specific and time-specific optimal decisions (the optimal lifetime reproductive strategy).

The current mating success, M_i , in a time interval was zero for bachelors and for the remaining tactics was given by the equation: $M_i = f(t) \times T_i \times B_i \times H_i$. $f(t)$ refers to the number of estrous females in a given time interval. Based on data from lekking ungulates (fallow deer, Clutton-Brock et al. 1988, blackbuck, Isvaran and Jhala 2000), I assumed that the distribution of estrous females over the breeding season showed a unimodal mating peak (represented by a Gaussian function) with the peak at day 8 (Figure 3-1). This assumes that females show some degree of estrous synchrony and by varying the nature of this mating peak one can vary the degree of estrous synchrony. T_i represents male-male competition associated with territory clustering; it takes a value of 1 for *mixed-sex herd* males and *solitary* territorial males, but for the clustering tactics it is inversely proportional to the number of males in that cluster (e.g., *join 1* has a value of 0.5, *join 2* has a value of 0.33). This assumes that males in territory clusters compete for visiting females and suffer a reduction in mating success that is proportional to cluster size (the number of males in a cluster). B_i and H_i represent a female bias for mating in clusters and the harassment of estrous females by intruders, respectively. They are described in greater detail below.

The model predicts a matrix of state-dependent optimal decisions for each time interval. I then iterated forward such that a population of 100 males, whose initial distribution of states followed a normal distribution with mean = 12 and SD = 6 units of energy, was run through time intervals t_1 to T . In each time interval, the males were assumed to adopt the optimal state- and time-specific decisions; the distribution of their

energy states was correspondingly modified and the new distribution entered the next time interval. At the end of the forward iteration, I calculated the percent of the population that adopted each tactic, averaged across time intervals (Mangel and Clark 1988).

Evaluating The Effect Of A Female Bias For Clustered Territories

I defined female mating bias as the probability that a female mates in a cluster of a given size. There are few data available on which to base patterns of female mating bias. Hence, I modeled female mating bias for increased territory aggregation, B_i , in three ways: as linear, accelerating, and saturating functions of cluster size. In each case, I kept the basic model parameters constant (Table 3-1) and the mating probabilities for alternative tactics were scaled so that they summed to 1. Thus, for simplicity, I assumed that each female mated only once per season. In this analysis, predation risk was assumed to be equal for all tactics (survivorship $s_i = 0.97$ for all tactics), and there was no harassment of females (i.e., $H_i = 1$).

I first modeled female bias as a linear increase from tactic 3 (*solitary territory*) to tactic 8 (*join 5*), i.e., $B_i = a + bi$, where i represents tactic 3 to 8. I varied the slope of the linear relationship from 0.01 to 0.04. Thus, female mating bias increases proportionally with cluster size, and since there is a similar increase in male-male competition T_i with cluster size, there is no per capita gain in male mating success. Based on data that suggest that mating success of males in mixed-sex herds is relatively low (Clutton-Brock et al., 1988; Nefdt, 1995) I maintained female bias for this tactic at 0.005.

I modeled a disproportionate increase in female bias for larger clusters using a power function, $B_i = i^b$ where i represents the different reproductive tactics and increases from mixed-sex herd to join 5 ($i = 1$ for *mixed-herd* males, 2 for *solitary territory*, 3 for

join I etc.). The exponent b represents the strength of female discrimination among the alternative tactics and was varied from 1.1 to 2.5 (Figure 3-2).

Finally, I used a logistic function, $B_i = \frac{e^{a+bi}}{1 + e^{a+bi}}$ (where i took values from 1 to 7,

as above), to represent a saturating female mating bias for large clusters. The parameters b , which again represents the strength of discrimination between the alternative tactics, and a (the point of inflection) were varied (Figure 3-3).

Evaluating The Risk Of Predation

I examined the hypothesis that predation may favor lekking if males experience a lower predation risk in larger territory clusters. In the model, predation risk was represented by the tactic-specific probability, s_i , of surviving each time interval. Bachelor and mixed-sex herd males were assigned high survivorship ($s_i = 0.97$) in all runs (assuming that survivorship was maximum in herds due to the advantages of group living). Data on predation risk at leks of different sizes are scarce but information on survivorship in bird and ungulate social groups suggests that survivorship might accelerate with group size (Cresswell 1994, FitzGibbon 1990). Because there are so few data available, I chose to model the change in survivorship across clusters due to predation risk in several ways: 1) as a linear function of cluster size; 2) as an accelerating (power) function (as suggested by some data); and 3) as a saturating function $s_i = \frac{ai}{1 + bi}$ (as expected from dilution of predation risk); i represents tactics 3 to 8. In each case, I varied the magnitude of the selective factor, from a weak effect in which survivorship of territorial males, s , ranged from 0.9 to 0.95 to stronger selection in which s ranged from 0.7 to 0.95. All other parameters were as in Table 3-1, and there was no differential

female mating bias or harassment. I also examined the interaction between predation risk and female mating bias by considering combinations of low and high risk and bias.

For a preliminary test of the model, I searched the literature for data on the probability of females mating with males at different cluster sizes and for cluster size distributions from the same population. I was unable to find suitable data on lekking ungulates. However, one study of a lekking bird (ruff, *Philomachus pugnax*) reports copulation rates over a wide range of clusters (Widemo and Owens 1995). I assumed that copulation rates represented female mating bias for different cluster sizes since female ruffs are reported to move freely among leks and among lek territories (Höglund et al. 1993). Widemo and Owens (1995) found that a logistic regression best described the relationship between overall copulation rates and lek size. I used the equation they presented to calculate female mating bias, B_i , in the model and used the basic model values for the other parameters. Since I was also interested in examining the importance of multiple factors in lek evolution, I then ran the model including female mating bias from Widemo and Owens (1995) as before and included an intermediate level of predation risk (a linear decrease of 3% in predation risk between successive clustering tactics). Including a reduction in predation risk with clustering is likely to be realistic, since several studies of lekking birds report that predation is rare at leks (Höglund and Alatalo, 1995) and one study has shown that predation risk decreases with increasing lek size (Trail 1987). I summarized the model outcomes as the proportion of males adopting different levels of clustering and compared them to data from Widemo and Owens (1995).

Evaluating Male Harassment

I could not directly address the spatial black hole model using dynamic modeling. However, the central tenet of the black hole model is that before mating, females move among territories; the main factor proposed to cause this movement is harassment by non-territorial males from nearby herds (Clutton-Brock et al. 1992). Hence, I used this model to evaluate whether harassment by non-territorial males can produce territory clustering. Unlike female bias, harassment has not been previously modeled. Further, empirical descriptions of variation in harassment across leks of different sizes are unavailable. I modeled harassment as the probability that females arriving at a cluster of a given size were not driven away by intruders, but remained to mate. I examined whether this probability might increase sufficiently with cluster size and thus favor territory clustering. I modeled harassment as a function of intruder pressure and the probability that intruders arriving at a territory cluster were successfully chased away by resident males. Both these factors varied with cluster size. For simplicity, I assumed that tactic-specific intruder pressure (h_i), i.e., the probability that an intruder arrives at a territory cluster of a given size, was directly proportional to the number of territorial males in a cluster and that all territorial males were equally capable of successfully driving an intruder away. Given a basic probability, d , that a territorial male chases an intruder away successfully, I calculated the probability P_i that, in a cluster of i territorial males, an intruder is chased away by at least one male in that cluster (following the binomial

theorem) as
$$P_i = \sum_{n=1}^i \frac{i!}{n!(i-n)!} d^n (1-d)^{i-n}$$

I then calculated H_i , the probability that a female stays to mate in the cluster of territories, as the sum of the probability that no intruders appear and the probability that an intruder that appears is successfully chased away: $H_i = (1 - h_i) + h_i \times P_i$.

The current mating success in a time interval, M_i , was calculated as $f(t) \times H_i \times T_i$; all other parameters were as described in Table 3-1. I varied both intruder pressure (h_i , from 0.1 to 1.0) and the basic ability of a territorial male to successfully drive an intruder away (d , from 0.025 to 0.7).

Sensitivity Analyses

Finally, I conducted analyses of other parameters in the basic model to examine how sensitive model results were to these parameters. I increased and decreased the relative differences among tactics in foraging yield y_i (Table 3-2) and evaluated their effect on model outcomes. The relative energetic cost c_i was varied in a similar manner (Table 2). I modified the distribution of estrous females across the breeding season (the degree of estrus synchrony, Figure 3-1) by manipulating the steepness of the mating peak and evaluated its effect on model predictions. I varied the total estrous female population and evaluated the effect of lower (half the population of the basic model) and higher abundances (double the population of the basic model) on model predictions. Finally, I varied the terminal fitness, Φ , which describes expected reproductive success in future breeding seasons (range: $\Phi = 0.01X(T)$ to $\Phi = 0.2X(T)$ where X is the state in the final time interval T). A small contribution of X to reproduction in future breeding seasons implies that an individual likely survives for only one breeding season irrespective of its condition at the end of that breeding season. On the other hand, a large contribution of X to future reproduction implies that an individual may expect substantial reproduction in

future breeding seasons depending on its condition at the end of the current breeding season. Each variation in a particular parameter in the basic model was run maintaining the original values of the other parameters.

Sensitivity analyses were not performed for all sets of values of female mating bias, predation risk, and harassment. Since there were numerous potential parameter combinations, I ran the sensitivity analyses under the conditions that had the greatest effect in the model, namely non-linear forms of female mating bias. Specifically, I considered three forms of female mating bias (with survival kept uniform and no harassment), a low ($B_i = i^{1.1}$) and a high intensity ($B_i = i^{2.0}$) power function, and an intermediate intensity ($b = 6$) logistic function with the inflection point at *join 3*. All simulations were run in Turbo Pascal 1.5.

Results

The model predicted state- and time-specific optimal tactics. I then used those predictions and the process of forward iteration to predict the proportions of the male population that adopted the different tactics in each time interval. Here I discuss both the state-dependent decisions and the population level predictions (i.e., the percentage of males that adopted each alternative tactic, averaged over the breeding season).

Most of the model runs resulted in the expression of not more than two alternative mating tactics. When the basic model was run setting female mating bias equal for all reproductive tactics, survivorship equal for all tactics, and removing male harassment, joining a mixed-sex herd was the optimal tactic for all states at all times. This is because since female bias was the same for all reproductive tactics (*mixed-sex herd*, and all territorial tactics), the current mating success in a time interval was highest for *mixed-sex*

herd males and *solitary territory* males. Males in clusters of different sizes suffered a reduction in mating success (T_i) proportional to the size of the cluster. Further, *mixed-sex herd* males performed better than *solitary territory* males since they experienced a higher foraging yield and a lower energetic cost (Table 3-1). Territorial options were optimal only when specific benefits were included, such as a female mating bias for an increased clustering of territories. Of the three selective pressures evaluated, namely female mating bias, predation risk, and male harassment, female mating bias had the greatest effect in this model. Below, I describe the patterns in territory clustering generated by manipulating each of these factors.

Female Mating Bias

I considered three alternative forms of female mating bias: linear, accelerating, and saturating increases in mating probability with cluster size. When female bias was modeled as a function increasing linearly with clustering, clustered territories were never the optimal decision. The tactic with the highest fitness for all states at all times was either to join a *mixed-sex herd* or to establish a *solitary territory*. This is because the increase in mating benefits was insufficient to offset the costs of mate competition (T_i), lowered foraging yield, and energetic costs in clustered territories.

However, when female mating bias accelerated with clustering ($B_i = i^b$), clustering was produced at relatively low levels of non-linearity (Figure 3-2). At the lowest level of non-linearity, $B_i = i^{1.1}$, holding *solitary territories* was the optimal tactic for all states in all time intervals (Figure 3-2A). As the rate of acceleration increased (i.e., b increased), clustering was predicted. Initially, only large clusters (tactic *join 5*) were predicted in the optimal decision matrix, the proportion of the male

population adopting clustering was low (Figure 3-2B), and the rest of the population held solitary territories. With further increases in b , a mixture of clustering tactics appeared; the majority of the population joined large clusters, and a small proportion joined small clusters (Figure 3-2C). As the exponent was increased further, extreme clustering (*join 5*) was the dominant mating tactic. Males with low energy states joined *bachelor* herds, probably because this allowed them to substantially increase their energy states through high foraging yields. An increased state would then allow them to adopt extreme clustering (tactic *join 5*) in the future, a tactic which yielded the greatest mating benefits but which also had high costs. Under high non-linear female bias, mating benefits are disproportionately high in large clusters, but they are very low in small clusters and do not compensate for the associated costs. This may explain why less than 5% of males adopted territorial tactics other than extreme clustering, *join 5* (Figure 3-2D).

When female mating bias showed a saturating relationship with male clustering (B_i followed a logistic function), patterns similar to those described for the power function were predicted. When females distinguished among tactics only weakly (low b), holding a solitary territory was the dominant tactic. As b increased, clustering also increased in frequency. However, the optimal cluster size depended on the point of inflection of the curve describing the relationship between female mating bias and cluster size. In general, the tactic succeeding the inflection point predominated (Figure 3-3). For example, when the inflection point occurred at *join 2*, *join 3* was the dominant tactic. Tactics beyond the inflection point were associated with diminishing mating benefits and hence, were not optimal.

In several model runs, a mixture of clustering tactics was predicted both within a time interval and across time intervals in a breeding season. This variation in clustering was associated both with energy state and time in the breeding season. The model predicted that males with relatively high energy states should adopt extreme clustering, while joining bachelor and mixed-sex herds and joining smaller clusters were the main outcomes for males with lower energy states. Further, males with higher states were predicted to adopt clustering tactics earlier in the breeding season than other males. These model outcomes can be explained by the relative costs of the different tactics. Joining larger clusters may yield higher mating benefits, but males also experience larger costs. Males with low energy states risk the possibility of dying if their energy state after incorporating energetic costs falls below zero. A better strategy might be to increase state by initially adopting low cost tactics, such as joining bachelor or mixed-sex herds, and later adopting costlier tactics that yield high mating benefits (such as extreme clustering). Indeed, one of the model outcomes was that males with lower energy states adopted high levels of clustering progressively, as the breeding season unfolded. For example, when female mating bias increased steeply with cluster size ($b = 2.0$), in the first four time intervals of the breeding season, clustering tactics were optimal only for males with very high energy states (greater than 20 units); for all other males, joining a bachelor herd was optimal. As the breeding season progressed, males with lower energy states adopted clustering; however, males with very low energy states (less than 3 units) rarely adopted clustering tactics since they were too costly. Furthermore, males who initially adopted highly clustered mating tactics later adopted less costly tactics largely because they fell in state because of large energetic costs associated with extreme clustering.

I preliminarily tested model predictions concerning female mating bias using data from ruff leks (Widemo and Owens 1995). When I ran the model using female mating bias from this study and using the basic model values for other parameters, model results reflected a large part of the variation in clustering seen in the field (Figures 3-4A and 3-4B). The model predicted that males should show intermediate clustering (*join 2*) and that none should adopt low or high levels of clustering. In the field, more than 50% of territorial ruffs were in leks of intermediate size. However, a significant proportion of lekking males were found on large leks, a pattern not predicted by the model. When I included a second factor, predation risk, model predictions from this simulation were very similar to lek size distributions seen in the field (Figure 3-4C).

Predation Risk

I modeled survivorship as linear, accelerating, and saturating functions of cluster size. When survivorship increased linearly with cluster size, clustering was predicted only when the slope was relatively high (0.05, 5% increase in survivorship between successive cluster sizes). Further, the extent of clustering was low; in the above example (slope = 0.05), 70% percent of the population, averaged across time intervals, held *solitary territories*, while only 19% adopted the *join 5* tactic (the rest of the population joined *bachelor* herds). Intermediate clustering tactics were not seen, largely because the benefits from increased survivorship did not exceed the costs associated with defending territories in clusters.

Unlike female mating bias, non-linearity in survivorship did not have a great effect on model predictions. When the range of survivorship probabilities was small (e.g., 0.90 to 0.95) clustering options were never optimal even when survivorship accelerated steeply from solitary territories to large clusters. Clustering was seen only when the range

in survivorship probabilities was large (i.e., 0.70 to 0.95). Within this range, increasing the rate of acceleration (i.e., the exponent of the power function) did not produce significant increases in the proportion of the male population adopting clustering tactics. This proportion was never more than 20%. Of the clustering tactics, extreme clustering (*join 5*) was the only optimal tactic predicted. The saturating survivorship function produced similar results. One reason why non-linearity in survivorship did not have the dramatic effect that non-linear female bias did on the model is probably that the difference in survivorship probabilities between low and high clustering tactics was never as large as the differences in female mating bias. However, the limited data on survivorship available in the literature suggest that the larger ranges in survival used in this model greatly exceed natural variation in survivorship.

Predation did, however, significantly modify patterns of clustering produced by other factors. Even a linear increase in survivorship produced clustering at low levels of female bias for all functions used to model female bias. For example, when female mating bias was modeled as a weakly accelerating function ($B_i = i^{1.1}$) and predation risk was equal for all tactics, holding a *solitary territory* was the dominant tactic and clustering was not seen. However, if this female bias function was combined with linearly increasing survivorship (slope = 0.03), 34% of the male population adopted the *join 5* tactic (Figure 3-5). This is because although each selective factor was relatively weak, the combined overall benefit to clustering was sufficiently high to favor clustering.

Male Harassment

I modeled the effect of male harassment of females on male mating strategy as the probability that a non-territorial male would enter a cluster to harass females, h_i , and the probability that at least one resident male would exclude that male, d , and thus permit

females to mate. Since data on harassment patterns in leks of different sizes are lacking, I assumed these probabilities and thus, the overall probability of females mating, were proportional to the number of males in the cluster. Male harassment never produced clustering. Establishing a solitary territory was always the optimal strategy.

Sensitivity Analyses

I conducted sensitivity analyses of five parameters in the basic model: foraging yield, energetic cost, terminal fitness, abundance of estrous females, and the variance in the distribution of estrous females over the breeding season. These analyses were conducted for three non-linear patterns of female mating bias B_i (see Methods). When female mating bias was weakly non-linear, manipulations of basic parameters did not affect model results. Therefore, the results presented below refer to sensitivity analyses conducted with relatively stronger non-linear functions of female mating bias. In general, changes in basic parameters did not result in qualitative changes in model outcomes; for example, clustering never disappeared following a sensitivity manipulation. Further, with few exceptions, parameter manipulations had only small effects on the patterns of male clustering.

Two manipulations that yielded significant changes in clustering patterns were a reduction in the differences between tactics in foraging yield and changes in estrus synchrony. When I reduced differences in foraging yield between successive tactics, the proportion of the male population adopting clustering tactics increased, especially extreme clustering (*join 5*) which increased to 0.6 from 0.35. In contrast, when differences in foraging yield were increased, the predicted pattern of clustering was similar to that produced under the original assumptions.

Increasing the synchrony of estrous females (Figure 3-1) resulted in an overall reduction in the reproductive activity of males. The proportion of *bachelors* increased by 20% and was matched by a decrease in the proportion of *solitary* males. This was largely because when synchrony was increased, there were no estrous females in the first two and the last two time intervals. Consequently, no mating tactic was chosen and joining a bachelor herd was the optimal tactic for these time intervals for all states. When females were distributed more uniformly through the breeding season (lower synchrony), the proportion of *join 5* increased by 20% and the proportion of *solitary* males similarly decreased compared with the original model.

The three other variables manipulated, namely energetic cost, female abundance and terminal fitness, had small effects on model outcomes. Increasing differences between tactics in energetic cost resulted in a slight decrease in the proportion of males adopting the costly tactic *join 5*. Halving the total female population resulted in a small decrease in the proportion of males adopting territorial tactics and a corresponding increase in bachelor males. Finally, increasing terminal fitness (expected reproductive success in future breeding seasons) reduced the proportion of the male population adopting more costly clustering tactics in the last few time intervals of the breeding season. This is because costly clustering tactics reduced the state of the individual thereby reducing expected future reproductive success (since terminal fitness was a function of the state in the final time interval). Therefore, less costly tactics were optimal towards the end of the breeding season. However, the reduction in more extreme clustering tactics was relatively small.

Discussion

I used a dynamic optimization approach to evaluate the relative merits of three alternative explanations for the evolution of lekking. The usefulness of this model comes not solely from its ability to generate testable predictions. The real strength of such modeling approaches is to clarify (1) the conditions under which a putative selective pressure is likely to favor the evolution of territory clustering and (2) the consequences of assumptions one makes about how a particular factor affects male territory clustering. I evaluated the potential of female mating bias, predation, and male harassment as selective pressures in lek evolution. The model generated quantitatively and qualitatively different predictions for these three factors. I found that female mating bias had the greatest potential to generate high levels of clustering. Male harassment never produced clustering in the model, while predation risk produced very limited clustering but may be important in conjunction with other factors.

Female Mating Bias

One of the most popular hypotheses of lek evolution suggests that lekking has evolved due to a female bias for mating with males in aggregations (Alexander 1975, Bradbury 1981, Gibson et al. 1990). I evaluated this hypothesis by manipulating female mating bias, defined as the probability that a female will mate in a cluster of a given size. This parameter had the greatest effect on male decisions and the shape that it took greatly influenced the outcome of the model. Linear functions did not produce clustering largely because when female mating bias was translated into mating benefits per male, there was no per capita increase in benefits with cluster size. However, when modeled as power and logistic functions, even small amounts of non-linearity produced extreme clustering (large leks).

When I assumed that female mating bias did not increase exponentially, but included a pattern of diminishing returns at some point, the model predicted that cluster sizes just past the point of inflection should predominate in the population (Figure 3-3). Thus, variation in this threshold among species or populations may explain observed variation in maximum cluster size.

The model highlights the importance of explicitly specifying the shape of the relationship between a putative selection pressure (here, female mating bias) and cluster size since the same parameter modeled in different ways led to very different patterns in territory clustering or did not produce clustering at all. However, quantifying female mating bias in the field is difficult since it may not be possible to collect data over a wide range of cluster sizes. In many species, lek size distributions are greatly skewed so that most territorial males are either on large leks or in small clusters and intermediate cluster sizes are often not seen in the field (Deutsch 1994b, Nefdt 1995). Interestingly, such lek size distributions are consistent with the predictions of the dynamic model for certain forms of underlying female mating bias (Figures 3-2B and 3-2C). Thus, quantifying the underlying bias for clusters of different sizes may only be possible by experimentally providing females with an array of clusters (including intermediate clusters) to assess.

For one study on birds in which these data are available (ruffs; Widemo and Owens 1995), the dynamic model predicted a large part of the variation in the size of territory clusters that is observed in the field, even though the model was run using crude estimates for all parameters other than female mating bias. Model predictions when female bias alone was incorporated predicted the large proportion of intermediate lek sizes observed, but did not predict the large leks recorded in the field (Figures 3-4A and

3-4B). Including an additional benefit of clustering (a linear decrease in predation risk with cluster size) led to predictions very similar to lek size distributions in the field and included large leks (Figure 3-4C). It is currently believed that, although predation risk may often decrease with increased territory clustering in lekking birds, it is unlikely to be a primary factor in lek evolution (Höglund and Alatalo, 1995). While supporting this conclusion, the modeling exercise using data from ruffs emphasizes the importance of studying multiple selective factors, including those that appear to have little effect when acting alone, since these factors could have a dramatic effect in combination with other factors.

Non-linear patterns of female bias, such as those reported for ruffs, have been documented for several lekking species (Alatalo et al. 1992, Lank and Smith 1992). For example, Alatalo et al. (1992) report that per capita male mating success of black grouse increased with lek size up to around 10 males and then reached a plateau. Similar patterns have been reported in the Uganda kob (Balmford et al. 1992, but see Deutsch 1994b). Such data suggest that non-linear patterns of mating bias are not uncommon in lekking species and that female mating biases for larger clusters may in fact be a significant factor in the evolution and maintenance of lekking as this dynamic model indicates.

What might explain these non-linear patterns in female bias? The shape of the relationship between female mating bias and cluster size may be governed by the way in which the payoffs to females scale with cluster size. A variety of costs and benefits to female choice between leks has been proposed, but few data exist on how costs and benefits to females vary with cluster size (Clutton-Brock et al. 1993, Höglund and Alatalo 1995). The proposed benefits to females from mating in larger clusters include

reduced predation risk, increased mate quality, and a reduction in harassment and courtship disruption (Alatalo et al. 1992, Clutton-Brock et al. 1993, Gibson et al. 1990, Nefdt and Thirgood 1997). A reduction in the costs associated with mate searching is suggested to favor the clustering of territories (Bradbury 1981), while an increase in travel costs to a few large leks might select against clustering (Gibson et al. 1990). The results from the dynamic model emphasize the importance of quantifying the nature of the relationship between these hypothesized costs and benefits and cluster size.

Another factor that is thought to be important in female choice in lekking species is mate-choice copying (Deutsch and Weeks 1992, Gibson et al. 1990, Höglund and Alatalo 1995). Mate-choice copying has largely been studied in the context of sexual selection within a lek with several authors (Deutsch and Weeks 1992, Höglund and Alatalo 1995) suggesting that copying can increase the variance in male mating success within a lek. Copying could potentially also increase variance in male mating success across leks. For example, if a few females display an initial, small, and disproportionate bias for mating in larger clusters, this weakly non-linear pattern could be significantly enhanced through copying by other females. Currently there are few data on patterns in copying across leks of different sizes.

Predation Risk

The predation hypothesis proposes that a reduction in predation risk to lekking males outweighs the costs associated with competition among clustering males. I modeled predation risk in three ways: as a simple linear increase in survivorship from solitary territories to the tactic *join 5*, as an accelerating function, and as a saturating function. Interestingly, in contrast to female mating bias, non-linearity in predation risk did not lead to extensive clustering. The parameter predation risk, whether modeled as

linear or as non-linear functions, produced clustering only when differences in predation risk among behavioral options were high (e.g., a difference in survivorship probabilities of 25% or more between solitary territories ($s_{solitary} = 0.7$ in each time interval) and clusters of 6 males ($s_{join5} = 0.95$ in each time interval)). Data on predation levels in ungulate populations suggest that such high levels of predation are very unlikely. For example, in Thomson's gazelles, *Gazella thomsoni*, the average probability of being killed by predators ranges from 0.0004 to 0.0006 per day (survivorship is 0.9996 to 0.9994; calculated from Borner et al. 1987). Likewise, in blackbuck, the average probability of being killed per day varies from 0.00008 to 0.0002 (calculated from Jhala 1993).

Data on the anti-predatory benefits of clustering are ambiguous. For example, in a Uganda kob population, there was no difference in per capita predation risk on and off leks (Balmford and Turyaho 1992), and risk may in fact be higher on leks since predators may view leks as a reliable source of prey. Similarly, studies of topi leks report that hyenas hunt disproportionately more frequently at leks than at solitary territories (Gosling and Petrie 1990). However, observational and experimental data from another Uganda kob population suggest that males pay attention to predation risk while establishing territories and prefer areas with greater visibility (Deutsch and Weeks 1992). Predation risk could also potentially affect female mating decisions. This model, which is focused on male mating decisions, did not explore this influence.

In the model, predation risk had interesting effects when it interacted with female mating bias. In general, combining a female bias for larger clusters with an increase (even small) in male survival in larger clusters increased the proportion of males adopting more

extreme clustering options. Furthermore, female mating bias functions with low levels of non-linearity that did not generate clustering when acting alone, produced clustering in combination with predation risk. Thus, the model emphasizes the importance of studying interactions among factors when testing hypotheses about lek evolution.

Male Harassment

I modeled male harassment of estrous females because it has been highlighted in recent studies as a primary factor in lek evolution (Clutton-Brock et al. 1993, Nefdt and Thirgood 1997, Stillman et al. 1996). It has been proposed as the factor most likely to cause female movement between territories, this movement in turn is necessary to produce clustering in the black hole model (Stillman et al. 1993). Unlike female bias, harassment has not been extensively modeled. I modeled male harassment of estrous females as the probability that a female entering a male's territory is not driven away by harassing intruders but remains to mate with him. I was especially interested in assessing whether male harassment of estrous females could favor clustering in the absence of any kind of a female mating bias for clustering. In the model, harassment did not produce clustering of territories. This is because of the way in which the two parameters, the probability of an intrusion, and the probability of at least one territorial male successfully driving away the intruder, scaled with cluster size. These two components of male harassment increased and decreased proportionately with cluster size. A disproportionate increase in the chance of an intruder being successively driven away in larger clusters may have produced clustering. However I did not have any a priori expectation of such a disproportionate increase.

One mechanism that might generate such a disproportionate increase in intruder repulsion is cooperation between males in driving away intruders, so that two males in a

cluster acting together are more likely to drive away an intruder than two males individually. Such cooperation between territorial males has not been systematically investigated in ungulate leks. However, studies of other territorial systems report that territory owners are often less aggressive towards neighboring territorial males than towards strangers (the 'dear enemy' phenomenon, e.g., Beletsky and Orians 1989). These studies suggest that males may favor neighbors over strangers since remaining among neighbors whose strengths have already been assessed may minimize the costs of aggression and territory defense. Observations of a lekking antelope suggest that the 'dear enemy' phenomenon may operate on ungulate leks too (Isvaran, unpublished data).

During prolonged fights between a territorial male blackbuck and an intruder, the fighting males typically moved out of the owner's territory and crossed into neighboring territories. When such a fighting pair continued to remain in a neighboring territory, the neighboring owner usually attacked the intruder. Following such an attack, the intruder usually ended the interaction and left the area. Male harassment of estrous females could also produce clustering if fewer intruders appeared at larger clusters. Data from antelope leks do not support this option since intrusions reportedly increase with cluster size (Nefdt and Thirgood 1997). According to the dynamic model, clustering in response to harassment is most likely when intruder pressure decreases with lek size and the probability of driving away intruders increases disproportionately with lek size, an unlikely combination. Thus, I conclude that male harassment of estrous females is unlikely to be the primary factor favoring the evolution of leks because it is unlikely to show a strongly non-linear relationship with cluster size. However, the black hole model does not rely solely on this factor in its argument about lek evolution; male harassment is

only one of several factors that can facilitate the black hole process by which females are retained better in larger clusters (Stillman et al. 1993, 1996).

Sensitivity Analyses

I manipulated the basic parameters of the model to assess the sensitivity of model predictions to these parameters. None of the manipulations I performed produced large qualitative changes in model outcomes. For example, none of them produced clustering when clustering was never the optimal tactic in the original model result. Similarly, clustering never disappeared following manipulations, although the level and extent of clustering sometimes changed. These results suggest that the parameters manipulated are unlikely to be primary factors underlying lek evolution. These results also suggest that the main model results are robust and do not rely on a restricted set of parameter assumptions.

Two particular manipulations resulted in significant changes in model outcomes. Reducing the difference between tactics in foraging yield (i.e., reducing the cost of clustering) resulted in a large increase in clustering. This suggests that males in habitats where forage is abundant and accessible are more likely to defend territories in large clusters than males with less access to forage. Lekking males usually forage close to their territory cluster and likely compete with other males in the cluster for forage. Hence, resources may constrain clustering. This argument is supported by results from a study of a lekking bird (capercaillie, *Tetrao urogallus*) which found that lek size and spacing was regulated by the quality of the habitat around each lek (Wegge and Rolstad 1986).

The second manipulation that had a relatively large effect on the predictions of the model was a reduction in estrus synchrony. When females were distributed more uniformly across the breeding season (while keeping the length of the breeding season

the same), extreme clustering increased and fewer males adopted solitary territories. One explanation for this pattern in the model is that a reduction in synchrony was associated with an increase in time intervals with a large number of females (Figure 1). Thus, the mating benefits to males adopting *join 5* were high enough to offset the large costs of extreme clustering in many more time intervals, rendering extreme clustering an optimal tactic in more time intervals. Previous models of mating system evolution have also predicted that in systems where males do not defend either females or important resources used by females, a decrease in estrus synchrony should favor leks.

Conclusions

The dynamic model produced distinct sets of predictions for the three selective factors that I evaluated. Female mating bias generated the greatest levels of territory clustering. Furthermore, empirical evidence suggests that it may naturally have the forms and strengths of non-linear relationships with cluster size that were essential to generate clustering. More generally, one of the most striking results of the model exploration is that lek-like clustering is consistently produced when there are certain non-linear increases in mating benefits associated with clustering. From this I conclude that any factor that generates such a relationship can potentially explain the evolution of lekking. This model also highlights the importance of studying multiple factors and their interactions. Factors in interaction predicted male mating decisions that were often different from predictions generated by the same factors acting alone.

Although this model is based on lekking ungulates, its results are applicable to other taxa, especially those that show similar lekking behavior (e.g., birds). Further, the structure of the basic model is general and the only factors that are based on data from ungulates are the costs to clustering. Similar increases in costs with cluster size have been

reported in lekking birds (Alatalo et al. 1992, Höglund et al. 1993). Of the three selection pressures evaluated, harassment of estrous females is the only one that is considered less important in other species, (e.g., highly mobile taxa like birds; Höglund and Alatalo 1995).

Nevertheless, this model is a simplification of natural lekking systems. Clustering is a phenomenon in which a male's behavior depends on that of other males in a population. For example, even if extreme clustering is optimal for a male of a given state, he may not be able to adopt it if there are no large clusters available for him to join. This is a system in which a game approach potentially describes the outcomes of male decision-making processes more realistically. However, adding a game component to this model greatly increases the complexity of the model and of inferences drawn from such a model. With this straightforward dynamic model that included some major costs and benefits I have been able to produce patterns in clustering similar to those seen in natural populations. I have also been able to evaluate the potential role of different factors in lek evolution and produce predictions that vary both qualitatively and quantitatively.

Table 3-1. Costs associated with each tactic.

Tactic, i	Energetic cost of tactic, c_i	Foraging yield y_i	Male competition T_i
Join all-male herd	0	5	0
Join mixed-sex herd	3	5	1
Solitary territory	4	4	1
Join 1 territory	4	3	0.5
Join 2 territories	5	3	0.33
Join 3 territories	5	2	0.25
Join 4 territories	6	2	0.2
Join 5 territories	6	1	0.17

Table 3-2. Parameter values used in sensitivity analyses of energetic cost and foraging yield. For each analysis the differences in parameter values among tactics were either increased or reduced compared with those in the basic model.

Tactic, i	Energetic cost of tactic c_i		Foraging yield y_i	
	Reduced differences	Increased differences	Reduced differences	Increased differences
Join all-male herd	0	0	5	6
Join mixed-sex herd	3	2	5	6
Solitary territory	4	3	4	6
Join 1 territory	4	4	4	5
Join 2 territories	4	5	4	4
Join 3 territories	5	6	3	3
Join 4 territories	5	7	3	2
Join 5 territories	5	8	3	1

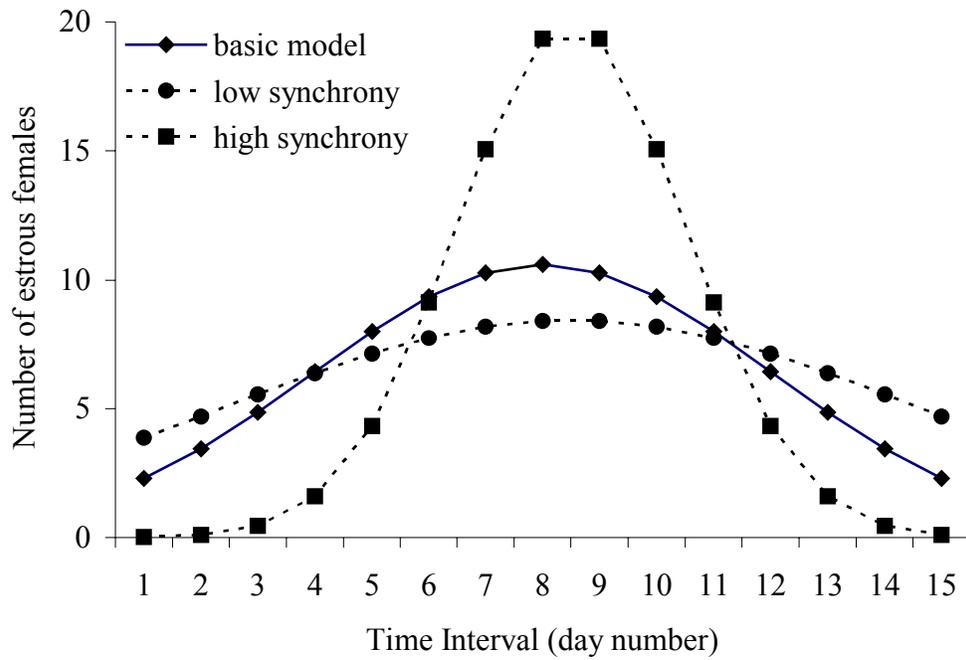


Figure 3-1. The number of estrous females (total = 100) in each time interval of the breeding season ($t = 1$ to 15 days). The distribution with peak at day 8 and with 50% of females in estrus during the mid five days (mid-season) of the breeding season was used in the basic model. The other two distributions representing low estrus synchrony (40% of the estrous female population appearing during the mid-season) and high synchrony (75% of estrous female population in the mid-season) were used in the sensitivity analyses.

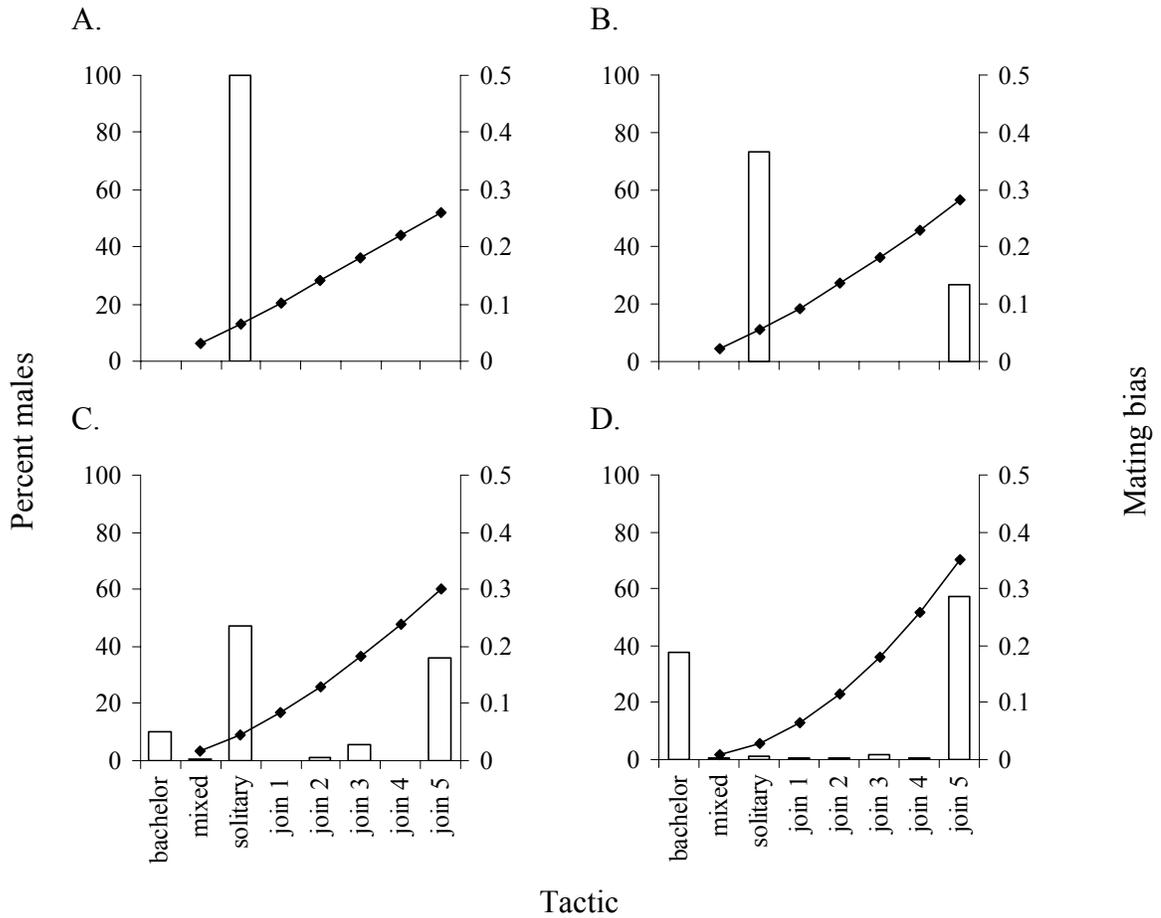


Figure 3-2. Model predictions of male mating strategies when female mating bias, B_i , was modeled as a power function, $B_i = i^b$, where i is mating tactic. Predictions are summarized as the percentage of the male population that follows a particular tactic (bar graphs); percentages are averaged across time intervals. The tactic-specific values of B_i are represented by line graphs. A. exponent, $b = 1.1$; B. exponent, $b = 1.3$; C. exponent, $b = 1.5$; D. exponent, $b = 2.0$.

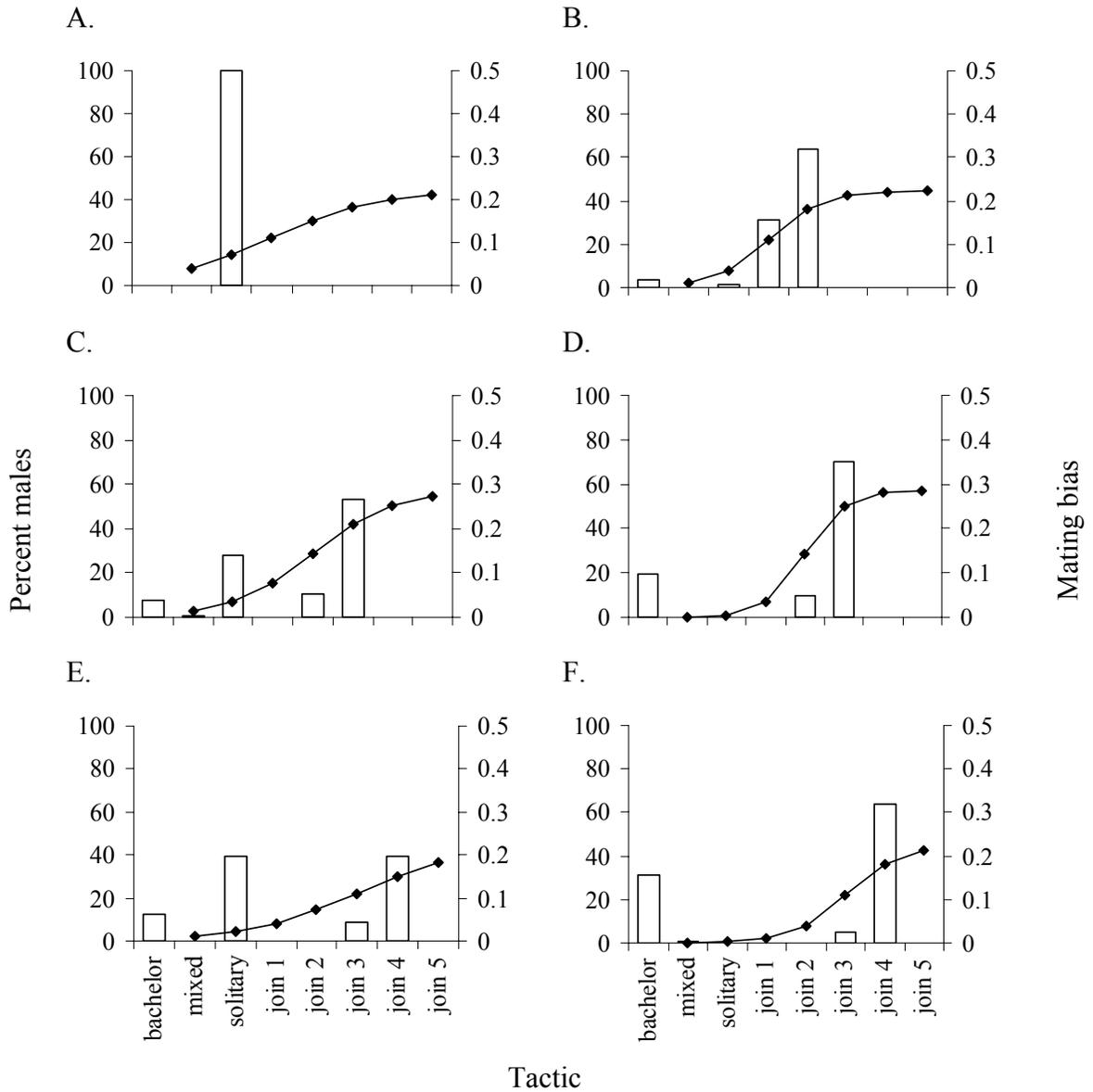


Figure 3-3. Model predictions when female mating bias B_i was modeled as a logistic function. The tactic-specific values of B_i are represented by line graphs. Predictions are summarized as the percentage of the male population that follows a particular tactic (bar graphs); percentages are averaged across time intervals. A. Point of inflection at tactic *join 1*, strength of bias, $b = 6$; B. Point of inflection at tactic *join 1*, strength of bias, $b = 12$; C. Point of inflection at tactic *join 2*, strength of bias, $b = 6$; D. Point of inflection at tactic *join 2*, strength of bias, $b = 12$; E. Point of inflection at tactic *join 3*, strength of bias, $b = 6$; F. Point of inflection at tactic *join 3*, strength of bias, $b = 12$.

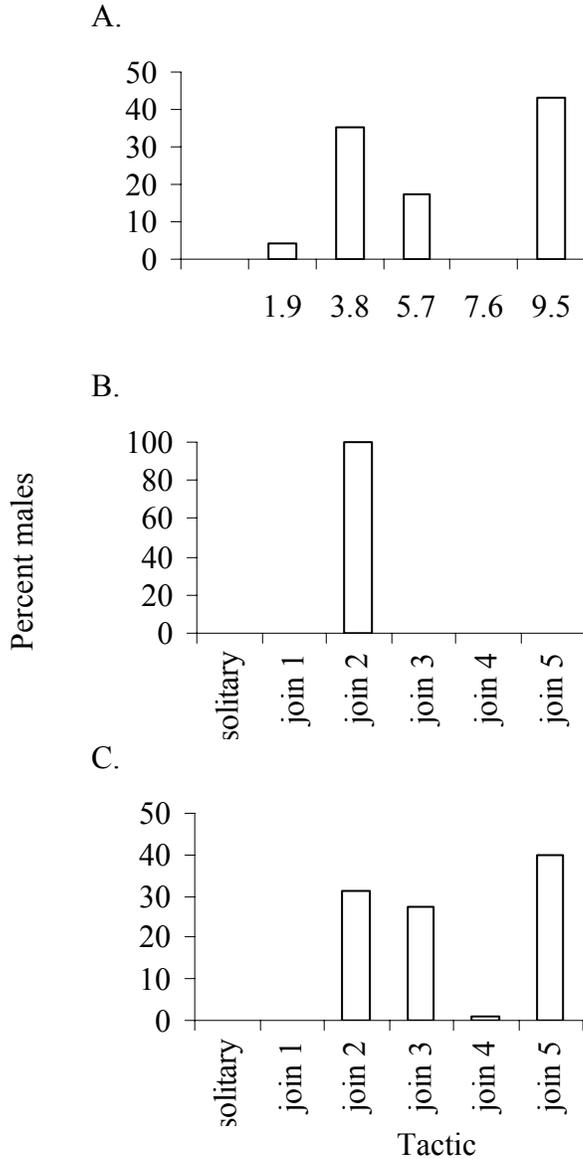


Figure 3-4. Comparisons of natural patterns of male clustering with model predictions. A. natural patterns of clustering for ruffs (summarized from Widemo and Owens, 1995); For each lek, Widemo and Owens (1995) report the average size (number of males) across the study period. I grouped these leks (territory-clusters) into five equal cluster-size classes; X-axis labels are the upper limits of cluster-size classes; B. model predictions of male clustering assuming the logistic form of female mating bias reported by Widemo and Owens (1995); C. model predictions of male clustering assuming the observed female mating bias and a linear increase in male survivorship (difference of 3% between successive tactics) with clustering.

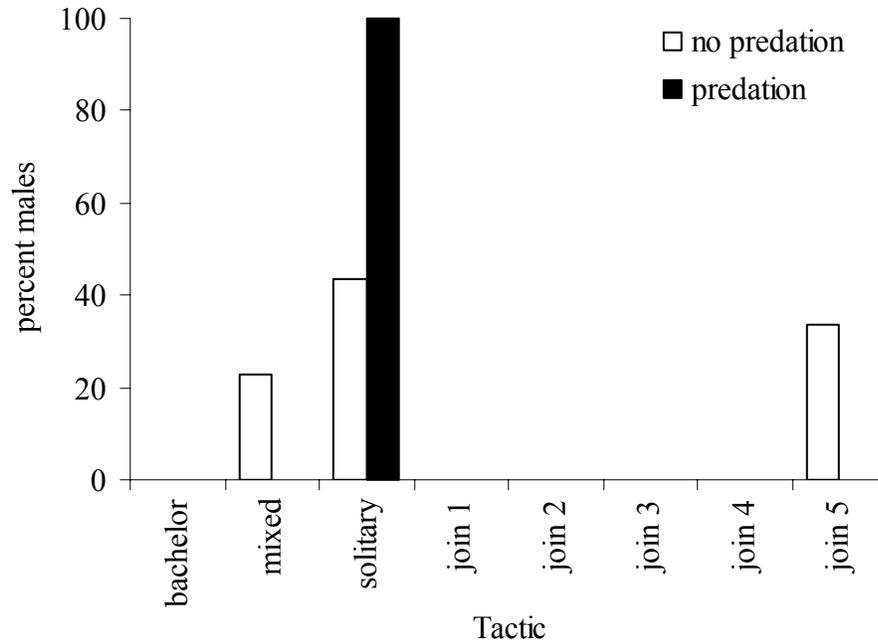


Figure 3-5. An example of the effect of an interaction between predation risk and female mating bias on model outcomes. Light bars display model predictions of male mating strategies when female mating bias is modeled as a weak power function, $B_i = i^{1.1}$, and survival is uniform for all males ($s_i = 0.97$). Darker bars display male mating strategies under the same weak mating bias in combination with linear decreases in predation risk with clustering (i.e., an increase of 0.03 in survival probabilities between successive clustering tactics).

CHAPTER 4
WHAT MAINTAINS THE SIZE OF MATING TERRITORIES IN A LEKKING
SPECIES? MODELS AND EMPIRICAL TESTS

Introduction

Lek territories are characterized by being clustered and unusually small (Bradbury 1981, Clutton-Brock 1989, Höglund and Alatalo 1995). Most studies of the evolution of lekking focus on male clustering (Bradbury et al. 1986, Höglund and Alatalo 1995, Stillman et al. 1993) with territory size receiving little attention. The typical explanation for the small size of lek territories is that males defend mating territories that females visit solely for mating (Bradbury 1981). Since mating territories do not involve the defense of conventional resources (such as forage and water) attractive to females, territory size is not expected to be related to mating success. However, comparisons across species suggest that territory sizes vary widely and therefore, demand an explanation. In some cases, this variation blurs the distinction between leks and other territorial systems. For example, in black lechwe (*Kobus leche smithemani*), male territories are clustered, a lek-like feature, but are large enough so that the resources within territories appear substantial, a feature of resource-defense polygyny (Thirgood et al. 1992). Similar observations have been reported from other species (e.g., bustard, *Tetrax tetrax*, Jiguet et al. 2000; grassquit, *Volatinia jacarina*, Almeida and Macedo 2001). Within species, territory sizes vary both among leks of different sizes and within a lek (Gosling and Petrie 1990, Ranjitsinh 1989). Since territory sizes vary so widely and

do not always covary with male clustering, understanding the factors underlying variation in territory size may provide important insights into lek evolution.

I used the flexible mating system of an Indian antelope, blackbuck (*Antelope cervicapra*), to explore processes that lead to variation in territory size. The blackbuck, like several other ungulates, displays a variable mating system in which males defend mating territories that may be solitary or clustered to different degrees including classical lekking (Isvaran and Jhala 2000, Mungall 1978, Ranjitsinh 1989). Territory size also varies in this species (Mungall 1978, Prasad 1989, Ranjitsinh 1989). Thus, territory distributions may differ dramatically among populations, from solitary, dispersed, large territories to tightly clumped classical leks with more than a hundred males. However, in all cases, these are primarily mating territories. Even large territories (1 to 20 ha, Mungall 1978), which are typically called resource territories because they are situated in feeding areas and contain forage, contain only a small proportion of resources used by females and are much smaller than the home range of female groups. Such territoriality is common in ungulates (Clutton-Brock 1989, Gosling 1986) and, thus, resource territories in ungulates are different from those in other taxa (e.g., many birds) in which males defend a large part of the resources used by females (Clutton-Brock, 1989). Thus, since territories in blackbuck are primarily mating territories, they can be analyzed together to investigate the factors influencing mating-territory size.

Since there are few explicit predictions about the patterns that mating-territory size should show, I first used simulation methods to construct alternative spatial models of territory size based on verbal explanations presented in the literature (Langbein and Thirgood 1989). I considered two processes thought to influence lek territory size. The

first process that I modeled was the interaction between neighboring territorial males. Langbein and Thirgood (1989) suggest that when the number of males in a cluster increases, the number of neighbors increases for a given territory, males experience greater male-male competition, and consequently defend smaller territories. Thus, variation in cluster size leads to variation in territory size through variation in the number of neighbors. I modeled interactions between neighbors in clusters of different sizes and generated predictions for how territory size should vary (1) locally within a cluster, and (2) across clusters with different numbers of males.

A large part of male behavior at leks is thought to be a response to female behavior when visiting leks (Höglund and Alatalo 1995). Therefore, the second process I considered was female movement in relation to mating. First, many studies report that most matings in lekking populations occur at restricted traditional sites (Widemo 1997, Wiley 1991). Experimental studies have shown that the occurrence of leks at these traditional sites is more likely driven by females moving to these sites to mate, than by the tendency of males to establish territories at particular sites (Apollonio et al. 1998, Nefdt 1995).

Second, in most lekking species, females move to and mate with males on central territories in leks (Bro-Jørgensen 2002, Deutsch 1994b, Gosling and Petrie 1990, Höglund and Alatalo 1995, Hovi et al. 1994, Isvaran and Jhala 2000). Along with higher female visitation and mating rates in central territories, these territories are also generally smaller than those at the periphery (Fryxell 1987, Gosling and Petrie 1990, Hovi et al. 1994). This suggests that males on central territories receive greater competitive pressure from other males seeking to establish territories in areas attractive to females, thereby

leading to a reduction in territory size towards the center of the lek. There are several explanations for female movement towards central territories on leks: females use territory position as an indirect cue in mate choice (Apollonio et al. 1989, Hovi et al. 1994); females prefer the center because predation risk is lower at the center of a group (Gosling and Petrie 1990); females prefer to mate with high quality males who are in the center of a group of less-popular males (Höglund and Robertson 1987); and females prefer males who are better able to defend them from harassing intruders (Clutton-Brock et al. 1993). In this chapter, I do not assess these explanations of female movement on leks. Instead, I evaluate whether this female movement within a cluster of territories can lead to spatial variation in territory size and whether this effect can vary with cluster size (the number of males in a cluster).

In this chapter, I first present spatial models of territory size to evaluate the influence of (A) interaction between neighbors, and (B) female movement in relation to mating on territory size. I used these models to generate predictions for how territory size should vary within a cluster and across clusters of different sizes. I then tested these predictions using data from six blackbuck populations.

Models Of Territory Size

Model 1. Effect Of Interactions Between Neighbors

Model construction

I evaluated the effect of male-male competition between neighbors in simulated territory clusters ranging in size from one to fifty territorial males. Each male's territory was represented as a square, k sq. units in area. At the beginning of a simulation, all territories in a cluster were equal in area (Figure 4-1A). Males were then allowed to interact with their neighbors. For simplicity, all males were assumed to be equal in

condition and dominance. Males were assumed to partition their energy so that they allocated equal energy towards defending each boundary that they shared with a neighbor. Thus, a male with four neighbors used 25% of his defense effort towards each neighbor. When two adjacent males had unequal numbers of neighbors, the male with fewer neighbors had relatively more energy to devote to that boundary and was assumed to take over one unit of his neighbor's territory. For example, if a male with three neighbors shared a boundary with a male who had four neighbors, the first male was able to devote one-third of his defense effort towards that boundary while the second could only devote one-fourth of his effort towards the same boundary. Therefore, the first male gained part of the second male's territory (Figure 4-1B). For each male, I calculated the number of spatial units (l) lost to neighboring males with fewer neighbors, and the number (g) gained from neighboring males with fewer neighbors than the focal male. Therefore, the size of a male's territory depends on both the immediate number of neighbors he experiences, and his neighbors' environment (the number of neighbors they experience). After all males interacted, effective territory sizes were calculated for all males as follows:

$$t_i = k - l + g$$

where t_i is the territory size of the i th male, l is the number of units lost, and g is the number of units gained. For these simulations, I considered the starting size a male's territory, k , to be nine sq. units.

Model outcomes

Within a cluster of a given size (number of males), males with relatively more neighbors had relatively smaller territories (Figure 4-2A). However, the reduction in territory size was slight since the number of neighbors only varied from one to four.

Territory size also varied with the distance from the center of a cluster (Figure 4-2B). The smallest territories were the ones intermediate between central and peripheral territories. This is because peripheral males had the fewest neighbors and exerted the most pressure on territories inner to them. On the other hand, territories further towards the center had similar numbers of neighbors and exerted similar pressure on each other.

Comparing across clusters with different numbers of males, mean territory size was not correlated with cluster size (the number of males in a cluster). As cluster size increased, mean territory size remained the same since the same area was redistributed among males so that males with fewer neighbors had larger territories.

Model 2. Effect Of Female Preference For Traditional Mating Sites

Model construction

To evaluate the effect of traditional mating sites on territory size, I modeled a mating ground consisting of 900 unit squares in which mating benefits decreased exponentially from the center of the ground to the periphery (Figures 4-3A and 4-3B). This pattern in mating benefits was meant to represent a strong female preference for mating at a traditional site (the center of the ground). At any one unit on this ground, mating success (M) was given by $M = p * e^{qd}$ where p and q are constants, and d is the distance of that unit from the center of the mating ground. Males sequentially entered this area and established a territory (maximum size = 9 units) in the part of the ground that maximized mating benefits devalued by the cost of male-male competition. Males could establish territories in unoccupied units and could also choose to overlap their territories with those of other males. Males did not experience any cost of competition in the unoccupied units, but in areas of overlap, males competed with others previously occupying these areas and, thus, suffered a cost that was proportional to the number of

males they were competing with (cost = cn where c is a constant and n is the number of males previously occupying a unit). Further, males were assumed to share mating benefits in the areas of overlap. To avoid a unit square being shared by an unrealistically large number of males, I assumed that the mating benefit in a square to a new male was zero if that square was already occupied by four males. Using these rules, each time a new male entered the territorial ground, the fitness (F_i) of all possible territories (each territory a set of 9 units) was calculated as $F_i = \sum_{u=1}^9 \frac{M_u}{n} - c.n$ where M_u is the mating success of each unit, c is the cost of overlap and n is the number of males using that unit (previously established males + new male). The territory with the maximum fitness was adopted by the new male. After all males sequentially established territories, I calculated final effective territory sizes. Areas of overlap were divided equally among males occupying them. I then calculated the mean size of territories in the cluster.

I ran the simulation varying cluster size (the number of males in a cluster) from a solitary territory ('cluster' of one), to a cluster of 50 males. To evaluate the effect on the model of the strength of female preference to mate at a restricted area, I varied the exponent (q) of the function describing mating benefits from 0.1 to 0.9.

Model outcomes

For a given cluster size, territories were most dense towards the center of the mating ground. This is because more territories were established towards the center than the periphery since mating benefits were highest in the center and declined steeply towards the periphery of the ground. Thus, territory sizes were smallest in the center and increased towards the periphery (Figure 4-3C). This pattern was clear in clusters of varying size, the exceptions being very small clusters (2-3 males) in which the number of

males was too small to display this correlation. Note that the area of the mating ground (900 unit squares) was never limiting. The size of the mating ground was large enough so that all males in the largest cluster size simulated (50 males) could choose to establish territories of the maximum size (9 units). However, because of the pattern in mating benefits, territory sizes were usually much smaller (Figures 4-3C and 4-3D) as males tried to establish territories in areas that maximized net benefits.

Comparing among clusters of different sizes (numbers of males), mean territory size decreased exponentially with cluster size (Figure 4-3D). This is because as cluster sizes increased, many more males established territories towards the center of the mating ground. Although males who established territories towards the center, in areas previously occupied by territories, faced high competition costs, the large mating benefits at the center outweighed these costs. Therefore, as cluster sizes increased, the competitive pressure from males attempting to establish territories in areas with high mating benefits also increased. The steepness with which territory size declined with cluster size depended on how steeply mating benefits fell away from the center, that is, how strong the female tendency to mate on the traditional site was (Figures 4-3 and 4-4).

Model 3. Female Preference To Mate In The Center Of An Aggregation

Model construction

A wide range of studies report that females move to and mate in the center of a cluster of males (Bro-Jørgensen 2002, Hovi et al. 1994). To model the effect of this behavior on territory size, the territorial ground was initially assumed to have uniform mating benefits. Once two territories were established, a female preference for mating in the center of an aggregation was modeled as follows. Mating benefits were assumed to decline exponentially from the centroid (mean x coordinate, mean y coordinate) of

previously established territories. I recalculated the mating benefit surface after every territory addition since the center of a territorial aggregation shifts with every new territory added. This process assumes (1) that females show a strong preference to mate in the center of the current territorial aggregation, and (2) the location of maximum female preference shifts to some extent as the center of the territorial aggregation shifts with the addition of each new territory. The cost structure and procedure by which the best territory was chosen by each new male were the same as described for Model 2.

Model outcomes

Results from Model 3 were very similar to those of Model 2. For a cluster of a given size (number of males), territory size increased from the center to the periphery. Mean territory size decreased exponentially with cluster size just as in the case of females mating at traditional sites (Model 2, Figures 4-3 and 4-4).

Comparison Of Predictions From Models 1, 2 And 3

Using simulation methods, I generated predictions regarding patterns in territory size across clusters of different sizes (numbers of males) and spatially within a cluster (summarized in Table 4-1). Model 1 (interactions among neighbors) made very different predictions from the two female movement models. Model 1 predicted no change in mean territory size with cluster size, in striking contrast to female movement models that predicted a strong exponential decrease. A second striking difference is the prediction relating territory size (within a cluster) to the distance from the center of the cluster. Model 1 predicted a quadratic pattern with smallest clusters being intermediate in location while Models 2 and 3 predicted an increase in territory size from the center to the periphery. The two female movement models (Models 2 and 3) made very similar predictions. The main difference between them was the location of the mating center (the

peak of the mating benefit surface). In Model 3 (female bias for the center of a territorial aggregation), the location of the mating center changed as territories were added to the cluster. This occurred because as territories were added to a cluster, the centroid of the aggregation changed, thereby changing the mating center. This is contrary to Model 2 in which the mating center remained fixed. I tested these predictions using data from six blackbuck populations.

Evaluating models using empirical data

Study Organism

The blackbuck is a small antelope (31 to 45 kg, Ranjitsinh 1989) native to the Indian sub continent. The blackbuck is a selective grazer. It is found in a wide range of habitats although it reaches its highest densities in open, semi-arid grasslands (Ranjitsinh 1989). This antelope is group living and group sizes range from two to several hundred animals. Mating typically occurs on mating territories that males defend. Although males have also been observed courting females in mixed-sex groups, these seldom end in successful matings (Mungall 1978, Prasad 1989, Ranjitsinh 1989, this study). Matings occur throughout the year. However, data on mating and fawning indicate two prominent annual mating peaks, one in March and April and another from August to October (Ranjitsinh 1989).

Study Sites

I measured patterns in territory size in six blackbuck populations in India from August to November 1998 and 1999 (Fall mating peaks). These sites were Tal Chappar in Rajasthan state, Velavadar and Savainagar in Gujarat state, Nannaj in Maharashtra state, Rollapadu in Andhra Pradesh state, and Point Calimere in Tamil Nadu state. Details of these study sites are presented in Chapter 2. They represent a wide range of habitat

conditions and blackbuck density and mating system. I also intensively studied one population, Velavadar in Gujarat, from February to May 2001.

Among-Population Variation In Territory Size

I spent two to four weeks (mean = 3 weeks, SD = 0.8) at each of the six populations surveyed. At each study site, I surveyed the area repeatedly and recorded all territorial males. Putative territorial males were observed during three to six (mean = 4) one-hour watches performed during morning and evening hours when territorial and mating activity is high (Isvaran and Jhala 2000). During these watches, I recorded the area used by males and interactions between males. Neighboring males often engage in displays (parallel walks, Mungall 1978) and fights at the boundaries of their territories (Mungall 1978, Ranjitsinh 1989). From these data I identified territory clusters, defined as territories that shared boundaries. Territory clusters were typically identified unambiguously since clusters were usually at least half a km apart (while the average nearest-neighbor distance between males within a cluster was 80m). Mean territory sizes were estimated for a sample of territory clusters (two to six, mean = 3.8, SD = 1.5) at each population. In each of these clusters, I measured the territory sizes for a sample of males (one to 15, mean = 5, SD = 4). During one hour focal watches, I noted the location of males every five minutes. Males were typically active and moved over the majority of the area subsequently recorded as their territories within the first half hour. At the end of these watches, I estimated territory size by pacing out the longest and shortest axes of the area used by each male during the watch. Territories varied in shape but were well approximated by an ellipse.

Within-population Variation In Territory size

Cluster size and territory size

Territorial and mating behavior was studied more intensively at Velavadar in Gujarat from Feb 5 to May 1, 2001. I studied the principal lek (maximum of 90 males) and four relatively small clusters (with a maximum of 7, 4, 4, and 3 males). Blackbuck use dung piles, formed by repeated defecation at a site, to mark territories and a territory typically contains a principal central dung pile and several smaller dung piles at the periphery and elsewhere in the territory (Isvaran and Jhala 2000, Mungall 1978, Prasad 1989). I mapped the principal dung pile of each territory in the clusters studied using a 30 m measuring tape and permanent markers on the territorial ground. I identified territory boundaries by observing interactions (Nose-up displays, parallel walks and fights; Mungall 1978, Ranjitsinh 1989) between neighboring males. I then estimated territory sizes by measuring (with a 30 m tape) the longest and shortest axes of the area used by males and using the formula for the area of an ellipse. I also identified individual males using horn characteristics (Isvaran and Jhala 2000). I recorded changes in the number of territories, and ownership at least once in three days at the main lek and once a week at the smaller clusters. Further, at the main lek, I intensively monitored the sizes of twenty territories (randomly chosen at the beginning of the study) throughout the mating peak. During two to three hour observation sessions conducted at least once a week during morning and evening hours when territorial and mating activity is high, I watched each territory for five to ten minutes and recorded the area used by the territorial male. Since territories are relatively small at the main lek (20m to 110 m in diameter), and since territorial activity is high, this time interval was likely sufficient to gain an estimate of the area used by each male.

Female movement on leks

To study spatial patterns in female movement and mating in a cluster, I recorded female location and behavior on the main lek during one hour scan sampling sessions. During each session, I scanned the lek every 15 minutes and recorded the location of all observed females and male intruders on territories. Females spend variable amounts of time at the lek (8 minutes to 120 minutes; Isvaran, unpublished data) and move among multiple territories during their visit. Therefore, observations across scans within a session are unlikely to be highly correlated. I also recorded any courtship (see Mungall 1978 and Isvaran and Jhala 2000 for descriptions) and mating activity seen during these sessions. Scan sessions for female numbers and location on the lek were conducted in the afternoons and evenings since mating activity is concentrated during these hours (Isvaran and Jhala 2000). I conducted these sessions at least once a week during the study period, and every two days during the peak in mating activity (28 February to 14 March). I also conducted one to three hour watches of the lek for courtship and mating activity at least once a week and more frequently during the peak in mating activity. During these watches, I recorded the location on the lek of courtships and copulations.

Analyses

I used linear and nonlinear regression methods to analyze relationships between cluster size and territory size across populations. I used similar methods to analyze within-cluster relationships between territory size and variables such as the number of males and the distance of the territory from the center of the cluster. The center of a cluster was defined as the center of gravity, centroid, of all territories in the cluster. For all analyses, I examined patterns in residuals to evaluate whether assumptions of normality or linearity were violated.

Results

Among-Cluster Variation In Territory Size

Territory sizes varied widely both among and within populations from territories 350 m² to 100,000 m² in area. Territory cluster sizes also ranged widely from solitary males (“cluster” size = 1) to clusters of 50 territorial males. Pooling together clusters from all six populations, the mean size of territories in a cluster was strongly negatively related to the number of males in that cluster. Mean territory size in a cluster declined exponentially with cluster size ($R^2 = 0.72$, $N = 23$, $P < 0.0001$; Figure 4-5). This pattern was also apparent among the smaller subset of clusters within each population (Figure 4-5).

Within-Cluster Variation In Territory Size

At Velavadar, the intensive study site, the number of territorial males varied at the main lek and at the smaller clusters throughout the study period. At the main lek, the number of territorial males increased from 35 males in the beginning of February to 90 males in the middle of March and then fell to 43 males in the end of April (Figure 4-6A). Corresponding to the change in territorial male numbers, the mean size of territories at the lek also changed (Figures 4-6B, $R^2 = 0.59$, $N = 23$, $P < 0.0001$). Mean territory size decreased with an increase in territorial male numbers in March and then increased again once territorial male numbers declined in April (Figure 4-6A).

Territory sizes of known individual males also changed both at the main lek and at the smaller clusters (Figure 4-7). Territories shrank in relation to an increase in the number of males at the cluster. Similarly, an expansion in territory size was associated with a reduction in the number of territorial males in a cluster. Interestingly, the degree to which territory size changed was associated with cluster size. Thus, for a given change in

cluster size (e.g., an addition of one territory) the change in territory size was higher in small clusters than at a large one (Figure 4-7).

Territory sizes at the main lek varied not only over time but also spatially in relation to the lek center (center of gravity of all lek-territories). Territory size at the main lek increased in an accelerating fashion with the distance from the lek center ($R^2 = 0.78$, $N = 34$, $P < 0.0001$; $\log Y = 5.9 + 0.01X$). Territory sizes also decreased with the number of immediate neighbors (Figure 4-8, $R^2 = 0.50$, $N = 34$, $P < 0.0001$; $\log Y = 9.4 - 1.6\log X$).

Female Behavior At The Main Lek

Female numbers on the lek were concentrated at the lek center and declined sharply from the center to the periphery. The mean number of females per scan (first averaged across scans within a session and then averaged across 18 scan sessions) was negatively correlated with distance from the center of the lek (Pearson's $r = 0.8$, $N = 10$ distance classes, $P = 0.005$). Matings and courtship were similarly concentrated in the lek center (Figure 4-9A). The mating center (centroid of locations at which matings and courtship events were observed) shifted during the mating peak (March-April 2001, Figure 4-9B). About 60% of lek territories were already established before females began visiting the lek regularly and before any courtship or mating was observed. The center of mating activity early in the mating peak was very close to the center of previously established territories. Finally, the location of the mating center was very similar across years (Figure 4-10; Spring 1995, Isvaran and Jhala 2000; Fall 2000 and Spring 2001, this study).

Discussion

Effect Of Male-Male Competition Between Neighbors

A simple model of competitive interactions between neighbors predicted that, within a cluster, territory sizes should decrease as the number of neighbors increased. The extent of the predicted decrease was limited, however, because variation in the number of neighbors is limited (one to four in the model). This limitation in the model is reasonable for blackbuck, since I found that the number of neighbors varied from one to six. The model also predicted that within a cluster territory sizes should decrease from the periphery to the center in a quadratic manner with the smallest territories lying in the region between the periphery and the center (Figure 4-2). However, across clusters of varying size, no change in mean territory size was predicted. This is because the same area is just partitioned differently among males as cluster sizes increase.

Empirical results from blackbuck did not support this model. While territory size was correlated with the number of immediate neighbors, territory sizes did not decrease from the center of the cluster to the periphery in the manner predicted by Model 1. Furthermore, one of the most striking empirical results, that mean territory size in a cluster was strongly related to the number of males in a cluster, is inconsistent with model predictions. Thus, data from blackbuck suggest that interactions among neighbors alone is insufficient to explain the observed patterns of variation in territory size.

Effect Of Female Movement In Relation To Mating

Empirical results from blackbuck supported the female movement models (Models 2 and 3). As predicted by the models, mean territory size was strongly associated with the number of territorial males in a cluster. This pattern was seen both across clusters from different populations (Figure 4-5), and at individual clusters as their sizes changed over

time (Figure 4-6). For example, mean territory size at the main lek in Velavadar decreased as the number of lekking males increased and then increased again as territorial males left the lek towards the end of the mating season. A third line of support was provided by changes in the territory sizes of known males. Again, individual territories expanded when the size of a cluster decreased and shrank when more males joined the cluster. This pattern was seen both at small clusters and at the large principal lek. Interestingly, the female movement models predicted that since territory size decreases disproportionately with cluster size, the incremental change in territory size should be greater at small clusters than at large clusters. This prediction was also supported by data from blackbuck (Figure 4-7).

The female movement models also made predictions about spatial patterns in territory size within a cluster. As predicted, I found that territory size increased from the center of the cluster to the periphery. This pattern has been reported in many lekking ungulates (Deutsch 1994b, Fryxell 1987, Gosling and Petrie 1990) and birds (Hovi et al. 1994, Wiley 1991).

Patterns in territory size variation with respect to cluster size and distance from the center do not allow us to distinguish between the two female movement models. The main prediction that distinguishes between these models is whether there is a change in the location of the mating center through the mating season. At Velavadar, the mating center shifted through the Spring 2001 mating season (Figure 4-9). Further, about 60% of lek territories seen during the mating peak were already established several weeks before females began visiting the lek. The location of the center of matings and courtship when females first visited the lek (in late February) was very close to the center of established

(early February) territories. This suggests that females display a bias towards mating in the center of a territorial aggregation. However, the location of the mating center was very similar across years (Figure 4-10) supporting the hypothesis that females mate on restricted traditional mating sites. Although in each mating season males establish territories before females arrive at the lek, males may be responding to the location of the mating center in the previous year. Thus, data from blackbuck do not allow us to distinguish unequivocally between the two female movement models.

Taken together, the lines of evidence presented above suggest that variation in territory size in blackbuck can be explained by two interacting factors: a female bias for mating on central territories (or restricted mating sites) and cluster size. A female bias for mating in the center of a territorial aggregation may lead to a reduction in the size of central territories. This can be explained by males attempting to establish territories as close as possible to the center preferred by females. Therefore, central territories receive more pressure from males and are smaller than peripheral ones. The number of males in a cluster also affects territory size since this pressure on central territories increases with the number of males in a cluster. Thus, female preference and cluster size interact so that the effect of a female preference is most obvious in large clusters. The smallest territories are in the center of the largest clusters. There are several reasons proposed for why females mate in the center of a cluster; this chapter focuses on the consequence of this behavior rather than the cause.

The main assumption of the female movement models, that mating benefits decline exponentially from the center (of the aggregation or a traditional site) to the periphery, was supported by data from blackbuck. Both female numbers and mating activity

declined exponentially from the lek center (Figure 4-9). Further, studies of many lekking species report similar spatial patterns in mating success (reviewed in Höglund and Alatalo 1995) suggesting that territory size variation may be related to a central territory advantage in a wide range of lekking species.

Although the main mechanism in the female movement model is a female bias for mating in the center, the model can be interpreted more generally as one in which benefits to territorial males are highest in the lek center, thereby generating increased competition for central territories. From this I conclude, more generally, that any process that results in greater benefits to males in the center compared to the periphery could lead to the kind of variation in territory size seen in the model and in empirical results from blackbuck. What are some factors (apart from female preference) that might result in this central territory advantage? Harassment of estrous females by non-territorial intruders, predation risk, and female copying are three factors that can result in disproportionately high benefits to central territories.

In many lekking species, courtship is often disrupted by intruding males harassing the female. In lekking ungulates, such intruders are usually young non-territorial males (Clutton-Brock et al. 1993). Several hypotheses for lek evolution propose ways in which harassment may favor male territory clustering (Clutton-Brock et al. 1992, Nefdt and Thirgood 1997). This factor has not been previously discussed in relation to territory size. Male intrusions might explain variation in territory size if patterns in intrusion rates lead to greater benefits to central territories than to peripheral ones. This might occur if it becomes progressively more difficult for intruders to penetrate into the center of leks because of the resistance from territorial males that they encounter during their progress

into a cluster. However, this argument is not supported by data from blackbuck since intrusion rates did not decrease from the lek periphery to the center. On the contrary, intrusion rates were highest in the center of the lek (Isvaran, unpublished data).

Predation risk is also expected to reduce from the periphery of a group to the center. However, theory suggests that anti-predatory benefits are unlikely to show a strong exponential increase from the periphery to the center of a group, the pattern required in the model to produce the observed territory size variation. Rather, antipredatory benefits are likely to show a pattern of diminishing returns from the periphery of an aggregation to the center (Hamilton 1971). Thus, territories would be expected to be large at the periphery and decrease in size inwards such that the decrease soon levels off. This is not the pattern predicted by the female movement models or found in data on blackbuck territories. There are few data on predation risk either at leks of different sizes or within a lek to evaluate spatial patterns in risk within territory clusters. One study of kob reported that the pattern of carcasses on a lek did not support any reduction in predation rates from the periphery of the lek to the center although peripheral males did show greater vigilance than central males (Balmford and Turyaho 1992). Thus, it remains to be investigated whether patterns in predation risk within clusters may resemble the benefit pattern that seems to explain observed variation in territory size in blackbuck.

Female copying, while difficult to assess in the field, is proposed to be an important source of variation in male mating success in several lekking species (Clutton-Brock et al. 1993, Höglund and Alatalo 1995, Gibson et al. 1990). Female copying could also influence territory sizes by leading to a strong decline in mating benefits from the center

of a cluster to the periphery. Let us assume that the first few females mate on a particular territory on the lek (either at random or choosing particular male characteristics or choosing the location where they mated the previous year). Suppose their mating preferences are copied by females for the rest of the season. This would give rise to a pattern of mating benefits that decline sharply from the site of initial female preferences. Selection would favor males joining the cluster to establish territories close to the area preferred by females. Such a female copying model is likely to make predictions similar to the model of female preference for mating in the center. Data from several lekking species suggest that the initial females making mate choice decisions and females visiting the lek alone do not randomly visit territories but preferentially visit central territories (Höglund and Alatalo 1995). Thus, there seems to be a preference to visit central territories that is independent of copying. However, it is possible that female copying affects territory size by enhancing a given mating pattern. For example, female copying could act on a female bias for mating on central territories to produce extreme mating benefit patterns strongly favoring central territories.

The two factors explored in the models, interactions among neighbors and female movement in relation to mating, were chosen based on observations from previous studies. The effect of these factors on territory size has not been systematically evaluated previously. Therefore, the main aim of the modeling effort in this study was to construct simple models of these factors and generate testable quantitative predictions. Potentially there are many ways in which the two factors might be modeled and the models presented here do not attempt to comprehensively evaluate these factors in multiple complex ways. Further, the models make some simplifying assumptions (e.g., no

differences among males in condition and dominance, males have perfect information about mating benefits and costs). Nevertheless, model results were similar to observed variation in territory size in blackbuck, which suggests that these simple models may capture the main factors influencing territory size.

Conclusions

Findings from this study suggest that understanding lek evolution requires that we examine both the causes of variation in male clustering and the causes of variation in territory size. Using a combination of models and empirical analyses I found that, in blackbuck, territory size is most likely influenced by the interaction between a female mating bias for central territories and cluster size. The small territories typically seen in classical leks may be explained by a female bias for mating on central territories leading to increased competition for these locations, which, in turn, leads to a reduction in territory size. In addition, this process likely intensifies with an increase in cluster size so that the smallest territories are found in the largest clusters. These findings have important implications for lek evolution. They suggest that even if male clustering, the factor that is typically explored by studies of lek evolution, is strongly favored, classical leks may not form if the conditions for a reduction in territory size are not met. For example, if there are very few males in a population, even if clustering is strongly selected for we may not see classical leks. This is because even if all males in a population cluster together, if the size of the cluster remains small, the model predicts that territory sizes will be relatively large. The territorial system is likely to resemble the clustered resource territories seen in some antelope (e.g., black lechwe) or the exploded leks seen in some bird species rather than classical leks. My study thus suggests that the

two main characteristics of lekking -male clustering and territory size - may not always co-vary and may be affected by different sets of factors.

Findings from this study also have implications for territorial systems other than lekking. First, the models of territory size suggest novel explanations for the occurrence of territorial systems intermediate between lekking and resource-based territories. Specifically, they show that by varying cluster size and by varying the central territory advantage we can get territorial distributions ranging from large solitary territories to classical leks. Variation in these two factors together with variation in the factors favoring male clustering may explain intermediate territorial distributions such as exploded leks and clustered resource territories. Second, the models presented in this paper may explain territory size in territorial systems other than lekking. For example, model predictions relating territory size to cluster size are supported by data from a non-lekking kob population. Fischer and Linsenmair (1999) report that a reduction in the number of territorial males over several years was associated with an increase in mean territory size. These results suggest that the factors captured by the two female movement models: (1) decline in benefits from the center of an aggregation (or location) to the periphery (leading to male-male competition for central locations); and (2) size of the aggregation (influencing the magnitude of the competition for more central locations) may be applicable to other territorial systems including nesting territories in fish and resource-defense territories in ungulates.

Table 4-1. Predictions from three models of territory size.

	Predictions from models		
	<i>Model 1.</i> Interactions between neighbors	<i>Model 2.</i> Female bias for traditional mating sites	<i>Model 3.</i> Female bias for center of territorial aggregations
<i>Pattern among clusters</i>			
Relationship between cluster size and mean territory size	Uniform	Exponentially decreasing	Exponentially decreasing
<i>Pattern within a cluster</i>			
1. Relationship between territory size and distance from the center of the cluster	Territories are smallest in the areas intermediate between the center and the periphery of a cluster	Territory size increases from the center to the periphery	Territory size increases from the center to the periphery
2. Location of mating center across years	No pattern	Same location	No pattern
3. Location of mating center during a mating season	No pattern	Fixed throughout territory-addition process	Changes during the territory-addition process

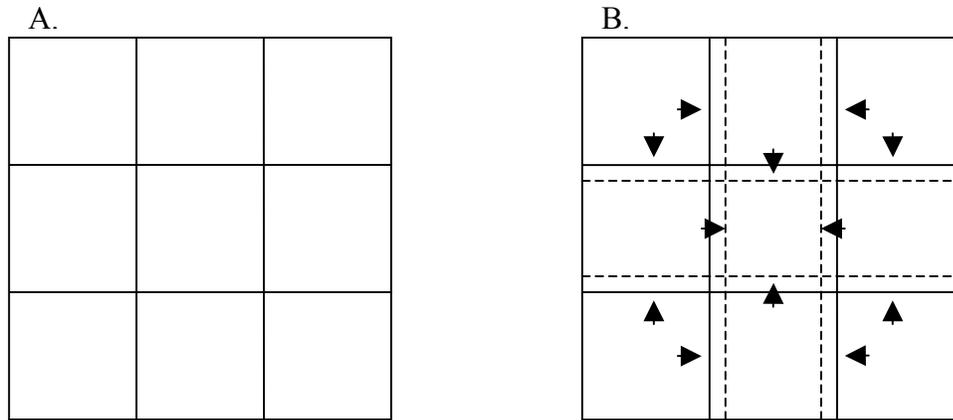
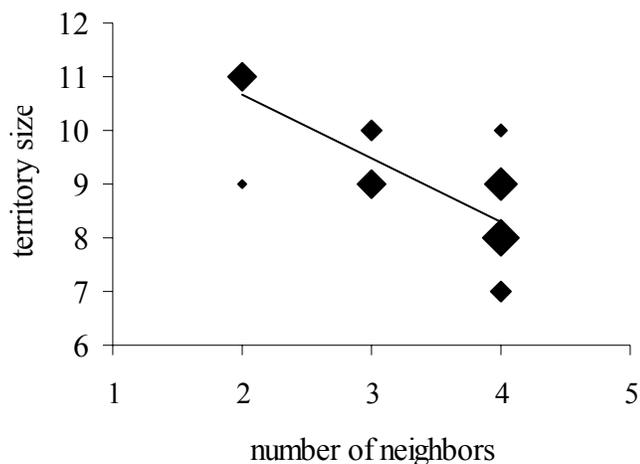


Figure 4-1. An example of interactions between neighbors in a cluster of 9 males. A. Arrangement of territories at the start of the simulation. B. Direction of movement of territorial boundaries (dashed lines) following interactions between neighbors. Arrows show net direction of movement of each territorial boundary. In each interaction between neighbors, the male with fewer neighbors gains part of the territory of his opponent.

A.



B.

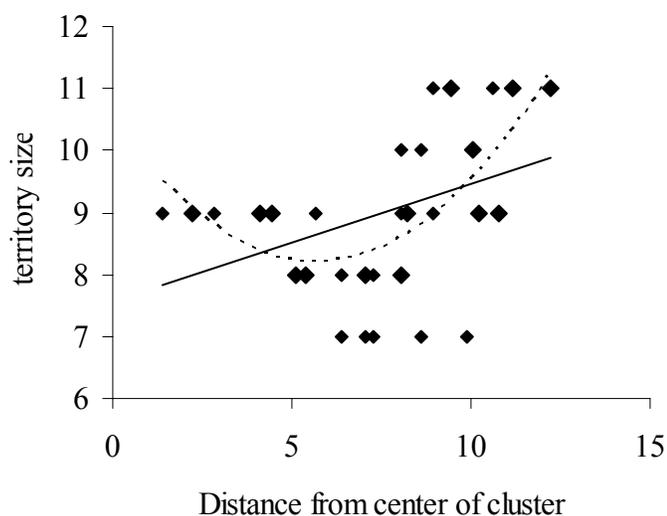


Figure 4-2. An example of model results from modeling the effect of male-male competition between neighboring territorial males on territory size. Patterns in territory size within a cluster of 44 males are shown. The size of diamonds is proportional to the number of observations. A. The size of a male's territory is correlated with the number of neighboring territories. $R^2 = 0.60$, $N = 44$, $P < 0.00001$. B. Territory size is correlated with the distance of the territory from the center of the cluster. Territories are smallest in the area between the center and the periphery. A quadratic model (dashed line) fits the model outcomes better than a linear model (solid line).

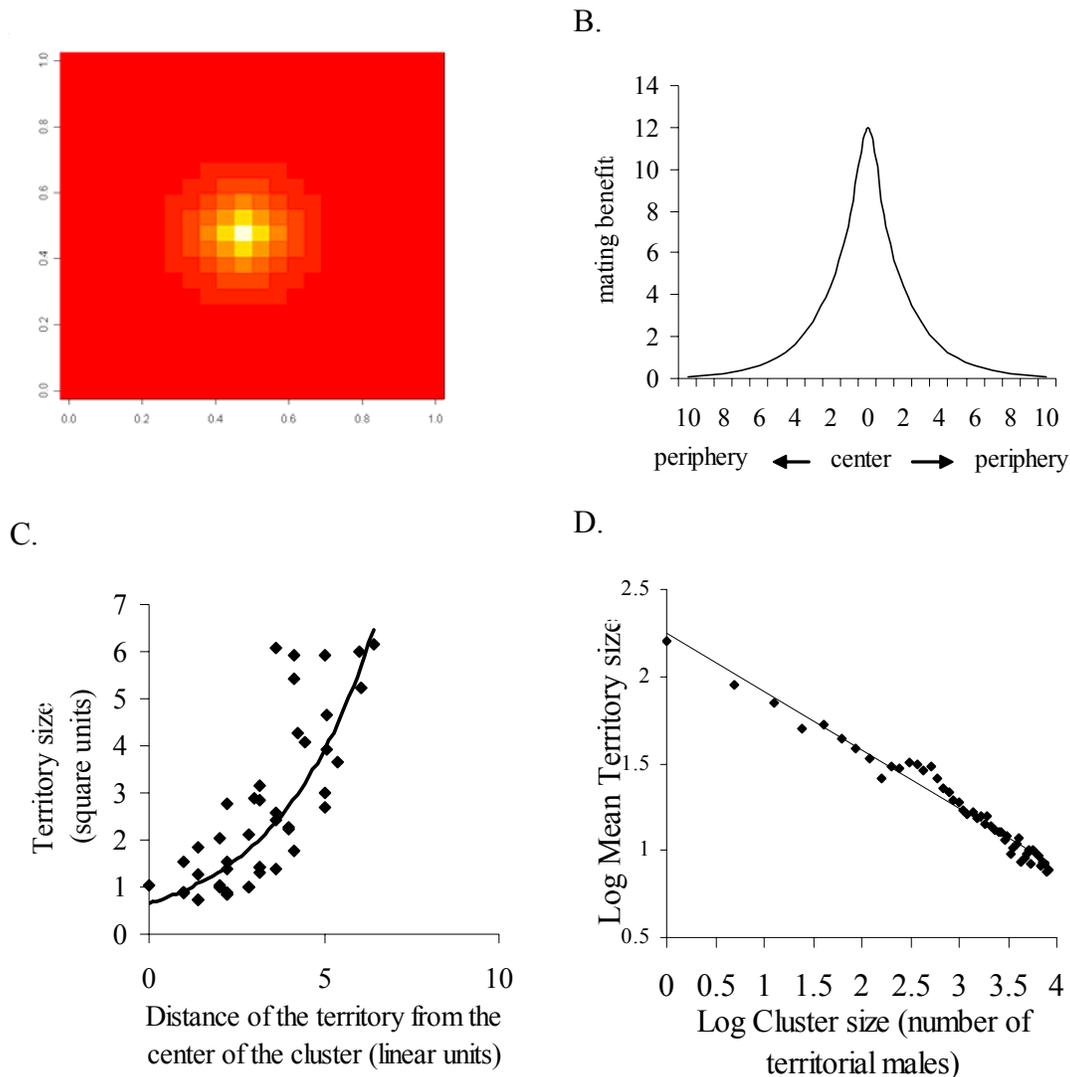


Figure 4-3. Results from the simulation of the effect of female movement patterns, specifically female preference to mate on traditional sites, on territory size (Model 2). A and B. Two- and one dimensional views of the decline in mating benefits from the center of the ground to the periphery (exponent = 0.5). C. The model predicts that, within a cluster, territory size should increase from the center of a cluster to the periphery. An example is shown for a cluster of 50 territorial males ($R^2 = 0.67$, $N = 50$, $P < 0.0001$). D. The model predicts that, across clusters varying in size, mean territory size should decrease nonlinearly with cluster size ($R^2 = 0.97$, $N = 50$, $P < 0.0001$). Model 3 results are very similar to those of Model 2.

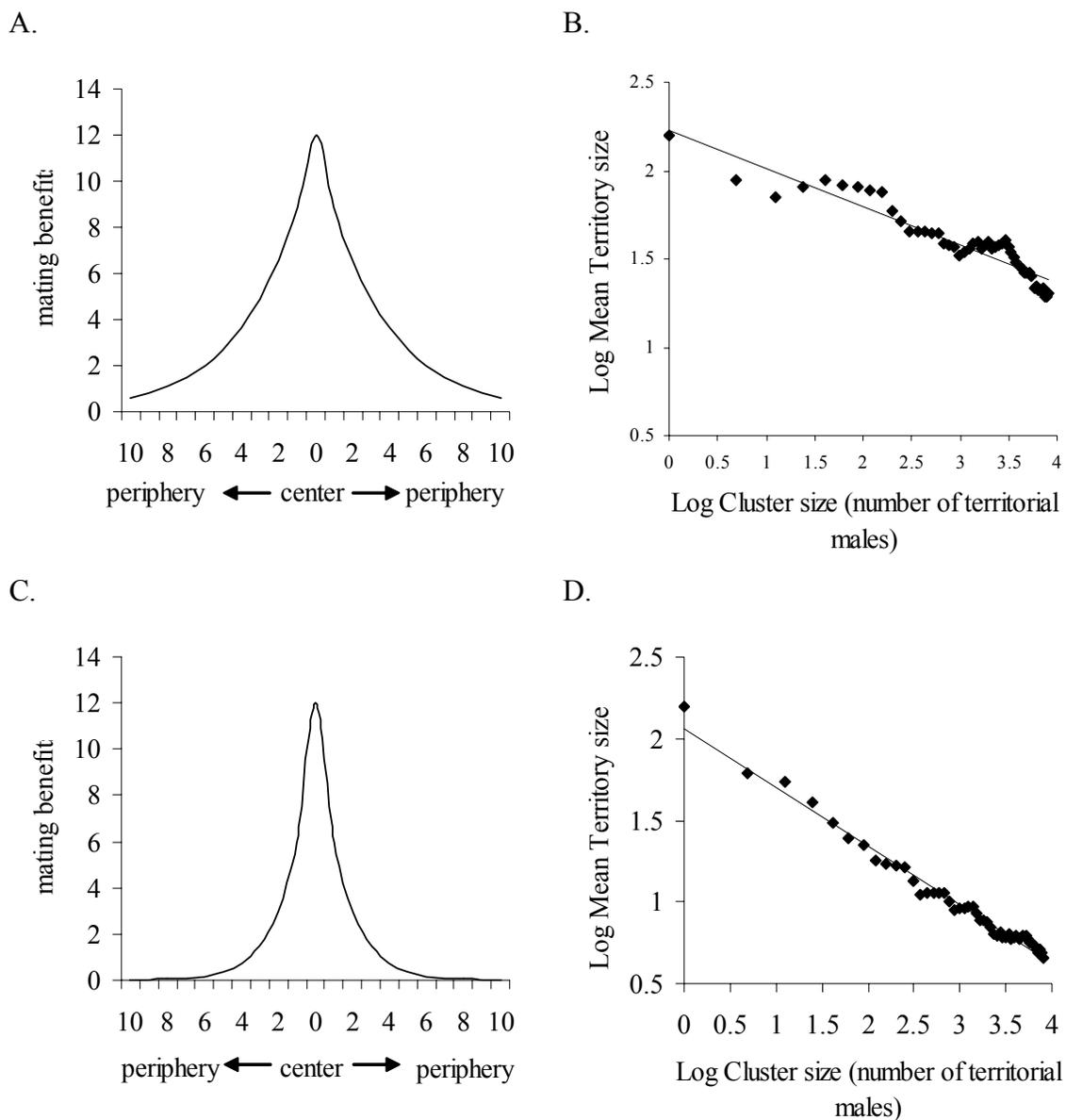


Figure 4-4. Examining the effect of the strength of a female preference for mating at a particular site (model 2). A. Weaker female preference relative to the original model (exponent = 0.3). B. Relationship between cluster size and mean territory size when exponent is 0.3. C. Stronger female preference relative to the original model (exponent = 0.7). D. Relationship between cluster size and mean territory size when the exponent is 0.7.

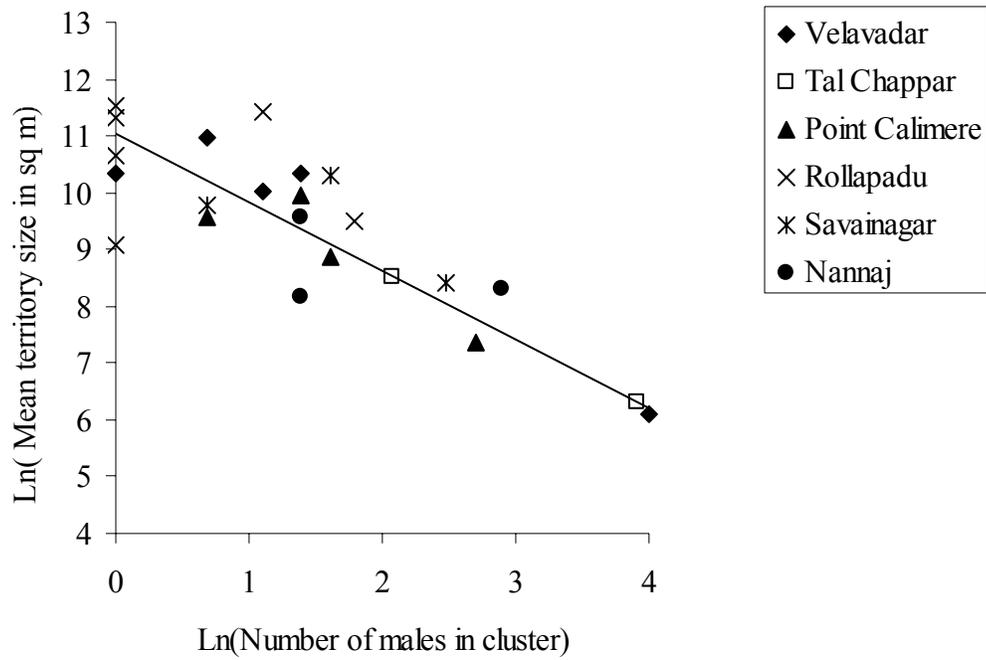
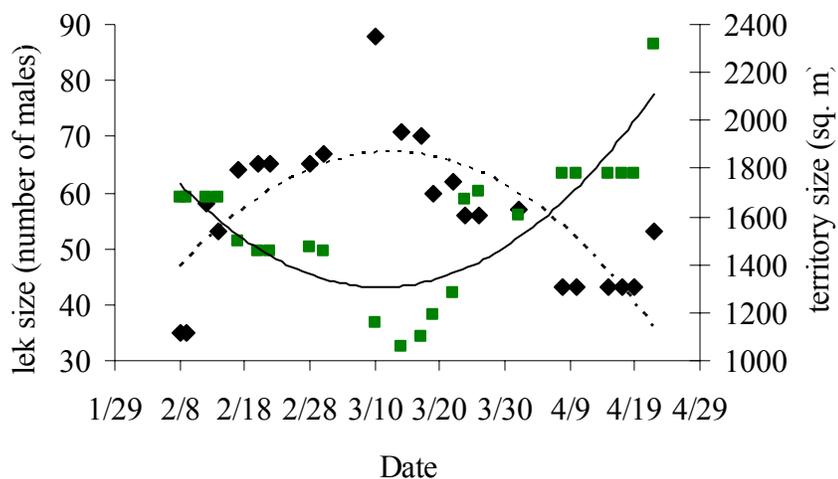


Figure 4-5. Relationship between cluster size (the number of males in a cluster) and mean territory size. Each data point represents a cluster and is an average of the size of a sample of territories from that cluster (range = 1-15 territories). The relationship is strongly nonlinear and hence the data have been log-transformed to obtain a better view of the pattern.

A.



B.

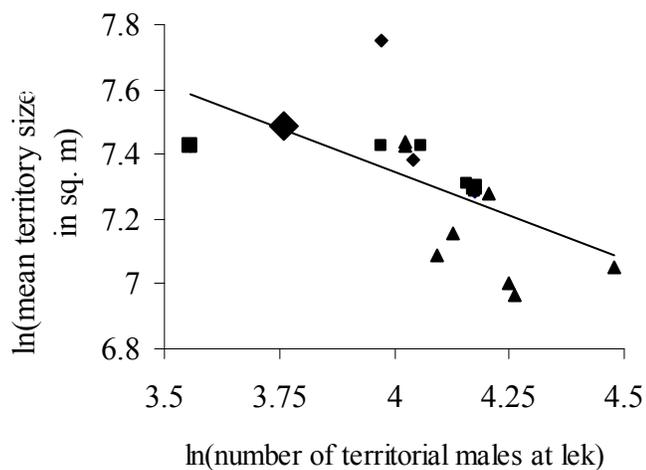
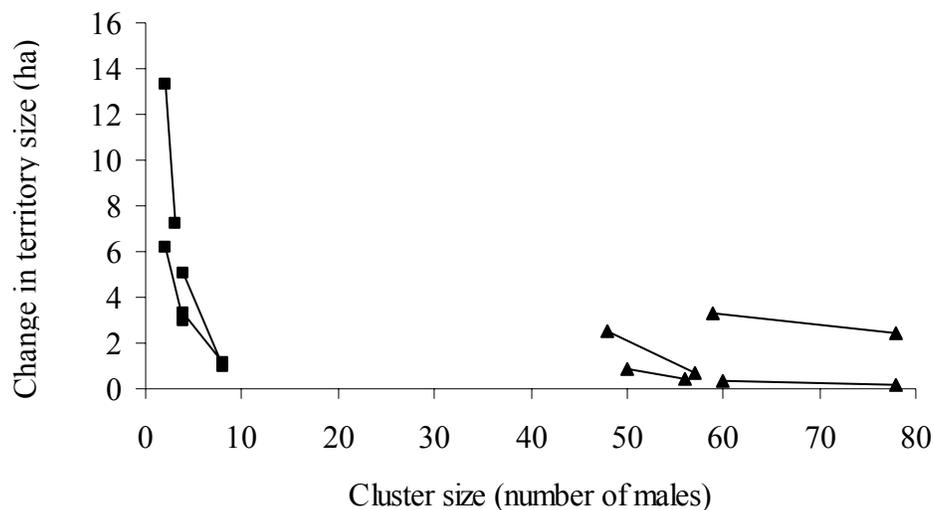


Figure 4-6. A. Trends in the number of territorial males (open diamonds, dotted line) and mean territory size (solid squares, solid line) over time at the main lek in Velavadar, Gujarat, from Feb 5 to May 1, 2001. B. An analysis of the relationship between the number of territorial males and mean territory size for the same data. Squares, triangles and diamonds indicate samples in February, March, and April respectively. Each data point is a day and the size of markers corresponds to the number of samples with that particular set of x and y values. Territory sizes are the means of 20 territories whose sizes were monitored throughout the mating peak.

A.



B.

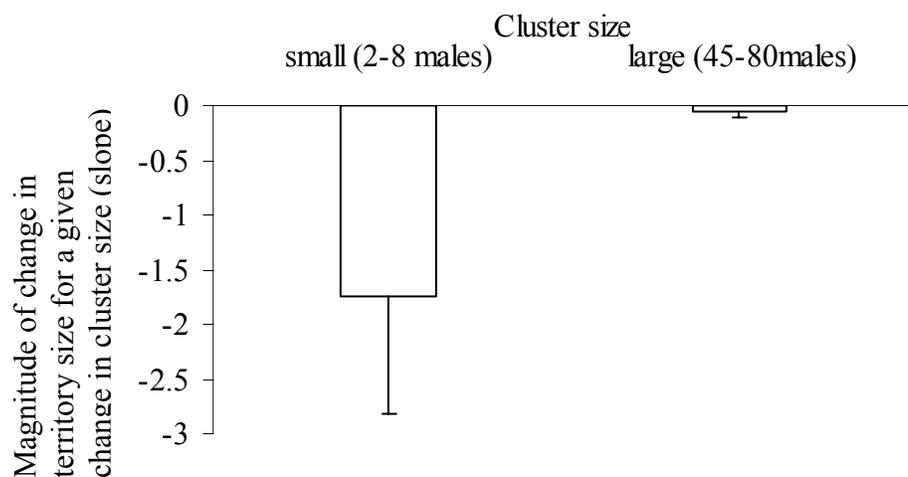


Figure 4-7. A. Examples of the change in the size of territories of known individuals in relation to change in the number of males in the territory cluster that the individuals belong to. Each pair of data points connected by a line represents the change in territory size for an individual male for a given change in cluster size. A subset of data is shown from small clusters (solid squares) and from the large main lek (triangles). B. Mean magnitude of change in territory size of known individuals corresponding to a given change in cluster size. Data are means (with standard deviations) for territories in small clusters ($N = 7$) and in the main lek ($N = 10$). The magnitude of change in territory size is the slope of the relationship between territory size and cluster size calculated for each individual male (slopes of lines such as those shown in Figure A).

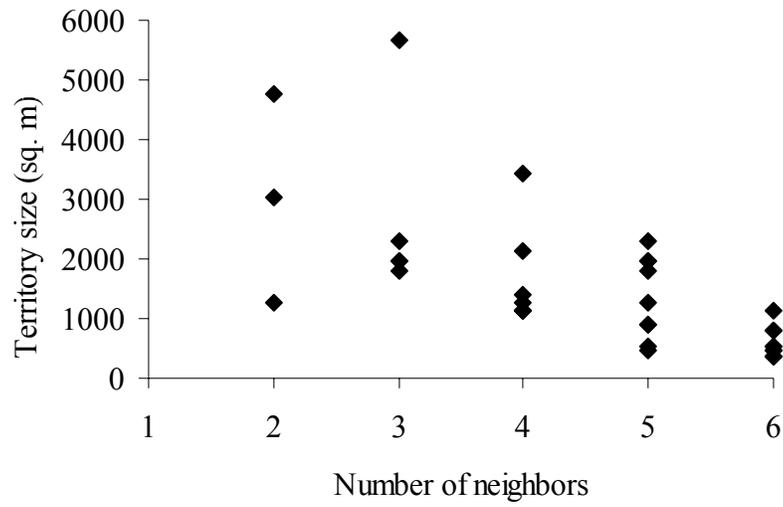
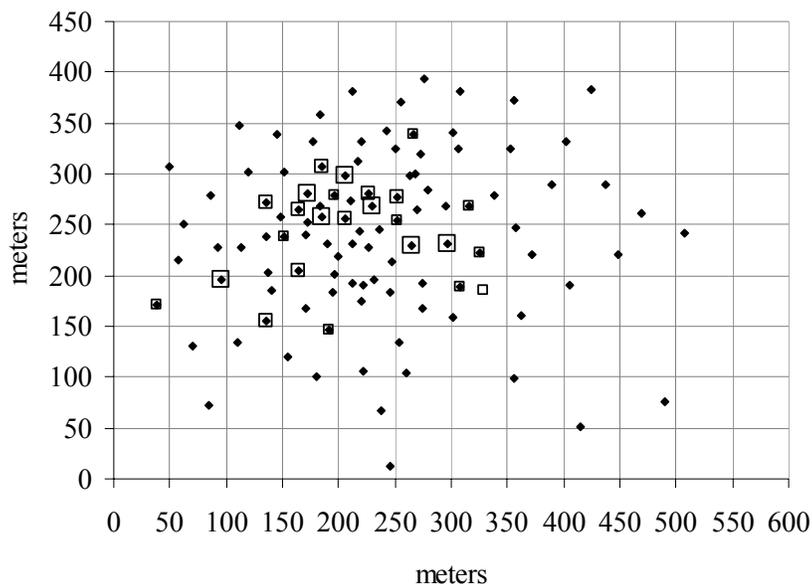


Figure 4-8. Relationship between number of neighbors and territory size ($N = 34$) at the main lek.

A.



B.

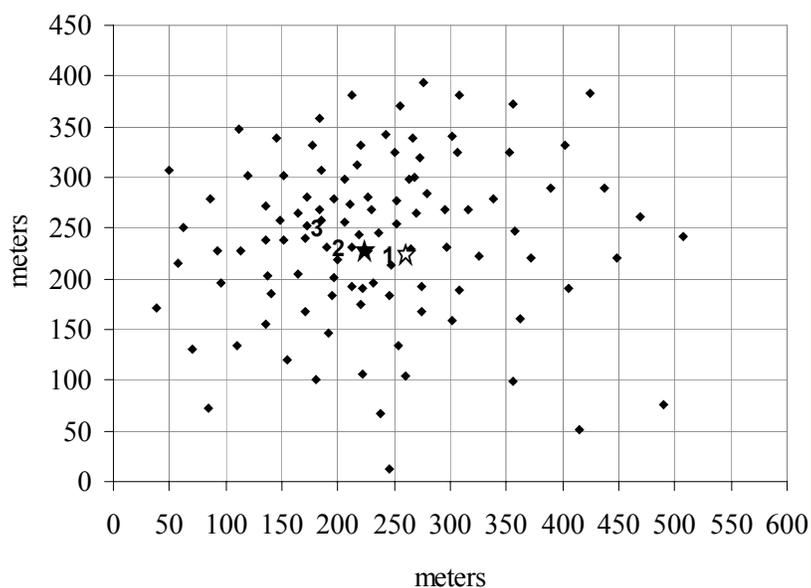


Figure 4-9. A. Distribution of matings at the main lek in Velavadar during the Spring 2001 mating peak (March-April). Solid diamonds represent principal dung piles marking approximate centers of territories. Open squares represent locations of matings and courtship events and the size of squares is proportional to the number seen at that location. B. “1”, “2” and “3” are the centers of matings/courtship events in the first, second and third parts of the mating peak. The open star is the center of territories before females begin to visit the lek (early February) and the solid star is the territory center in the middle of the mating peak (mid March).

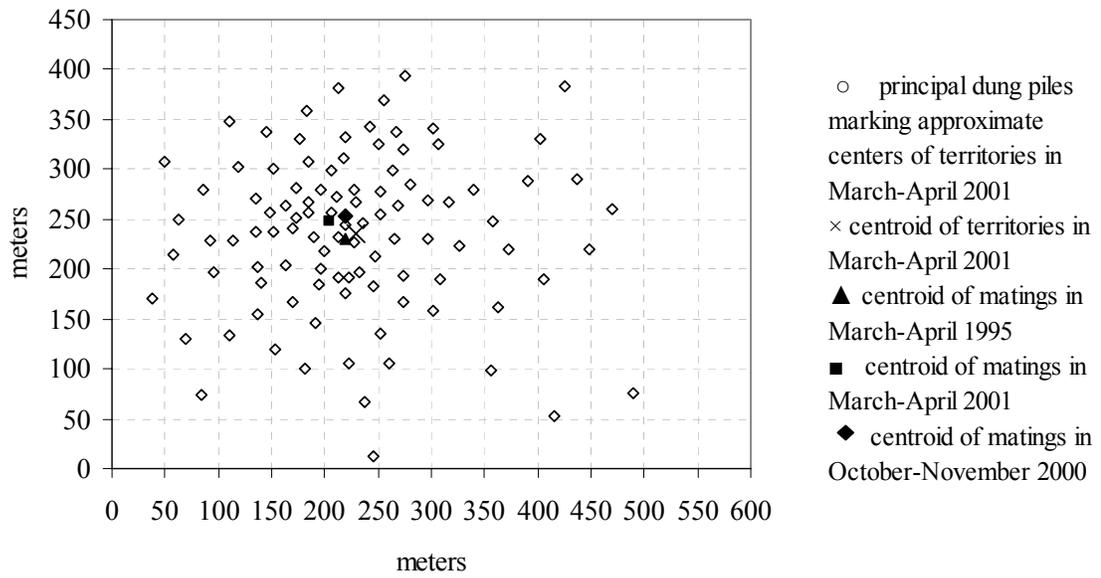


Figure 4-10. Location of centers of mating/courtship on the main lek in Velavadar during three different mating peaks (October-November 2000 and March-April 2001, this study; March-April 1995, Isvaran and Jhala 2000).

CHAPTER 5
MAINTENANCE OF INTRASPECIFIC VARIATION IN GROUP SIZE IN AN
INDIAN ANTELOPE: INSIGHTS FROM COMPARATIVE AND ECONOMIC
APPROACHES

Introduction

Grouping patterns, a primary feature of the social organization of a population, vary widely in nature from populations in which individuals are primarily solitary to those in which most animals live in large aggregations of hundreds, even thousands, of individuals (Lott 1991). How do we explain this wide variation in group size? Many ungulates show extensive intraspecific variation in social organization (e.g., fallow deer *Dama dama*, Thirgood et al. 1999; oribi *Ourebia ourebi*, Arcese et al. 1995, Brashares and Arcese 2002; topi *Damaliscus lunatus*, Gosling 1986; Uganda kob *Kobus kob* Fischer and Linsenmair 2000; sika deer *Cervus nippon*, Borkowski and Furubayashi 1998), and offer the opportunity to investigate the processes underlying such behavioral variation. I studied the relative importance of factors influencing variation in group size among and within populations of an Indian antelope, the blackbuck (*Antilope cervicapra*).

Group size distributions can be viewed as the outcome of decisions made by multiple individuals evaluating the benefits and costs associated with being in groups of different sizes (Pulliam and Caraco 1984). A wide range of costs and benefits to group living have been proposed. Benefits include reduced predation risk (Jarman 1974, Waterman 1997), maintenance of forage at an immature and nutritious stage (Fryxell 1991), increased hunting success (Bednarz 1988), better access to information about resources (Pacala et al. 1996), better defense of feeding resources or mates (Creel and

Creel 1995), and reduced risk of infanticide (Treves and Chapman 1996) in groups compared to solitary animals. Proposed costs to group living include increased feeding competition (Andelman 1986, Chapman et al. 1995), greater risk of acquiring diseases (Bertram 1978), and greater conspecific aggression (Gittleman 1989). Of all these variables, minimizing predation risk is arguably the most general and prominent benefit to grouping, especially in large herbivores such as macropods, bovids, and cervids (Brashares and Arcese 2002, Estes 1974, Gosling 1986, Hirth 1977, Jarman and Southwell 1986, Molvar and Bowyer 1994). Group living may reduce per capita predation risk because (1) predators are detected earlier (FitzGibbon 1990, Terborgh 1990), (2) the presence of other individuals reduces the probability that a particular individual is attacked (dilution effect, Hamilton 1971), (3) the rapid movement of many individuals confuses the predator (confusion effect, Pulliam and Caraco 1984), or (4) individuals cooperate and defend against predators (Crook 1972). Individuals in groups may also experience related benefits associated with predation such as spending less time in vigilance and more time feeding compared to solitary animals (Underwood 1982). The primary cost to group living is generally considered to be feeding competition (Chapman et al. 1995). Animals in groups may have to forage over larger areas and/or spend more time searching for food compared to solitary animals (Chapman et al. 1995, Terborgh and Janson 1986). Given these costs and benefits to group formation, factors that influence the shape and magnitude of the relationship between group size and any cost or benefit are likely to generate variation in group size.

The main factors thought to affect the payoffs to group formation are predator density, habitat structure, and resource abundance and distribution (Figure 5-1, Brashares

and Arcese 2002, Lott 1991). Predator densities influence the magnitude of predation risk experienced by individuals and thus affect the magnitude of benefits that individuals gain by joining larger groups. An increase in predator density is predicted to favor an increase in group size (Brashares and Arcese 2002). The second factor, habitat structure, is thought to affect group size by changing the payoffs to group formation in relation to predation. While group formation is an effective strategy against predation in open habitats with little predator cover (e.g., grasslands), hiding strategies are thought to be more effective against predation in closed forested habitats (Jarman 1974, Walther 1977). Therefore, group size is predicted to increase with habitat openness. The third factor, resources, is proposed to affect grouping primarily by constraining group size. Feeding competition, one of the main costs of group living, is expected to be modified by the abundance and distribution of resources (Chapman et al. 1995). Thus, when resources are abundant and distributed in large patches, animals are predicted to form large groups. However, when resources are relatively scarce and/or distributed in small, distant patches, large group sizes are not economical since the cost of competing for food outweighs the benefits from predation. Thus, group sizes are predicted to vary with forage abundance and distribution.

While studies from a range of taxa provide support for each of these factors, their relative importance in wild populations is rarely assessed simultaneously and is thus still not well understood. In this chapter, I use data from ten blackbuck populations (nine in India and one in U.S.A.) to evaluate the relative importance of predator density, resource distribution and abundance, and habitat structure towards large-scale variation in group

size. I also examine the correlates of variation in group size at a smaller scale, within a single population in a heterogeneous habitat.

To explore the processes by which different ecological factors, such as resources, might influence the payoffs to group size, I quantified the shape of the relationship between group size and various costs and benefits. The main cost I measured was distance moved while foraging (expected to be larger for larger groups). The benefits I measured were the probability of detecting a predator (expected to be better in larger groups) and the time allocated to foraging versus vigilance (expected to be greater in larger groups). The other main predation-related benefits, dilution and confusion effects, are difficult to measure since predation events in the wild are relatively rare. For similar reasons, it is difficult to measure actual risk of predation in groups of different sizes. Instead, I experimentally quantified the relationship between group size and the probability of detecting a predator, one of the main ways in which grouping is thought to reduce predation risk. In this chapter, I describe the shape of the relationship between group size and the various potential costs and benefits. I then discuss how the three ecological factors I focus on might modify the costs and benefits of grouping and thus lead to variation in group size.

Finally, I experimentally evaluated a main assumption underlying this study, that animals vary their behavior in response to changes in the costs and benefits to grouping. I report results from an experiment in which I quantified the relationship between group size and the probability of detecting a predator in two habitats that are expected to vary in predation risk. The habitats in which this experiment was conducted were open grasslands and grasslands with scattered shrubs. Predators are thought to be able to

approach groups better in habitats with greater cover (grasslands with scattered shrubs) than in open grasslands (Brashares and Arcese 2002, Hirth 1977, Jarman 1974). Thus, individuals in the first habitat were expected to detect predators earlier than those in open grasslands, controlling for group size. This is because individuals in habitats with greater cover are expected to be more vigilant.

Methods

Study Species

The blackbuck is an endangered antelope native to the Indian sub continent. It is a group living grazer found in a wide range of habitats from semi-arid grasslands to open forest. The main social groups found in blackbuck are (1) all-male groups (males of all age classes); (2) female groups (females of all age classes and immature males); and (3) mixed-sex groups (males and females of all age classes). Group sizes are reported to vary widely both among and within populations from solitary animals to groups of more than 500 animals (Ranjitsinh 1989). Groups do not defend territories but have overlapping home ranges (Prasad 1981). Groups are typically unstable and may split and re-form several times during a day (Mungall 1978).

Study Sites

I studied nine populations in India from August to November 1998 and 1999, and one in U.S.A. in May 1999. The nine Indian populations were Tal Chappar in Rajasthan, Savainagar and Velavadar in Gujarat, Rehekuri and Nannaj in Maharashtra, Rollapadu and Vanasthali in Andhra Pradesh, and Guindy and Point Calimere in Tamil Nadu. These sites were spread throughout the range of blackbuck in India and displayed a wide range of habitat type, predator density, and blackbuck density (details in Chapter 2). I also studied a free-ranging blackbuck population at Kyle ranch in Texas, U.S.A. Blackbuck

were introduced in Texas about 80 years ago and have multiplied rapidly (20,000 animals estimated in 1998, Mungall 1998). Blackbuck in Texas allow one to examine whether correlates identified for the Indian populations hold in a new environment.

I studied within-population variation in group size and individual behavior more intensively at Velavadar, Gujarat. This site, 36 km² in area, consists of a mosaic of grasslands, shrublands and mudflats. It holds one of the largest populations of blackbuck in India. The population size has fluctuated around 1850 animals since 1969 (Jhala 1993). Wolves, the main predators of adults, are reported to kill 35 to 39 blackbuck per wolf per year at this site (Jhala 1993).

Among-Population Variation In Group Size

Group sizes

Individuals were placed in the same group if they were within 50m from at least one of the other individuals (Clutton-Brock et al. 1982, Lingle 2001). Groups could be typically identified unambiguously since distance between neighbors within a group was usually less than 20m while distances between groups were more than 200m. At each study site, I quantified group sizes through total counts or transects. Total counts are a recommended census technique for species like blackbuck that aggregate and that inhabit relatively open areas (Sutherland 1996). At seven of the ten study sites, I conducted three to five total counts during morning or evening hours when animals were most active. During each total count, I systematically surveyed the whole study area and recorded the number and sex of individuals in each group I encountered. At three sites (Guindy National Park, Point Calimere, and Kyle ranch), the vegetation (forest with grassy openings) was too dense to perform total counts. At these sites, I walked six to seven 1 km strip transects 100 m wide and recorded the number and sex of individuals in all

encountered groups. Territorial males were not included in the estimation of group sizes since the factors that influence territory location and clustering are thought to differ from those affecting social group sizes.

Ecological variables

At each study site, I divided the area into four to seven units (depending on the area of the site), and laid a one km line transect in each unit. I measured habitat structure and resource abundance and distribution along these transects.

Habitat openness. The main aspect of habitat structure that is thought to influence grouping is the extent and distribution of open habitat. Therefore, I placed habitats in two categories – open and closed habitats (Chapter 2). Open habitats included those with less than ten percent of woody shrubs and trees more than one m high (mainly grasslands with or without occasional shrubs and trees, and bare ground). Closed habitats were defined as those with more than ten percent of woody shrubs and trees more than one m high (mainly shrublands and forest). At 50 meter intervals along each transect, I visually estimated the percentage of the area occupied by open and closed habitats in circular plots of 10 m radius. Habitat openness was calculated as the mean percentage of open habitat in a plot (estimates were first averaged across plots and then across transects).

Habitat homogeneity. For each transect, I counted the number of successive sampling points with open habitat as the major habitat type; thus, each transect can be broken down into segments of varying lengths (1 to 20), where each segment consists of successive points with open habitat. These segments are an index of the size of open habitat patches through which a transect ran. A transect that did not go through any open habitat was assigned a value of zero. A transect with all 20 points falling in open habitat represented maximum homogeneity of open habitat (value of 20). The mean length of

segments of open habitat was averaged across transects to obtain a measure of habitat homogeneity at each study site.

Forage abundance. At each sampling point along a transect, I measured grass height and visually estimated the percentage of area covered by grass in circular plots of one meter radius. Grass height \times percent cover was used as an index of forage abundance.

Forage homogeneity. Since patchiness of resources is proposed to influence grouping, I broadly estimated the patchiness of the main forage, grass. As in the case of habitat homogeneity, for each transect I counted the number of successive sampling points with grassland as the main habitat type. These segments are an index of the size of forage patches. For example, a transect in which all points lie in grassland habitat receives a score of 20, representing maximum homogeneity of forage. I then calculated forage homogeneity as the mean length of segments of grassland, first averaging across segments within a transect and then across transects. This index incorporates both the size of grassland patches and the distance between patches.

Predator density. I obtained estimates of the number of predators (i.e., wolves) of adult blackbuck known to use a study site from Forest Department records and from information obtained from researchers working at the sites. Using these estimates, I calculated predator density (number of wolves per km²) for each site.

Within-Population Variation In Group Size

I examined the correlates of variation in group size within a population at Velavadar in Gujarat from January to April 2000. I divided the study site into fourteen 1.1 \times 1.1 km sampling units. Every two to three weeks, I performed total counts of blackbuck in the study area three to five times on consecutive days. Total counts were

conducted in morning or evening hours and the number and sex of all individuals in the encountered groups were recorded. I measured habitat structure and resource abundance and distribution in the different spatial units. In each unit, I laid two 500m transects at random. Along each transect, I measured habitat characteristics and resources as described in the among-population comparison. Further, in each 1 m radius circular plot in which I measured overall grass abundance, I also visually estimated the percentage of area covered by three of the most preferred forage species (Jhala 1997) *Dichanthium annulatum*, *Chloris virgata*, and *Sporobolus madraspatensis*. The first species dominates the annual diet of blackbuck (30% to 70% seasonally). Together, they contribute 48% to the annual diet of blackbuck (Jhala 1997).

Individual Behavior

To quantify the shape of the relationship between group size and potential costs and benefits, I followed 60 adult female blackbuck in different groups varying in size in grasslands at Velavadar from February to April 2000, during October 2000, and from February to April 2001. These follows were performed on 36 different days spread throughout the study periods. I focused on adult females to control for the confounding effects of age and sex. All individual follows were ten minutes long and were performed during morning and evening hours, times when foraging activity is high (Mungall 1978, Jhala 1997). I focused on foraging periods since some of the main costs and benefits, such as feeding competition and time spent in vigilance versus foraging, are related to foraging activities. During each follow, I recorded the frequency and duration of several behavior patterns: (1) Alert (head up, ears held forward, still or moving) (2) Feeding (head down, ingesting or chewing, still or moving) (3) Standing (head up, ears held normal, still) (4) Food-searching (head down, moving, without ingesting or chewing) 5)

Moving (head up, moving, ears held normal or forward). To estimate potential travel costs associated with foraging in larger group sizes, I followed 24 different groups of varying size for one hour during morning and evening hours. Blackbuck show peaks in foraging activity in early morning and evening hours that are about two hours in duration (Mungall 1978, Ranjitsinh 1989). Thus, one hour follows are likely representative of behavior during peaks in foraging activity. During each group follow, I recorded the number of individuals in the group, noted the location of the centroid of the group at the beginning and the end of the one hour follow, and paced out the distance between these two locations. I used this distance as a measure of travel costs associated with foraging in groups of different sizes.

Finally, I conducted an experiment to test if animals in larger groups detected predators earlier and if this relationship was influenced by habitat type. I approached individuals in groups of different sizes from a fixed distance of 250 m (measured with a Nikon range-finder). Individuals were chosen at random from along the periphery or near-periphery of the group. Once the individual appeared to be alert to my approach (defined as alert behavior with the individual's head oriented in my direction), I halted and used a range-finder to measure the distance from my position to the individual. This experiment was also conducted during foraging periods (morning and evening hours). I conducted this experiment with 18 adult females in grassland habitat with scattered shrubs and with nine adult females in grassland habitat without any tree or shrub cover. Hunting by humans does not occur within Velavadar but has been known to occur outside the protected area (Ranjitsinh 1989). Since animals do move to some extent outside the protected area and since blackbuck showed alert behavior towards humans in all

populations, the experiment described above likely reflects the behavior of individuals towards a ‘predator.’

Analysis

For both among and within population comparisons, I used two measures of group size. I first calculated *mean group size* by first averaging group sizes within each transect (or total count) and then across transects (or total counts). Mean group size represents the size of the group that an observer would encounter on average in a population. However, this measure does not reflect the average group size that an individual associated with. To represent the social environment that individuals experienced, I used Lloyd’s *crowding index* (Lloyd 1967)

$$\frac{\sum_{i=1}^n x(x-1)}{N}$$

where x is the number of individuals in a group, n is the number of groups and N is the total number of individuals. A solitary male was counted as a group of 1 and was thus assigned a crowding index of 0. The crowding index represents the mean number of animals that an individual associated with. The crowding index was first calculated for each total count or transect and averaged across total counts or transects.

For among-population comparisons, I used parametric correlation analyses to explore relationships and stepwise regression procedures to identify the factor(s) that best explains the variation among populations in crowding index and in mean group size. Both group size measures were log-transformed to linearize their relationship with habitat openness and the homogeneity measures. The independent variables entered into the regression analysis were habitat openness, habitat homogeneity, forage abundance (log-

transformed) and forage homogeneity. Predator density could not be estimated in all populations (Texas) and hence was not included in the regression.

For within-population comparisons, I again used multiple regression analysis to identify the factors explaining the most variation in crowding index and mean group size among one km² sampling units. Mean group sizes were calculated by first averaging across groups within a census, then across censuses within a time period (3 to 5 days), and then across time periods. All variables were log-transformed.

In both among- and within-population comparisons, the results from analyses of the crowding index and mean group size were very similar. Here I mainly focus on results from the analysis of crowding index (See Tables 5-1 and 5-2 for results from the analysis of group size).

I used the observations from ten minute follows of adult female blackbuck to quantify the relationship between group size and potential costs and benefits. From the individual follows I calculated (1) frequency of alert behavior (number of alert events in ten minutes); (2) time spent in alert behavior (minimum = 0; maximum = duration of follow, 600 seconds); (3) frequency of feeding bouts (number of bouts in ten minutes, a bout was defined as feeding behavior lasting at least a second); (4) time spent in feeding behavior (minimum = 0; maximum = duration of follow, 600 seconds). I estimated the relationship between group size and these behavioral measures using regression analyses on log-transformed data (to meet linearity and normality assumptions). For the experiment testing the effect of habitat type on the relationship between group size and the distance to detection I used an Analysis of Covariance on log-transformed data.

Results

Among-Population Variation In Group Size

Mean group size varied among populations from three at Kyle ranch (maximum group size = 19) to 53 in Velavadar (maximum group size = 420). The crowding index better reflected the large differences among populations in the group size that individuals associated with. The crowding index ranged from a mean of 5 individuals in Guindy and Texas to a mean of 222 individuals in Velavadar. Group sizes also varied within each of the populations surveyed (Figures 5-2 and 5-3). Group size distributions were typically discontinuous (Figure 5-2 and 5-3).

Of the measured ecological correlates, variation in crowding index among populations was most closely correlated with habitat homogeneity (Pearson's $r = 0.80$, $N = 10$, $P = 0.005$; Table 5-1; Figure 5-4). Large groups were associated with areas where the main habitat consisted of large stretches of open habitat. Conversely, group sizes were smaller in woodlands where open habitat was sparse and found in small patches. The crowding index was less strongly correlated with habitat openness (Pearson's $r = 0.65$, $N = 10$, $P = 0.04$). Finally, the crowding index was weakly positively correlated with forage homogeneity ($r = 0.59$, $N = 10$, $P = 0.08$) and tended to increase with forage abundance ($r = 0.50$, $N = 10$, $P = 0.17$). In a stepwise regression with crowding index as the dependent variable and the above habitat and forage variables as independent variables habitat homogeneity was the only variable that entered the model ($R^2 = 0.69$, $N = 10$, $P = 0.003$; $\ln Y = 1.17 + 0.14X$). However, this result must be interpreted cautiously since habitat homogeneity was strongly correlated with two of the other three independent variables, habitat openness ($r = 0.91$, $N = 10$, $P = 0.0002$) and forage homogeneity ($r = 0.87$, $N = 10$, $P = 0.001$). I used annual rainfall as another measure of

forage abundance but found no relationship between rainfall and the crowding index ($r = -0.49$, $N = 10$, $P = 0.14$).

The crowding index was not correlated with predator density ($r = 0.07$, $n = 9$, $P = 0.84$). Since I relied on information from secondary sources for predator density estimates in several populations and since such densities are difficult to estimate in the absence of intensive sampling, the error around these estimates is uncertain. Therefore, a categorical analysis of predator density may be more appropriate. I placed populations in Low (wolves absent) and High (wolves present) categories of predation pressure and tested for a difference in crowding index between the two categories. The crowding index differed in the expected direction (Low: crowding index = 44, $SD = 66$; High: crowding index = 86, $SD = 94$). However, this difference was not significant (t-test on log-transformed data: $t = 1.07$, $df = 7$, $P = 0.32$).

Within-Population Variation In Group Size

Group sizes at Velavadar varied from solitary animals to groups of over 400 animals. Variation in crowding index among one km^2 sampling units was closely correlated with forage abundance (Pearson's $r = 0.77$, $N = 14$, $P = 0.0007$; Figure 5-5C) and forage homogeneity ($r = 0.79$, $N = 14$, $P = 0.001$; Figure 5-5D), but was not correlated with either habitat openness ($r = 0.14$, $N = 14$, $P = 0.63$; Figure 5-5A) or homogeneity ($r = 0.19$, $N = 14$, $P = 0.51$; Figure 5-5B). The habitat structure variables and the forage variables were not cross-correlated ($r < 0.5$, $P > 0.05$ in all cases). In a stepwise regression, forage homogeneity was the only variable that entered the analysis and explained a large part of the variation in crowding index among sampling units ($R^2 = 0.62$, $N = 14$, $P = 0.001$; $\ln Y = 1.3 + 1.2 \ln X$). The measure of forage abundance used (the

abundance of all grass species) was closely correlated with the abundance of three preferred forage species ($r = 0.98$, $N = 15$, $P < 0.0001$).

Individual Behavior

Females in larger groups were alert less frequently (Figure 5-6A, $R^2 = 0.42$, $N = 60$, $P < 0.0001$; $\ln Y = 2.9 - 0.3 \ln X$) and spent less time in alert behavior (Figure 5-6B, $R^2 = 0.47$, $N = 60$, $P < 0.0001$; $\ln Y = 5.8 - 0.7 \ln X$) than females in smaller groups. Both these relationships decreased disproportionately (as power functions) with group size. Females engaged in increasingly fewer (Figure 5-6C, $R^2 = 0.26$, $N = 60$, $P < 0.0001$; $\ln Y = 2.8 - 0.2 \ln X$) and longer feeding bouts ($R^2 = 0.40$, $N = 60$, $P < 0.0001$; $\ln Y = 2.9 + 0.3 \ln X$) when in larger groups. The time spent in feeding increased rapidly with group size (Figure 5-6D, $R^2 = 0.36$, $N = 60$, $P < 0.0001$; $Y = 317 + 48 \ln X$). However, larger groups moved over longer distances while foraging and this increase was proportionate to group size (Figure 5-7, $R^2 = 0.35$, $N = 24$, $P = 0.002$; $Y = 98 + 0.7X$).

Animals in larger groups detected my approach farther away than those in smaller groups (Figure 5-8). The distance to detection increased with group size in both open grasslands ($R^2 = 0.89$, $N = 9$, $P = 0.000$; $\ln Y = 4.32 + 0.16 \ln X$) and in grasslands with scattered shrubs ($R^2 = 0.60$, $N = 18$, $P = 0.000$; $\ln Y = 4.42 + 0.20 \ln X$). The relationship was decelerating in both habitats. Further, individuals in the habitat with greater cover (grasslands with scattered shrubs) detected my approach sooner than individuals in open grasslands (ANCOVA; $\ln(\text{Group size})$: $F = 31.13$, $df = 1$, $P < 0.0001$; Habitat: $F = 12.38$, $df = 1$, $P = 0.002$; $\ln(\text{Group size}) \times \text{Habitat}$: $F = 0.64$, $df = 1$, $P = 0.43$, Figure 5-8).

Discussion

I simultaneously evaluated three hypothesized selective pressures acting on group size and found that all three likely influenced group size variation in blackbuck, although their relative importance appeared to vary at different spatial scales.

Among-Population Variation In Group Size

Large-scale variation in group size among ten blackbuck populations was most closely correlated with predation-related factors, namely habitat homogeneity and openness. Groups were largest in sites dominated by large stretches of open habitat. Habitat structure is primarily thought to affect grouping by interacting with predation pressure and influencing the magnitude of anti-predatory benefits that animals experience from joining larger groups. Several authors have proposed that group formation reduces predation risk to a greater degree in open habitats than in closed habitats (Estes 1974, Jarman 1974). They argue that, in open habitats, predation risk is best reduced by grouping to improve detection of predators and to take advantage of dilution and confusion effects. In closed habitats, on the other hand, predation risk is best reduced by hiding and by reducing the probability of being detected by predators. Thus, individuals are expected to occur singly or in small groups in closed habitats (Estes 1974, Jarman 1974). In support of these arguments, an increase in group size with habitat openness has been reported both from interspecific (Estes 1974, Jarman 1974, Kaufmann 1974) and intraspecific comparisons (Barrette 1991, Hirth 1977, Walther 1977). The results from blackbuck further strengthen this argument, especially since a principal criticism of previous studies is that they only focused on habitat structure without including other potential correlates, particularly resources (Brashares and Arcese 2002). In blackbuck, variation among populations in group size was more strongly related to habitat structure

than to forage abundance or distribution. However, since habitat structure was correlated with one aspect of forage (homogeneity), more work is needed to evaluate whether habitat may have a stronger effect on large scale variation in group size than forage.

Interestingly, the density of the main adult predators of blackbuck, wolves, was not correlated with group size variation across populations. Since the error around some of the predator density estimates I obtained from secondary sources was uncertain, I also tested for the effect of predation by comparing mean group size of populations where predators are reportedly absent (at least in the past decade) and those where they are reported to be present. The difference between group sizes was not significant. It is possible that I was unable to detect a relationship because of a small sample size (nine populations). It is also possible that my measures of predation pressure (density and presence/absence of wolves) may not be adequate. The two other potential predators of adult blackbuck are village dogs and humans. I did not attempt to quantify either of these factors since they are not reported to be significant sources of mortality of adult blackbuck at the study sites I surveyed (Ranjitsinh 1989). For example, intensive studies at Velavadar indicate that kills of adult blackbuck by village dogs are very infrequent although dogs have been observed to chase adults (Ranjitsinh 1989). There are few reports of hunting by humans within the study populations in India although it may occur outside these protected areas. However, these two factors have not been studied as intensively as wolf predation and it is possible that even if village dogs and humans do not account for much actual mortality this may only reflect the success of attacks and not the frequency. Brashares and Arcese (2002) similarly report a lack of a relationship between predator density and group size for an African antelope. They suggest that first,

individuals may be responding to predation levels on a longer time scale than measured by current studies. For example, at many of the Indian populations wolves were reported to be present till as recently as fifty years ago (Ranjitsinh 1989). Alternatively, Brashares and Arcese (2002) suggest that predation may not be the primary selective factor influencing oribi social organization. Their conclusion is bolstered by their finding that another principal factor related to predation, habitat structure, was also not related to oribi group size. Unlike in oribi, the strong relationship between habitat structure and group size in blackbuck suggests that blackbuck show large-scale variation in group size primarily in response to variation in anti-predatory benefits associated with grouping. This variation in anti-predatory benefits of grouping likely arises from an interaction between variation in predation pressure and variation in habitat structure.

Variation in group size among blackbuck populations was not related to forage abundance but was positively correlated with forage homogeneity consistent with the hypothesis that the size and dispersion of resource patches can constrain group size (Chapman et al. 1995). However, this relationship was not as strong as the relationship between group size and habitat structure suggesting that resources are unlikely to be the primary factor influencing large-scale variation in social organization in blackbuck. It is possible that my measure of forage abundance (grass height * percent cover) did not sufficiently describe variation in abundance, especially of preferred forage species. Further, this measure does not incorporate forage quality. I chose the measure based on the trade-off between time spent at each study site and the number of study sites that I could survey. Annual rainfall has been shown to be a good predictor of primary productivity and has been used previously as an indirect measure of food quality and

abundance (Jarman 1979, Maher 2000). When I re-analyzed the data using annual rainfall instead of forage abundance, I still did not find a relationship with group size. Further, at Velavadar, the intensive study area, along with the overall abundance of grass, I also measured the abundance of the three main preferred grass species in each plot. The two measures were strongly correlated suggesting that overall grass volume is a good measure of forage abundance. Thus, while the distribution of forage may limit group size as suggested by the positive relationship between forage homogeneity and group size, forage is unlikely to be the primary factor influencing among-population variation in group size.

Within-Population Variation In Group Size

Contrary to the among-population comparison, variation in group size at a smaller spatial scale, within a population, was strongly related to forage distribution and abundance and unrelated to habitat structure. Groups were largest in sampling units with large grassland patches and smallest in units with small, scattered grassland patches. This is consistent with the hypothesis that resources influence group size. Why does habitat structure show a strong relationship with group size at the among-population level but not within a population? The most likely explanation is that the interaction between predation pressure and habitat structure varied much more across populations than within a population. There are two lines of evidence supporting this explanation. First, at the intensive study site (Velavadar) predation pressure appeared to be high over the whole study area. Wolf kills and movement were observed throughout the area (pers obs.). Given a strong predation pressure across the whole area, variation in habitat structure is unlikely to lead to much spatial variation in anti-predatory benefits to grouping. Secondly, although the habitat at Velavadar is heterogeneous, the variation in habitat

structure within this site (Coefficient of Variation in habitat openness = 22%) was not as high as the variation among populations (CV = 56%). Taken together, these observations suggest that the anti-predatory benefits to grouping did not vary much across the one km² sampling units at Velavadar and therefore group size was not related to habitat structure. The differences in group size among sampling units might then be best explained by resource conditions. Variation in forage homogeneity and abundance among sampling units could lead to variation in feeding competition and thus modify the costs to grouping to different degrees. For example, in sampling units with forage distributed in small patches, the costs of feeding competition may exceed the benefits from reduced predation risk, thus favoring small group sizes. On the other hand, in sampling units with large grass patches, resources may be sufficient to support large groups.

An interesting finding of the within-population comparison is that group size was more strongly related to forage distribution than forage abundance. This suggests that to predict grouping patterns information on forage abundance is not sufficient and information on resource distribution is essential. While there are some descriptions of the effect of food dispersion on ungulate social organization (Jarman 1974), most studies of ungulates largely focus on the relationship between food abundance and group size. Further, the few studies that address food distribution focus on differences in the dispersion of qualitatively different food sources (e.g., grass versus browse); less attention has been paid to variation in the dispersion of the same resource. In primates, a taxon in which food dispersion has received much more attention, studies show that in frugivorous species group size may be influenced by the size, density and dispersion of resource patches (Chapman 1988, Chapman et al. 1995). Interestingly, less is known

about the effect of food dispersion on folivores since they are often viewed as utilizing resources that are either non-depleting or less depleting compared to frugivores (Gillespie and Chapman 2001). The results from blackbuck (a grazer comparable to a folivore rather than a frugivore) suggest that patchiness in food resources may be as important in species that utilize apparently non-depleting patches as in species in which patches are clearly discrete and depletable.

Individual Behavior: Trade-offs Associated With Group Size

To identify the processes by which ecological factors such as habitat structure affect grouping, a description of the relationship between group size and potential costs and benefits to individuals is first needed. We can then study how ecological factors affect the nature and magnitude of these trade-offs and thus affect grouping. I studied the behavior of individuals in groups of different sizes and found that grouping in blackbuck appears to involve a trade-off between predation-related benefits and feeding-competition costs. While measuring actual predation risk is difficult, I was able to quantify the ability of individuals in groups of varying size to detect predators. This is one of the main ways in which grouping is thought to reduce the risk of predation (Pulliam and Caraco 1984). When I approached individuals in groups of different sizes from a fixed distance, individuals in larger groups detected my approach at a greater distance than those in smaller groups. The relationship between group size and distance to detection was decelerating. This function matches predictions from theoretical models of grouping that predation-related benefits should show a pattern of diminishing returns with group size (Pulliam 1973, Dehn 1990). Such a relationship also suggests that individuals gain the greatest incremental benefits from joining relatively small groups. Another proposed benefit to grouping, time allocation towards feeding versus vigilance, also showed a

pattern of diminishing returns with group size in blackbuck. The time spent feeding by an individual increased rapidly (as a logarithmic function) with group size while the time spent in alert behavior (generally assumed to represent vigilance, Underwood 1982) decreased rapidly with group size.

I also quantified a major cost associated with joining larger groups, namely increased travel costs while foraging (likely due to increased feeding competition in larger groups). I used the distance traveled by a focal group during one hour of foraging as a measure of travel costs. I found that individuals in larger groups moved over longer distances than those in smaller ones. The relationship between group size and the distance moved during an hour of foraging suggest that travel costs for an individual increase linearly with group size. Travel costs are not well studied in ungulates, but several primate studies report that larger groups travel further than smaller ones (van Schaik and van Noordwijk 1988).

The information on the relationship between group size and major costs/benefits can be used to predict optimal group size distributions in blackbuck. Per capita benefits increased rapidly, either as logarithmic or decelerating functions, with group size. Costs on the other hand appeared to increase less rapidly with group size. Since these benefits and costs were measured in different currencies (distance to detecting a predator, time spent in vigilance and foraging, distance moved), it is difficult to compare costs and benefits directly and arrive at quantitative estimates of net benefits. However, assuming that, when expressed in a common currency, the general shapes of the cost and benefit functions remain similar (although their relative magnitudes may change), it is possible to predict the general shape of optimal group size distributions. When I assumed a

decelerating benefit function and a linear cost function (Figure 5-9A), net benefits increased rapidly, peaked at intermediate group sizes and decreased slowly (Figure 5-9B). Individuals in a population are expected to adopt the group size with the greatest net benefits. Therefore, group size distributions might be expected to follow a unimodal distribution with the mean at the optimal group size and some error around the mean arising from variation in costs/benefits and in decision making (Figure 5-9C). However, observed group size distributions in blackbuck are very different (Figure 5-2). Unlike predicted distributions, they are not unimodal and they are typically discontinuous. Further groups are often much larger than expected given that predation- and foraging-related benefits asymptote rapidly at intermediate group sizes.

What might explain the discrepancy between predicted and observed distributions?

(1) The costs and benefits I measured may not fully describe the true costs and benefits. However, both theoretical treatments and empirical studies from other species (e.g., Blumstein et al. 2001), describe cost and benefit functions similar to those in blackbuck suggesting that the lack of sufficient information is currently an unlikely explanation. (2) Discontinuous distributions may result because condition affects optimal decisions. For example, if animals in poor condition minimize feeding costs while those in good condition maximize survivorship the group size distribution of such a population would display two peaks, one at small and one at large group sizes. This explanation predicts that condition is positively related with group size. However, condition in blackbuck showed a weak negative relationship with group size (Isvaran, unpublished data). Further, blackbuck groups were very fluid and groups formed, split, and re-joined through the day (this study, Mungall 1978). Individuals were also observed to move between groups of

different sizes suggesting that a simple relationship between condition and group size is unlikely. (3) Suboptimal and discontinuous distributions can result when group size distributions are viewed as the outcome of a game played by individuals in a population (Pulliam and Caraco 1984). For example, consider a population of 100 individuals in which the optimal group size is 80. The eighty-first individual has the option of joining the group and increasing the group size to 81, which would result in a reduction in fitness to all individuals. Alternatively, the individual could choose to remain solitary, an option that is associated with low fitness. The individual would be expected to join the larger group as long as its fitness is higher in the larger group than when it is solitary. The realized group size would then be sub optimal and larger than expected (Clark and Mangel 1984, Pulliam and Caraco 1984). Further, once groups reach a size beyond which a new individual joining the group experiences a lower fitness in the group than when it is solitary (the extreme end of the X axis in Figure 5-9B), new individuals would then be expected to either be solitary or form small groups. Thus, discontinuous distributions may result because individuals in nature are limited in the sizes of groups that they can join. Few empirical observations are available to test this argument since studies of grouping in ungulates typically focus on average group size in a population rather than on group size distributions. My findings from blackbuck suggest that to understand grouping patterns we need to study (1) the nature of the functions relating costs and benefits to group size; (2) variation in these costs/benefits arising from variation in ecological factors as well as variation in individual condition; and (3) interactions among individuals in a population.

General Conclusions

I found that habitat structure and resource abundance and distribution were strongly related to group size variation. Interestingly, their relative importance varied at different spatial scales. Habitat structure showed a stronger relationship with large-scale, among-population variation in group size. This suggests that large-scale variation in blackbuck group size is primarily in response to variation in the anti-predatory benefits of grouping. On the other hand, small-scale spatial variation in group size within a population was more strongly related to resource distribution and abundance than to habitat structure. Thus, within a population, spatial variation in resources appeared to lead to variation in group size by modifying the costs to grouping to different degrees at different locations in the study site.

I estimated the major costs and benefits associated with grouping and found that individuals in larger groups experienced larger travel costs. However, individuals in larger groups also experienced greater benefits, namely an increase in time spent feeding, a reduction in the time spent in vigilance, and the earlier detection of an observer. Interestingly, individuals in a habitat with greater predator cover (and presumably greater predation risk) detected an approaching observer sooner than individuals in more open habitats. These patterns in individual behavior taken together with patterns in the movement of individuals suggest that individuals are sensitive to changes in costs and benefits both associated with changing social conditions (group size) and with changing ecological conditions (habitat structure). Groups in Velavadar typically move through different habitats, often changing in size when they do so. Further, individuals were observed to move among groups of different sizes during the same day. Thus, the observed patterns in group size and in individual behavior likely reflect individuals

responding flexibly to immediate conditions rather than intrinsic differences among individuals or among populations.

Table 5-1. Estimates (mean±SE) of mean group size, crowding index, and ecological variables in 10 blackbuck populations.

	Guindy	Nannaj	Point Calimere	Rehekuri	Rollapadu	Savainagar	Tal Chappar	Texas	Vanasthali	Velavadar
Habitat openness (percent open habitat)	25±9	90±3	61±15	19±5	93±5	89±5	92±5	54±10	4±2	95±5
Habitat homogeneity (mean length of open habitat segments)	2±.5	9±2	7±3	2±.4	15±3	10±4	15±3	3±1	1±.3	15±3
Forage abundance (mean grass volume)	99±38	257±61	104±15	687±216	592±88	64±29	135±16	5±2	1±.1	742±343
Forage homogeneity (mean length of grassland segments)	4±0.9	5±1	2±3	2±.5	19±1	7±2	16±3	3±.7	.3±.3	10±4
Predator density (number of adult wolves per sq. km)	0	0.4	0	0	1	0.5	0	-	0	0.1
Crowding index	5±1	75±20	25±12	14±1	37±3	12±5	161±29	5±2	15±6	222±32
Mean group size	4±.6	19±2	8±3	6±1	10±2	6±2	37±5	3±1	3±1	53±6

Table 5-2. Results from correlation analyses between mean group size and ecological variables. Analyses were performed on both among- and within- population variation in mean group size. All data are log-transformed in the within-population analyses. Group size and forage abundance are log-transformed (to meet linearity assumptions) in the among-population analyses. Correlation coefficients (Pearson's r), number of populations/sampling units (N), and significance (P) are shown.

Variable	r	N	P
<i>Among-population comparison</i>			
1. Habitat openness	0.72	10	0.020
2. Habitat homogeneity	0.83	10	0.003
3. Forage abundance	0.62	10	0.054
4. Forage homogeneity	0.60	10	0.069
<i>Within-population comparison</i>			
1. Habitat openness	0.15	10	0.59
2. Habitat homogeneity	0.20	10	0.48
3. Forage abundance	0.69	10	0.004
4. Forage homogeneity	0.76	10	0.0001

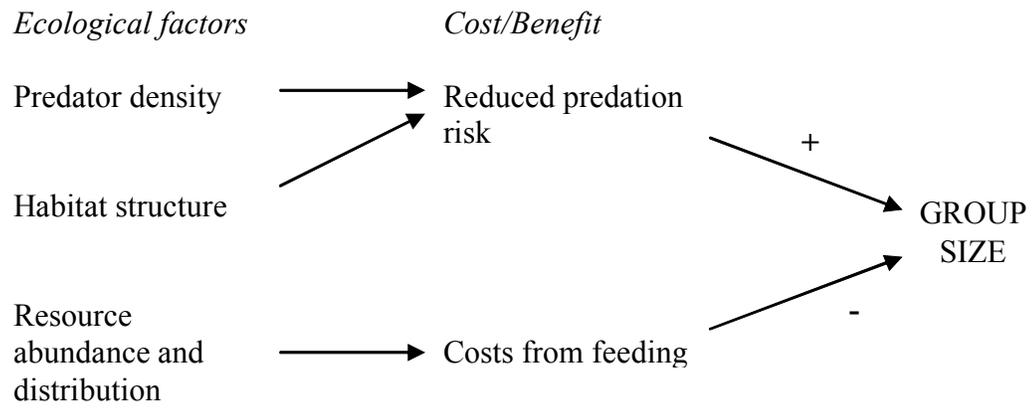


Figure 5-1. A general model of ecological factors affecting payoffs to group size.

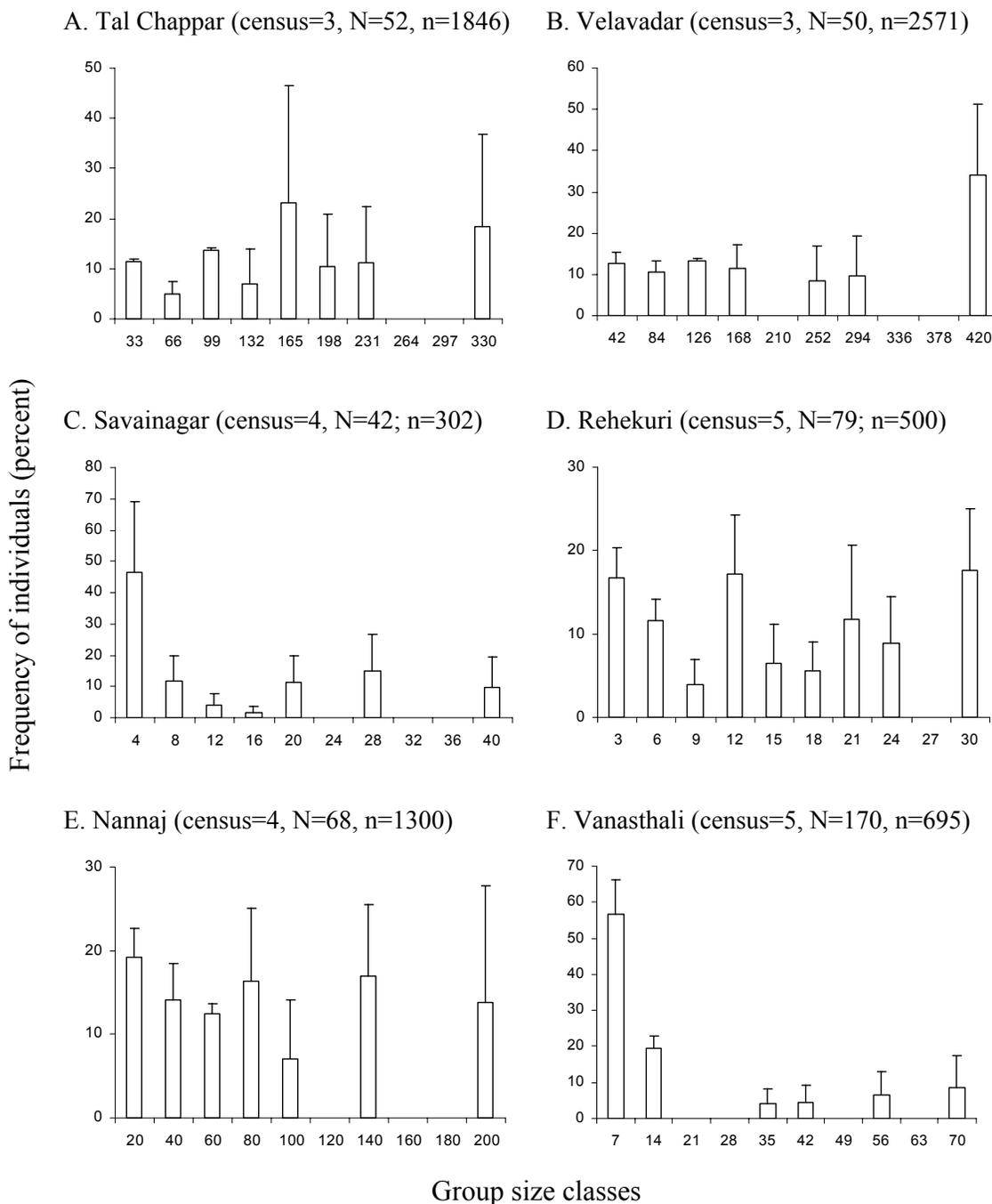


Figure 5-2 (A – F). Frequency distribution of individuals in groups of different sizes in six blackbuck populations. For each population, percent frequencies are means (with standard errors) of three to five censuses. N = number of groups (pooled over censuses); n = number of individuals (pooled over censuses). X-axis labels show upper limits of group size classes.

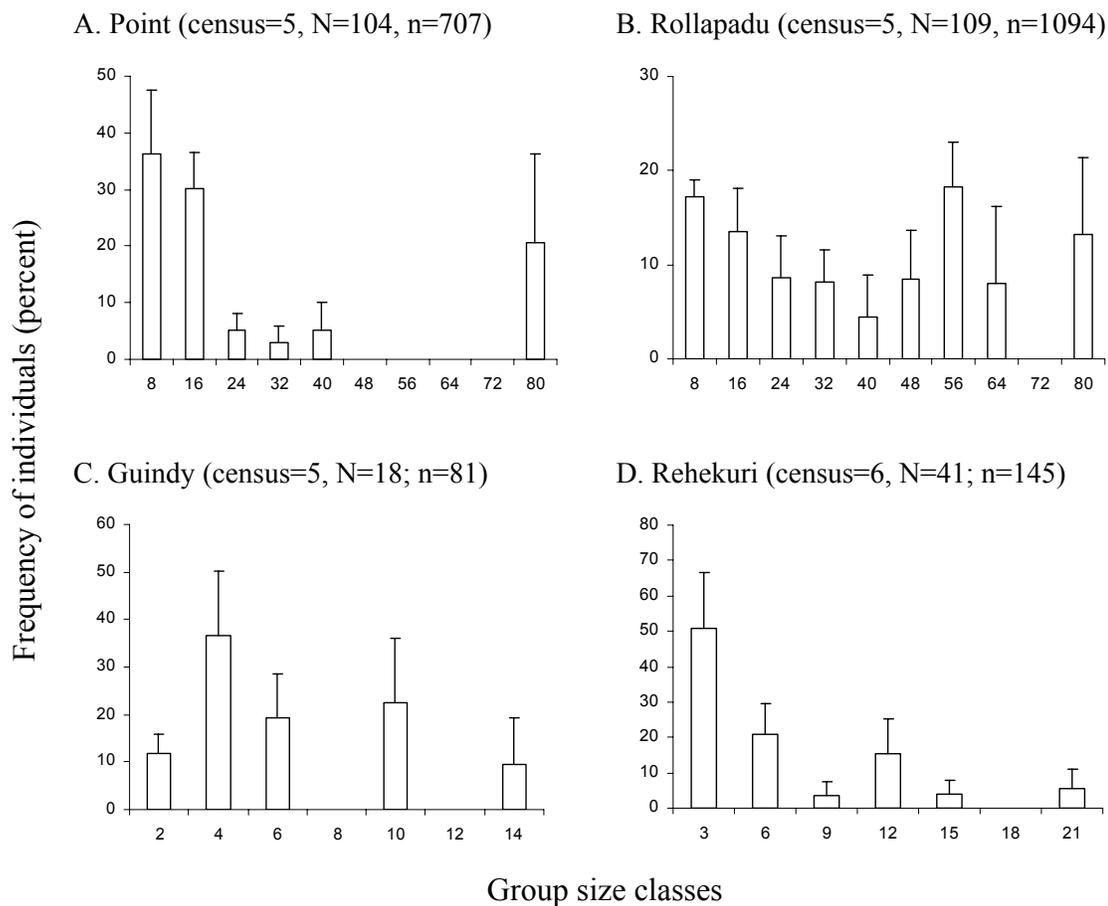


Figure 5-3 (A – D). Frequency distribution of individuals in groups of different sizes in four blackbuck populations. For each population, percent frequencies are means (with standard errors) of three to five censuses. N = number of groups (pooled over censuses); n = number of individuals (pooled over censuses). X-axis labels show upper limits of group size classes. In C and D, seven rather than ten group size classes were used since maximum group sizes were small.

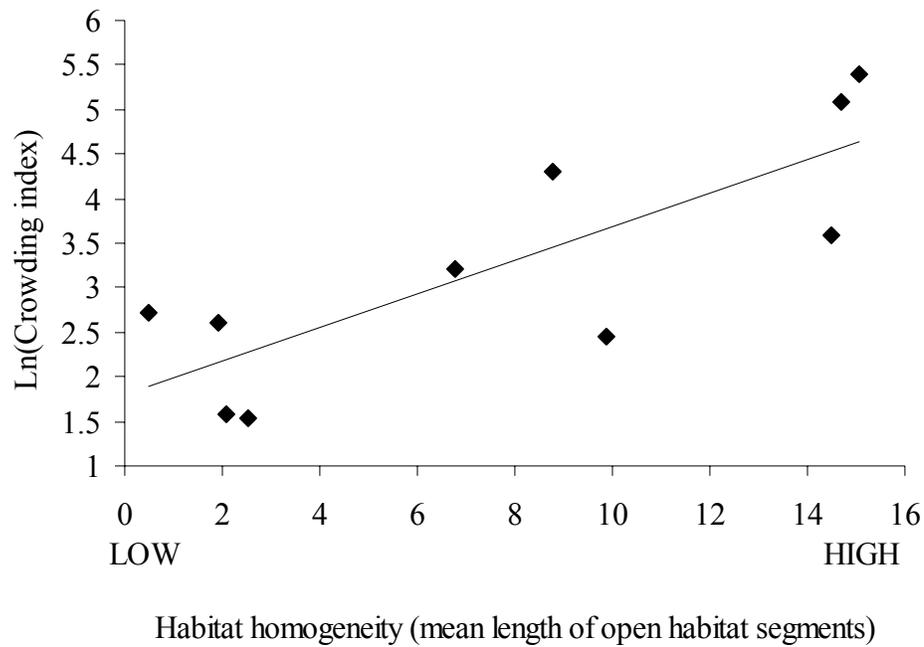


Figure 5-4. Relationship between habitat homogeneity and among-population variation in group size (Crowding Index). Each data point is a population. Since an exponential relationship provided the best fit (compared with other simple functions such as power, linear, and logistic) to this relationship, habitat homogeneity is plotted against log(crowding index) to linearize the exponential relationship.

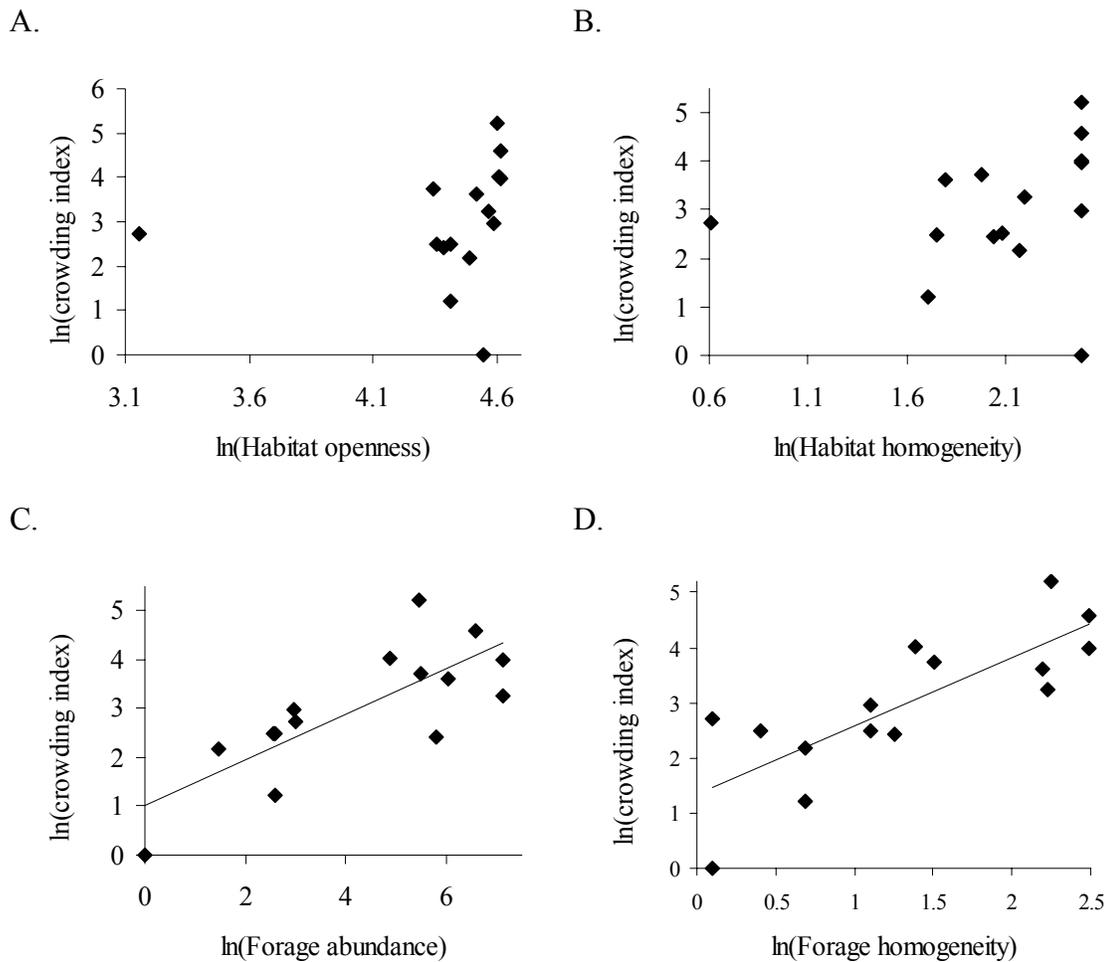


Figure 5-5. Relationship between within-population variation in mean crowding index and ecological variables: A. Habitat openness (mean percent of open habitat), B. Habitat homogeneity (mean length of open habitat segments), C. Forage abundance (mean grass height \times grass cover) *, D. Forage homogeneity (mean length of grassland segments) *. Each data point is a one km² sampling unit. * Significant correlations. Patterns of statistical significance were the same even when the outlier was removed in A and B.

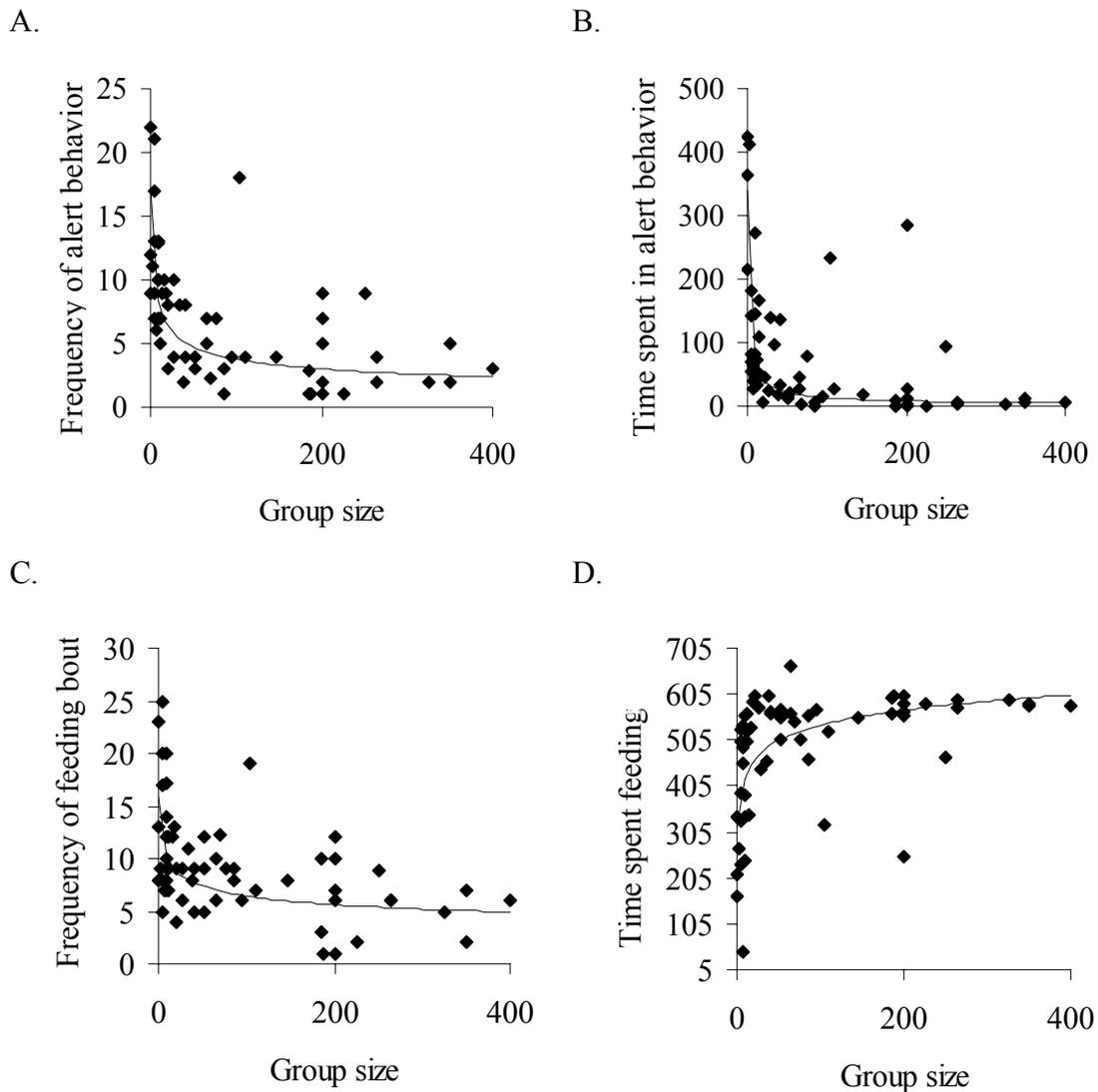


Figure 5-6. Relationship between group size and feeding and alert behavior: A. Frequency of alert behavior (occurrences in 10 minutes), B. Time spent in alert behavior (time in seconds during a 10 minute follow), C. Frequency of feeding bouts (occurrences in 10 minutes), D. Time spent feeding (time in seconds during a 10 minute follow). Each data point is an adult female blackbuck (N = 60).

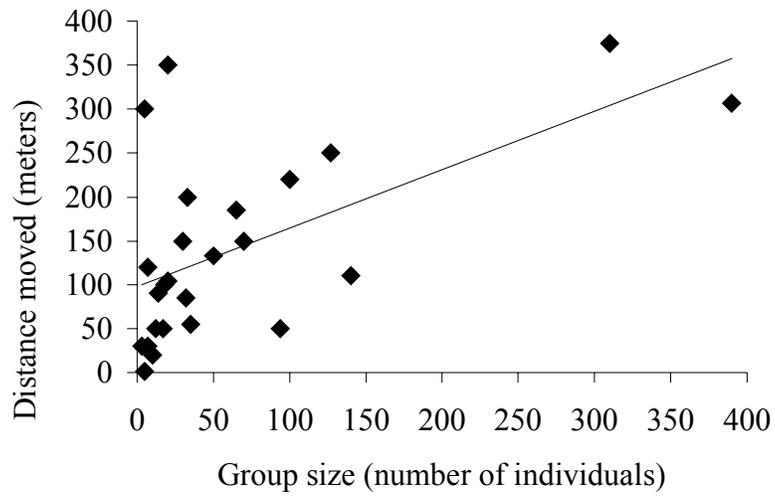


Figure 5-7. Distance moved while foraging by groups of different sizes during one hour group follows. Each data point is a group.

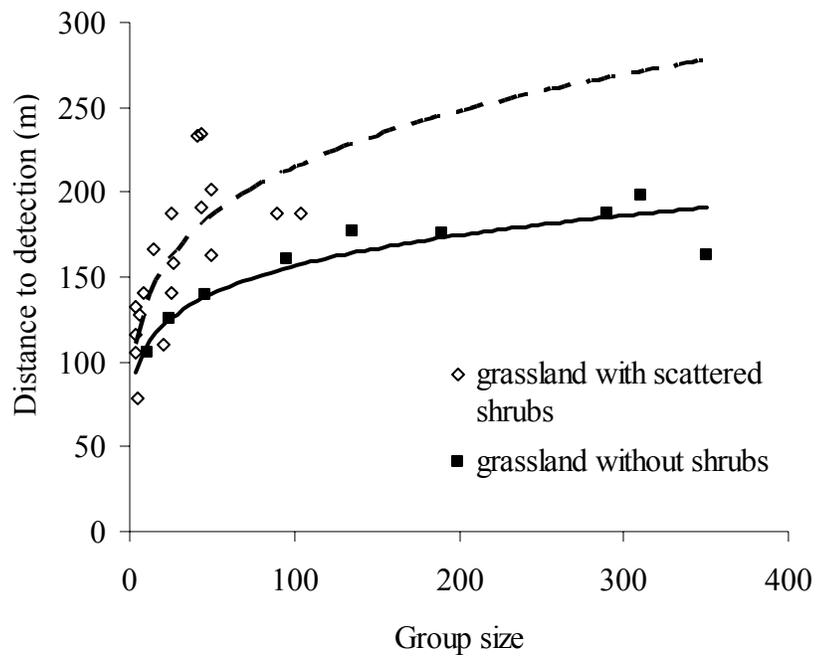


Figure 5-8. Relationship between group size and the distance at which the focal animal detects a potential predator in two different habitats. Open diamonds and dashed lines represent the relationship in grassland with scattered shrubs while solid squares and line represent the relationship in open grasslands.

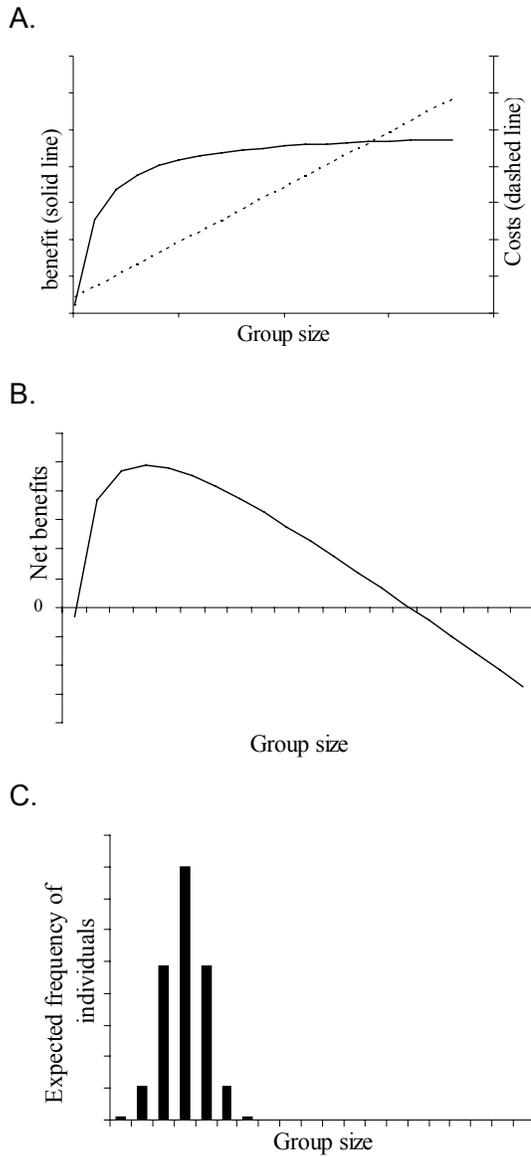


Figure 5-9. Predicting the general shape of optimal group size distributions in blackbuck given the observed general shape of functions relating costs and benefits to group size. A. An example of (1) a benefit function that incorporates the pattern of diminishing returns found in data on vigilance, foraging, and distance to predator detection, and (2) a cost function that is linear as indicated by data on travel costs. B. The net benefits arising from the benefits and costs shown in A. C. Group size distribution expected based on the pattern of net benefits (and assuming some random variation in cost/benefit and in decision-making).

CHAPTER 6 GENERAL DISCUSSION

In this dissertation, I sought to identify the selective pressures that currently influence the maintenance of a lek-mating system. I used a combination of modeling and empirical approaches and focused on a species with flexible mating behavior. I found that multiple factors acting at different spatial scales and on different aspects of mating behavior are likely to favor lekking.

In the first component of this study (Chapter 2), I focused on identifying the ecological, demographic and social conditions associated with large- and small scale variation in mating system. I studied nine populations in India and one in Texas, U.S.A. I also studied spatial variation in mating behavior more intensively at Velavadar, Gujarat. Rather than using discrete mating system categories, I described the mating system of a population in terms of the degree of clustering of mating territories. A striking finding of this component of the study was that territory clustering varied widely among blackbuck populations from solitary dispersed territories to large classical leks. The wide variation in territorial patterns suggests that lekking is best viewed as one extreme in an array of territory distributions. The main correlate of mating system variation in blackbuck was female group size. This factor explained most of the variation in male territory clustering both among populations and, at a smaller spatial scale, within a population. Extreme clustering (lekking), in particular, was associated with large female groups. Similar findings have been reported from many lekking bird and antelope species (Clutton-Brock et al. 1993, Höglund and Alatalo 1995). In contrast to the results from several studies,

(Balmford et al. 1993b, Thirgood et al. 1999), I found no relationship between territory clustering and population density. Thus, my findings suggest that territorial males respond to local patterns in female distribution (represented by group size) rather than population-level patterns when making decisions regarding territory location. A third important factor identified by previous studies (Clutton-Brock et al. 1993), female ranging, was less strongly correlated with territory clustering in blackbuck. However, like other studies (Clutton-Brock et al. 1993, Wiley 1991), I found that group size and ranging were correlated, with larger groups ranging over greater distances (Chapter 2, Chapter 5). Previous studies have not attempted to separate the relative effects of group size, population density, and female ranging on male mating behavior. The results from my blackbuck study suggest that, of the three important factors highlighted by previous studies, female group size is the primary correlate of large-scale variation in male clustering. While this is a correlational result, experimentally separating the effect of these factors may be difficult in wild populations of large mammals, like blackbuck. Interspecific comparisons may provide another way to evaluate the relative effects of density, group size, and ranging on mating system.

The results from examining mating system variation can be used to evaluate hypotheses of lek evolution. The hypothesis best supported by the strong correlation between territory clustering and female group size is the hot spot hypothesis (Bradbury et al. 1986, Gosling and Petrie 1990), that males establish territories in areas with high female encounter rates. Two other prominent hypotheses involving predation risk and male harassment of estrous females (Nefdt and Thirgood 1997) were not supported (Chapter 2).

While local female distribution may predict territorial male distribution and clustering among populations and within a population at the spatial scale of 1 km², this factor was insufficient to explain territory clustering at finer scales. Within each sampling unit, territory clusters occupied a very small part of the area used by females. For example, in the area of highest local female numbers (280 females/ km²) males did not defend dispersed territories covering the whole area; instead, they defended small territories, often less than 20 m in diameter. This suggests that, at scales less than 1 km², other selective factors (e.g., female choice, male-male competition, male harassment) must shape the sizes and clustering of territories.

Because female group size emerged as the main correlate of large-scale mating system variation in blackbuck, I also examined the factors influencing grouping patterns in this species (Chapter 5). I did not focus on females alone and addressed a larger question, the factors influencing variation in the size of social groups (female, bachelor, and mixed-sex groups) among and within blackbuck populations. I found that habitat structure and resource abundance and distribution were strongly related to group size variation. Similar findings have been reported from other large vertebrates (e.g., ungulates, Brashares and Arcese 2002; macropods, Jarman and Southwell 1986; primates, Chapman et al. 1995). Interestingly, I found that the relative importance of habitat structure and resources varied at different spatial scales. Habitat structure showed a stronger relationship with large-scale, among-population variation in group size. On the other hand, small-scale spatial variation in group size within a population was more strongly related to resource distribution and abundance than to habitat structure. However, since habitat structure and resources were correlated to some extent, especially

in the among-population comparison, more research is needed to establish their relative contributions to variation in group size.

I also estimated some of the main tradeoffs to grouping and found that individuals in larger groups experienced higher travel costs. However, individuals in larger groups also experienced greater benefits, namely an increase in time spent feeding, a reduction in the time spent in vigilance, and the earlier detection of an observer. Interestingly, individuals in a habitat with greater predator cover (and presumably greater predation risk) detected an approaching observer sooner than individuals in more open habitats. These patterns in individual behavior taken together with patterns in the movement of individuals suggest that individuals are sensitive to changes in costs and benefits both associated with changing social conditions (group size) and with changing ecological conditions (habitat structure). Thus, as in the case of male mating behavior, the variation in grouping behavior appears to reflect individuals responding flexibly to immediate conditions rather than intrinsic differences among individuals or among populations (Chapter 5).

While I used a comparative approach to address variation in male territory clustering at relatively coarse spatial scales, I used a modeling approach to investigate the factors influencing clustering at finer scales (Chapter 3). Using dynamic state variable modeling (Clark and Mangel 2000), an approach that can incorporate much complexity, I evaluated the factors influencing the decision of males to either display alone, join clusters of different sizes or join mixed-sex or bachelor herds. The factors evaluated were female mating bias for large clusters (female choice hypothesis, Bradbury 1981), reduction in predation risk in large clusters (predation hypothesis, Koivisto 1965), and

reduced male harassment of estrous females in large clusters (black hole hypothesis, Stillman et al. 1993). The dynamic model produced distinct sets of predictions for the three selective factors. Female mating bias generated the most extensive territory clustering. Furthermore, empirical evidence from several lekking species (Alatalo et al. 1992, Balmford et al. 1992, Höglund et al. 1993) suggests that female mating bias may naturally have the forms and strengths of nonlinear relationships with cluster size that were essential to generate clustering in the model. The model also emphasized the importance of estimating the shape of the relationship between a hypothesized selection pressure (here, female mating bias) and cluster size, since the same parameter modeled in different ways led to very different patterns in territory clustering or did not produce clustering at all.

More generally, the dynamic model highlighted the conditions most likely to lead to extreme clustering of male mating territories. Lek-like clustering was consistently produced when there were certain nonlinear increases in the benefits associated with clustering. Thus, any factor that generates such a relationship can potentially explain the evolution of lekking. Current literature (Balmford and Turyaho 1992, Nefdt 1995) suggests that predation risk and harassment, the two factors evaluated along with female bias, are unlikely to display the kinds of nonlinear relationships that led to clustering in the model. However, data on these two factors at clusters of different sizes are only available from a few studies (Balmford and Turyaho 1992, Nefdt and Thirgood 1997). More work is needed to examine the nature of their relationship with territory clustering. A second general result from the dynamic model was that factors, in interaction, predicted male mating decisions that were often different from predictions generated by

the same factors acting alone. For example, although predation risk did not favor much clustering when acting alone, in combination with female bias it enhanced the extent of clustering adopted by males in a population. Finally, a third general result from the dynamic model was the shape of the distributions of the mating options adopted by males in a population. Most of the model runs resulted in the expression of not more than two alternative mating tactics. The distributions of the proportion of males adopting different clustering tactics were often bimodal. This is consistent with empirical observations of lek sizes. In many lekking ungulate populations, males are found in small or large leks and intermediate lek sizes are rare (Deutsch 1994b, Balmford et al. 1992). Data from blackbuck also display this pattern (Chapter 2). Thus, the dynamic model presents some general ways in which the costs and benefits to clustering might interact to produce the lek size distributions seen in wild populations. Taken together, the results from the mating system comparison (Chapter 2) and the dynamic model (Chapter 3) suggest that large-scale variation in male clustering can be explained by the local distribution of females (hotspot hypothesis), whereas finer scale variation in clustering is best explained by a female preference to mate in larger clusters (female choice hypothesis).

In the comparative study (Chapter 2) and the dynamic model (Chapter 3) I focused on understanding lekking by examining variation in male territory clustering. However, another aspect of lekking that has received less attention is the size of male territories. Since mating territory sizes vary widely and do not always covary with male clustering, understanding the factors influencing variation in territory size may be important to understanding lek evolution. I constructed spatial models of territory size to examine the effects of two prominent factors: (1) competition between neighbors, and (2) female

movement in relation to mating on territory size. I tested predictions from these models using data from six blackbuck populations (Chapter 4). The models and empirical analyses suggested that, in blackbuck, territory size is most likely influenced by the interaction between a female mating bias for central territories and cluster size (the number of males in a cluster). The small territories typically seen in classical leks may be explained by a female bias for mating on central territories leading to increased competition for these locations, which, in turn, leads to a reduction in territory size. In addition, this process likely intensifies with an increase in cluster size so that the smallest territories are found in the largest clusters. Many studies of lekking species report a female preference for central lek-territories (Brø-Jorgensen 2002, Gosling and Petrie 1990, Höglund and Alatalo 1995) suggesting that this factor may influence territory size in other lekking species. Some studies also report a decrease in territory size towards the center of leks (Hovi et al. 1994), but few examine patterns in territory size across clusters of different numbers of males. Thus, the generality of the results from the models of territory size remains to be explored.

The findings from territory size variation in blackbuck have important implications for lek evolution. They suggest that even if male clustering, the factor that is typically explored by studies of lek evolution, is strongly favored, classical leks may not form if the conditions for a reduction in territory size are not met. For example, if there are very few males in a population, even if clustering is strongly selected for we may not see classical leks (clustering with small territories). This is because even if all males in a population cluster together, if the size of the cluster remains small, the model predicts that territory sizes will be relatively large. Comparative data from blackbuck provide

some evidence for this prediction. For example, the Point Calimere and Texas populations show similar levels of male clustering (standardized clustering indices of 2.0 and 2.1 respectively; Chapter 2). In both populations, about 50% of males adopted the lowest level of clustering while 50% of males adopted intermediate levels of clustering. However, the size of the territorial male population and absolute cluster sizes differed considerably between the two populations. The largest cluster in Texas contained five males while the largest at Point Calimere contained 15 males. Corresponding with this difference, the mean territory size at the largest clusters was 3 ha in Texas and 0.6 ha at Point Calimere. Therefore, although the two populations displayed similar relative levels of clustering, the territory distribution at Point Calimere could be characterized as exploded leks while that at Texas was hardly lek-like; instead, territorial males were found in much smaller aggregations (five males or fewer) with much larger territories. Hence, these data suggest that territory size is related not only to the relative level of clustering but also to the number of males in a cluster.

What might lead to variation in the number of males in a cluster (cluster size)? The first two parts of this study (Chapter 2 and Chapter 3) together suggest that variation in cluster size can be explained by variation in local numbers of territorial males and in the strength of selection for territory clustering. If the local number of territorial males is high (most likely in response to high local female numbers, Chapter 2), and if clustering is strongly favored (perhaps by a female mating bias, Chapter 3), then we might expect territorial males to form large clusters (Figure 1). Large cluster sizes are then predicted to lead to the small territories typical of classical leks (Chapter 4) Thus, understanding the

maintenance of lekking requires that we examine both the causes of variation in male clustering and the causes of variation in territory size (Figure 1).

Taken together, my work suggests that classical leks are an outcome of multiple factors acting at different scales on different aspects of male mating behavior. Large scale variation in the location of territories was best explained by local patterns in female distribution. Specifically, classical leks were associated with large female groups. A likely explanation of this pattern is that the number of females in an area (represented by group size) reflects the maximum potential mating opportunities for males in that area. Thus, extreme male clustering may not be favored in populations in which females move in small groups, since mating benefits may be too few to outweigh the costs of male-male competition in large clusters. While female distribution may explain patterns in the distribution of territories at relatively coarse scales, the dynamic model highlighted the type of factors that is most likely to favor male clustering at finer scales. Of the three factors evaluated in the model, female mating bias appeared to be most likely to show strongly nonlinear patterns with cluster size and thereby favor extreme clustering of male mating territories. Finally, the study of territory size variation identified two factors that may favor reduced territory sizes and hence classical leks: female bias for mating at the center of a territorial aggregation (or at restricted mating sites) in interaction with large cluster sizes (the number of males in a cluster).

This dissertation makes several important contributions to the understanding of lekking and, more generally, to an understanding of the evolution of mating systems. First, my work reinforces the argument that to understand a complex pattern of behavior, such as a mating system, we need to consider multiple factors acting on different male

and female behavioral traits (Davies 1991). Thus, the attempts by some previous studies to focus on a single aspect of male mating behavior (clustering of territories) and to isolate a single important selective factor may have led to conflicting results and the resulting controversy surrounding lek evolution. I found that multiple factors influence lekking in blackbuck. Second, my findings suggest that it is important to consider the spatial scale at which selective factors may act. For example, I found that the hotspot hypothesis was supported at relatively coarse spatial scales while the female choice hypothesis was supported at finer scales. These results also highlight the usefulness of studying behavioral variation at different spatial scales. Third, my modeling work emphasizes the importance of explicitly considering the shape of the relationship between cost and benefit factors and the trait of interest. I found that the same factor modeled in different ways led to very different predictions about male mating behavior. The models of the clustering and size of mating territories developed in this dissertation provide clear testable predictions. Investigating their generality to other lekking species represents a promising avenue of future research. Fourth, my work stresses the importance of female behavior in the evolution of mating systems. Female group size, female preference for mating in larger territorial clusters, and female preference for mating in the center of territory clusters were three prominent selective factors identified in this study. However, the role of female preference in lekking, especially in ungulates, is controversial. While some studies report that female preference might explain differences in male mating success within and between leks (Brö-Jorgensen 2002, Gosling and Petrie 1990), others emphasize the role of male-male competition and male harassment of estrous females (Clutton-Brock et al. 1993, Nefdt 1995, Thirgood et al. 1999). It is likely that all three

factors, female preference, male-male competition, and male harassment, influence mating patterns to different degrees in different species (Clutton-Brock et al. 1993, Höglund and Alatalo 1995); however, their interactions and relative contributions to variation in mating success have rarely been studied simultaneously. In particular, detailed observational and experimental data on the mating behavior of females are still lacking and my study underscores the argument that to understand lekking it is essential to understand the evolution of female mating behavior (Clutton-Brock et al. 1993, Höglund and Alatalo 1995). Results from blackbuck also suggest that it is important to study female mating behavior in relation to variation in male mating behavior (e.g., do females show similar preferences for mating in the center in small and large territory clusters?).

Through this dissertation, I have shown that the extraordinary lek mating system can be understood by (1) viewing the mating system as the outcome of multiple mating decisions that individuals make, such as where to locate territories, how many males to cluster with, and how large the territory should be; (2) examining the costs and benefits associated with different mating decisions; and (3) studying how ecological, demographic, and social conditions influence these costs and benefits and, in turn, the mating system. I have shown how different aspects of male mating behavior, including the defense of tiny territories in dense clusters in the face of intense aggression, can be explained by the behavior of females. This study also identifies the evolution of female mating behavior as an important focus for future studies.

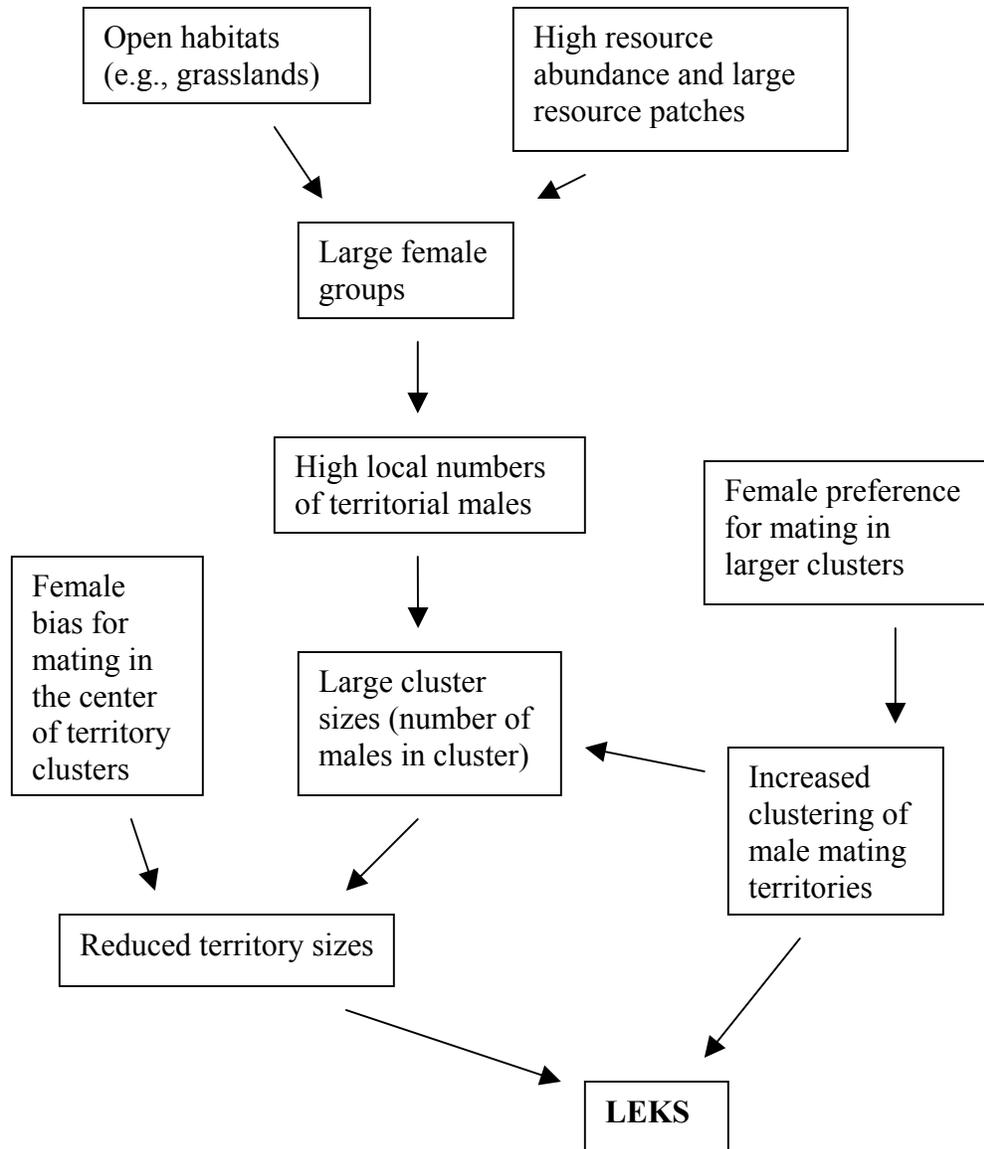


Figure 6-1. A schematic of the conditions favoring leks in blackbuck.

APPENDIX
CALCULATION OF THE STANDARDIZED CLUSTERING INDEX

Calculation of the Standardized Clustering Index (SCI) for one population. This measure of territory clustering reflects the level of territory clustering adopted by the average male in the population and is independent of the number of territorial males in a population. For example, in the Nanaj population, there were 30 territorial males distributed among 6 clusters. The sizes of clusters were 18, 4, 4, 2, 1, 1 individuals. The maximum possible cluster size was 30. This number was taken and divided into six equal intervals of cluster sizes that represent 6 levels of clustering from low (1-5 males) to high (26-30 males). The territorial males were then assigned to these levels of clustering depending on the size of the cluster they were found in:

Level of Clustering	Number of males
1 (1-5)	12
2 (6-10)	0
3 (11-15)	0
4 (16-20)	18
5 (21-25)	0
6 (26-30)	0

SCI (the mean level of clustering adopted by the average male) was:

$$(12 \times 1 + 18 \times 4) / 30 = 2.8$$

Similarly, at Vanasthali I observed 6 territorial males, four of which were solitary while two defended adjacent territories.

Level of Clustering	Number of males
1 (1-5)	4
2 (6-10)	2
3 (11-15)	0
4 (16-20)	0
5 (21-25)	0
6 (26-30)	0

The SCI was $(4 \times 1 + 2 \times 2) / 6 = 1.3$.

LIST OF REFERENCES

- Alatalo RV, Höglund J, Lundberg A, Sutherland WJ, 1992. Evolution of black grouse leks – Female preferences benefit males in larger leks. *Behav Ecol* 3:53-59.
- Alexander RD, 1975. Natural selection and specialized chorusing behavior in acoustical insects. In: *Insects, Science and Society* (Pimental D, ed). New York: Academic Press.
- Almeida JB, Macedo RH, 2001. Lek-like mating system of the monogamous Blue-black Grassquit. *Auk* 118:404-411.
- Andelman SJ, 1986. Ecological and social determinants of cercopithecine mating patterns. In: *Ecological aspects of social evolution*. (Rubenstein DI, Wrangham RW, eds). Princeton: Princeton University Press; 201-216.
- Anonymous, 1999. Climatological tables of observatories in India, 1951-1980. Government of India Publications.
- Anonymous, 2002. Comparative climatic data for the United States [1971-2000]. Southern Regional Climate Center.
- Apollonio M, 1989. Lekking in fallow deer: just a matter of density? *Ethol Ecol Evol* 1:291-294.
- Apollonio M, Festa-Bianchet M, Mari F, 1989. Correlates of copulatory success in a fallow deer lek. *Behav Ecol Sociobiol* 25:89-97.
- Apollonio M, Festa-Bianchet M, Mari F, 1990. Site-specific asymmetries in male copulatory success in a fallow deer lek. *Anim Behav* 39:205-212.
- Apollonio M, Festa-Bianchet M, Mari F, Bruno E, Locati M, 1998. Habitat manipulation modifies lek use in fallow deer. *Ethology* 104:603-612.
- Apollonio M, Festa-Bianchet M, Mari F, Mattioli S, Benedetta S, 1992. To lek or not to lek: mating strategies of male fallow deer. *Behav Ecol* 3:25-31.
- Arcese P, Jongejan G, Sinclair ARE, 1995. Behavioral flexibility in a small african antelope - group-size and composition in the oribi (*Ourebia ourebi*, Bovidae). *Ethology* 99:1-23.

- Balmford A, 1992. Social dispersion and lekking in Uganda kob. *Behaviour* 120:177-191.
- Balmford A, Turyaho M, 1992. Predation risk and lek-breeding in Uganda kob. *Anim Behav* 44:117-127.
- Balmford A, Albon S, Blakeman S, 1992. Correlates of male mating success and female choice in a lek-breeding antelope. *Behav Ecol* 3:112-123.
- Balmford A, Bartos L, Brotherton P, Herrmann H, Lancingerova J, Mika J, Zeeb U, 1993a. When to stop lekking: Density-related variation in the rutting behaviour of sika deer. *J Zool* 231:652-656.
- Balmford A, Deutsch JC, Nefdt RJC, Clutton-Brock TH, 1993b. Testing hotspot models of lek evolution: data from three species of ungulates. *Behav Ecol Sociobiol* 33:57-65.
- Barrette C, 1991. The size of axis deer fluid groups in Wilpattu-National-Park, Sri-Lanka. *Mammalia* 55:207-220.
- Bednarz JC, 1988. Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). *Science* 239:1525-1527.
- Beehler BM, Foster MS, 1988. Hotshots, hotspots and female preferences in the organization of lek mating systems. *Am Nat* 131:203-219.
- Beletsky LD, Orians GH, 1989. Familiar neighbors enhance breeding success in birds. *Proc Natl Acad Sci USA* 86:7933-7936.
- Bertram BCR, 1978. Living in groups: predators and prey. In: *Behavioural ecology: an evolutionary approach*. (Krebs JR, Davies NB, eds). Sunderland, Massachusetts: Sinauer Associates; 64-96.
- Blumstein DT, Daniel JC, Evans CS, 2001. Yellow-footed rock-wallaby group size effects reflect a trade-off. *Ethology* 107:655-664.
- Borkowski J, Furubayashi K, 1998. Seasonal and diel variation in group size among Japanese sika deer in different habitats. *J Zool* 245:29-34.
- Borner M, FitzGibbon CD, Borner M, Caro TM, Lindsay WK, Collins DA., Holt ME, 1987. The decline in the Serengeti Thomson's gazelle population. *Oecologia* 73:32-40.
- Bradbury J, 1981. The evolution of leks. In: *Natural selection and social behavior* (Alexander RD, Tinkle TW, eds). New York: Carron Press; 138-169.

- Bradbury JW, Gibson RM, Tsai IM, 1986. Leks and the unanimity of female choice. In: Evolution: essays in honour of John Maynard Smith (Greenwood PJ, Harvey PH, Slatkin M, eds). Cambridge: Cambridge University Press; 301-314.
- Bradbury JW, Gibson RM, McCarthy CE, Vehrencamp SL, 1989. Dispersion of displaying male sage grouse. II. The role of female dispersion. Behav Ecol Sociobiol 24:15-24.
- Brashares JS, Arcese P, 2002. Role of forage, habitat and predation in the behavioural plasticity of a small African antelope. J Anim Ecol 71:626-638.
- Bro-Jørgensen J, 2002. Overt female mate competition and preference for central males in a lekking antelope, P Natl Acad Sci USA 99: 9290-9293.
- Chapman CA, 1988. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. Behaviour 105:88-116.
- Chapman CA, Wrangham RW, Chapman LJ, 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol and Sociobiol 36:59-70.
- Clark CW, Mangel M, 1984. Foraging and flocking strategies: information in an uncertain environment. Am Nat 123:626-641.
- Clark CW, Mangel M, 2000. Dynamic state variable models in ecology: methods and applications. Oxford: Oxford University Press.
- Clutton-Brock, TH, 1989. Mammalian mating systems. Proc R Soc Lond B 235:339-372.
- Clutton-Brock TH, Deutsch JC, Nefdt RJC, 1993. The evolution of ungulate leks. Anim Behav 46:1121-1138.
- Clutton-Brock TH, Guinness FE, Albon SD, 1982. Red deer: Behavior and ecology of two sexes. Edinburgh: Edinburgh University Press.
- Clutton-Brock TH, Price O, MacColl A, 1992. Mate retention, harassment and the evolution of ungulate leks. Behav Ecol 3:234-242.
- Clutton-Brock TH, Green D, Hiraiwa-Hasegawa M, Albon SD, 1988. Passing the buck: resource defense, lek breeding and mate choice in fallow deer. Behav Ecol Sociobiol 23:281-296.
- Creel S, Creel NM, 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Anim Behav 50:1325-1339.
- Cresswell W, 1994. Flocking is an effective anti-predator strategy in redshanks, *Tringa totanus*. Anim Behav 47:433-442.

- Crook JH, 1972. Sexual selection, dimorphism, and social organization in the primates. In: Sexual selection and the descent of man. (Campbell B, ed). Chicago: Aldine; 1871-1971.
- Davies, NB, 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Anim Behav* 33:628-648.
- Davies NB, 1991. Mating systems. In: Behavioural Ecology. 3rd ed. (Krebs JR, Davies NB, eds). Oxford: Blackwell.
- Dehn MM, 1990. Vigilance for predators: detection and dilution effects. *Behav Ecol Sociobiol* 26:337-342.
- Deutsch JC, 1994a. Lekking by default: female habitat preferences and male strategies in Uganda kob. *J Anim Ecol* 63:101-115.
- Deutsch JC, 1994b. Uganda kob mating success does not increase on larger leks. *Behav Ecol Sociobiol* 34:451-459.
- Deutsch JC, Weeks P, 1992. Uganda kob prefer high visibility leks and territories. *Behav Ecol* 3:223-233.
- Deutsch JC, Weeks P, 1992. Uganda kob prefer high visibility leks and territories. *Behav Ecol* 3:223-233.
- Estes RD, 1974. Social organization of the African Bovidae. In: The behaviour of ungulates and its relation to management. (Geist V, Walther F, eds). Morges: IUCN; 166-205.
- Fischer F, Linsenmair KE, 1999. The territorial system of the kob antelope (*Kobus kob kob*) in the Comoé National Park, Côte d'Ivoire. *Afr J Ecol* 37:386-399.
- Fischer F, Linsenmair KE, 2000. Changes in group size in *Kobus kob kob* (Bovidae) in the Comoe National Park, Ivory Coast (West Africa). *Zeitschrift Fur Säugetierkunde* 65:232-242.
- FitzGibbon CD, 1990. Mixed-species grouping in Thomson's and Grant's gazelles: The antipredator benefits. *Anim Behav* 39:1116-1126.
- FitzGibbon CD, 1990. Why do hunting cheetahs prefer male gazelles? *Anim Behav* 40:837-845.
- FitzGibbon CD, Lazarus J, 1995. Antipredator behavior of Serengeti ungulates: Individual differences and population consequences. In: Serengeti II: Dynamics, management, and conservation of an ecosystem (Sinclair ARE, Arcese P, eds). Chicago: The University of Chicago Press; 274-296.

- Fryxell JM, 1987. Lek breeding and territorial aggression in white-eared kob. *Ethology* 75:211-220.
- Fryxell JM, 1991. Forage quality and aggregation by large herbivores. *Am Nat* 138:478-498.
- Gibson RM, Taylor CE, Jefferson DR, 1990. Lek formation by female choice: A simulation study. *Behav Ecol* 1:36-42.
- Gillespie T, Chapman CA, 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological constraints model. *Behav Ecol Sociobiol* 50:329-338.
- Gittleman J, 1989. Carnivore group living: comparative trends. In: *Carnivore behavior, ecology and evolution*. (Gittleman J, ed). Ithaca: Cornell University Press; 183-207.
- Gosling LM, 1986. The evolution of mating strategies in male antelopes. In: *Ecological aspects of social evolution* (Rubenstein DI, Wrangham RW, eds). Princeton: Princeton University Press; 244-281.
- Gosling LM, 1991. The alternative mating strategies of male topi, *Damaliscus lunatus*. *Appl Anim Behav Sci* 29:107-119.
- Gosling LM, Petrie M, 1990. Lekking in topi: a consequence of satellite behaviour by small males at hotspots. *Anim Behav* 40:272-287.
- Hamilton WD, 1971. Geometry for the selfish herd. *J Theor Biol* 31:295-311.
- Hirth DH, 1977. Social behavior of white-tailed deer in relation to habitat. *Wildlife Monographs* 53:1-55.
- Hjorth I, 1970. Reproductive behaviour in Tetraonidae. *Swedish Wildlife* 7:190-596.
- Höglund J, Alatalo, RV, 1995. *Leks*. Princeton: Princeton University Press.
- Höglund J, Montgomerie R, Widemo F, 1993. Costs and consequences of variation in the size of ruff leks. *Behav Ecol Sociobiol* 32:31-39.
- Höglund J, Robertson JGM, 1987. Female preference, male decision rules and the evolution of leks in *Gallinago media*. *Anim Behav* 40: 15-22.
- Houston AI, McNamara JM, 1999. *Models of adaptive behaviour*. Cambridge: Cambridge University Press.
- Hovi M, Alatalo RV, Höglund J, Lundberg A, Rintamaki PT, 1994. Lek center attracts black grouse females. *Proc Roy Soc Lond B* 258:303-305.

- Isvaran K, Jhala YV, 2000. Variation in lekking costs in blackbuck (*Antelope cervicapra*): Relationship to lek-territory location and female mating patterns. *Behaviour* 137:547-563.
- Jarman PJ, 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.
- Jarman PJ, 1979. Impala social behaviour: territory hierarchy, mating and the use of space. *Advances in Ethology* 21:1-92.
- Jarman PJ, Southwell CJ, 1986. Grouping, associations, and reproductive strategies in eastern grey kangaroos. In: *Ecological aspects of social evolution: birds and mammals* (Rubenstein DI, Wrangham RW, eds). Princeton: Princeton University Press; 399-428.
- Jhala YV, 1991. Habitat and population dynamics of wolves and blackbuck in Velavadar National Park, Gujarat, India. Ph.D. Dissertation. Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Jhala YV, 1993. Predation on blackbuck by wolves in Velavadar National Park, Gujarat, India. *Conserv Biol* 7:874-881.
- Jhala YV, 1997. Seasonal effects on the nutritional ecology of blackbuck *Antelope cervicapra*. *J Appl Ecol* 34:1348-1358.
- Jiguet F, Arroyo B, Bretagnolle V, 2000. Lek mating systems: A case study in the Little Bustard *Tetrax tetrax*. *Behav Proc* 51:63-82.
- Kaufmann JH, 1974. The ecology and evolution of social organization in the kangaroo family (Macropodidae). *Am Zool* 14:51-62.
- Koivisto I, 1965. Behavior of the black grouse, *Lyrurus tetrix*, during spring display. *Finn Game Res* 26:1-60.
- Kokko H, 1997. The lekking game: can female choice explain aggregated male displays? *J Theor Biol* 187:57-64.
- Langbein J, Thirgood SJ, 1989. Variation in mating systems in fallow deer (*Dama dama*) in relation to ecology. *Ethology* 83:195-214.
- Lank DB, Smith CM, 1992. Females prefer larger leks: field experiments with ruffs (*Philomachus pugnax*). *Behav Ecol Sociobiol* 30:323-329.
- Lewis RA, 1985. Do blue grouse form leks? *Auk* 102:180-184.
- Lingle S, 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. *Ethology* 107:295-314.

- Lloyd M, 1967. Mean crowding. *J Anim Ecol* 36:1-30.
- Lott DF, 1991. *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge: Cambridge University Press.
- Maher CR, 2000. Quantitative variation in ecological and hormonal variables correlates with spatial organization of pronghorn (*Antilocapra americana*) males. *Behav Ecol Sociobiol* 47:327-338.
- Mangel M, Clark C, 1988. *Dynamic modeling in behavioral ecology*. Princeton: Princeton University Press.
- Molvar EM, Bowyer RT, 1994. Costs and Benefits of Group Living in a Recently Social Ungulate - the Alaskan Moose. *J Mammal* 75:621-630.
- Mungall EC, 1978. *The Indian Blackbuck Antelope: A Texas View*. Kleberg Studies in Natural Resources, College Station.
- Mungall EC, 1998. Bucks in the black: India vs. Texas. *Exotic Wildlife* 8:1-3.
- Nefdt RJC, 1995. Disruption of matings, harassment and lek-breeding in Kafue lechwe antelope. *Anim Behav* 49:219-429.
- Nefdt RJC, Thirgood SJ, 1997. Lekking, resource defense, and harassment in two subspecies of lechwe antelope. *Behav Ecol* 8:1-9.
- Pacala SW, Gordon DM, Godfray HCJ, 1996. Effects of social group size on information transfer and task allocation. *Evol Ecol* 10:127-165.
- Prasad NLNS, 1981. Home range, dispersal, and movement of blackbuck (*Antelope cervicapra*) population in relation to seasonal change in Mudmal and environs. Ph.D. dissertation, Dept. of Biosciences, Saurashtra University, Rajkot, India.
- Prasad NLNS, 1989. Territoriality in the Indian blackbuck, *Antelope cervicapra* (Linnaeus). *J Bombay nat Hist Soc* 86:187-193.
- Pulliam HR, 1973. On the advantages of flocking. *J Theor Biol* 38:419-422.
- Pulliam HR, Caraco T, 1984. Living in groups: Is there an optimal group size? In: *Behavioural ecology: an evolutionary approach*. (Krebs JR, Davies NB, eds). Sunderland: Sinauer Associates; 122-147.
- Ranjitsinh MK, 1989. *The Indian Blackbuck*. Dehradun: Natraj Publishers.
- Stillman R, Clutton-Brock TH, Sutherland WJ, 1993. Black holes, mate retention and the evolution of ungulate leks. *Behav Ecol* 4:1-6.
- Stillman R, Deutsch JC, Clutton-Brock TH, Sutherland WJ, 1996. Black hole models of ungulate lek size and distribution. *Anim Behav* 52:891-902.

- Sutherland WJ, 1996. Mammals. In: Ecological Census Techniques (Sutherland WJ, ed). Cambridge: Cambridge University Press; 260-278.
- Terborgh J, 1990. Mixed flock and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *Am J Primatol* 21:87-100.
- Terborgh J, Janson CH, 1986. The socioecology of primate groups. *Ann Rev Ecol Syst* 17:111-135.
- Thirgood S, Langbein J, Putman RJ, 1999. Intraspecific variation in ungulate mating strategies: The case of the flexible fallow deer. *Adv Study Behav* 28:333-361.
- Thirgood SJ, Robertson A, Jarvis AM, Belbin SV, Robertson D, Nefdt RJ, 1992. Mating system and ecology of black lechwe (*Kobus*: Bovidae) in Zambia. *J Zool* 228:155-172.
- Trail PW, 1987. Predation and anti-predator behavior at Guianan cock-of-the-rock leks. *Auk* 104:496-507.
- Treves A, Chapman CA, 1996. Conspecific threat, predation avoidance, and resource defense: implications for grouping and alliances in langurs. *Behav Ecol Sociobiol* 39:43-53.
- Underwood R, 1982. Vigilance behaviour in grazing African antelopes. *Behaviour* 79:81-108.
- Walther FR, 1977. Social grouping in Grant's gazelle (*Gazella granti*) in the Serengeti National Park. *Zeitschrift für Tierpsychologie* 31:348-403.
- Waterman JM, 1997. Why do male Cape ground squirrels live in groups? *Anim Behav* 53:809-817.
- Wegge P, Rolstad J, 1986. Size and spacing of capercaillie leks in relation to social behavior and habitat. *Behav Ecol Sociobiol* 19:401-408.
- Widemo F, 1997. The social implications of traditional use of lek sites in the ruff *Philomachus pugnax*. *Behav Ecol* 8:211-217.
- Widemo F, Owens IPF, 1995. Lek size, male mating skew and the evolution of lekking. *Nature* 373:148-151.
- Wiley, RH, 1974. Evolution of social organization and life-history patterns among grouse. *Q Rev Biol* 49:201-227.
- Wiley RH, 1991. Lekking in birds and mammals: behavioral and evolutionary issues. *Adv Study Behav* 20:201-291.

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