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ASPECTS OF DOE PRONGHORN SOCIAL STRUCTURE ON THE NATIONAL BISON RANGE

By

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Aspects of Doe Pronghorn Social Structure on the National Bison Range (95 pp.)

Director: Lee H. Metzgar

Studies of ungulate social systems have emphasized the role of the male. To gain an overall view of an ungulate social organization, however, aspects of female social structure must also be studied. Pronghorns (*Antilocapra americana*) are appropriate for such studies because they are diurnal and highly visible. In the summers of 1975 and 1976, observations of single and grouped pronghorns on the National Bison Range, Moiese, Montana, provided data on pattern of doe use, doe group size, and interactions between does and territorial bucks. Observations of naturally marked and ear-tagged does were used to collect information on doe home range size and association between does.

Doe home ranges covered several buck territories. There was no evidence of herd home ranges. Does used relatively small areas of the study area at any point in time, showing seasonal movement throughout the home range. A seasonal trend in doe group size was apparent, with the largest groups occurring in May and early September, and smallest groups in June during the fawning season and in late September during the rut. Doe groups accompanied by a territorial buck were larger than unaccompanied groups, and doe groups with fawns contained more does than groups without fawns.

Doe group composition changed often. Known does formed moderately strong, random or negative associations with does occurring in the same area.

Does showed differential association with territorial bucks during the summer. Criteria for mate selection by females were not clear; in one area, most does bred with the buck does were seen with most often in the summer, but this was not the case in the other area.

The summer doe pronghorn social system, with varying group size and composition, was flexible and probably well adapted to changing environmental conditions and effective predator defense. Pronghorn social organization is comparable to the social organization shown by similar African bovids.

ACKNOWLEDGEMENTS

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I am very grateful to the women of 707 Dickinson, who lightened the sometimes heavy load of graduate student existence with their encouragement, support, and, most of all, their unfailing good humor. Special thanks to Patricia Dolan for her help and friendship.

I would like to thank my family for interesting me early in the wonders of the outdoors, and for their never-ending interest and support in whatever I have chosen to do.

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CHAPTER I

INTRODUCTION

The uniquely North American pronghorn (Antilocapra americana) is well known ecologically, but its social structure has only recently been investigated. Specific aspects of pronghorn social organization studied include territoriality (Bromley 1969 and 1977, Gilbert 1973, Kitchen 1974, Kitchen and Bromley 1974); buck, doe, and fawn social behaviors and interactions (Kitchen 1974); social groups (Prenzlow 1965, Pyrah 1970, Fichter 1972); courtship (Bromley and Kitchen 1974); and fawn behavior and socialization (Bromley 1969, Autenrieth and Fichter 1975). Interest in social systems has grown rapidly in recent years and focuses on the relations between individuals and the environmental conditions to which their social behavior is adapted (Crook 1970). Studies of ungulate social systems have concentrated on savannah-dwelling African species (Buechner 1961 and 1974, deVos 1965, Estes 1969 and 1974, Jarman 1974, Leuthold 1966, 1970, and 1977, Spinage 1969 and 1974). These large, diurnal, open country ungulates, like the pronghorn, are well suited to studies in social behavior because the animals can be observed without disturbing them. North American ungulates are generally difficult to observe, but some social behavior has been studied in elk (*Cervus elaphus*) (Altmann 1952, McCullough 1969, Knight 1970), moose (*Alces alces*) (Houston 1974), white-tailed deer (*Odocoileus virginianus*) (Brown 1974, Moore and Marchinton 1974), bison (*Bison bison*) (Fuller 1960), and mountain sheep (*Ovis canadensis*) (Geist 1971).

In pronghorn and most other vertebrate social systems studied, emphasis has been on the role of the male in the social system. The role of the female has generally been examined in much less detail, even though the behavior of the female is also of great importance. The female mammal generally makes a great parental investment, feeding and protecting the young until they can care for themselves. Factors affecting female as well as male reproductive success must be considered when examining the adaptive value of mating systems (Orians 1969, Downhower and Armitage 1971). To gain an overall view of a social system, it is therefore important to know how females are interacting with other females and with males.

Because a female is physiologically limited in the number of offspring she can produce compared to a polygamous male, she should maximize the fitness of her offspring by picking the best possible mate. Closer examination of female social organization may lead to greater understanding of mate selection by females. The mechanism of female choice, which operates when a female influences what male will sire her offspring, has received less attention and is a more controversial subject than male-male competition (Ghiselin 1974). Mate selection by females is harder to document in the field, perhaps because it is less physical and obvious (Wilson 1975). Even where female choice has been demonstrated, little is known about the basis on which females choose (Cox and Leboeuf 1977).

Geist (1974) proposed a theory relating ungulate social structure to ecological parameters. If certain basic ecological facts are known about an ungulate (e.g., open or closed habitat structure, food density and concentration, climax or seral stage), Geist's (1974) theory can be used to predict aspects of that ungulate's social structure (e.g., territoriality, monogamy or polygamy, sexually mono or dimorphic). I used this theory as a hypothetical base to predict the social structure of doe pronghorns on the National Bison Range, Moiese, Montana.

In terms of ecological variables needed for prediction from Geist's (1974) theory, pronghorns on the National Bison Range are inhabitants of an open, climax stage ecosystem on good to excellent range with high quality, diverse forage. From the theory, I then predicted the following pronghorn social characteristics:

a. development of a home range tradition and cohesion among individuals;

b. development of territoriality in males;

c. less territorial females maximizing energy available towards reproduction and lactation by lessening intra-specific aggression;

d. males that maximize fitness by capturing a high quality habitat and advertising to females; and

e. females that maximize fitness by selecting the male with the best quality habitat.

From these characteristics, I hypothesized a social system where a dominant male keeps and breeds a harem of females. The male, and to a lesser extent the females, would defend that territory against other males and perhaps other females after some female carrying capacity is reached. A male that establishes and defends a high quality habitat would attract, support, and breed females. A female choosing a male with a high quality habitat would copulate with a superior male and receive good forage for herself and her fawns. To successfully breed, a male should have a territory that could completely support at least two animals (himself and one doe). Therefore, an area where pronghorns breed would contain one or more buck territories, each with a doe or does. There would be no migration between doe groups (harems), so doe groups would be stable in terms of numbers and individuals. Association would be high among members of a group, and low or nonexistent between members of different groups. In any one doe group, individuals would have roughly the same individual home range, which would be very similar to the territory of "their" buck.

Kitchen (1974) conducted one of the most extensive studies of pronghorn social structure. His work, which was conducted on the National Bison Range from 1969 to 1971, concentrated on behavioral interactions between bucks, does, and fawns, and expanded Bromley's (1969) work on male territoriality on the National Bison Range. Dominant bucks establish territories and defend them against other bucks from March or early April through the rut in early fall. Kitchen found territories in three areas of the Bison Range.

According to Kitchen (1974), does formed three loosely organized herds from April to early October, and each herd occupied a separate home range in an area containing buck territories. Each of the three doe herd home ranges contained all the buck territories in that area. Kitchen found no rigid social structure within each doe herd. Doe group size and composition changed daily or even hourly. His work suggested considerable migration between doe groups within each doe herd home range. Association between does of the same herd was loose, with individual does and their fawns being the most consistent social unit. Kitchen observed no stability in size or composition of doe groups, and individual doe home ranges encompassed several buck territories.

Large discrepancies exist between the social structure I predicted from Geist's (1974) theory and Kitchen's (1974) observations. This study reexamines aspects of doe social structure on the National Bison Range. Specific objectives were to:

1) determine the relationships of does to geographic sites by looking at individual doe home ranges, areas used, and pattern of use;

2) determine the relationships of does to other does by measuring association between does;

3) determine the relationships of does to territorial bucks in terms of association with bucks and their territories; and

4) evaluate Geist's (1974) theoretical framework by comparing my results to the predicted social system.

CHAPTER II

STUDY AREA

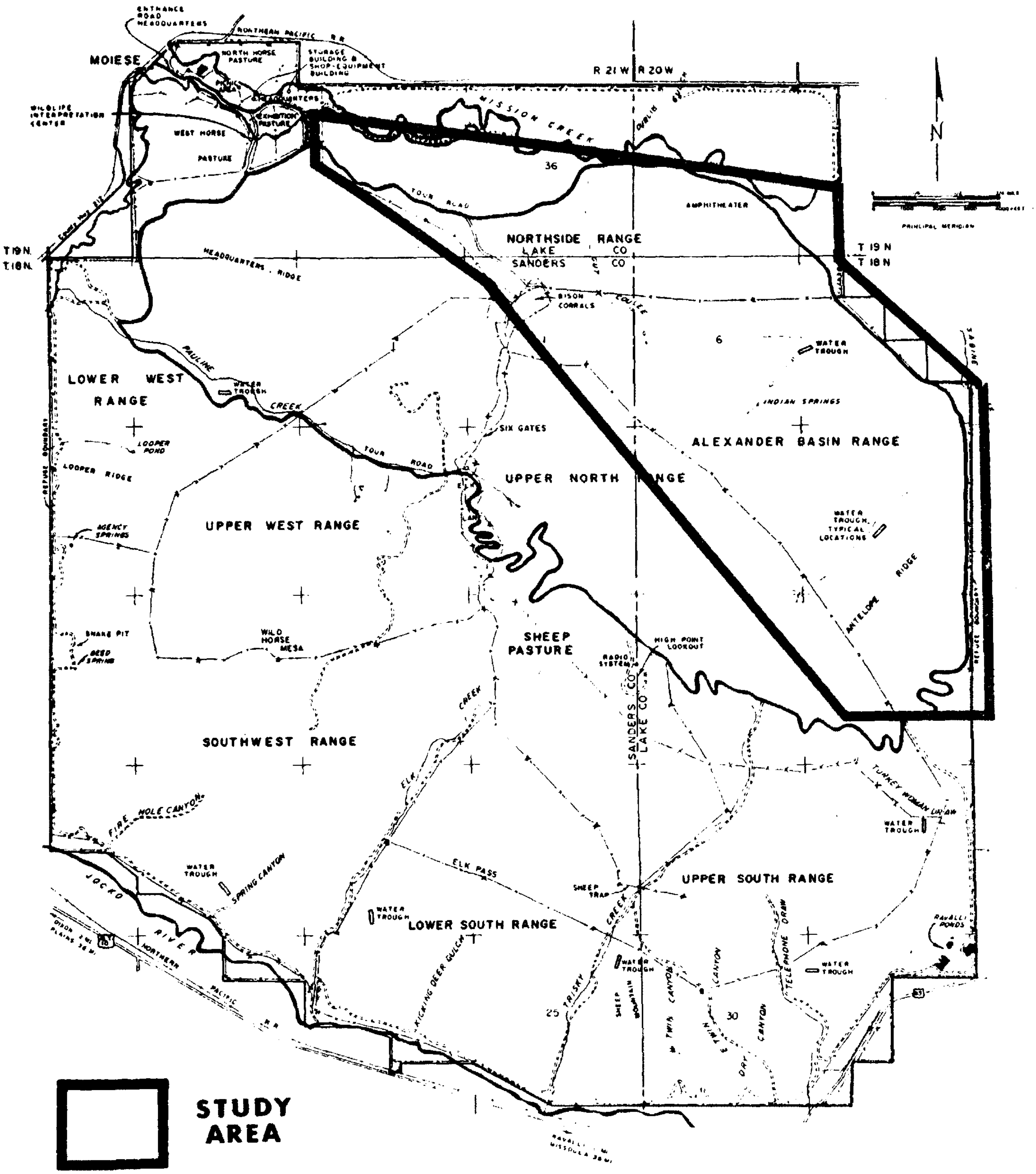
Description

The National Bison Range is located near the southern end of the Flathead Valley in Lake and Sanders Counties, Montana. The Range encompasses over 7,700 ha and ranges in elevation from 696 to 1,361 m. Pronghorns use the northern half of the Bison Range, which is predominantly grassland with small basins separated by low ridges. A 32 km gravel tour road runs through the center of the Bison Range, and circles back near the northern boundary.

The principle study area in 1975 was Alexander Basin. In 1976, I expanded the area studied to include the area along Mission Creek near the northern boundary (Fig. 1). These two areas correspond to Kitchen's (1974) "Alexander Basin" and "Northside" doe herd home ranges. The areas are separated by a fenced ridge.

The Bison Range is primarily a Palouse Prairie grassland typified by bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and rough fescue (*F. scabrella*). Major forbs are arrowleaf balsamroot (*Balsamorrhiza sagittata*), and aster (*Aster falcatus*). Snowberry (*Symphoricarpus occidentalis*) and fringed sage

Fig. 1. National Bison Range.



PROPOSED PLAN

NATIONAL BISON RANGE

Moiese, Montana

(*Artemesia frigida*) are the major browse species (Morris and Schwartz 1957, Kitchen 1974, Anonymous 1975, Reichel 1976).

Animals

Big game species present on the Bison Range include bison, elk, white-tailed deer, mule deer (*O. hemionus*), pronghorns, bighorn sheep, and mountain goat (*Oreamnos americana*). Pronghorns, mule deer, white-tailed deer, bison and elk were seen on the study area. The Bison Range is completely enclosed to restrict big game movements. It is divided into eight bison pastures but all other big game animals move through the Range. The internal fences are raised 0.3 to 0.6 m off the ground to allow pronghorns to pass under them.

Pronghorns are not endemic to the Bison Range. Fifteen were released on the Bison Range from 1910 to 1916, but that herd dwindled and finally disappeared in 1926. Pronghorns were reintroduced during 1951 in connection with a research project at the University of Montana. Those animals prospered, and currently there are approximately 120 pronghorns on the Bison Range. Pronghorn numbers are slowly decreasing because fawn mortality has been high since 1970 (Anonymous 1956-1975).

CHAPTER III

METHODS AND MATERIALS

Field work was conducted during two summers. I spent 49 days in the field between 26 June and 26 October 1975, mostly during July, August, and early September. During that time, I became familiar with the area and with the general habits of the pronghorns. In 1976, the study area was expanded, and 453 observations were collected in 67 days from 4 April to 11 August 1976. Unless otherwise specified, the data in this paper were gathered in 1976.

Known Animals

To gather information on locations of and associations between individual pronghorns, I had to be able to recognize individual animals. Several does and bucks had easily identifiable ear tags from previous studies. In 1975, I attempted marking does with paint spots using 7 cc Cap-Chur marking syringes and a Cap-Chur gun. This method was discontinued because of several problems. Range was necessarily very limited (< 30 m) to achieve high accuracy in placing paint spots where they would be most visible (flank or rump) and to avoid injuring animals by impact of the syringe. A low charge was used in the marking syringe because a high or medium charge sprayed the paint too quickly, atomizing the paint instead of spraying it on the animal. Three does and two fawns were marked with paint spots, but the paint spots were only visible for a day or two after the animals were marked. None of those pronghorns had unusual natural markings, so I could not tell if they had left the area or lost the paint spots. This paint (RamCote Vinyl Plastic Finish, Ramcote Products, Inc., Evergreen Park, Illinois) had been used to mark eagle feathers (O'Gara, personal communication), but had not been used on mammal hair. Dye has been used successfully to mark pronghorns in other studies (Hepworth 1965).

In some pronghorns, variation in horn structure and in white markings on the heads, necks, and bodies was large enough so I could readily recognize them. For positive field identification of individuals, I carried sketched outlines (after Kitchen 1974) on which I had drawn horns and markings of known individuals.

The ear-tagged animals, animals with very unusual horns or markings, or animals I had learned in 1975 could be recognized at the start of the 1976 field season. Less extreme differences between animals became more apparent as more and more time was spent observing pronghorns. Consequently, individuals became "known" at different times in the field season. Table 1 lists the

Table 1. Date first recognized, and histories of known pronghorns.

Pronghorn	Date recognized (1976)	History
Territorial bucks		
TH	4 April	Gained territory in 1973*
HH	4 April	
SB	4 April	Born 1970; gained territory in 1975*
AB	18 June	
LTH	27 June	Born 1969; held TH territory in 1972; in 1973 TH moved him off of it, and LTH moved to present territory.*
ST	20 July	
ORSL		Born 1969-71*
Does		
ORYL	4 April	
OO	4 April	Born in West Horse Pasture, 1969-71*
SH 1	4 April	
SH 2	4 April	
SSO	4 April	
YY	4 April	Born 1975 on Northside**
YL	4 April	Born 1975 on Northside**
NN	16 May	
HB	17 May	
LHB	5 June	
RSH	25 June	
RCH	26 June	
RHO	10 July	

*D. Kitchen, personal communication.

**J. Reichel, personal communication.

known pronghorns in 1976, the date on which they were first recognized, and partial history of a few of the animals.

Most recognizable does were ear tagged or had unusual horns. In general, neck markings were only used to confirm identification. The majority of pronghorn does have horns, but because horns are shed at irregular intervals (O'Gara 1969), they cannot be used as permanent identifying marks. I recognized more does than are listed in Table 1, but unlisted does were only recognized a few times during the field season. This could be because the does cast their horns and thus lost their identifying characteristics. For most of the field season, doe ORYL was recognizable both by her ear tags and her right horn which curved down over her right eye. When she was seen on 19 July 1976, she had lost the right curving horn and could only be identified by her ear tags.

Observations

Pronghorns were observed most easily from vehicles, having become habituated to the large volume of tourist traffic. Most of the study area could be observed from the tour road or the service roads. Several areas could only be reached by walking to them. Pronghorns could not be approached as closely on foot as in a vehicle, but I could still get close enough to identify known individuals. Both binoculars and a 15-60 variable power spotting scope were used to identify individuals.

To collect information on pronghorn associations and locations, I drove around the tour road in the morning and evening when the pronghorns were most active and most easily observed (Prenzlow 1965, Taylor 1972, Bromley 1977). I stopped periodically to scan the area to be sure I was seeing all pronghorns in the area, and I walked to the areas that could only be checked on foot. Any time one or more pronghorns were sighted, time, date, location, group size by age (fawn or adult) and sex, and known individuals present (if any) were recorded on data sheets, and location was marked on copies of an enlarged topographic map of the area. One set of maps covering the entire study area was used per day to record all pronghorn sightings. I observed groups until I was sure I had seen all does clearly enough to identify any of my known does that were in the group.

Once a day early in the morning, I scoped Alexander Basin from a high vantage point near the junction of the tour road and the Trisky Creek service road. From this point I had a clear view of the entire basin. Location and sex of every pronghorn in the basin was marked on a topographic map of the basin. Individuals could not be recognized from that distance.

Groups

Singles were distinguished from groups by being at least 30 m from other pronghorns or exhibiting independent action or movements. Any pronghorn within 30 m of any other pronghorn was considered a group member. At times, subgroups of perhaps three to five animals were discernible within larger groups. Subgroup membership was not recorded because continued observation of the entire group showed that subgroups were not maintained.

Analysis of Data

Before map location data could be analyzed statistically, it had to be reduced to a numerical record. To do this, doe locations were compiled on maps of the study area. For example, when examining doe home ranges, all sightings of a known doe for the field season were put on a map of the study area. When analyzing patterns of doe use, locations of all does seen during a 2-week time period were compiled on a map of Alexander Basin or the Northside. A grid was then placed over the map in question, dividing it into blocks, and the number of sightings per block was then recorded. This numerical record of doe locations was then compared to locations of other does, or to doe sightings taken during other time periods. Specific analyses are included in the appropriate results section.

CHAPTER IV

RESULTS

Doe-Area Relationships

Several types of information about doe-area relationships were available from the data collected on doe locations. The size of the area used and the pattern of use were determined both for all does seen during the field season and for the individual known does. This information was then used to examine doe social structure in several different ways.

Doe Home Range Size

I needed to determine the size of individual doe home ranges, because home range size influences the associations does form. In the predicted system, does have small home ranges and would therefore only associate with the few other does in their group. Kitchen (1974) reported doe home ranges as large as the regional doe herd home ranges which included several buck territories. In that system, each doe in the herd home range associated with all herd does and most territorial bucks in the area. Specifically, I needed to determine if doe home ranges covered one territory (predicted system), a discrete doe herd home range such as Alexander Basin or the Northside (Kitchen), or an even larger area.

Two tests of individual doe home range size were used. First, I tabulated the number of territories on which each known doe was seen (Table 2). Alexander Basin contained three territories and the Northside contained four territories on which does were seen. One Alexander Basin doe (OO) was only seen on two different territories, but the rest of the known does were seen on three or more different territories (mean for 13 known does = 4 territories). This disagrees with the predicted system, but is consistent with Kitchen's (1974) observation that does use more than one buck territory. Use of three or more territories also indicates that doe home ranges were at least as large as Alexander Basin or the Northside.

Second, I determined if does used an area larger than reported by Kitchen (1974). Known does were frequently seen in both Alexander Basin and the Northside (Table 3). Eight of the 13 known does were seen in both areas. Kitchen did not observe any doe migration between Alexander Basin and the Northside. Reichel (1976), in a short study of pronghorn fawn mortality on the National Bison Range in 1975, reported the movement of one doe from Alexander Basin to an area not included in this study, but did not observe any doe movements between Alexander Basin and the Northside.

Table 2. Number of buck territories each known doe was sighted on.

Doe	Number territories seen on
ORYL	5
SH 1	3
SH 2	4
SSD	5
YY	4
YL	5
OO	2
NN	3
HB	4
LHB	4
RSH	5
RCH	4
RHO	4

Table 3. Number of sightings of each known doe in the two areas of the study and the number of times each doe was known to change from one area to the other.

Doe	Number of sightings Northside	Alexander Basin	Total sightings	Shifts between areas (runs)
ORYL	20	18	38	7
SH 1	12		12	
SH 2	22		22	
SSD	37	1	38	
YY	3	38	41	3
YL	22	18	40	9
OO		33	33	
NN	22		22	
HB	26	1	27	2
LHB	7	16	23	4
RSH	4	5	9	
RCH	11	1	12	
RHO	7		7	

Five of the does seen both in Alexander Basin and the Northside were seen more than once on both areas. When those does switched areas, they usually stayed on that area for several weeks before moving again. All these does showed significantly fewer shifts between Alexander Basin and the Northside (one-sample runs test yields $p < .05$) than would be expected if the does were moving from one area to the other randomly.

Pattern of Use

Home range size is useful, but gives incomplete information on how does use an area. A doe could have been seen on more than one buck territory but still concentrated her activity in a subarea of her total home range, or a doe could have used all areas of her home range equally. To determine how individual does shared Alexander Basin and the Northside with other does, I compared individual doe use to general doe use as shown by all does on both areas throughout the field season.

General doe use was shown by compiling all doe sightings for the field season on one map of Alexander Basin or the Northside. A grid placed over the maps divided them into 4.05 ha blocks. Each block containing doe sightings was numbered consecutively, and the number of doe sightings per block counted, giving a numerical record of doe sightings in each section of Alexander Basin or the Northside.

A separate map was also kept for each known doe, showing the location of her sightings. These individual maps were divided into the same blocks and the number of sightings per block recorded. The proportion of sightings per block for each individual doe was compared to the corresponding proportion of sightings per block for general doe use using the Spearmann Rank Correlation Coefficient.

A doe using the same areas of Alexander Basin or the Northside in the same relative frequencies as other does would show a correlation of 1.0. If a doe used only a portion of Alexander Basin or the Northside or used very different sections than the rest of the does, the correlation coefficient would be negative. If a doe used the areas randomly in comparison to general use shown by other does, the correlation coefficient would be close to zero. To confirm this behavior of the correlation coefficient, the locations of a known doe were randomly placed on the Northside or Alexander Basin grids. The correlation between general doe use and the "randomized" doe was computed. These correlations were all close to zero (mean r_s for 13 known does = -.0437).

Most of the correlation coefficients for known doe use vs. use by all does were strongly positive (mean r_s = +.4418) (Table 4), indicating that each known doe tended to use the same areas in the same frequencies as other does. In other words, individual does contributed similarly to the composite maps, and did not show

Table 4. Spearmann Rank Correlation Coefficients and corresponding Z values comparing use by all does with use by known does.

	Northside		Alexander Basin	
Doe	r_s	Z	r_s	Z
ORYL	+.54	+3.48	+.18	+1.31
SH 1	+.42	+2.66		
SH 2	+.42	+2.67		
SSD	+.63	+4.06		
YY	+.38	+2.42	+.57	+4.13
YL	+.66	+4.20		
OO			+.64	+4.66
NN	+.48	+3.07		
HB	+.70	+4.47		
LHB	+.33	+2.12	+.57	+4.17
RSH	-.10	- .67	+.25	+1.84
RCH	+.38	+2.45		
RHO	+.44	+2.81		

differential use of subareas. The one negative correlation value was the result of RSH being seen a few times in one area of the Northside that does used infrequently.

Sightings for each known doe for the 1976 field season may not give a complete picture of the actual home range of those does. Sometimes after inspecting all the visible doe groups in Alexander Basin and the Northside, I still did not locate all my known does. Either I could not see the does, a possibility in the undulating hills, especially if the pronghorns were bedded (Bromley 1977), or the does were using areas not included in my study area.

To determine if there was a bias against seeing pronghorns in Alexander Basin, I recorded location and size of doe groups in two ways. First, early morning locations of pronghorns were mapped from the junction of the tour road and the Trisky Creek service road (Trisky Creek maps), overlooking the entire Alexander Basin. Second, I mapped the locations and sizes of doe groups seen from the tour road (daily maps). Alexander Basin contains five draws and many small hills that can hide pronghorns when viewed from the tour road. Daily maps may reflect this bias, and doe locations differed significantly between daily maps and Trisky Creek maps ($X^2 = 191.4$, 20 d.f., $p < .01$).

The differences in the two sets of data could reflect a bias against seeing does in Alexander Basin from the tour road, or it could reflect differential use of the basin during different times of the day. The Trisky Creek maps were always taken early in the morning while the daily maps were taken later in the morning and/or evening. In view of this possible bias, the actual home ranges of the known does could be larger than is apparent from the locations I recorded. The pattern of use shown could also be slightly different.

The Typical Doe Home Range

Some attributes of a typical doe home range on the National Bison Range can be generated from the above data and from my observations. Does used areas of the Bison Range that were relatively flat grasslands separated by low ridges. Does did not use all areas in Alexander Basin or the Northside equally; they were seen more often in lower areas such as draws and areas fairly close to water. Doe home ranges rarely extended outside areas not included in a buck territory. In size, a typical doe home range was larger than Alexander Basin or the Northside, although activity would be centered in one of these areas at any point in time. The movement of individually known does could not be distinguished from the collective movements of all does.

Seasonal Use of Alexander Basin and the Northside

I examined seasonal use to determine if the pattern of use shown in the previous section was the result of does using that entire area throughout the summer, or the result of differential seasonal use. If a certain number of does inhabit a large area with no seasonal change, the possibility of one doe meeting another particular doe is relatively low. The possibility of two particular does meeting is much higher if only small areas within the larger area are used by the does at any point in time.

Separate analyses for Alexander Basin and the Northside described doe use of each area throughout the field season. The field season was divided into 2-week periods. Fewer observations were taken in the spring than in the summer, so sightings in the first two time periods in Alexander Basin and the first three time periods in the Northside were lumped to obtain large enough numbers for analysis. Sightings of all does seen during each time period were compiled on maps and divided into blocks as before. This time, however, 16.2 ha blocks were used to obtain adequate sample sizes. The hypothesis of no seasonal change in doe locations was tested by chi-square. Significant differences in number of sightings per block for all time periods were found in Alexander Basin ($X^2 = 722.4$, 120 d.f., $p < .01$) and the Northside ($X^2 = 348.1$, 60 d.f., $p < .01$), indicating that does used areas in different frequencies during the course of the field season.

Alexander Basin seasonal use. Throughout the field season, does used the area along the tour road in Alexander Basin (Fig. 2). In late June and early July, does also started using the middle of the basin, and by mid-July they were often seen in the Indian Springs area. The does continued to use the lower area (Indian Springs and along the tour road, especially Sabine Creek) throughout July and early August.

Not all areas of Alexander Basin were used by does. The middle of the basin and the area around Indian Springs were not used until late June, though they were used frequently after that time. Does were rarely seen on or at the base of Antelope Ridge, or in the southeastern section of Alexander Basin.

Northside seasonal use. The areas of most intensive use in the Northside were the Amphitheater and the flat areas around the tour road as it comes from Alexander Basin (Fig. 3). These areas were used throughout the field season. For a short time near the end of June and beginning of July, does were seen on the ridge top between the Amphitheater and the Fawn Bowl. In early August does also started using the ridge top along the southern boundary fence between the Northside and Alexander Basin. At the same time, several doe groups were sighted west of the Fawn Bowl, at the junction of the tour road and the road leading to the slaughterhouse

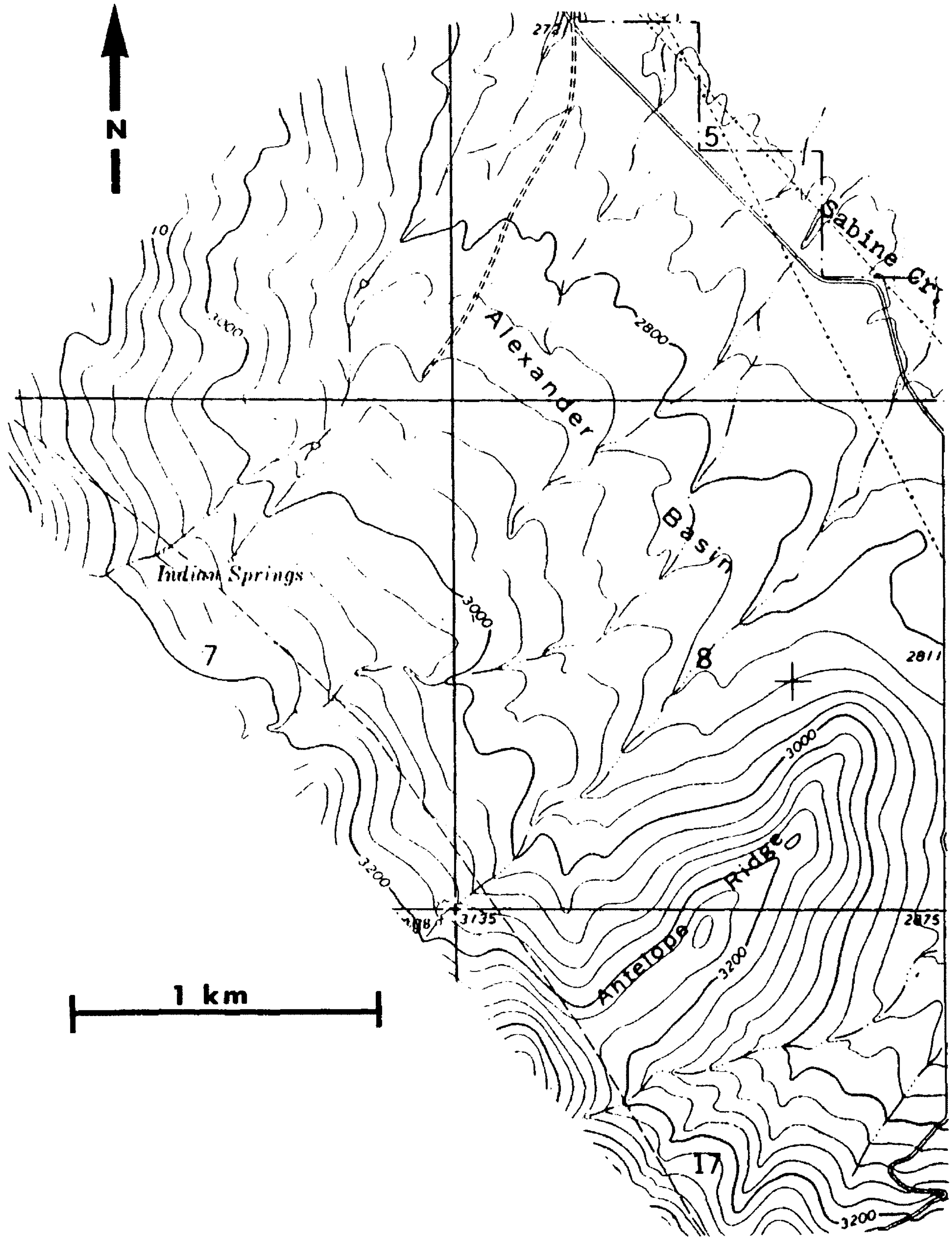
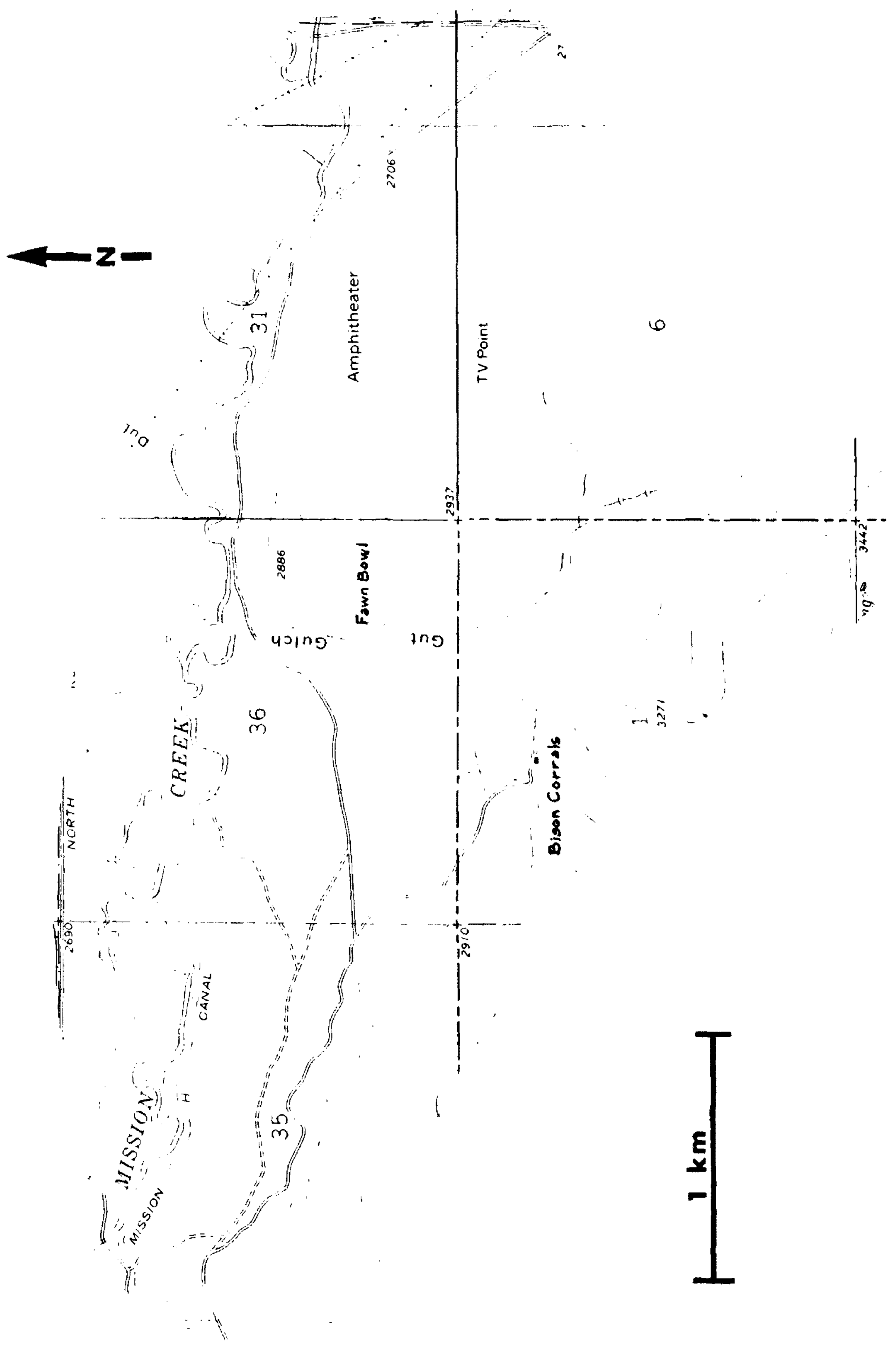

N
1 km
Alexander Basin
Sabine Cr
Indian Springs
Antelope Ridge
5
7
8
17
2800
3000
3000
3200
3200
3200
2811
2875
3135

Fig. 3. Northside, showing Amphitheater and areas along tour road used by does.


N
1 km
Amphitheater
TV Point
6
31
2706
27
2937
2886
Fawn Bowl
Gulch
Gut
36
1
3271
3442
Bison Corrals
CREEK
NORTH
2690
2910
CANAL
MISSION
MISSION
35

and bison corrals.

Does were not seen north of the tour road around Mission Creek. Does were rarely seen in the Fawn Bowl or around the slaughterhouse.

Doe-Doe Relationships

Relationships between does were analyzed by examining the stability in size and composition of doe groups. Theoretically, two basic options are open for both the size and composition of doe groups. The size of doe groups can be constant or can fluctuate over a period of time. Groups can always be composed of the same does, or groups can contain different combinations of individuals. The interaction of group size and composition leads to several possible arrangements of does that differ widely in how does interact with one another: a) constant doe group size and composition, b) constant doe group size and changing group composition, and c) changing doe group size and composition. Situation (a) was predicted from Geist's (1974) theory. To illustrate this situation, consider Alexander Basin with 14 does, arranged in one group of eight and one group of six. The same does would always be in the same group, so does would associate only with the does in their group.

In situation (b), the 14 does in Alexander Basin might be arranged in a group of eight does and a group of six does, but membership would not be stable. Does would shift between groups, and would associate with all 13 other does seen in Alexander Basin. This might occur, for instance, if subareas within Alexander Basin had foraging room for only a certain number of animals. In this case, the group of eight might always be found in the same area, and the group of six in a different area. Shifting between groups might occur if each subarea contained different desirable forage.

Situation (c) is the system described by Kitchen (1974). He observed daily or even hourly changes in group size and composition. The 14 does in Alexander Basin might be arranged in one group of 14 one day while the next day they might be arranged in a group of three, a group of six, and a group of five. The third day they might still be in groups of three, six, and five, but different does might make up these groups.

Typical Doe Group Size and Composition

The size and composition of doe groups on the National Bison Range on 28 July 1976 is fairly typical and illustrates the grouping tendencies of pronghorns. During the morning in Alexander Basin, three groups of does were seen: one group of eight containing known does LHB, YL, and YY was accompanied by territorial buck TH; after 20 minutes, the second group of three does merged with the first group; the third group of 12 unknown does, located at the opposite side of the basin from the first group, was accompanied by territorial buck LTH. That evening in Alexander Basin, one doe group of 10 containing YY and LHB was seen near Sabine Creek, unaccompanied by a territorial buck, though they were in TH's territory.

In the Northside, one group of nine does containing SSD, SH 2, HB, RCH, and one fawn, was seen with territorial buck AB in the Amphitheater during the morning. In the evening a group of 10 does with ORYL, YL, SSD, SH 2, NN, HB, and one fawn was seen again with AB, but the group had moved from the Amphitheater over a ridge to an area closer to the tour road.

The data from 28 July illustrates several traits of pronghorn doe groups that I observed to be characteristic: changing group size, changing group composition, and doe groups not always accompanied by a territorial buck.

Doe Group Size

The size and composition of doe groups, defined in this study as any animals within 30 m of each other, changed daily or even hourly. Some immediate causes of this were obvious. When chased or on the appearance of danger, smaller pronghorn groups would band together into one large group when fleeing. When the danger disappeared, these larger groups would break up into smaller groups immediately or would stay together for a while before disbanding. Territorial bucks also actively influenced the size of doe groups by herding stray does into their group or trying to stop does from leaving the group that was with the buck at the time.

I needed to know if any trends or factors not immediately observable influenced the size of doe groups. The following factors were investigated.

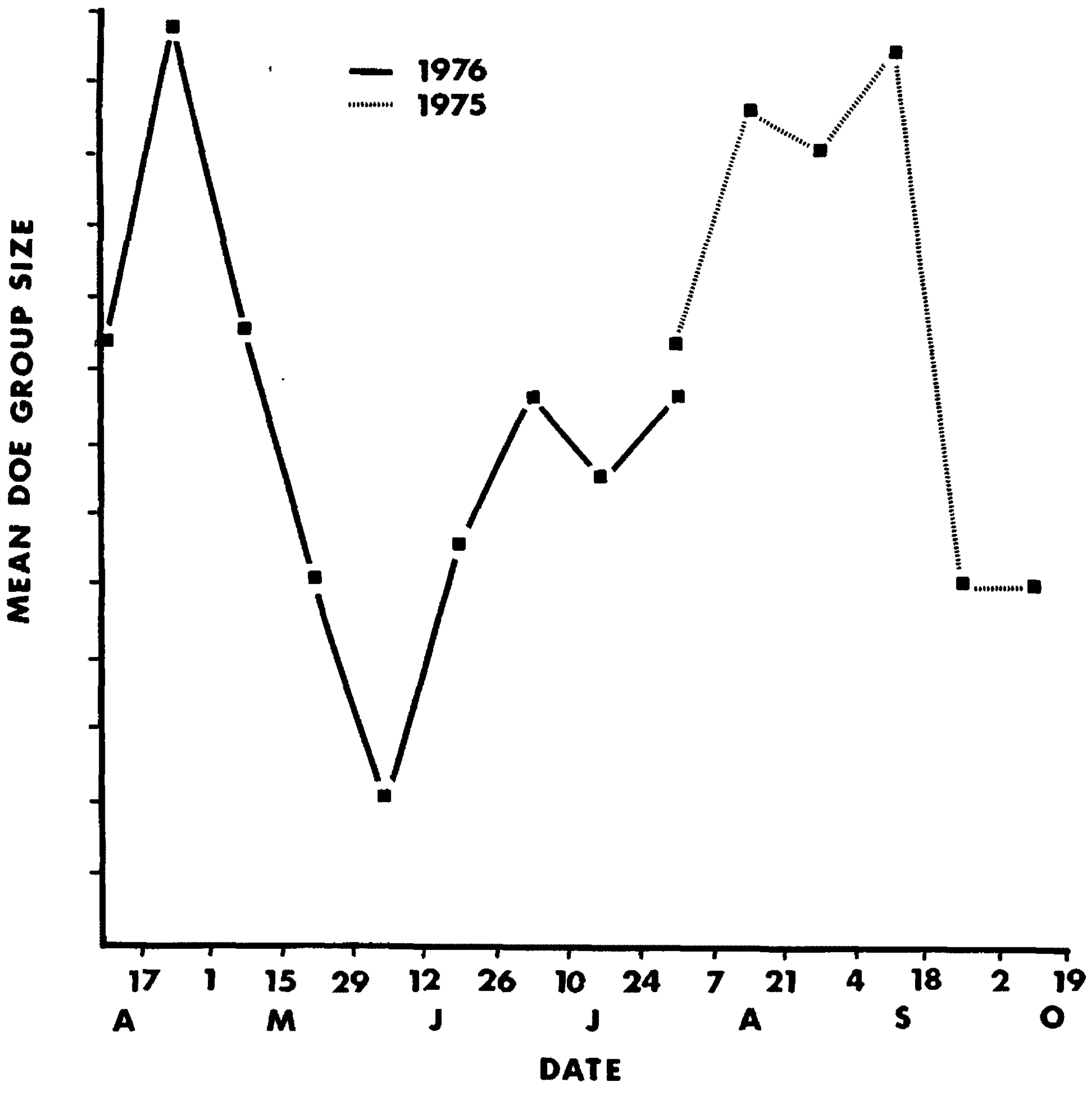
Seasonal differences. To analyze for seasonal differences in sizes of doe groups, I divided the field season into 2-week periods and calculated mean group sizes by averaging the number of does in groups seen during each period. In these analyses, the term group includes a single individual.

Even though the range of doe group sizes is large for any time period (Table 5), a definite seasonal trend exists in the size of doe groups (Fig. 4). Mean doe group size peaked in late spring, dropped drastically during June and early July, increased through August, and peaked again in early September. This trend coincides with the major events in the life cycle (Kitchen 1974). During parturition in late May and early June, does seek semi-isolation and move away from doe groups. After fawns are born, does return to groups, leaving periodically to nurse their hidden fawns. The small group size in June reflects the large number of does seen singly or

Table 5. Mean doe group size, group size range, and number of groups observed.

		Overall			With territorial bucks			Without territorial bucks			With fawns			Without fawns		
		Mean group size	Group size range	Number of groups observed	Mean group size	Group size range	Number of groups observed	Mean group size	Group size range	Number of groups observed	Mean group size	Group size range	Number of groups observed	Mean group size	Group size range	Number of groups observed
1976	4/4 - 4/17	8.1	1-23	19	7.9	4-13	7	7.8	2-23	11						
	4/18- 5/1	12.8	9-20	4	15.0	10-20	2	9	9-12	2						
	5/2 - 5/15	8.5	6-12	4	10.0	8-12	2	7	6-8	2						
	5/16- 5/29	5.1	1-14	20	7.0	3-14	10	3.2	1-11	10						
	5/30- 6/12	2.0	1-8	12	4.0	2-4	2	1.1	1-8	9						
	6/13- 6/26	5.6	1-15	37	8.4	1-15	18	3.0	1-7	19	8.5	1-15	10	4.6	1-18	27
	6/27- 7/10	7.7	1-22	32	8.5	4-18	17	6.4	1-22	16	10.1	4-22	7	7.1	1-18	27
	7/11- 7/24	6.5	1-18	63	8.6	1-18	34	3.7	1-18	24	10.2	1-18	25	3.9	1-12	39
	7/25- 8/11	7.7	1-24	66	8.9	1-24	41	5.4	1-15	23	9.7	2-24	29	6.4	1-16	36
1975		8.3	4-11	6												
	8/12- 8/21	11.7	9-14	6												
	8/22- 9/4	11.1	1-18	13												
	9/5 - 9/18	12.5	2-19	11												
	9/19-10/2	5.0	1-20	22												
	10/3 -10/19	5.0	2-11	13												

Fig. 4. Mean doe group size.


1976
1975
MEAN DOE GROUP SIZE
17
1
15
29
12
26
10
24
7
21
4
18
2
19
A
M
J
J
A
S
O
DATE

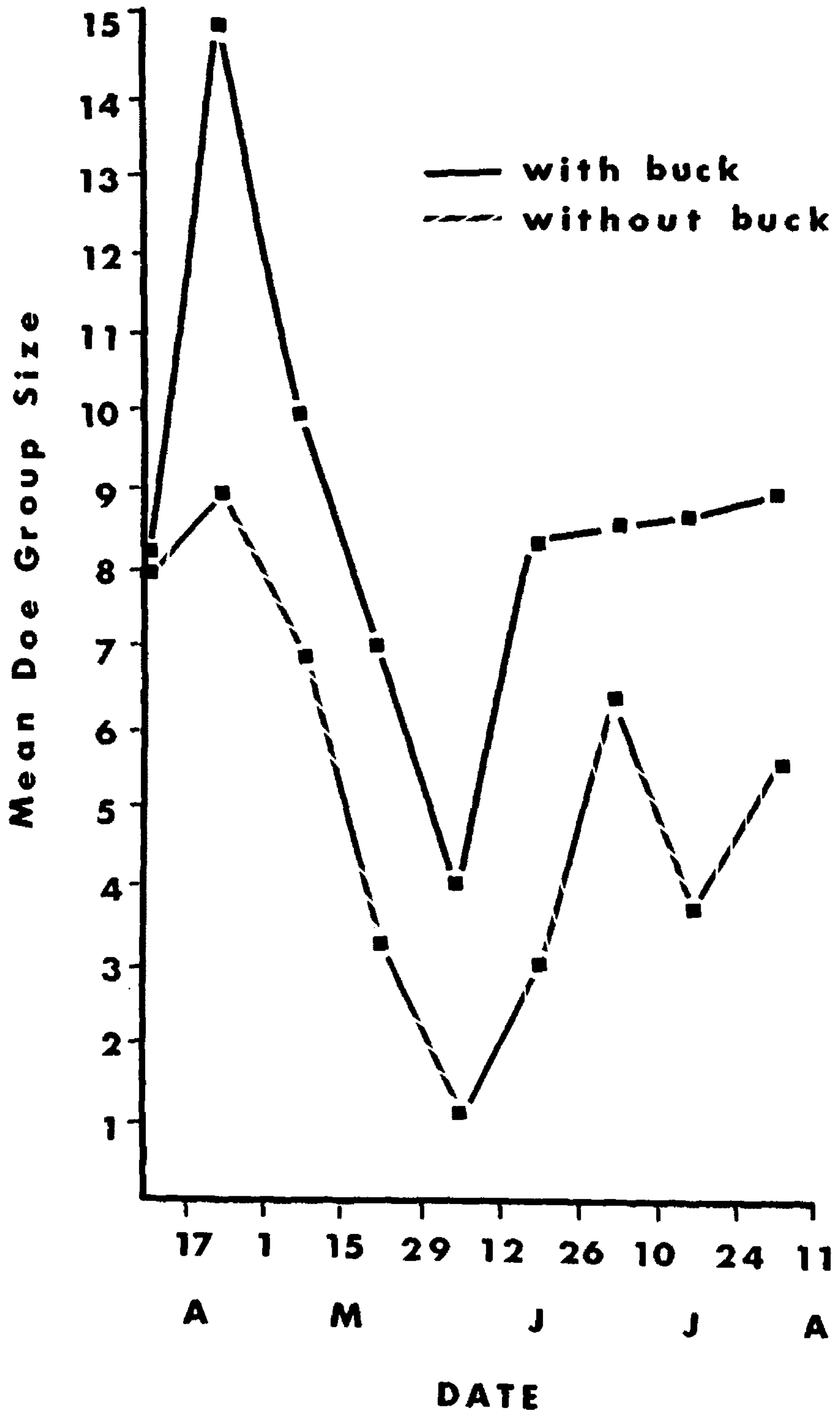
in groups of two or three. Several weeks after fawns are born, they join their dams in a doe group. The size of doe groups increases throughout July and August, peaking in early September. As rut starts in mid-September and progresses into October, doe group sizes drop sharply, reflecting increased harassment by territorial and bachelor bucks.

The range of doe group sizes per 2-week period is large for almost all time periods, and only superficially follows the trend shown by mean doe group size. Single does as well as fairly large groups were seen during almost every 2-week period.

Presence of bucks. Doe groups that were accompanied by a territorial buck were significantly larger than unaccompanied doe groups ($t = 5.52$, 8 d.f., $p < .01$) (Fig. 7, Table 5), indicating that attempts by territorial bucks to entice and keep does with them were successful during the summer.

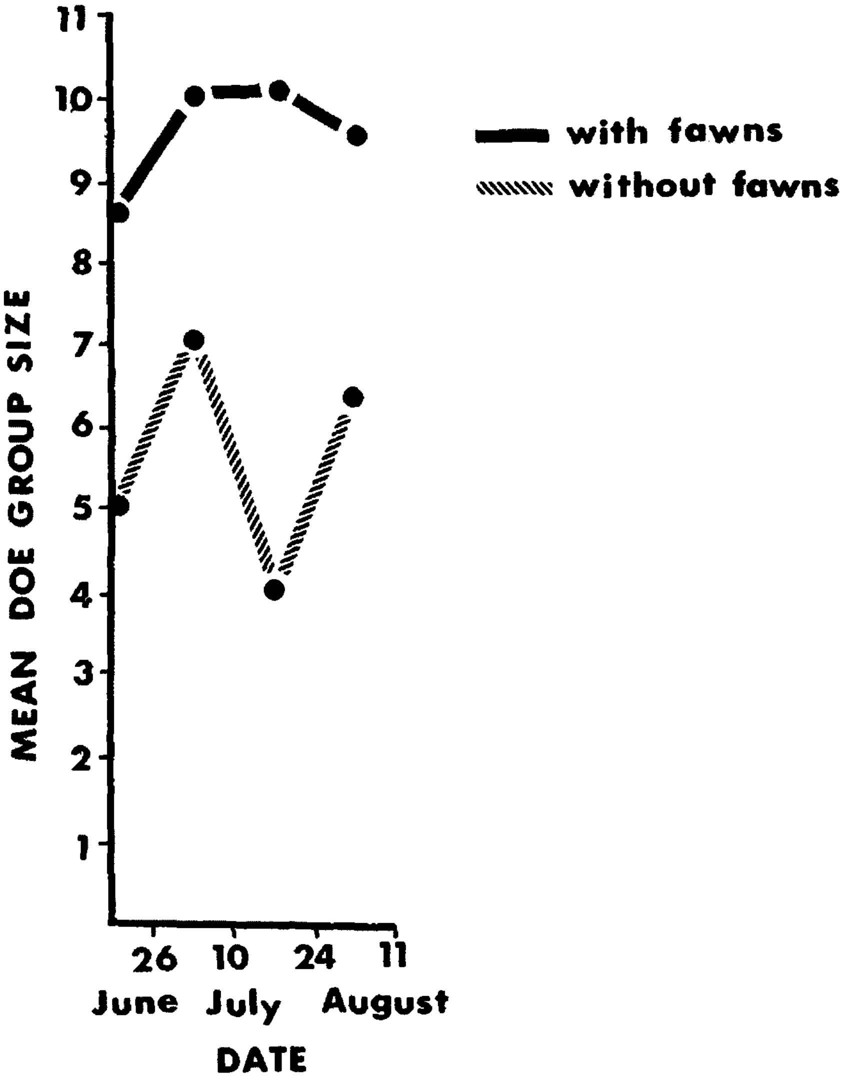
Presence of fawns. After fawns joined their dams in doe groups, groups with fawns contained significantly more does than groups without fawns ($t = 5.40$, 3 d.f., $p < .02$) (Fig. 6, Table 5). Two possible explanations exist. Does with fawns may have sought larger groups to gain better protection from predators. Fawn mortality was high in 1976 so there were few fawns, indicating heavy predator pressure. Also, fawns may have been seen with larger

Fig. 5. Mean doe group size with and without territorial bucks, 1976.



with buck
without buck
Mean Doe Group Size
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
17
1
15
29
12
26
10
24
11
A
M
J
J
A
DATE

Fig. 6. Mean doe group size, with and without fawns, 1976.


11
10
9
8
7
6
5
4
3
2
1
MEAN DOE GROUP SIZE
26
June
10
July
24
11
August
DATE
with fawns
without fawns

groups because the chances of a doe with a fawn being in a group increased as the number of does in the group increased.

Number of Groups

The mean number of groups in Alexander Basin or the Northside per morning or evening observation was calculated for each 2-week period during the field season (Fig. 7, Table 6). As expected, the mean number of doe groups increased as the mean doe group size decreased. The range of doe group sizes was large though, and there did not appear to be any specific break-off point which, if reached, caused the does to split into two groups instead of remaining in one large group. A paired sample t test comparing the number of doe groups seen early in the morning (from Trisky Creek maps) and the number of groups seen later in the day (Alexander Basin daily maps) indicates that time of day may have had an effect on the number of groups does formed. Significantly more doe groups were observed per observation period on the early morning maps than the late morning/evening maps ($t = 4.29$, 8 d.f., $p < .01$). This supports the idea raised previously that does showed a different pattern of use in Alexander Basin in the early morning.

Doe Group Composition

Because the size of doe groups changed, groups obviously did not always contain the same individuals. I anticipated two

Fig. 7. Mean number of doe groups per observation period in Northside and Alexander Basin.

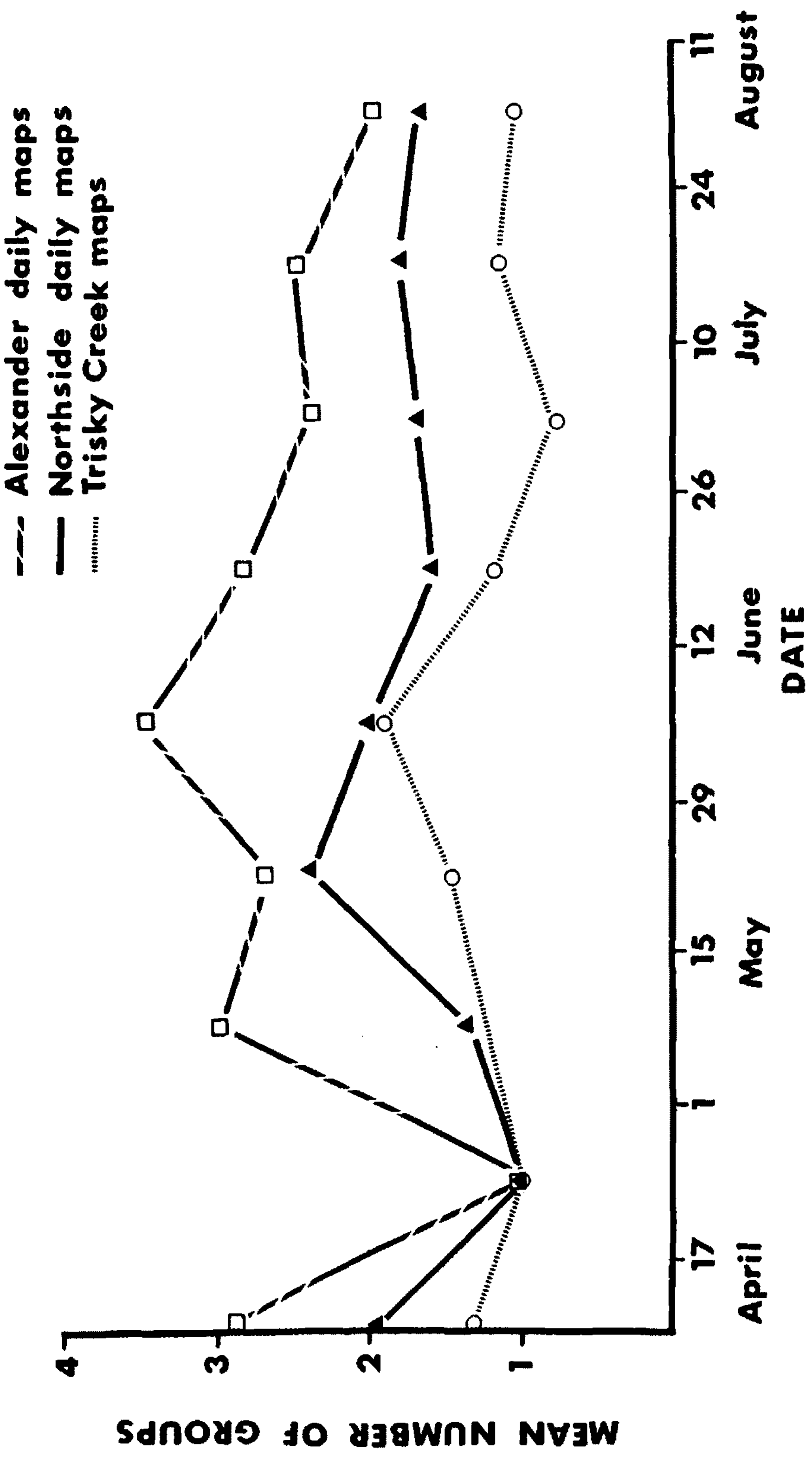

Alexander daily maps
Northside daily maps
Trisky Creek maps
MEAN NUMBER OF GROUPS
4
3
2
1
17
1
15
29
12
26
10
24
11
April
May
June
July
August
DATE

Table 6. Mean number of doe groups, range, and number of groups per 2-week time period.

				Alexander Basin					
	Northside			Daily maps			Trisky Creek		
	Mean number of groups	Range	Number of groups	Mean number of groups	Range	Number of groups	Mean number of groups	Range	Number of groups
4/4 -4/17	1.3	1-2	4	1.8	1-2	5	3	3	1
4/18-5/1	1.0	1	1	1.0	1	2	1.0	1	1
5/2 -5/15	--	--	--	1.3	1-2	3	3.0	3	1
5/16-5/29	1.5	1-3	6	2.4	1-5	7	2.7	2-5	6
5/30-6/12	1.8	1-2	4	2.0	2	1	3.5	3-4	2
6/13-6/26	1.4	1-3	9	1.6	1-4	14	2.8	1-5	6
6/27-7/10	1.1	1-2	8	1.7	1-3	14	2.4	1-5	7
7/11-7/24	1.4	1-2	14	1.8	1-3	19	2.5	1-5	11
7/25-8/11	1.3	1-2	24	1.7	1-3	23	2.0	1-4	15

possible doe interactions within this framework. First, does could form bonds with certain other does, staying with them and thus forming small subgroups. These subgroups might be composed of related does. Larger groups would be composed of various subgroups. If some does were positively associated (same subgroup), those does would necessarily be randomly or negatively associated with other does not in their subgroup. Does not in the same subgroup would meet sometimes, if and when their respective subgroups joined in a larger doe group. If association was measured between all does, some does would be positively associated (same subgroup), some would be negatively associated (different subgroups meeting rarely or not at all), and some might show random association (different subgroups meeting occasionally).

The second possibility is that does form no strong positive or negative associations with other does. Doe groups would then be aggregations of individuals, with does joining or leaving groups randomly. In this case, does would be seen in about the same frequency with other does in the same area. An association measure would show random association between does.

Several tests were run to indicate how does interacted. These tests were based on the number of times each possible pair of known does was seen in the same group.

Doe association. To investigate the degree of association among known does, a 2 x n contingency table ("observed tables") was constructed to determine the association of each known doe with the n other known does. For the doe in question, each observation of her after the n^{th} other doe had been identified was classified as seen with that n^{th} doe or as not seen with that n^{th} doe. A related 2 x n table representing the "expected" frequencies (of the n other does being seen with the doe in question) under the hypothesis of random association permitted one-sample chi-square evaluation of doe association. If does formed subgroups, they would have positive association with does in their subgroups and random or negative associations with does not in their subgroup. In this case, the expected values would differ significantly from the observed values. If does did not form bonds with some does and avoid others, observed and expected values would not be significantly different.

Two or three tests were run for each known doe. Each doe was seen most frequently in either Alexander Basin or the Northside, and one test was run against the other does seen principally in the same area. For does seen frequently in both areas, this was repeated for the secondary area. Each doe was also tested against all other known does. The fact that each known doe showed significant associations when compared with all known does (Table 7, last column) is understandable because almost all the known does

Table 7. Association of known does using chi-square tests.

	Northside			Alexander Basin			Northside and Alexander Basin		
Doe	X^2	d.f.	Prob. level	X^2	d.f.	Prob. level	X^2	d.f.	Prob. level
ORYL	20.66	7	<.01	3.21	3	n.s.	32.33	11	<.01
SH 1	21.50	7	<.01				39.66	11	<.01
SH 2	8.05	7	n.s.				48.00	11	<.01
SSD	13.86	7	n.s.				51.29	11	<.01
YY	54.80	7	<.01	10.37	3	<.02	78.64	11	<.01
YL	27.85	7	<.01	15.87	3	<.01	43.03	11	<.01
OO				18.55	3	<.01	88.77	11	<.01
NN	33.28	7	<.01				57.21	11	<.01
HB	32.88	7	<.01				64.60	11	<.01
LHB	22.13	7	<.01				70.00	11	<.01
RSH				7.2	3	n.s.	21.25	11	<.05
RCH	17.03	7	<.02				33.60	11	<.01
RHO	19.04	7	<.01				40.33	11	<.01

centered their activities in either Alexander Basin or the Northside, thereby forming two large subgroups. The chi-square values among does of the same area are also large and mostly significant (Table 7, first and second columns), showing that does formed smaller subgroups within Alexander Basin and the Northside.

The percentage of times each known doe pair was sighted was relatively low compared with the frequency at which they could have been together (mean = 30 percent), indicating that subgroups were small or that members of a subgroup were not always seen together.

Doe pair association. I needed a measure of association between two individual does to examine the kinds of subgroups formed, the strength of associations within subgroups, and the associations between subgroups.

The observed and expected contingency tables for each known doe showing association with all known does (see previous section) were also used to measure association between individual does. For example, association between does ORYL-SH 1 was measured using the contingency table for ORYL and the table for SH 1. Using ORYL's table, the observed and expected number of times ORYL was and was not seen with SH 1 were used in the formula $\frac{(O - E)^2}{E}$ and summed to obtain a single number. If does were seen together more than the expected value, the number was designated positive, and if the does were seen together fewer times than expected, the number was designated negative. Another association value for the ORYL-SH 1 pair was similarly obtained from the contingency tables constructed for SH 1. The two numbers for the doe pair were then averaged to give a single number describing ORYL-SH 1 association. Association values for the 78 pairs of does (Table 8) show a wide range (-4.59 to +17.51). Thirty-nine of the doe pairs have values greater than zero, 25 of which are relatively strong associations. Thirty-nine of the pairs are negative, with 25 pairs showing strong negative associations.

The association values shown by does ORYL and NN are typical and point out some interesting features of this association measure. NN was seen exclusively in the Northside while ORYL was seen almost an equal number of times in Alexander Basin and in the Northside. The range of association values between NN and the other known does was -3.50 to +6.88. ORYL had a smaller range of values (-2.80 to +2.35). Both does showed positive, random, and negative associations with does occupying similar home ranges, again indicating small subgroups. Interestingly, the magnitude of positive association values shown by ORYL and NN for other Northside does is similar although NN spent all her time in the Northside while ORYL was only seen in the Northside half the time.

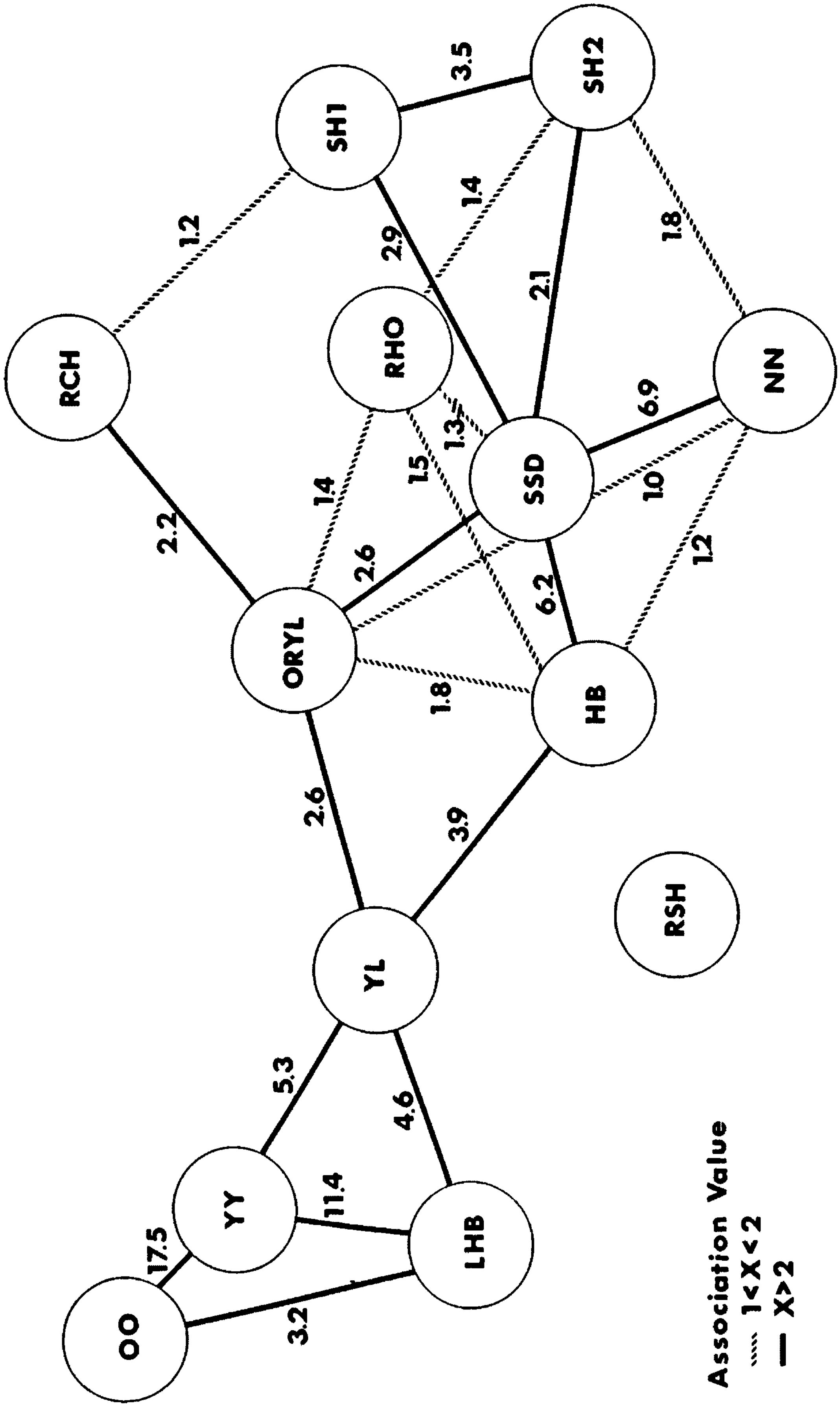
Table 8. Individual doe chi-square associations, 1976.

	ORYL	SH 1	SH 2	SSD	YY	YL	OO	NN	HB	LHB	RSH	RCH	RHO
ORYL		-2.80	.90	2.25	.14	2.40	-1.56	1.02	1.79	-.72	.91	2.24	1.41
SH 1			3.47	2.94	-2.78	-4.15	-1.52	-1.41	-2.68	-1.90	-1.12	1.18	-.21
SH 2				2.10	-3.47	.46	-3.45	1.82	1.89	-2.65	-.50	.63	1.40
SSD					-2.14	.73	-4.59	6.88	6.19	-.44	.11	1.28	1.43
YY						5.59	17.51	-2.20	-.60	11.35	.04	-1.31	-1.69
YL							-.67	.40	3.88	4.59	-.86	.58	-.50
OO								-3.50	-2.69	3.32	-.06	-1.87	-1.27
NN									1.17	-.79	.36	.02	-1.01
HB										.03	-2.43	-.72	1.50
LHB											-2.00	-1.26	-1.87
RSH												.54	-1.24
RCH													-1.82
RHO													

Association values vary somewhat with the number of times each doe of the pair was seen, but even so, most positive association values were relatively low.

Using association values greater than 1, I diagrammed the relationships among all the known does (Fig. 8). The length of lines linking does is inversely proportional to the strength of the association. Solid lines show association values greater than 2 while dotted lines show association values between 1 and 2. Two groups are immediately recognizable, one to the left composed of does seen mostly in Alexander Basin (OO, YY, LHB) and the other on the right of does seen mostly in the Northside (HB, SSD, NN, SH 1, SH 2, RCH, RHO). YL, ORYL, and RSH appear peripheral to the two main groups and were seen regularly in both Alexander Basin and the Northside. Looking at association values greater than 2 (solid lines), several small groups are evident. Closer examination, however, reveals that members of these subgroups are not always found together. For example, SSD had five associations greater than 2, but only two of these (SH 1 and SH 2) were closely associated with each other. Doe SSD was associated closely with HB (+6.2) and NN (+6.9). If these positive values represented more-or-less constant companionship, HB and NN would have been closely associated themselves. However, NN and HB showed fairly low positive association (+1.2). Even the highest positive associations represent

Fig. 8. Positive association among known does.


OO
YY
LHB
YL
ORYL
RCH
RHO
SH1
SH2
SSD
NN
HB
RSH
17.5
3.2
11.4
5.3
4.6
2.6
3.9
2.2
1.4
2.6
1.8
1.2
1.4
2.9
1.3
1.5
6.2
2.1
3.5
1.4
1.8
6.9
1.0
1.2
Association Value
1<X<2
X>2

flexible and dynamic companionship patterns.

The strongest associations were between pairs of does, not larger groups. Does appeared to have a few does with which they associated closely, and then more does with which they were seen less often, but with which they still had positive associations. Each doe seemed to have her own nested hierarchy of does she associated with. Even for closely associated does, these hierarchies were not the same.

I anticipated a system of either small discrete subgroups or of random interactions between does. The system revealed by these associations appears to be intermediate. Does formed moderately strong bonds with a few other does, but did not stay with those does exclusively. This system appears to be flexible, with does moving about as individuals rather than in discrete groups. This system of doe association fits well with the findings that does seasonally use different sections of Alexander Basin and the Northside. Because does use relatively small areas at any one time, the opportunities for meeting and associating with other does and other doe groups are greater than if does are spread over a large area.

Doe Home Range Correlation

Additional information about doe association can be gathered by comparing individual home range location. If the amount of home range overlap shown by doe pairs positively correlates with the association values, that would indicate that associations between does is based on their being in the same area. If the two does have roughly the same home range, but are negatively associated, those does may be intentionally avoiding each other by using the same areas at different times.

Doe home range size and pattern of use were compared by using individual maps showing sightings of each known doe. Each map was divided into 4.05 ha grid blocks and the number of sightings per block recorded. The Spearmann Rank Correlation Coefficient was used to compare the number of sightings per block for the two members of each doe pair (Table 9). Sixty-six of the 78 doe pairs were negatively correlated; 12 pairs were positively correlated. The large number of negative correlations indicates that though does generally used the same areas in Alexander Basin and the Northside, there was much individual variation in exactly what areas were used and the pattern of use. It also emphasizes the independence of individual does.

The association values and the home range correlation measures were compared for all pairs of does using the Spearmann Rank Correlation Coefficient (r_s = +6841, 77 d.f., $p < .001$). The two measures were strongly positively correlated, indicating that does tended to associate when they were in the same area. If does

Table 9. Comparison of known doe locations and statistical significance.

	ORYL	SH 1	SH 2	SSD	YY	YL	OO	NN	HB	LHB	RSH	RCH	RHO
ORYL		-.56 * *	-.38 *	-.35 *	-.33 *	-.21	-.38 *	-.36 *	-.51 * *	-.48 * *	-.33	-.01	-.54 * *
SH 1			-.35	+.39	-.71 * *	-.40 *	-.93 * *	-.16	-.14	-.51 * *	-.73 * *	-.37	-.72 * *
SH 2				+.55 * *	-.78 * *	-.04	-.96 * *	+.30	+.34	-.63 * *	-.40	-.18	+.04
SSD					-.77 * *	-.22	-.74 * *	+.41 *	+.40	-.54 * *	-.37	+.09	-.15
YY						-.14	+.27	-.79 * *	-.71 * *	-.16	-.30	-.57 * *	-.78 * *
YL							-.38 *	-.14	-.11	+.03	-.21	+.05	-.34
OO								-.91 * *	-.84 * *	-.35	-.59 * *	-.80 * *	-.90 * *
NN									-.08	-.58 * *	-.15	-.22	-.21
HB										-.77 * *	-.62 * *	-.30	-.30
LHB											+.06	-.07	-.85 * *
RSH												-.12	-.85 * *
RCH													-.99 * *
RHO													

☐ - Spearmann Rank Correlation Coefficient (r_S)
- Statistical significance $* p < .05$
$* * p < .01$

were negatively associated, it was because they used different areas, not because they were actively avoiding each other by using the same areas at different times.

When chi-square association values and home range correlations for each pair of does are graphed (Fig. 9), points lie in all four quadrats. Quadrat I contains points of 11 doe pairs that showed both positive association and positive home range correlation. Quadrat III contains 28 doe pairs that were both negatively associated and negatively correlated. One point in Quadrat IV describes the LHB-RSH doe pair that was negatively associated, but occupied positively correlated home range area. Quadrat II contains points for doe pairs that showed positive association, but occupied negatively correlated locations. These negative correlations were not large, indicating that these does shared a few areas, but mostly used different areas. The positive association between these pairs must indicate that when they were in the same area they associated in the same group.

Doe-Buck Relationships

Does were seen almost exclusively on buck territories. There were four territories in the Northside and three territories in Alexander Basin where does were seen during the 1976 field season (Fig. 10). Bachelor bucks, in groups or singly, stayed in areas

Fig. 9. Graph of chi-square association measures and home range correlations per known doe pair.

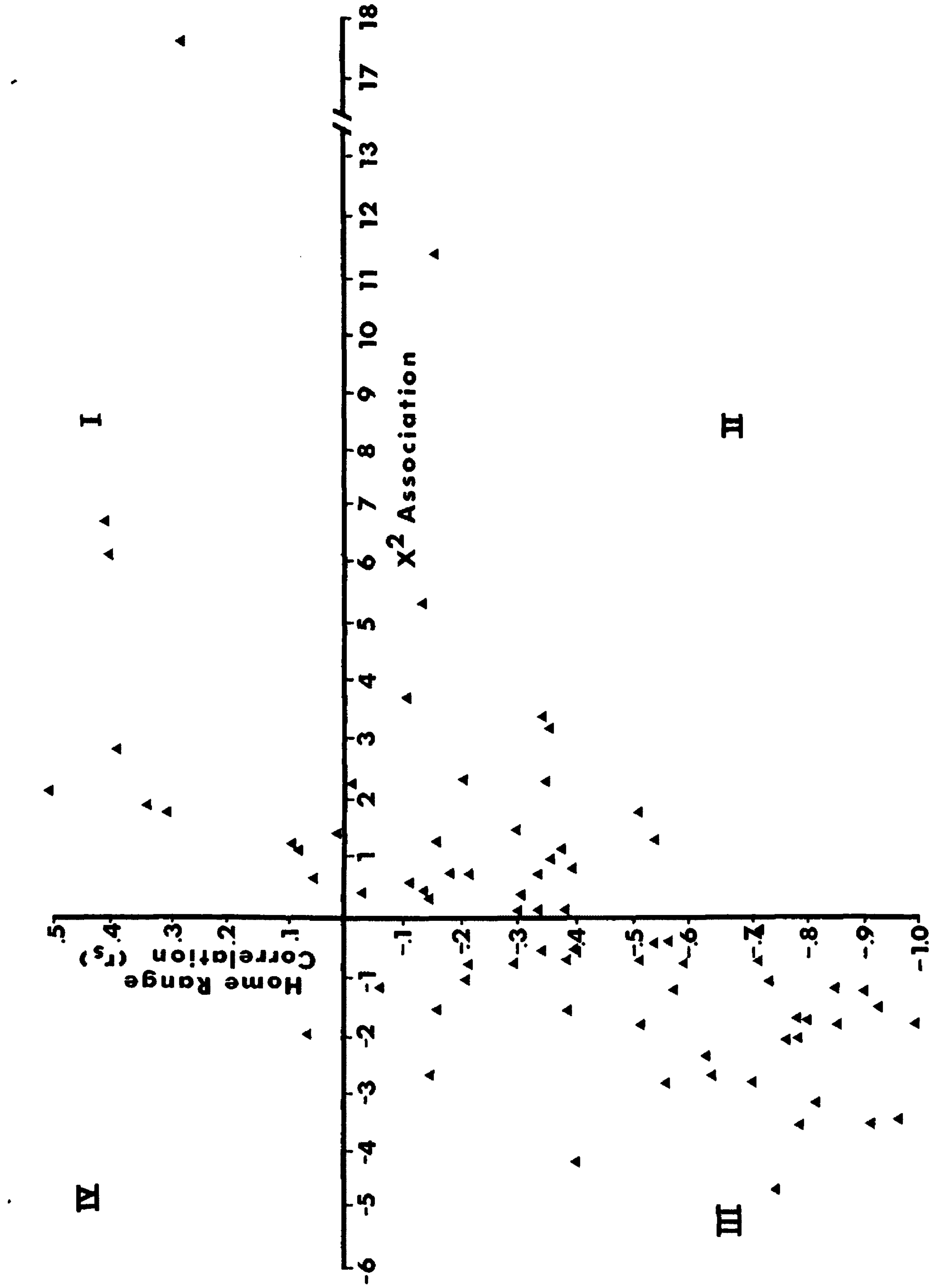
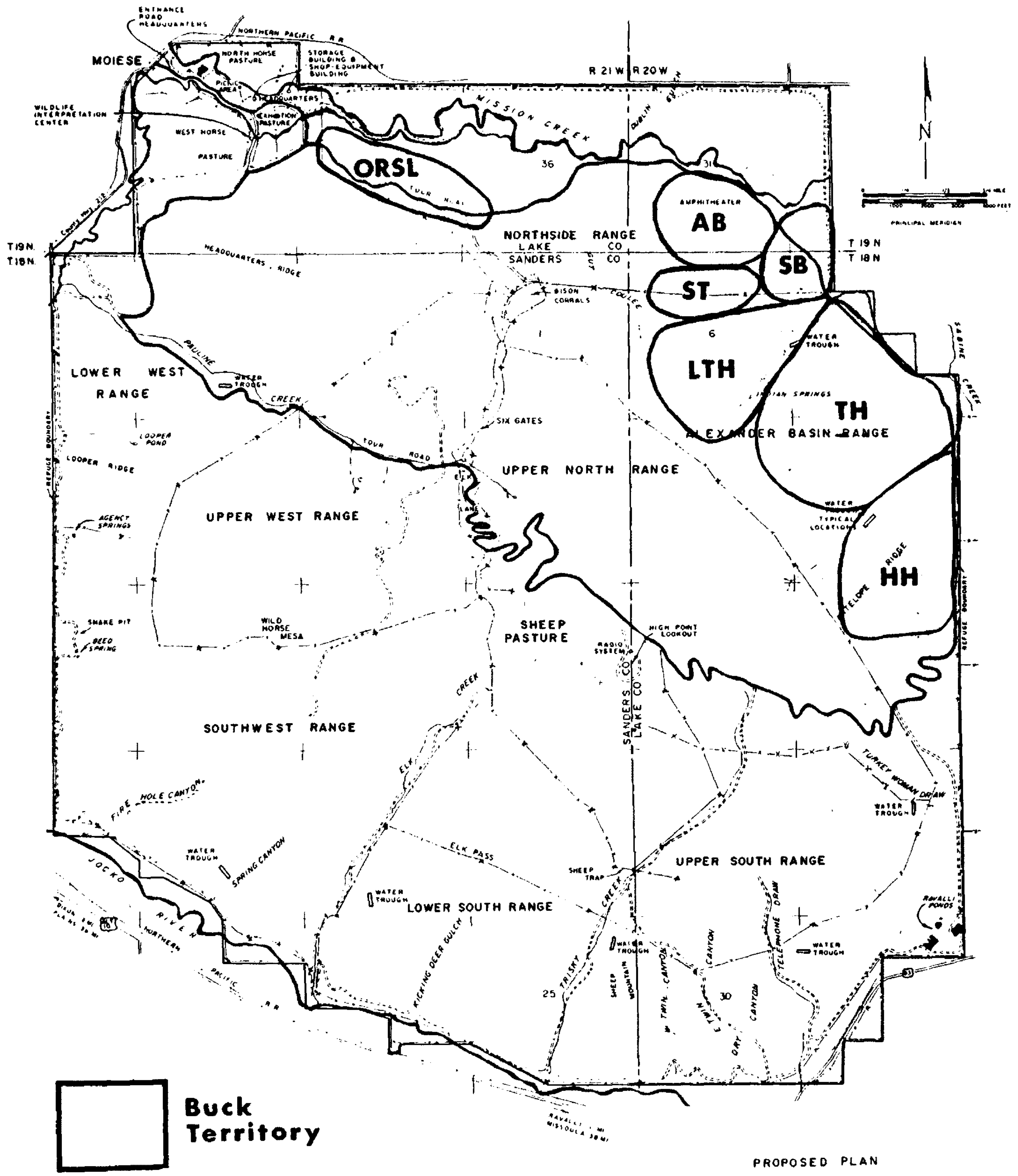

Home Range Correlation (r_s)
X² Association
I
II
III
IV
.5
.4
.3
.2
.1
-.1
-.2
-.3
-.4
-.5
-.6
-.7
-.8
-.9
-1.0
-6
-5
-4
-3
-2
-1
1
2
3
4
5
6
7
8
9
10
11
12
13
17
18

Fig. 10. Locations of buck territories, Northside and Alexander Basin, 1976.



NATIONAL BISON RANGE

Moiese, Montana

close to territories, presumably remaining as close to females as possible.

Doe social structure, as it emerges from the previous sections, is flexible in terms of doe group size and composition. A study of doe-buck relationships throughout the field season gives some insights into mate selection and its relationship to doe social organization.

There are two basic types of mate selection by females among territorial species. First is the site hypothesis, in which females choose the male with the highest quality territory, thereby equating territorial quality with genetic fitness. Second is the behavioral difference hypothesis, in which females choose the male with the best courtship display (Hartzler 1972). For the site hypothesis to be true, does must be able to distinguish between territories. Presuming does attempt to eat the highest quality forage to maximize energy available for pregnancy and lactation, they should spend as much time as possible in territories with the best forage, and therefore with the best buck. If the site hypothesis is true, there should be a positive correlation between the amount of time does spent on a buck's territory during the summer and his breeding success during the rut in September and October. If the behavioral difference hypothesis is true, there need not be a correlation between amount of time spent on a buck's territory and his breeding success.

Two tests were run to determine how does used buck territories. First I compared territorial buck sightings with or without does. These sightings measured preference for a territory. Does showed differential association with territorial bucks ($X^2 = 41.0$, 6 d.f., $p < .01$) (Table 10). Among Alexander Basin bucks, TH was seen with does 80 percent of the time compared to 61 percent for LTH. HH was only rarely seen with does (9 percent of his observations). In the Northside, however, does did not show a real preference. Does were seen in 83 percent of ST's and ORSL's observations, but these bucks were seldom seen. Does were also seen almost equally with SB and AB (57 and 58 percent respectively).

The other test was run using sightings of individual known does with territorial bucks. This second test determined if the known does differed in preference for territorial bucks. In this case, 2 x n contingency tables like those used in measuring doe-doe association were constructed for each territorial buck. An observed table showed the number of times each of the n known does was or was not seen with that territorial buck. Expected values were generated under the hypothesis that all known does were seen equal proportions of times with that particular buck. A one-sample chi-square test was used to evaluate the differences between the observed

Table 10. Total territorial buck sightings with and without does, 1976.

Buck	Seen with does	Alone	Total sightings	Percent with does
Alexander Basin				
TH	52	13	65	80
LTH	11	7	18	61
HH	2	22	24	9
Northside				
ST	5	1	6	83
SB	24	18	42	57
AB	23	17	40	58
ORSL	5	1	6	83
Total	122	79	201	61

and expected tables for each buck (Table 11). Does were not seen in significantly different ratios with any of the territorial bucks tested (HH and ORSL were not seen with enough known does to be tested). Does did not differ in their preference for various bucks. Although all known does spent roughly the same proportion of time with a particular buck, the total amount of time with does was not the same for each territorial buck. In Alexander Basin, known does were in 57 percent of TH's observations, but only 16 percent of LTH's. Sightings of all does in the Northside did not show any preference for SB or AB, but known does were seen slightly more often with AB (44 percent of sightings) than SB (35 percent). ST was seen with known does 28 percent of the time.

When they held territories, bucks attempted to herd the does on their territories. The territorial buck stayed apart from his does in a position to best head off any that tried to stray.

According to a partial breeding history of Northside-Alexander Basin bucks (D. Kitchen, personal communication), the most successful buck in Alexander Basin was territorial buck TH, (Table 12). In the Northside, territorial buck AB did most of the breeding. Territorial buck SB had no observed copulations, even though both AB and SB had does with them approximately the same number of times during the summer.

Table 11. Comparison of frequency associations of territorial bucks with known does using X^2 tests, 1976.

Buck	X^2	Probability level	d.f.	% observations with known does
Alexander Basin				
TH	4.473	$p > .20$	4	57
LTH	6.962	$p > .15$	4	16
Northside				
ST	2.728	$p > .20$	7	28
SB	6.865	$p > .20$	9	35
AB	5.415	$p > .20$	9	44

Table 12. Observed breeding history of territorial bucks (D. Kitchen, personal communication).

Buck	Breeding history
Alexander Basin	
TH	Has held territory since 1973; has bred approximately 16 percent of all females in the population to date (average, six does per rut).
LTH	Has held territory since 1973; has bred eight does.
Northside	
SB	Has held territory since 1975; no observed copulations.
AB	Has bred 8-10 does.
ST	No observed copulations.
ORSL	Bred two does in 1976.

CHAPTER V

DISCUSSION

The doe social system I predicted from Geist's (1974) theory and the system I observed on the Bison Range differed in several ways. In the predicted system, does form stable harems that each associate with a single territorial buck. Doe home ranges are the size of a buck territory, and does associate only with does in their own harem and their territorial buck. In actuality, doe home ranges were known to cover several buck territories, and does occurred in groups of variable size and composition. Does associated closely with a few does, but all associations seemed to be flexible, and does were seen sometime with almost all known does in the area (Alexander Basin or the Northside).

Two explanations exist for the discrepancies between the predicted system and the system I observed. The theory appears too general for forming such predictions and the ecological parameters I used may have been in error.

Geist's (1974) theory appears too general for predicting specific aspects of social systems. He related certain ungulate behaviors to basic ecological parameters. However, I was unable to predict some behaviors that are integral parts of the social system from these ecological facts. Using Geist's theory, only general characteristics such as presence or absence of territoriality can be predicted.

One of the points of Geist's (1974) theory that I used was that females should maximize energy available for reproduction and lactation by lessening intraspecific aggression. The best interpretation of this seemed that does would form stable groups, each staying with one territorial buck. In any group, does would form a dominance hierarchy and not associate with nongroup members or other bucks. Other predictions are also possible, however. The does on the Bison Range, for example, reacted passively to others leaving or joining their group. This behavior may or may not have evolved to reduce aggression. It does accomplish that and also allows other potential benefits such as group size that varies with environmental conditions.

Another reason for the discrepancies between the predicted and the observed systems may lie in the ecological parameters I used to make the predictions. I characterized pronghorns on the National Bison Range as inhabitants of an open, climax stage ecosystem on good to excellent range with high quality, diverse forage. Because I assumed forage was abundant, I also assumed that a buck territory was large enough to completely support the buck and several does throughout the growing season. This may not be the case. The Bison Range contains good forage for bison, but bison and pronghorns differ in their diets and style of feeding (Schwartz and Nagy 1976). Pronghorns are selective feeders, taking small distinct bites from rather specific portions of each plant species (Ellis and Travis 1975). Because pronghorns only select certain plant parts, food items are dispersed more widely than if pronghorns utilized more parts of each plant. This style of feeding also removes the desirable food, so pronghorns leave an area once it has been gleaned until new growth appears (Bromley 1977). These factors probably make doe home ranges larger than one buck territory.

If I had initially assumed does needed home ranges larger than a buck territory, I would have predicted a different social system. Using the basic points from the theory, several doe social systems are possible when home ranges are larger than one territory. Using the strategy of stable groups to lessen female aggression, does might have joined in larger stable groups that would maintain group home ranges covering several territories. The system I observed is another possible social system with large doe home ranges.

Doe Strategy and Social Organization

A doe should place herself in the social and ecological environment where she can maintain the highest rate of energy fixation, and obtain the best possible male genes for her offspring (Bromley 1977). A high rate of energy fixation is necessary because pregnant and lactating females have the highest nutritional needs of all ungulates (Sadleir 1969). Doe social organization should provide the means by which does maximize energy fixation, by allowing does access to the best available forage while limiting as much as possible the amount of energy expended. Doe social organization should also provide the means by which a doe can select the best possible mate. I have already briefly described one way in which does reduced energy expenditure by lessening intraspecific aggression. Other ways in which doe social organization reflects doe strategy are discussed in this chapter. Pronghorn doe social structure is also compared to social organizations shown by other ungulates in comparable habitats, to see how other female ungulates have realized basic doe strategy as stated at the beginning of this paragraph.

Home Range Size

Doe home range size is important for two reasons. At its lowest limit, the size of an individual's home range indicates the amount of land she needs. In the predicted system, a buck territory is a Type A territory, containing sufficient resources to completely support the buck and his harem. In the system I observed, does used an area covering several buck territories.

Individual doe home range size influences the associations does form. Does in stable groups on small, nonoverlapping group home ranges would only associate with does within their group, while does on large, overlapping home ranges would associate with most does and territorial bucks in an area.

Doe home ranges covered several territories in this study. Little work has been done with marked pronghorns to determine if does typically use several territories. Does used several buck territories in Wind Cave National Park in South Dakota (Bromley 1977). In central Montana, Cole (1956), Cole and Wilkins (1958), and Pyrah (1970) found that doe groups used several buck territories as well as areas outside buck territories. Wentland (1968) found that females had larger home ranges than did territorial bucks in Montana.

Among open-country territorial ungulates, females generally have home ranges overlapping different male territories (Estes 1974, Jarman 1974, Owen-Smith 1977). This had been specifically recorded in impala (*Aepyceros melampus*) (Leuthold 1970), puku (*Kobus vardoni*) (deVos 1965), Uganda kob (*K. kob*) (Leuthold 1966), bontebuck (*Damaliscus dorcus*) (David 1973), and Coke's hartebeest (*Alcelaphus buselaphus cokei*) (Gosling 1974). Kiley-Worthington (1965) found that in defassa waterbuck (*K. defassa*), male territories and female home ranges were approximately the same size, but did not exactly coincide, so that a female home range overlapped several territories. Other researchers indicated that defassa waterbuck female home ranges covered as many as four or five territories (Hanks et al. 1969, Spinage 1969 and 1974).

Two of the widest ranging known does in the study (YY and YL) were yearlings, indicating young does might have larger home ranges than older does. Defassa waterbuck females range more widely when young, decreasing their home range with increasing age (Spinage 1969). Spinage (1974) felt that young defassa waterbuck females leave the doe group in which they were raised when they are 18 months old and form "spinster" groups that wander over large areas like bachelor buck groups. The females settle when they are about 3 years old, in the doe home range where they have their first fawn. I knew birth sites for three of my known pronghorn does. Doe OO was seen only in Alexander Basin during this study and had apparently left the Pauline Creek area where she was born (D. Kitchen, personal communication). Does YY and YL were born in the Northside in 1975 (J. Reichel, personal communication). In 1976, YY was seen a few times in the Northside, but stayed mostly in Alexander Basin. YL was seen regularly in both the Northside and Alexander Basin. This shows a tendency for pronghorn does to leave the area where they were born.

The size of pronghorn doe home ranges is not related to how far pronghorns can range. Fifty-nine transplanted pronghorns in

Nebraska moved from 0 to 125 miles from the release site (mean = 26 miles). Six of the seven pronghorns which moved 60 miles or more were does (Menzel and Suetsuyii 1966).

Several species of ungulates similar to the pronghorn show female group home ranges, which I did not find in pronghorns. In lesser kudu (Tragalephus imberbis) (Leuthold 1974) and defassa waterbuck (Spinage 1974), home ranges appear to be owned by groups of females, with little interchange of females between different group home ranges. Feral Soay sheep (Grubb and Jewell 1966) form ewe group home ranges that overlap slightly. In all three of these species, though home range group membership is relatively large, group members move within the home range as individuals in small, dynamic groups.

Kitchen (1974) reported doe herd home ranges in his 1969-1971 Bison Range study of pronghorns. He found three doe herd home ranges: the Lower Westside (around Pauline Creek), and two in my study area, Alexander Basin and the Northside. Kitchen found no doe migration between the Northside and Alexander Basin. Five years later, however, I found considerable doe movement between these two areas, along with generally larger doe home ranges than reported by Kitchen. One factor influencing wider doe dispersal may be availability of desirable pronghorn forage. Pronghorns on the Bison Range depend heavily on forbs; rumen contents of Bison Range pronghorns killed in 1965-1967 contained an average of 67 percent forbs, 18 percent browse, and 15 percent grasses (O'Gara and Greer 1970). The number of forbs available for pronghorns may have decreased since Kitchen's study because range condition has "improved" since then. Most of the Bison Range is now classified as being good or excellent range, based on a system that relates the present plants to the climax plant community. Grasses are generally more abundant in the good to excellent range condition classes. The general improvement in range condition on the Bison Range may have lessened the availability of forbs, causing pronghorns to search larger areas than before to find good forage (B. O'Gara, personal communication).

Pattern of Use and Feeding Style

The pattern of use shown by the does (differential use of a large area through the summer) fits in well with the feeding style of pronghorns. Pronghorns are selective feeders, picking high quality plant parts in one area and then moving on (Hoover 1972). During the growing season, they can glean an area, return later and reglean, in effect following a local grazing circuit (Bromley 1977). While this is probably true, does also appear to move in response to new forage (Hoover 1972) and to moisture. In spring, does occupy areas that green up earliest and then move in response to various forbs as they flush (D. Kitchen, personal communication). As forage dries in late summer, does are seen more often near areas containing water, such as Sabine Creek and Indian Springs in Alexander Basin. Kitchen (1974) found a significant positive correlation between wet forage weight and the size of doe groups on different zones of buck territories during the rut.

Pronghorn foraging patterns may also be influenced by bison use. In the Serengeti, larger ungulates appear to open up the herb layer for the smaller ungulates by removing the upper layers of coarse, lower protein plant parts (Gwynne and Bell 1968, Bell 1971). In the same way, bison may increase access to desirable forage for pronghorns. Bison herds are periodically rotated among pastures, so bison are in the same pastures as the pronghorns for approximately 3 months of the year, not necessarily during the growing season.

In this study, does used areas inside buck territories from which bachelor bucks were generally excluded. By staying in territories, does avoided the harassment of bachelor bucks (Cole and Wilkins 1958, Gilbert 1973, Kitchen 1974, Bromley and Kitchen 1974, Buechner 1974). Territories also contain better forage than other areas (Bromley 1977). It has also been suggested that by excluding other territorial bucks and bachelor bucks from his territory, a territorial buck increases the amount of forage available for does and his fawns. A quantitative estimate for impala indicated that this gain is only 3-5 percent (Jarman and Jarman 1973). Owen-Smith (1977) further pointed out that females of most species range widely, so the extra available forage would benefit offspring other than the territory holder's.

Doe home range size and pattern of use reflect doe strategy of maximizing energy fixation. Does maximize energy intake by utilizing areas with the best forage. Does reduce energy expenditure by using territories and avoiding bachelor bucks, and probably ranging only as far as they have to to find food. Moving across several territories also allows does to examine several territories or territorial bucks before rut.

Jarman (1974) categorized the African antelopes according to feeding styles. He divided the various types of feeding styles into five classes, ranging from class a, in which species feed very selectively on a wide range of mostly browse plants in small, exclusive, home ranges, to class e, in which species feed unselectively on a wide range of mostly grasses, moving in large herds seasonally within a very large home range. Feeding style is generally related to body size (a = smallest, e = largest), and also to social organization. In this system, pronghorns fit very nicely into class c in terms of feeding style and body weight. Class c species feed rather selectively on a range of grasses, forbs, and browse within a fairly large home area. As examples of this feeding style, Jarman (1974) lists greater kudu (T. strepsiceros), nyala (T. angasi), waterbucks, kob, puku, impala, and gazelles (Gazella spp.).

Doe Groups

Size. Doe group size showed a definite seasonal trend. Does were found more often in large groups during May and early September, and in smaller groups during June and late September. Similar trends in doe group size were also documented by Kitchen (1974) and Bromley (1977). Autenrieth and Fichter (1975) found Idaho does dispersed during fawning and during the latter part of September when does were coming into estrous. Decrease in doe group size during rut was noted by Einarsen (1948), Prenzlow (1965), and Fichter (1972).

The drop in doe group size at the onset of rut corresponded to increased harassment by territorial and bachelor bucks. At the beginning of the breeding season, bachelor bucks intensified their attempts to associate with females. Territorial bucks tried to keep bachelors away from females, but often left doe groups on their territories unattended while pursuing single females. The unattended doe groups were then broken up by bachelor bucks that invaded the territories (Cole and Wilkins 1958).

The largest groups (up to 22 does) were seen in August and early September, a time when forage was drying. Does could have been concentrating in the few areas still containing succulent forage. Defassa waterbucks group into larger herds during the dry season and small herds during the wet season (Hanks et al. 1969). Jarman (1974) also reports a correlation between group size and available food in impala.

In pronghorn and impala, respectively, Bromley (1977) and Leuthold (1970) noted that female herds without territorial males were smaller than female herds accompanied by a territorial buck. Wentland (1968) found that pronghorn does averaged 59 percent greater distances between successive observations when they were not accompanied by a territorial buck. These observations indicate that male herding attempts were at least partially successful, and showed that perhaps some does were forced to associate with more does than they might otherwise have been with (Bromley 1977).

Association. Use of marked or recognizable animals is necessary to determine how animals are associating. Marked does have been part of several pronghorn studies, but usually only general impressions of female social organization have been recorded.

Several studies have found some stability in pronghorn doe groups. In central Montana, marked does remained with the same herds for several years of a study (Pyrah 1970). Pyrah used an association index (Knight 1967) to measure association between does. He found high coefficients of association among members of a doe group, and low association coefficients between does from different groups. Pyrah also found that when summer groups mixed, they almost invariably separated into the original herds. Unfortunately, Pyrah did not define groups or herds, or give an indication of group or herd size, making it difficult to compare to the data from this study. Ingold (1969, in Autenrieth and Fichter 1975) saw a lack of stability in large pronghorn groups, but considered it only the result of movements of small functional social units that remained intact both upon merging and parting. It is unclear whether Ingold used marked animals.

Several other studies found no order among pronghorn does. Fichter (1972) found summer pronghorn groups in Idaho very fluid. One mature, naturally marked buck was seen 42 times in the summer of 1965, 39 of which were with pronghorn groups. This buck was never seen with the same number and/or combination of individuals twice consecutively. Comparable data were also gathered on 14 other marked pronghorns.

More comprehensive studies on female associations have been done in other ungulate species. Knight (1967), studying associations between individual elk in the Sun River elk herd in Montana, found little or no evidence of group stability. With only a few exceptions, no two individuals other than a cow and her current calf were closely associated for more than several days. Some animals had a high degree of association, but this only seemed to last for a single season. Knight thought it doubtful that individual elk of the Sun River herd were grouped into subunits of any size that had a lasting association throughout the year.

Several different types of association are evident in African ungulates similar in size to pronghorns. No associations with the possible exceptions of mother-daughter or same age group associations were evident in impala (Schenkel 1966, Leuthold 1970, Jarman and Jarman 1974) or defassa waterbuck (Spinage 1969 and 1974, Hanks et al. 1969). Spinage (1969) found that no two defassa waterbuck females associated for more than 50 percent of their total observations. Bontebuck, on the other hand, form female groups in which association between members are of an enduring nature. Female groups in bontebuck are semi-exclusive in character. When a new female was seen with an established group, there was a marked rise in aggressive activity among the females. The new female usually only stayed with the new group for a day or two (David 1973). Wildebeest female herds are also stable in composition for at least 5 months following the calving season, reflecting semi-closed associations between adult females. Outside females that attempted to join established herds were usually harassed and/or excluded

(Estes 1969).

Lesser kudu seem to have associations most like those I found for pronghorns. Leuthold (1970) found that a female had a few close friends with which she formed a temporarily stable nuclear group, even though a doe may associate with a considerable number of other females within her core area.

Limits on group size. Jarman (1974) contends that the upper limit on group size is determined by feeding style. Feeding style in most antelope species places a limit on the maximum number of individuals that can feed together as a coordinated, cohesive group. The effect of one animal feeding on the food available to others is important in the boundary size of the herd. If the animals are selective feeders, selecting distinct plant parts as they progress through their pastures (Jarman feeding styles a, b, c), they completely remove the food items they eat, and affect the dispersal of food items available to the animals following them. Because food items would be more widely dispersed for animals not in the lead, animals which followed would have to spread out to get sufficient forage, and group cohesion would be lost. In contrast, less selective feeders (Jarman feeding styles d, e), that are capable of eating almost all parts of a plant, do not affect the dispersal of food items as they pass through their foraging areas, but only reduce the size of each item. Therefore, animals following the lead animals can still stay close together in a coordinated herd. As expected, animals with feeding styles a, b, or c, such as pronghorns, occur singly or in relatively small groups (2 to 60) during the growing season. Animals with feeding styles d and e often form very large herds numbering hundreds or even thousands.

In almost all cases, animals would have the best chance at the food resources if they occurred singly. The medium to large antelopes never or rarely occur singly, so some other factors must be responsible for the lower limits on herd size. Jarman (1974) credits predation as the other major determinant of herd size.

Avoidance of predators has often been given as a reason for grouping (Pulliam 1973, Estes 1974, Geist 1974, Jarman 1974, Treisman 1975). When animals group, there are many pairs of eyes and ears to detect potential danger, and there are many conspecifics to hide behind (Vine 1971). Estes contends that bovids were only able to emerge from hiding and live in open grasslands after they began forming herds.

African antelopes suffer from many predators. For pronghorns, predation is probably a more important factor in the winter than summer. Coyotes have killed pronghorns in deep snow in winter, but pronghorns do not run from coyotes in the summer (Einarsen 1948, VanWormer 1969, Bruns 1970). I observed a coyote near a group of five does and a fawn for approximately 30 minutes on 14 July 1976. The coyote came within 3 m of the feeding does, but the does showed no sign of alarm other than keeping themselves between the coyote and the fawn. Because predation is less of a threat in summer (by the time fawns join doe herds, they can outrun most predators), groups should not have to be as large as during winter.

Group size depends on two factors (Jarman 1974). Large groups are favorable in terms of defense against predators, but single animals obtain the best forage. Because does are not locked into stable groups, adjustments in group size to optimize both foraging and predator protection are more easily made. The changing number of doe groups from early morning to afternoon reflects this flexibility. Early in the morning [one of the most intensive feeding periods (Prenzlow 1965)], does in Alexander Basin were in more, smaller groups than later in the day when feeding was not as important an activity. Also, if danger did appear, small groups banded together to escape from predators, thereby gaining the advantages of being in a large group.

Small groups may have contained some doe-fawn or same-age group associations. Jarman and Jarman (1974) found that the majority of female impala in groups often shared a common physiological state such as being nursing mothers or even being in good or poor physical condition.

The loose structure of doe groups was possible because does accepted the presence of new does in a group. If the coming or leaving of does from a group caused disruption, a loose structure would take too much energy and time to be advantageous. Recognition of an individual doe by other does was recorded by Kitchen (1974) and seems likely because variations in markings were large enough so I could recognize some does individually. This raises the possibility of formation of dominance hierarchies among all does that associate with each other, another means of reducing female aggression. Kitchen (1974) recorded doe dominance hierarchies with his Alexander Basin and Northside doe herds.

Because doe groups were flexible in size and composition, perhaps each group should not be considered as a separate entity, but should be considered a unit of the pronghorn herd, for example, the pronghorns in Alexander Basin at any point in time. Calhoun (personal communication in Fichter 1972) thought that the seemingly loose cohesiveness may be evidence that a high level of group organization exists. Fichter (1972) further added that because pronghorns can maintain visual contact over considerable distances and because pronghorns come together quickly when threatened, pronghorn herds are "well" organized even when widely scattered.

Doe-Buck Relationships

The offspring of a female and a superior male should survive better than offspring sired by an inferior male, so to maximize her own fitness, a doe should mate with the best possible male. The female should use the easiest possible method available to her to choose the fittest male. If males are nonterritorial, the female may choose the dominant male, or may incite males to fight and then mate with the winner. If males are territorial, the female should pick the male with the best territory (Cox and Leboeuf 1977).

Pronghorn does do show some mate selection in that they mate almost exclusively with territorial bucks (Bromley and Kitchen 1974). The data from this study combined with breeding data from 1976 give contrasting views concerning doe selection of specific territorial bucks, however. If the site hypothesis is true and the amount of time a doe spent with a buck was directly proportional to the probability that doe would mate with him, more does in Alexander Basin should have mated with TH than LTH or HH because does spent more time with TH than the others. Similarly, breeding in the Northside should have been divided among AB, SB, ST, and ORSL because does spent approximately the same proportion of time with all of them. In support of the site hypothesis, does in Alexander Basin seemed to select a particular male, TH. This did not appear to be the case in the Northside, however, because one buck did most of the observed breeding.

Further support of the site hypothesis comes when examining breeding data from Kitchen's (1974) study. The territorial buck with the most copulations in the 1969-1971 study occupied the same territory as TH, one of the most successful breeding bucks in 1976. It appears that the buck that occupies this territory in the northeast section of Alexander Basin is successful in breeding does.

There are several indications that territorial status is sufficient to insure some breeding success. Almost all territorial bucks did some breeding (Kitchen 1974 and personal communication), while bachelor bucks did almost none (Bromley and Kitchen 1974). Also, doe home ranges covered an average of four territories, while the number of territories immediately accessible to them was seven (three in Alexander Basin and four in the Northside). Does did not seem to go out of their way to cover all territories in the Northside-Alexander Basin area to find the best territory or best male. Two possibilities for mate selection by females exist: 1) does chose a territory (which included a fit male) from among those within her home range, or 2) does used other criteria for judging males and therefore were not necessarily confined to choosing from among males in her home range. One step towards an answer to this problem would be observed copulation between known bucks and does.

The courting technique of the buck at least partially determines his breeding success. In Wind Cave National Park, yearling and 2-year-old bucks were inept in performing courtship displays, either because of inexperience or because of the threat of bigger bucks. These young bucks completed fewer courtship displays because the does escaped before the display was finished (Bromley 1977). As Geist (1971) pointed out, no male ungulates are equipped physically to grab and hold on to the female, copulating with her despite her struggles. Copulation can only come about with the cooperation of the female, another reason for female mate selection to take place.

Bromley (1977) presents evidence of a dominance hierarchy among territorial bucks in Wind Cave National Park, based on age and length of time on a territory. This might be discernible by does, and influence their choice of a mate. Uganda kob have a dominance hierarchy, but it is reflected in ownership of territories. Uganda kob have a lek-type breeding system, so breeding territories are small. Young territorial bucks, or those low on the territorial dominance hierarchy hold peripheral territories. As they become dominant, they fight and gain territories towards the center, where most of the breeding takes place (Buechner 1961). In pronghorns, those low on the dominance hierarchy have no territories while dominant males hold territories. Reproductive success is strongly tied to territorial ownership (Bromley and Kitchen 1974).

If better territories mean more does will come there to be bred, it would be logical for bucks to challenge for better territories as they move up the dominance hierarchy. It seems this would be simpler for pronghorns to do this than some other antelopes because pronghorn bucks must reestablish territories each spring rather than holding them yearlong. Because pronghorn bucks do not change territories, another possibility is that older, more dominant bucks can improve their territories by altering boundaries in their favor when territories are reestablished in the spring.

There are advantages to retaining the same territory. Pronghorn territories are large, and intimate knowledge of the terrain is helpful in escaping predators and in keeping does in the territory. Kitchen (1974) and Bromley (1977) found that bucks used corners, hills, and other natural and man-made barriers to contain does, especially during rut.

Comparison of Pronghorn and African Ungulate Social Systems

Pronghorns are the only medium sized, open country ungulates in North America. African open country ungulates are numerous and are well enough studied that several classification systems based on their social organizations have been derived. Aspects of pronghorn social structure have been compared to those of some African ungulates throughout this discussion, but how does pronghorn social organization compare in general to those shown by similar African species? If pronghorns fit well into the classification systems, there would appear to be a general set of answers for how best to maximize energy fixation, and choose a mate for certain sized ungulates under certain environmental conditions. If pronghorns do not fit into these classification systems, this is not the case, or conditions are different in North America, and so different social systems have evolved to adapt to them.

Estes (1974) surveyed the known types of social organization in African Bovidae and attempted to relate them to ecological niche. He classified all bovids as: 1) solitary/territorial; 2) solitary/nonterritorial; 3) gregarious/territorial; or 4) gregarious/nonterritorial. Solitary species which generally live in closed habitats have such traits as: small size; females slightly larger or the same size as males; short inconspicuous horns; are browsers and selective feeders; cryptic, noncontrasting coloration; hide in reaction to danger; and a crepuscular or nocturnal main activity period. Gregarious species, on the other hand, are open country dwellers; large; have conspicuous horns; males are larger than females; are mainly grazers; have revealing, contrasting coloration; take flight in reaction to danger; and have diurnal, early morning and late afternoon main activity peaks. Based on these characteristics, pronghorns under this system would fall into the third category--gregarious/

territorial.

Characteristically, gregarious/territorial African bovids have three different social classes: herds of females and young, bachelor herds of juvenile to mature males, and territorial males. Female herds never spend all their time in one territory, and female herds are usually accompanied by one territorial buck. Association between females appears to generally be loose, with the possible exception of mother-daughter bonds. These features of gregarious/ territorial African bovids apply equally well to the social system of pronghorns, so pronghorns fit well into Estes' (1974) classification system.

Jarman (1974) also related social organization of African antelopes to their ecology. His classification of antelope feeding styles was presented earlier. Pronghorns fit into class c in terms of feeding style and body weight. Related class c social organization has the following attributes. During at least part of the year, a proportion of the adult males hold territories. During the territorial season, nonterritorial adult and subadult males form bachelor herds. Females gather in fairly large groups (6 to 150 or so, depending on the species), with open membership. Females are not confined to single territories. Females leave the herd to give birth, and the calf lies out for varying lengths of time before joining the herd. For the part of the year when territories are not defended, all sexes commonly mix. These class c characteristics also aptly describe pronghorn social organization.

Pronghorns fit very well into the classification systems proposed by Estes (1974) and Jarman (1974), even though these systems were devised for African species. Through convergent evolution, pronghorns and the similar African antelopes arrived at very similar social systems, indicating that this system is best suited to realization of doe strategy.

CHAPTER VI

SUMMARY

The summers of 1975 and 1976 were spent studying pronghorn social structure on the National Bison Range, Moiese, Montana. An increasing amount of work is being done on ungulate social systems, but emphasis has been on the male, not the female, components of the social system. Knowledge of female interactions, and female-male relationships is necessary to form a complete picture of pronghorn social organization.

Using sightings of known does, I determined that Bison Range doe home ranges covered an average of four buck territories. I observed considerable doe movement between Alexander Basin and the Northside. Does showed differential seasonal use of Alexander Basin and the Northside, probably moving in search of more succulent or new forage as the summer progressed. The pattern of use shown by known does was similar to the use pattern shown by all does, indicating that does did not spend the summer in separate subareas of Alexander Basin and the Northside.

Although doe group size and composition changed frequently, a seasonal trend in the size of doe groups was apparent. Doe groups were largest in May and early September, while doe group size dropped sharply in June during the fawning season, and in late September at the onset of the rut. The range of doe group sizes was generally large, and did not follow the seasonal trend shown by mean doe group size per 2-week period. Doe groups accompanied by territorial bucks were larger than unaccompanied groups, and doe groups with fawns were larger than doe groups without fawns.

Based on the number of times known does were observed in the same groups, does seemed to form subgroups within each area. As measured between known doe pairs, associations between does were fluid. Does formed a few close associations with other does, but even these closely associated doe pairs were not seen together in all observations. Does formed random or negative associations with other does in the area.

Another measurement of doe-doe interactions was calculated comparing sightings of each possible pair of known does. These home range correlations were largely negative, indicating the independence of individual does. Their measure correlated positively with the doe pair associations, indicating that a few does associate consistently when they are in the same section of Alexander Basin or the Northside.

Does showed differential use of buck territories in Alexander Basin, while does in the Northside used all territories about equally. In defense of the site hypothesis theory of female mate selection, the territorial buck in Alexander Basin that does mostly associated with during the summer did most of the observed breeding in that area. In the Northside, however, one buck did most of the observed breeding even though does had used Northside territories equally during the summer.

Pronghorn social organization fits very well into systems classifying social organization of African bovids and antelopes, indicating convergent evolution in social systems of the North American pronghorn and similar African ungulates.

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