Habitat use and distribution of bison in Theodore Roosevelt National Park
by Jack Eugene Norland

A thesis submitted in partial fulfillment of the requirements for the degree Master of Science in Range Science
Montana State University

Abstract:
This study described the habitat use and distribution of bison in Theodore Roosevelt National Park. Data was collected by direct observation of bison herds and by use of fecal transects. Additional data was collected through the use of 4 marked bison cows. Both percent use from direct observation and the fecal transect index gave comparable estimates of habitat use. The close agreement meant that habitat use observed in 1982-83 was not different from the previous years, and absence of mature bulls in the direct observations did not effect use patterns. Flat grasslands were preferred with use higher than availability would indicate. Areas of rugged terrain or dominated by trees and shrubs were avoided with use lower than availability. Habitat use changed over time with levels of use varying widely in some habitats.

Home ranges of individuals and the overall distribution were very similar. Virtually the whole park was used by bison, with few areas avoided. Restricted distribution was found during certain parts of the year. Herds were uniformly distributed during a 15 day period in the immediate area of use. Grazing activity was significantly different over the habitat types in the park, but not over a more generalized land classification scheme. Resting and other activities were significantly different over the habitats. Grazing and other activities had signifcantly different levels over time. Daily activities had a crepuscular pattern with grazing being the deterministic factor. Bison -moved 1.65 kilometers per day which did not significantly differ over time. Bison daily changed sites of use and habitats. The second and third weeks after initial location the distances moved by bison individuals from the initial location were in a random pattern.

The combined results characterize the bison as a nomadic animal which had preferences for habitats and localities. Bison are very similar to other large, herding bovids which inhabit grasslands.

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A thesis submitted in partial fulfillment
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APPROVAL

of a thesis submitted by

Jack Eugene Norland

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date 12-3-84

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ABSTRACT

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Home ranges of individuals and the overall distribution were very similar. Virtually the whole park was used by bison, with few areas avoided. Restricted distribution was found during certain parts of the year. Herds were uniformly distributed during a 15 day period in the immediate area of use. Grazing activity was significantly different over the habitat types in the park, but not over a more generalized land classification scheme. Resting and other activities were significantly different over the habitats. Grazing and other activities had signifcantly different levels over time. Daily activities had a crepuscular pattern with grazing being the deterministic factor. Bison moved 1.65 kilometers per day which did not significantly differ over time. Bison daily changed sites of use and habitats. The second and third weeks after initial location the distances moved by bison individuals from the initial location were in a random pattern.

The combined results characterize the bison as a nomadic animal which had preferences for habitats and localities. Bison are very similar to other large, herding bovids which inhabit grasslands.

INTRODUCTION

Knowledge of the habitat use and distribution of an animal is essential to understanding its ecology and management. Because the American bison has declined from millions of animals freely roaming the grasslands of North America to small populations restricted to a fraction of their former range, much of the historical information does not apply to the bison's current situation (Reynolds et al. 1982). New studies are needed to redefine how bison use their present habitats.

This study specifically looked at a population of bison in Theodore Roosevelt National Park (TRNP), North Dakota. The objectives were to describe the habitat use and distribution of bison in the park, in order to define the spatial and temporal use of the available resources in the park. This study was done in conjunction with a larger study meant to determine carrying capacities of bison in the park (Marlow et al. 1984).

LITERATURE REVIEW

The American bison (*Bison bison*) has been present on the North American continent since its evolution 4,000-5,000 before present (McDonald 1981). The bison is believed to have originated on the Northern Great Plains and from there radiated to other provinces. At the time of contact with western man, bison were distributed from the foothills of the Appalachian Mountains to the Great Basin and from the boreal forests of northwest Canada south to northern Mexico. The original environment of the bison was characterized by wide open spaces covered by large grasslands. Eventually, the bison did adapt to habitats dominated by forests and shrublands.

Before the changes brought by western civilization bison were characterized as highly mobile animals utilizing large land areas during the year (Garretson 1938, Larson 1940, Roe 1970, and Dary 1974). Bison preferred grasslands, and their diets were made up mostly of graminoid species. How the bison influenced its environment has been debated for years. Weaver and Clements (1938) stated that the plant communities in the grasslands were influenced primarily by climate and soils, and bison affected only short term changes. Larson (1940) and Malin (1956) felt that bison were a major influence keeping the grassland in a disclimax.

The bison's environment has undergone many changes since the coming of western civilization. The vast original grasslands have been fragmented leaving only small tracts of grassland in which the bison can live. Since the great slaughter of the herds almost all bison have been managed as captive animals with only Yellowstone National Park and Wood Buffalo National Park having herds descended from and resembling wild animals (Reynolds et al. 1982).

Several recent studies have investigated the bison in their present situation. Popp (1981), working in Wind Cave National Park, reported that bison chose grassslands for the majority of use, and forested areas were only used as travel corridors. Sites dominated by cool season grasses tended to be preferred in the spring and early summer by the cow herds while warm season grass sites were preferred in the mid and late summer. The cool season sites were again preferred in the fall. Bull groups had different usage patterns with the warm season sites being preferred throughout the year. Also, forest openings were used more often by the bull groups. Prairie dog towns received heavy use during the rut (midsummer to early fall). The largest herds found in the park were on the prairie dog towns during the rut.

Coppock et al. (1983), working in Wind Cave, reported specifically on bison use of prairie dog towns. They found a definite selection for prairie dog towns during midsummer. Herds would use the most recently colonized areas for grazing while the older portions of the towns were used for other activities. This usage pattern was related to differences in vegetation structure and forage quality brought about by the herbivory of the prairie dogs.

In Utah Van Vuren (1979 and 1983), working with an isolated population of bison in the Henry Mountains, reported that bison differed from cattle in several respects. Bison tended to use habitats farther away from water sources, steeper landforms, and higher elevations. Bison used habitats which were dominated by their preferred forage, grass and grasslike plants. Cattle avoided the same sites because of the distance from water, steepness, and elevation.

Van Vuren (1979 and 1983) additionally reported that bison were a highly mobile animal staying an average of 1.9 days at a site but rarely longer than 3 days. The changes in bison distribution during the study were attributed to seasonal and yearly differences in forage and weather patterns. The home ranges of several bison cows overlapped with the average size being 52 square kilometers (km^2). Herds tended to include 15 individuals or fewer, but the size of herds was positively correlated with the size of forest openings. Social structure of the herds and the association of individuals was described as fluid.

Lott and Minta (1983) reported on group stability and individual associations of bison cows on Santa Catalina Island, California. They reported that mature cows associated in a random pattern, and the only close association reported was between cows and calves. The cow-calf association eventually became random after calves reached ages of 8-19 months. Herd size did not follow a random pattern but was influenced by environmental factors. Some of the environmental factors mentioned were watering locations, topography, forage quality and phenology, and social interactions such as the rut. Home ranges for cows averaged 56.1 km^2 with portions of all home ranges overlapping. Movement of individuals in a straight line averaged 2.8 kilometer (km) per day. This did not change significantly over the seasons but did increase somewhat during the rut. The authors characterized the bison as a highly mobile animal, with similar home ranges, and being driven individually by environmental rather then social factors.

Several authors have described habitat use by bison in Wood Buffalo (Soper 1941, Reynolds et al. 1982) and Yellowstone National Parks (McHugh 1958, Meagher 1973). Both parks are dominated by forests although bison almost exclusively choose areas dominated by graminoids. The distribution of the grasslands limited the range of bison in the parks. Although other habitats and locations were chosen during the year, this was thought to be related to snow depths and local climatic conditions.

McHugh (1958) investigated the behavior of bison herds in Yellowstone National Park and several other locations. He reported that the home range for Yellowstone National Park bison was approximately 31 km^2 in the summer and 93 km^2 in the winter. Movement of bison in the Whichita Mountains National Wildlife Refuge averaged 3.4 km per day and this daily movement was common to all the herds. He observed bison going to water only once a day.

Peden et al. (1974), working with cattle and bison in northeast Colorado, reported that bison used uplands more than cattle. Cattle were found more often in the drainageways. Schwartz and Ellis(1983), working in the same area, reported that bison were selecting for the most abundant forage the dominant grasses. They theorized that bison, because of their large size and energy needs, would have to select for the most available forage in an area.

From the literature review it appears that the bison of today: 1) prefer grasslands, 2) will change habitat preference during the year, 3) have differences in habitat preferences between the sexes, 4) have large home ranges, 5) will utilize most all of the available habitat, 6) move constantly from site to site, and 7) have a fluid social structure with no long term associations. Differences in the home range sizes were related to the different sizes of available preferred habitat.

STUDY SITE

The entire study was conducted in Theodore Roosevelt National Park. The Park was created in 1978, but had previously been Theodore Roosevelt Memorial Park established in 1947. The Park is composed of two units, the North Unit (NU) and South Unit (SU) (Figures 1 and 2). The SU is 18,756 hectares in size and the NU 9,741 hectares in size. Both units are located in western North Dakota, the SU near Medora, North Dakota and the NU 80 kilometers (km) directly north. Bison were reintroduced into the Park in 1956.

The dominant features in both units are the Little Missouri River and the valley and badlands that it has formed. During the most recent glaciation the mouth of the Little Missouri River was lowered which accelerated the erosional forces in the soft sedimentary rock producing the badland formations found in the Park (Hansen et al. 1980). The past and ongoing erosion has produced a varied topography which results in a variety of vegetational communities in the Park.

Two different schemes were used to describe the land in the Park. One scheme involved dividing the units into physiographic/vegetational classes (from now on referred to as classes) based on appearance, landform origin, and the gross structure of the associated vegetation (trees, grasslands, shrubs, etc.). A total of 14 different physiographic/vegetational classes were identified. Seven classes were unique to one or the other units, while the others were present in both units (Table 1). Figures 3 and 4 indicate where in the units each class is found. A general description of each class follows:

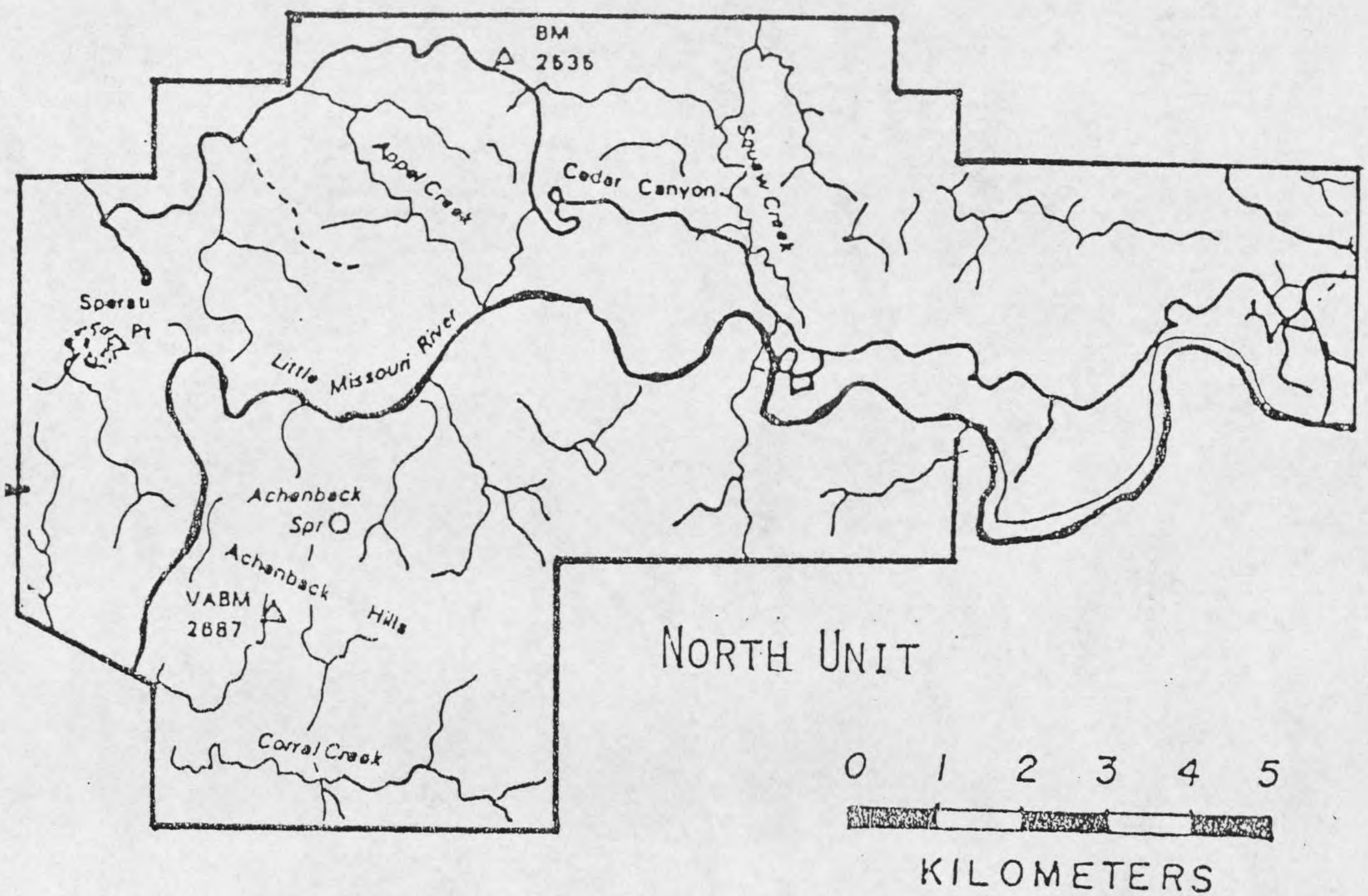

Figure 1. Map of North Unit, Thoedore Roosevelt National Park.

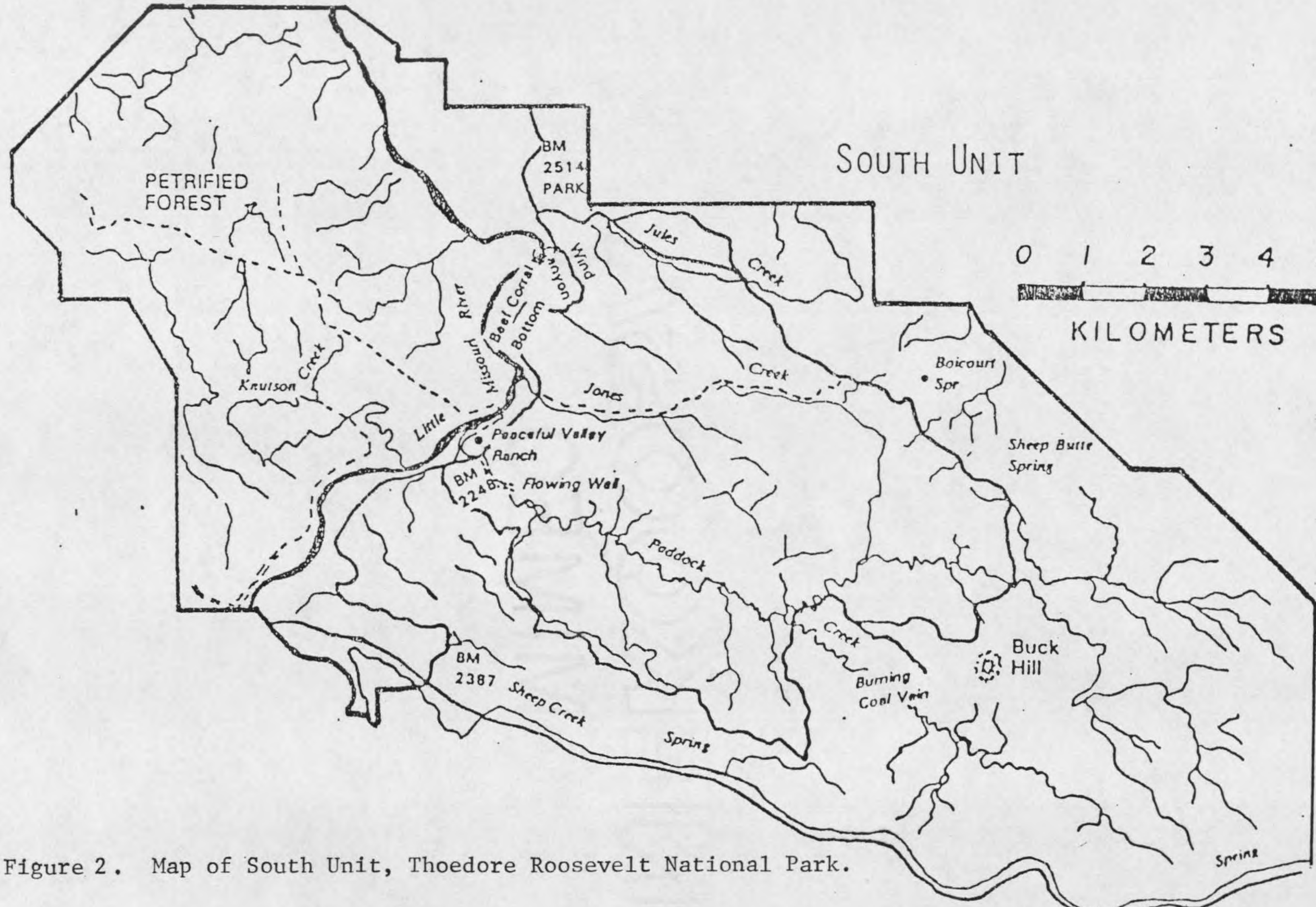

Figure 2. Map of South Unit, Thoedore Roosevelt National Park.

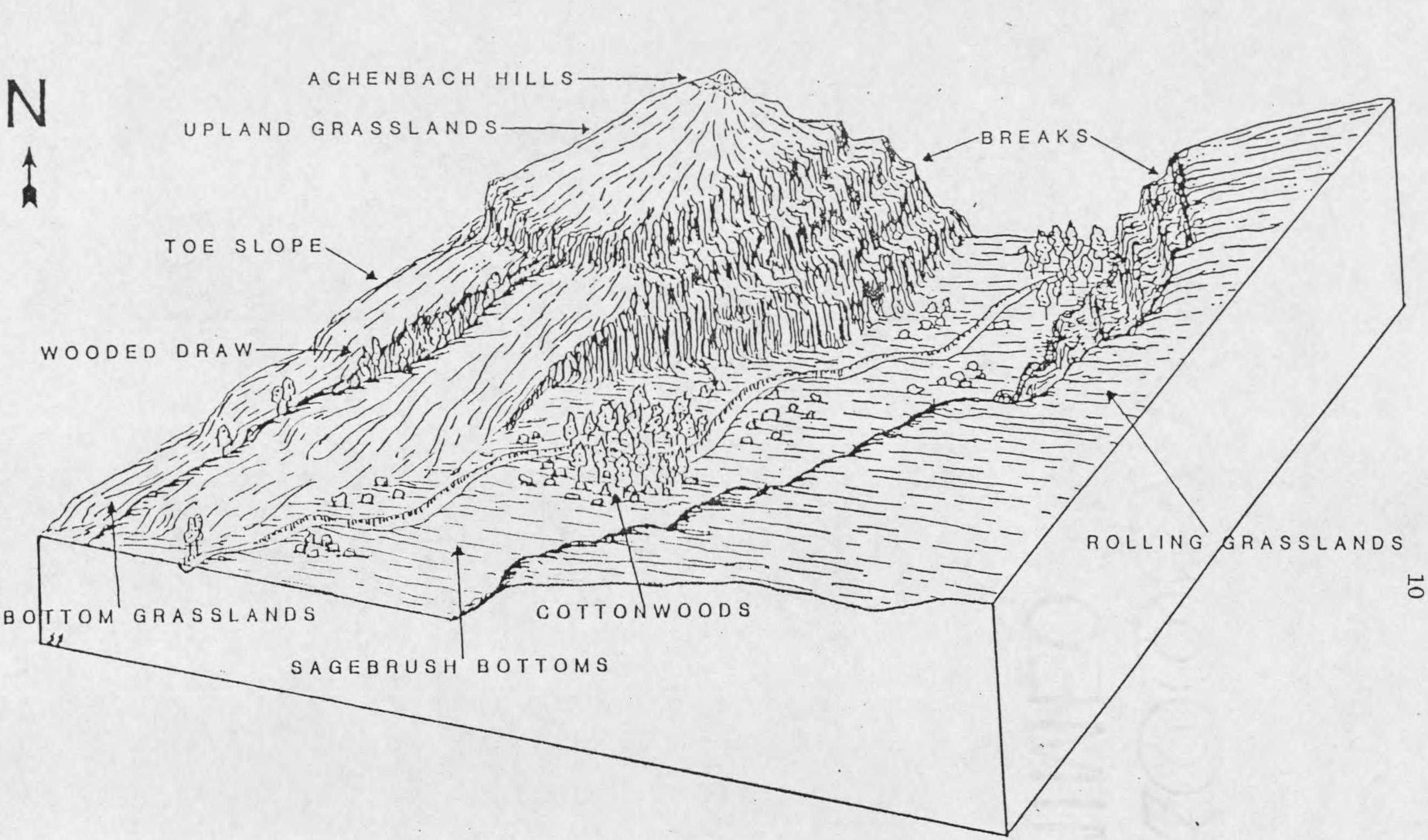

Figure 3. A view of the physiographic/vegetational classes within an idealized landform of the North Unit.

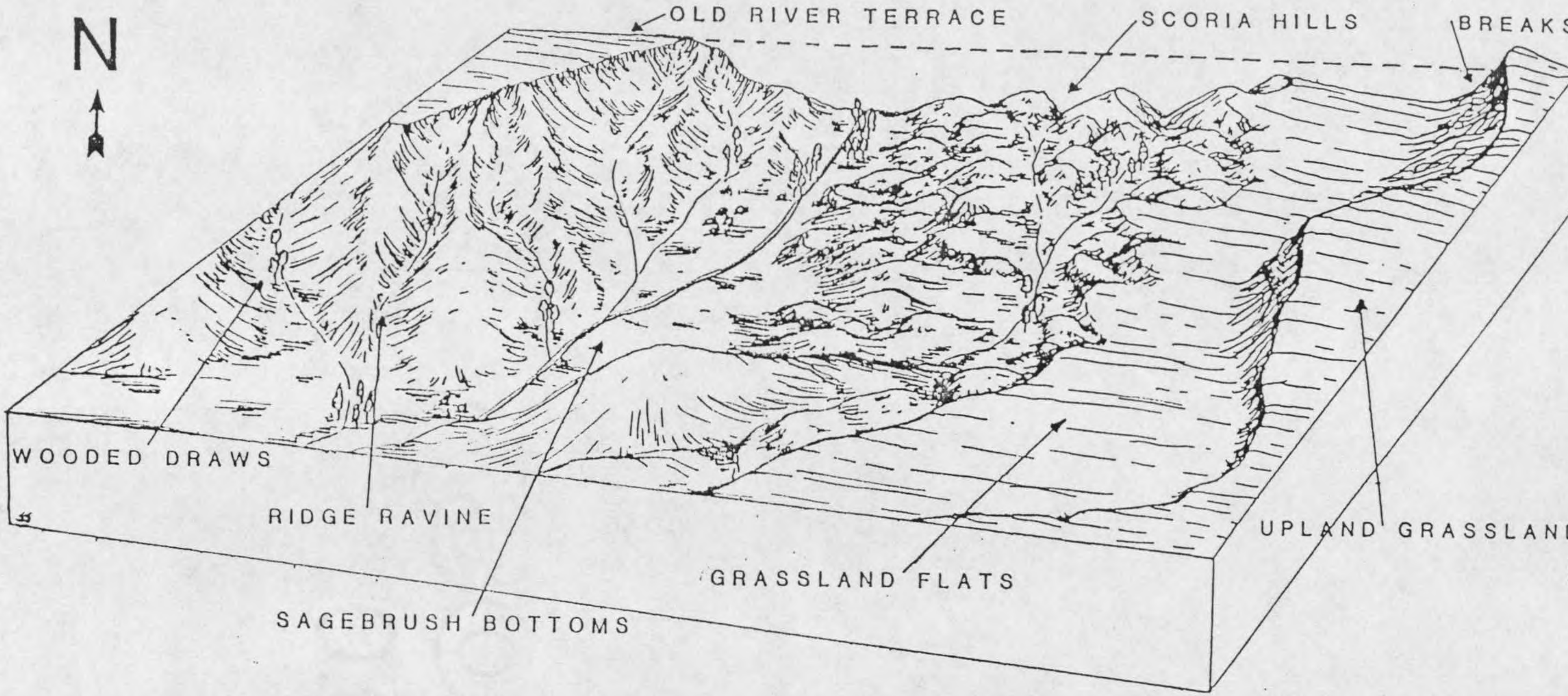

Figure 4. A view of the physiographic/vegetational classes within an idealized landform of the South Unit.

1. Breaks: consist of areas noticeably devoid of vegetation or if vegetation does exist, it is situated on steep slopes.

2. Cottonwood Forests: gallery forests along perennial water courses dominated by plains cottonwood (Populus deltoides). Large expanses in the NU are devoid of a dense shrub understory and have instead a dense cover of grass and forbs.

3. Wooded Draws: woody stringers dominated by either green ash (Fraxinus pennsylvanica) or aspen (Populus tremuloides). The wooded draws are uniformly scattered over both units of the Park.

4. Upland Grasslands: level to rolling grasslands found on the plains above the river valley. These lands are typical of the northern Great Plains.

5. Old River Terraces: level grasslands 200 to 500 feet above the river which are situated on terraces formed before the rapid down-cutting of the river.

6. Grassland Flats: large flat grassed alluvial deposits found 100 to 200 feet above the river valley.

7. Bottom Grasslands: large flat grassed alluvial deposits found on higher floodplains of the Little Missouri and its larger tributaries.

8. Toe Slopes: gradually sloping lands formed by slumping and alluvial deposition. The land is covered with grass, shrubs, and trees.

9. Rolling Grasslands: level to rolling grasslands found on the glaciated plains above the river valley.

10. Achenbach Hills: hills found 650 feet above the river which are covered by grass and shrubs. The large boulder fields on the slopes of the hills are the debris of a bedrock cap.

11. Ridge and Ravine: lands highly dissected by watercourses and covered by various grasses, shrubs, and trees.

12. Scoria Hills: lands influenced by scoria (a clinker formed from the baking of clays adjacent to burning coal veins) which produces a differential weathering

of the land. This weathering produces a very rugged and varied topography which is covered by various grasses and shrubs.

13. Sagebrush Bottoms: floodplains dominated by silver sagebrush (Artemisia cana) along with a substantial grass cover.

14. Prairie Dog Towns: lands which have been or are being influenced by prairie dogs. At the edges of towns plants are still characteristic of the former plant community. Nearer the center, vegetation is absent or dominated by unpalatable perennial plant species.

Table 1 gives the area of each class found in the different units.

Table 1. Number of hectares classified in the different physiographic/vegetational classes for both units (river channels included).

	Hecterage	
Physiographic/Vegetational Classes	SU	NU
Breaks	3578.3	2904.1
Sagebrush Bóttoms	1174.8	911.4
Wooded Draws	424.1	373.5
Upland Grasslands	1010.5	419.5
Prairie Dog Town	168.3	48.1
Cottonwood Forests	88.6	519.6
River Bottom	87.4	171.4
Grassland Flats	1949.0	-
Bottom Grassland	-	895.8
Ridge & Ravine	6879.5	-
Toe Slopes	-	1956.3
Old River Terraces	1012.5	-
Achenbach Hills	-	77.0

The second scheme was based on habitat types (HT) which have been previously described by others working in the immediate area (Whitman 1978, Hansen et al. 1980, K. Hirsch (personal communication, North Dakota State University), M. Girard (personal communication, North

Dakota State University), and Soil Conservation Service (range site guidelines for the Badlands of North Dakota). The habitat types were defined as the vegetation assemblages that eventually would develop on a site given a specific climate and substrate. Table 2 shows each HT recognized and the corresponding classification by the authors.

Table 2. Comparison of habitat type (HT) and mapping unit (MU) names used in this study with other systems developed in North Dakota (Whitman 1978, Hansen et al. 1980, K. Hirsch (personal communication, North Dakota State University), M. Girard (personal communication, North Dakota State University), and Soil Conservation Service (range site guidelines for the Badlands of North Dakota).

Agropyron smithii - Stipa viridula HT	
Hirsch:	Agropyron smithii - Stipa viridula*
Whitman:	Agropyron - Stipa viridula - Bouteloua and Agropyron - Stipa viridula - Mixed
SCS:	Clayey range site
Agropyron smithii - Stipa comata HT	
Hirsch:	Agropyron smithii - Stipa comata*
Whitman:	Agropyron - Stipa - Bouteloua
Hansen et al.:	Agropyron smithii - Carex filifolia
SCS:	Silty range site
Stipa comata - Bouteloua gracilis HT	
Hirsch:	Stipa comata - Bouteloua gracilis*
Whitman:	Stipa - Calamovilfa - Carex
Hansen et al.:	Stipa comata - Carex filifolia
SCS:	Sandy range site
Artemisia cana HT	
Hirsch:	Artemisia cana*
Hansen et al.:	Artemisia cana - Agropyron smithii
Andropogon scoparius - Juniperus horizontalis HT	
Hirsch:	Andropogon scoparius - Juniperus horizontalis*
Hansen et al.:	Juniperus horizontalis - Andropogon scoparius
SCS:	Very shallow range site

Table 2. Continued

Artemisia tridentata - Atriplex confertifolia HT

Hirsch:	Artemisia tridentata - Atriplex confertifolia*
SCS:	Shallow clay range site

Artemisia tridentata - Bouteloua gracilis HT

Hirsch:	Artemisia tridentata - Bouteloua gracilis*
Hansen et al.:	Artemisia tridentata - Agropyron smithii
SCS:	Shallow clay range site

Andropogon scoparius HT

Hirsch:	Andropogon scoparius*
Whitman:	Andropogon - Stipa - Bouteloua
Hansen et al.:	Andropogon scoparius - Carex filifolia
SCS:	Shallow range site

Andropogon gerardii HT

Hirsch:	Andropogon gerardii*
Whitman:	Andropogon - Stipa - Sporobolus

Agropyron smithii - Bouteloua gracilis - Distichlis spicata

Hirsch:	Agropyron smithii - Bouteloua gracilis - Distichlis spicata var. stricta*
SCS:	Thin claypon range site

Grassed Sand Floodplains HT

SCS:	Sandy range site*

Hardwood Draws HT

Hansen et al.:	Fraxinus pennsylvanica - Prunus virginiana and Fraxinus pennsylvanica - Symphoricarpos occidentalis*
Girard:	(Has a similar HT proposed)

Juniperus scopulorum - Oryzopsis mircantha HT

Hansen et al.:	Juniperus scopulorum - Oryzopsis mircantha*
Girard:	(Has a similar HT proposed)

Populus deltoides - Juniperus scopulorum HT

Girard:	Populus deltoides - Juniperus scopulorum

Table 2 Continued

Populus tremuloides - Betula occidentalis HT

Hansen et al.: Populus tremuloides - Betula occidentalis#
Girard: (Has a similar HT proposed)

Marsh MU

SCS: Wetland range site#

Brush MU

Hansen et al.: Symphoricarpos occidentalis# (this includes only a few sites, the rest may have been dominated by Prunus virginiana or Prunus americana)

Introduced Grass MU

Classified by author

Prairie Dog Towns MU

Classified by author

Willows MU

Classified by author

Man-Managed MU

Classified by author

#Denotes the description which was used in this study for the habitat type or mapping unit.

Besides the 15 HT, seven mapping units were also recognized. Mapping units (MU) were defined as vegetation assemblages which have been disturbed by natural or anthropogenic forces or were in the early stages of succession. Several MU had no comparable designations by the previously mentioned authors. The charateristics which were used to differentiate these MU were:

1. INTRODUCED GRASSES MU - disturbed areas replanted to introduced grasses to reduce erosion hazards. The grasses most often used were crested wheatgrass (Agropyron cristatum) or smooth brome (Bromus inermis).

2. PRAIRIE DOG TOWNS MU - vegetation drastically altered by prairie dogs.

3. RIVER BOTTOMS MU - areas subject to frequent flooding.

4. WILLOWS MU - areas dominated by densely growing willow (Salix spp.) with little other plant growth.

5. MAN-MANAGED MU - those lands whose vegetation was altered by ongoing human activities (roadsides, campgrounds, etc).

At several locations in both units, habitat types or mapping units were so small or so intermixed as to make it difficult to differentiate specific assemblages. These mosaics were classified as complexes. Table 3 shows the four complexes and the percent contribution of each HT and MU. Areas not classified as a HT, MU, or complex were placed into a separate category: unvegetated. Collectively the HT, MU, and complexes will be referred to as habitat divisions.

Appendix A shows the area of each HT, MU, and complex as it occurs in each of the classes. Mapping of all classes, HT, MU, and complexes was done with the use of color-infrared photos. Photos were interpreted through the use of a photo enhancing computer and by extensive ground truthing. All classes, HT, MU, and complexes were placed on a base map of 1:12000 scale and digitized.

Table 3. List of each vegetational complex and the proportion of each HT or MU that comprised the complex.

Achenbach Hills Complex -

.4	Agropyron smithii - Stipa comata
.3	Stipa comata - Bouteloua gracilis
.15	Andropogon scoparius
.05	Andropogon scoparius - Juniperus horizontalis
.05	Brush
.05	Andropogon gerardii

Petrified Forest Complex -

.4	Agropyron smithii - Stipa comata
.3	Agropyron smithii - Stipa viridula
.1	Andropogon scoparius
.05	Andropogon gerardii
.15	Stipa comata - Bouteloua gracilis

Rolling Scoria Complex -

.25	Andropogon scoparius
.2	Agropyron smithii - Stipa viridula
.2	Stipa comata - Bouteloua gracilis
.15	Agropyron smithii - Stipa comata
.1	Andropogon scoparius - Juniperus horizontalis
.1	Agropyron smithii-Bouteloua gracilis-Distichlis stricta

Steep Scoria Complex -

.3	Andropogon scoparius
.25	Andropogan scoparius - Juniperus horizontalis
.15	Agropyron smithii - Stipa viridula
.15	Stipa comata - Bouteloua gracilis
.1	Artemisia tridentata - Atriplex confertifolia
.05	Agropyron smithii-Bouteloua gracilis-Distichlis stricta

METHODS

Data were gathered in two basic categories: habitat use by bison and distribution of bison. Data on habitat use were collected by the direct observation of bison herds and by the use of fecal transects. Direct observations were started in July 1982 and ended in July 1983. No observations were made from January to early March 1983. Observations averaged 8 hours per day and were taken between dusk and dawn. During the direct observations the following information was collected at each 15-minute observation point:

1. The location of the herd (recorded on a 1-25,000 topographic map).
2. The number of bison using the classes and habitat divisions.
3. The number of bison engaged in grazing, resting, and other activities within the classes and habitat divisions. Grazing was defined any activity that would end in a plant being eaten. Resting was used only for bison reclining on the ground. Other activity was anything that was not grazing or resting; this could include social interactions, watering, walking, running, etc. Each bison was classified as doing only one of the activities at any one observation point.

A total of 5,281 observations were taken at the 15-minute observation points which translated into 298,016 bison minutes. The hours of observation were varied to prevent bias resulting from observations taken during only one part of the day. No night observations were taken because of the difficulty and danger involved, even though bison were active at night. Large herds were selected for direct observations whenever possible because small herds contained only a small portion of the population and could possibly bias the observations toward habitats used excessively by small herds. All direct observations were done in the SU because of time and travel constraints. Eleven different time periods were delineated during the study. Table 4 gives the dates of each period and how many observation days were completed in each period.

Table 4. Time periods with starting and ending dates along with the number of direct observation days in the period.

	Period	Start		End	Number of Observation Days
1.	April	3/28/83	to	4/14/83	14
2.	May	5/ 1/83	to	5/19/83	14
3.	June	6/27/83	to	7/ 7/83	14
4.	August 1	8/ 3/82	to	8/15/82	10
5.	August 2	8/16/82	to	8/31/82	13
6.	September 1	9/ 1/82	to	9/15/82	11
7.	September 2	9/16/82	to	9/30/82	11
8.	October 1	10/ 2/82	to	10/15/82	10
9.	October 2	10/16/82	to	10/28/82	11
10.	November	11/10/82	to	11/26/82	14
11.	December	12/ 4/82	to	12/15/82	10

Fecal transects consisted of walking a transect 500 meters long and 1 meter wide, with all recognizable bison chips counted within the transect. By running several transects within the same area transects of this length and width adequately sampled the density of chips within a 100 hectare area of a class. Transects were distributed in a stratified random manner in both units. The SU was divided into 9 blocks and the NU into 5 blocks. Within each block transects were placed randomly in each of the classes in the block. The number of transects placed into each class was proportional to the area it covered in the block. All classes had a minimum of 3 transects per unit. Fecal transects were read during the summer of 1983. A total of 52 transects were read in the NU and 100 in the SU (Table 5).

Home range and herd associations were established through the use of 4 characteristically marked animals. These animals had individually recognizable horn configurations. Locations of these animals were recorded whenever they were encountered during the study.

Several methods of statistical analysis were employed in the study. The Chi-square test for independence was used to test differences in availability (area covered by the class) and bison use of different classes (Zarr 1984). The Chi-square test for independence compared the various distributions of bison to a random distribution (Poisson), and compared each of the various distributions amongst themselves. Coefficients of dispersion were calculated for the home ranges and various distributions of bison based on the number of locations per km^2 (Sokal and Rohlf 1981). A coefficient of dispersion of 1 indicates random distribution, less than 1 means the distribution is uniform, and greater than 1 means the distribution is clumped.

Analysis of the activities of bison was based on the percent of the herd engaged in each activity at the 15-minute observation point. Activities were then averaged over all the 15-minute observation points within each time period. Those averages based on fewer than 20 observations were considered an inadequate sample and dropped from further analysis. The regression model of analysis of variance (ANOVA) with unequal replication for a two-factor experiment was used to test for significance among the main effects: either the classes and time periods, or the habitat divisions and time periods (Neter and

Wasserman 1974). F-tests for the main effects followed this equation:

$$\frac{SSE(R)-SSE(F)}{DF(R)-DF(F)} \Big/ \frac{SSE(F)}{DF(F)}$$

where:

SSE(R)= Error sum of squares for the reduced model for the other main effect.

SSE(F)= Error sum of squares for the full model.

DF(R) = Error degrees of freedom for the reduced model for the other main effect.

DF(F) = Error degrees of freedom for the full model.

Because of the unequal replication no interaction effects could be analyzed, and it will be assumed there were none. If only one main effect was significant, then that significant effect was subjected to separation of means as a one factor analysis using Tukey's method (Sokal and Rohlf 1981). If both main effects were significant, an adjustment of the percents in the classes and habitat divisions was done in the form of:

$$X_{ij}-X_i=Z_{ij}$$

where:

X_{ij}= The original percent observation in each class and habitat division.

X_i = The mean of the percents found in that time period.

Z_{ij}= The transformed observation.

The adjusted values were then used in the separation of means by one-factor analysis using Tukey's method. The purpose of the adjustment was to reduce the effect of the time periods on the values in the classes and habitat divisions. No suitable form of adjustment was found to reduce the effect of the classes and habitat divisions on the time periods, but they were graphically represented so trends could be observed. An arcsine transformation was done on all of the activity percentages.

The daily distance moved among the time periods was analyzed by analysis of variance (Sokal and Rolhf 1981). A logarithimic transformation was done on the distances because of heteroscedasticity and the fact that the standard errors were proportional to the means. The G-test (Sokal and Rolhf 1981) was used to test for independence among the distances between two random points and the distances bison moved from an original location. The G-test was also employed to test independence between the distances that a random transect was from water compared to the distance from water during a herd's daily movement.

RESULTS AND DISCUSSION

Direct Observations

The average herd size in the direct observations was 71 animals (standard error (SE)=25, range 25-126). The herds in the Park consisted of all ages of females and males up to 4 years of age. Mature bulls were found as solitary individuals or in small groups. The only time when large numbers of mature bulls were found in herds was during the rut, and this was the only time when direct observations included significant numbers of mature bulls. Herds under observation varied in size between and within days.

Fecal Transects

The average number of chips per fecal transect and associated standard error for each class appears in Table 5. The large variation within some of the classes evidently reflected the disproportionate levels of use among different areas of the Park.

Habitat Use

The percent use of each class in the SU from both fecal transects and the direct observations is given in Table 6. Both fecal transects and direct observations gave comparable (r=.95) estimates of use for the classes, but the methods did differ in what they were estimating. These differences were:

1. The fecal transects estimated the accumulated use over two years or more, while direct observations estimated use only during the study period.

2. The fecal transects estimated use by the whole population while direct observations estimated herd use, ignoring mature bull use for most of the year.

3. Fecal transectswere only an index of use while direct observations were an actual measure of use (at least during the daylight hours).

The high correlation between the estimates of both methods suggested that: 1. use of classes in 1982-83 was similar to that in the previous year or years, 2. use of classes by the entire population was not radically different from the use exhibited by the herds, and 3. the fecal transect index arrived at the same relative use as did the real estimates from the direct observations.

Table 5. Number of transects and average number of chips per fecal transect and standard error in the classes for both units.

Class	South Unit			North Unit		
	transects	chips	SE	transests	chips	SE
Breaks	21	1.5	2.0	9	1.0	1.2
Cottonwood forests	3	0.3	0.6	6	2.3	1.9
Wooded draws	9	2.2	1.9	5	4.0	2.0
Upland grasslands	9	17.8	13.5	4	33.5	14.9
Old river terraces	8	41.9	31.2	-	-	-
Grassland bottoms	-	-	-	5	14.8	8.9
Grassland flats	11	8.7	7.7	-	-	-
Toe slopes	-	-	-	5	31.6	28.3
Rolling grasslands	-	-	-	5	15.4	9.3
Ridge & Ravine	11	9.6	7.9	-	-	-
Scoria hills	15	8.7	5.8	-	-	-
Achenbach hills	-	-	-	3	11.6	2.1
Sagebrush bottoms	9	6.4	9.2	6	9.5	5.6
Prairie dog towns	4	23.5	12.4	3	50.7	51.1

Table 7 compares the percent availabilty of each class, i.e. the area of coverage, and the bison use estimated by fecal transects.

Table 6. Percent use of classes from direct observations and fecal transects in the South Unit.

Class	Observations	Transects
Breaks	1.3	1.2
Cottonwood forests	2.9	0.3
Wooded draws	1.3	1.8
Upland grasslands	7.2	14.7
Old river terrraces	35.9	34.7
Grassland flats	8.0	7.2
Ridge & Ravine	6.0	7.9
Scoria hills	10.6	7.2
Sagebrush bottoms	8.8	5.3
Prairie dog towns	17.9	19.5

Table 7. Average number of bison fecal chips per transect and availability (percent coverage) of classes. Significance found by using Chi-square analysis.

class	South Unit		North Unit	
	% coverage	chips	% coverage	chips
Breaks	17.3^A	1.5^B	37.2^A	1.0^B
Cottonwood forests	0.7^A	0.3^B	4.6^C	2.3^C
Wooded draws	3.0^A	2.2^B	3.9^C	4.0^C
Upland grassland	5.5^A	17.8^B	6.3^A	33.5^B
Old river terrace	5.8^A	41.9^B		
Grassland flats	11.8^C	8.7^C		
Grassland bottoms			4.5^A	14.8^B
Toe slopes			19.1^A	31.6^B
Rolling grasslands			11.6^C	15.4^C
Achenbach hills			1.9^A	11.6^B
Ridge and Ravine	19.2^A	9.6^B		
Scoria hills	29.7^A	8.7^B		
Sagebrush bottoms	5.5^C	6.4^C	10.3^A	9.5^B
Prairie dog town	1.5^A	23.5^B	0.5^A	50.7^B

A,B,C Pairs with different superscripts are significantly different at $p<0.01$.

Those classes with use significantly different from their availability were identified using the Chi-square test of independence. Significantly higher use was interpreted as preferance for a class, and lower use was interpreted as avoidance of a class. Several classes were neither strongly avoided nor preferred. The classes which were preferred were flat and dominated by grasslands. The classes which were avoided had either rugged topography or were dominated by trees or shrubs. Those classes with no definate preference or aviodance had characteristics that were found in both the avoided and preferred classes.

The observed use of the habitat divisions along with their availability is given in Table 8. Because of the non-independence of the observations, no statistical tests were done. Those HT, MU, and complexes with use much higher than availabilty were dominated by grasses and occurred on level or gently rolling sites. Those with lower use were dominated by woody vegetation or were found on rugged sites. Those in which use approximated availability had characteristics of both high use and low use habitat divisions.

The high preference for grasslands throughout the year was probably the result of bison diets being composed of 87% graminoids (Marlow et al. 1984), and bison being large animals with high absolute energy requirements and a tolerance for low quality forage (Schwartz et al. 1981). In addition, bison had no need for protective cover, either from environmental conditions or from predators, and foraging in the winter is easiest on grasslands because of the lower snow cover (Reynolds et al. 1982).

Table 8. Percent use from the direct observations and percent coverage of habitat types, mapping units, and complexes in the South Unit.

HT, MU, & Complexes	%Use	%Coverage
Agropyron smithii-Stipa comata	22.5	4.3
Agropyron smithii-Stipa viridula	22.0	15.5
Stipa comata-Bouteloua gracilis	3.9	2.0
Artemisia cana	6.5	5.5
Andropogon scoparius-Juniperus horizontalis	0.9	3.6
Artemisia tridentata-Atriplex confertifolia	2.2	2.3
Artemisia tridentata-Bouteloua gracillis	0.2	0.6
Andropogon scoparius	4.5	10.1
Hardwood draws	0.4	2.3
Juniperus scopulorum-Oryzopsis mircantha	-	1.9
Populus deltoides-Juniperus scopulorum	0.7	0.5
Introduced grasses	3.9	1.0
Prairie dog town	17.8	1.0
River bottom	2.8	0.5
Man-managed	2.4	0.2
Steep scoria complex	1.7	13.0
Rolling scoria complex	3.1	7.8
Petrified forest complex	0.1	0.1
Watering area	0.4	-
Unvegetated areas & river	0.1	27.8
Brush	-	0.1
Populus tremuloides	-	0.1

Seasonal Use of Habitats

The direct observations allowed seasonal use to be examined in each class and habitat division. Use over the 11 different time periods for each class and habitat division can be found in Appendix B. Heavily used classes had widely fluctuating values from period to period while those with little use did not fluctuate as widely. The same was true for the habitat divisions. Some of the classes, such as the prairie dog towns and old river terraces, had a definite seasonal pattern to their use. The prairie dog towns had high use during the summer and low use at all other times while the old river terraces had low use during the summer and high use at other times. There were other classes, such as the scoria hills which fluctuated, but showed no set pattern. Examples can also be found in the habitat divisions of seasonal and irregular use patterns.

Prairie dog towns make up only a small part of the Park (1.5%), but received high use by bison. This high preference has been noted and investigated by several other authors (Popp 1981, Coppock et al. 1983). Coppock et al. (1983) reported that preference is the result of plants on the edges of the towns being changed physically and genetically by the herbivory of the prairie dogs. Such changes cause plants to be more preferred and palatable to bison. Another reason could be that bison are drawn to prairie dog towns for rutting activities (Popp 1981, Shult 1972). Use of prairie dog towns increased in the study from almost zero at the start of the rut to a high level at the peak of the rut and then dropped back to zero at the end of the rut (Figure 13).

Two other preferred MU were the river bottoms and man-managed. During the summer the river bottoms became favorite loafing sites. This was because they provide easy access to water for drinking and cooling off, and being nearly devoid of herbaceous vegetation the river bottoms became quite hot. This produced conditions unfavorable to flies which were a nuisance to bison during the summer. Man-managed areas may have been preferred because the vegetation was manipulated by mowing, watering, and seeding. This manipulation produces a preferred and palatable forage.

Individual and Herd Associations

No long-term associations between the four identifiable cows were observed nor were individuals associated with specific herds. Instead there was often a day-to-day interchange of individuals within herds. At some point during the study every marked animal was associated with all of the other marked animals.

Home Range and Distribution

Home ranges of bison were determined for two of the four characteristically marked animals (Figures 5 and 6). The home range of each surviving bison appeared to encompass the whole of the Park. Certain areas in the Park had locations clumped together, indicating bison preference for certain classes and habitat divisions at these sites. Areas devoid of locations were dominated by avoided classes and habitat divisions, lacked permanent water, were not easily accessible due to rough terrain, and/or lacked suitable forage.

Coefficients of dispersion established for animals 0001 and 0002, were 2.1 and 1.4, respectively. Both coefficients suggest that these animals exhibited a clumped rather than a random or a uniform distribution. This clumping was presumably related to the preferences for classes and habitat divisions which were themselves not distributed evenly over the Park.

The overall distribution of the herds and bison in the Park is in Figure 7. Both the individual home ranges and the overall distribution were similar in that locations were found from one end of the

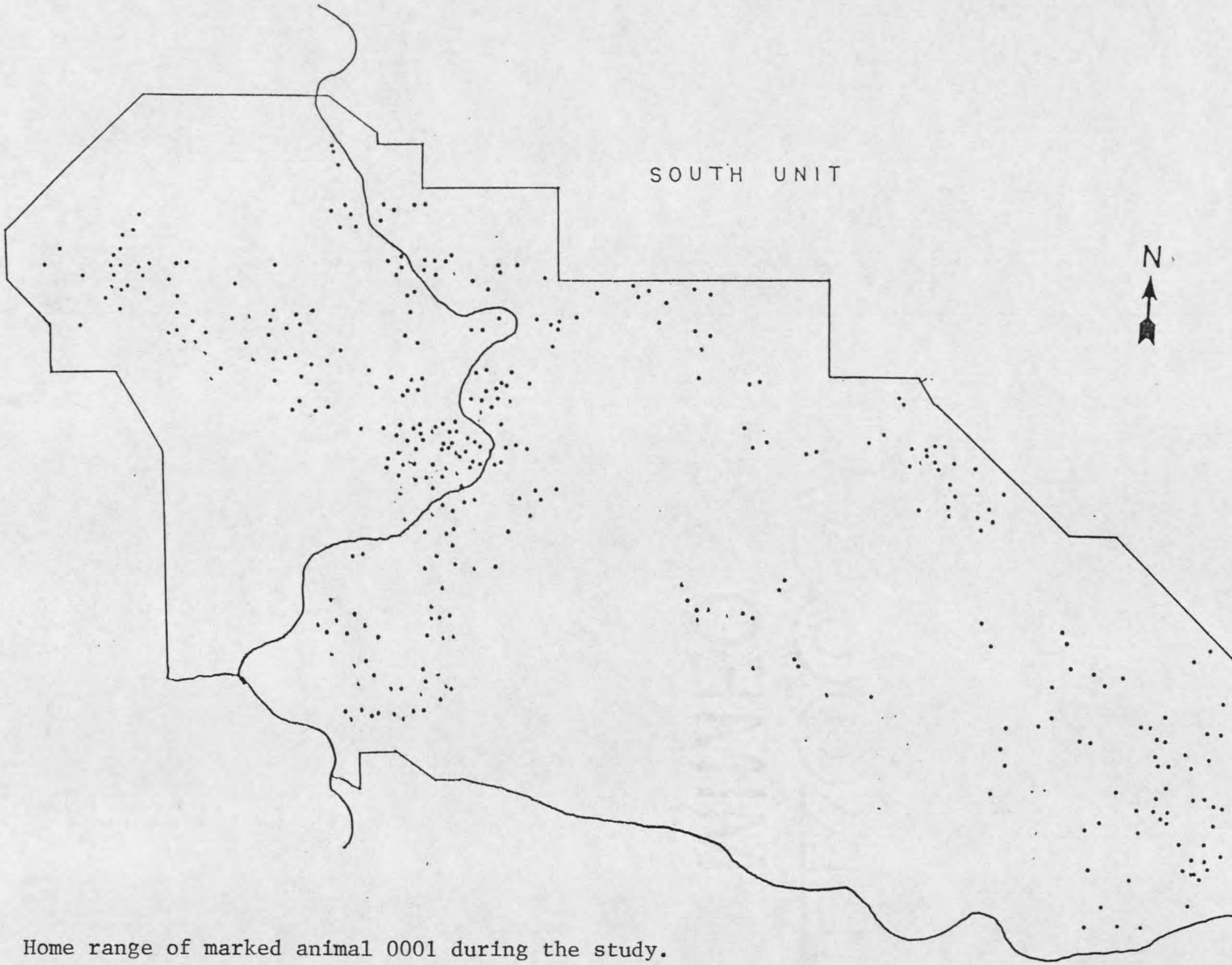

Figure 5. Home range of marked animal 0001 during the study.

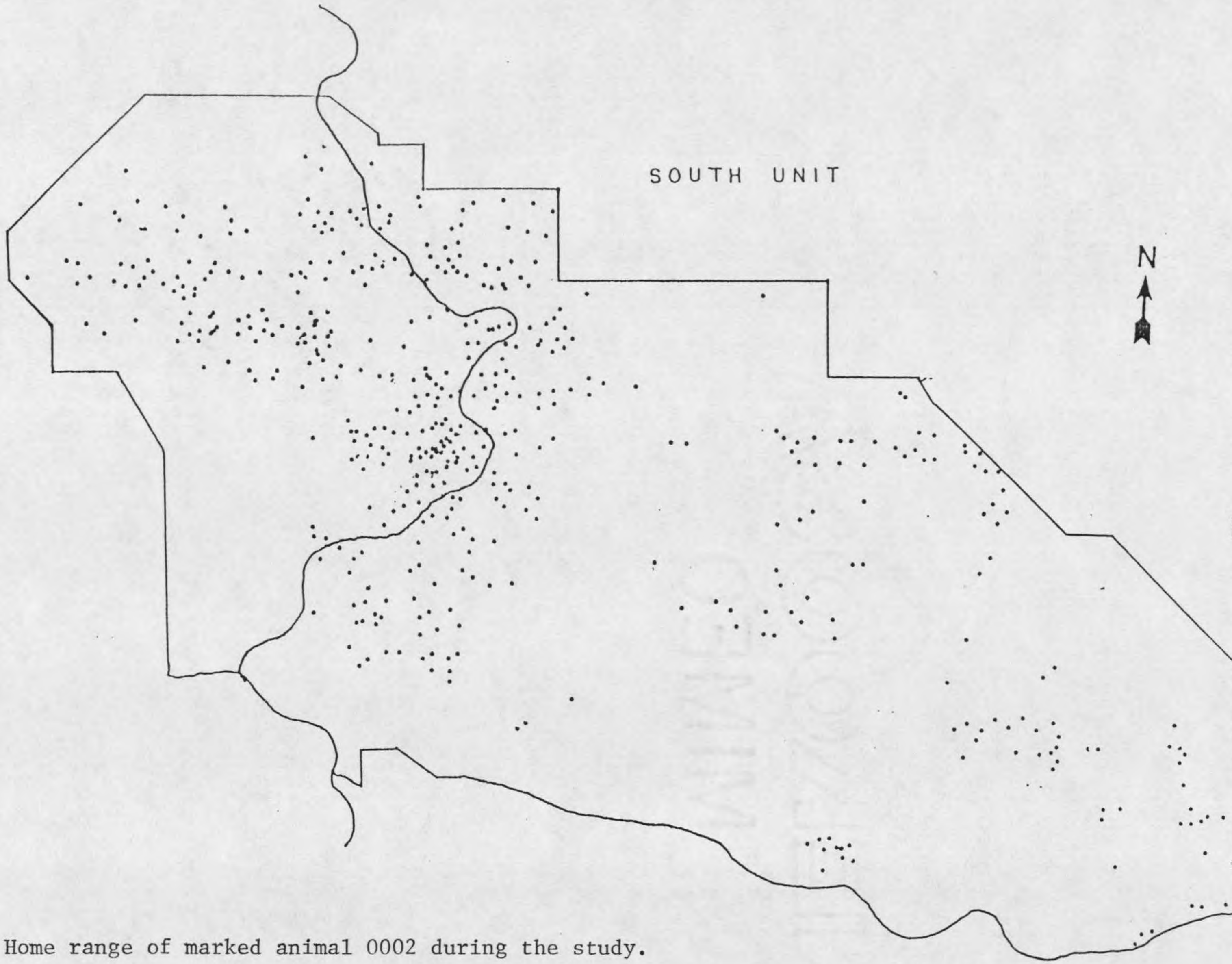

Figure 6. Home range of marked animal 0002 during the study.

Figure 7. Locations of all herds observed during the study.

park to the other. Yet, the coefficient of dispersion 0.94 was less than both the individual home ranges, and animal 0001 had a significantly different ($p<0.001$) distribution. A possible reason for the difference could be that individually bison were selecting certain locations for use, but collectively there was enough variation among individuals to produce a more uniform distribution. All of these distributions significantly differed from a random distribution.

Direct observations recorded only the distribution of herds. The fecal transects on the other hand did record mature bull and herd use. In areas with few if any herd locations, but with preferred habitat, use was recorded in the fecal transects. Evidently the areas that herds did not frequent had some use by mature bulls or by herds during previous years. Home ranges of mature bulls were probably similar to or larger than those of cows since most bison escaping from the Park were mature bulls.

Seasonal Distribution

Each time period had all locations plotted and a collapsing polygon placed around the perimeter points (Appendix C). Using only the area inside the polygon as the effective range for bison herds during that time period, a coefficient of dispersal for all locations over the time periods was 0.84. This distribution was significantly different from random. A low coefficient of dispersion suggests a uniform distribution of locations. Apparently, once the bison chose an area to use, the use occurred evenly over it.

Distribution of the bison herds in the Park did change over the

11 time periods (Appendix C). The most noticable restriction in distribution of bison herds was during the early spring when herds were found exclusively in the northwest section of the Park. This restriction limited use to basically only two classes, the old river terrace and the ridge and ravine. As larger parts of the Park were used bison use was spread over more classes.

Activity Patterns

The activities of bison were divided into three categories: grazing, resting, and other. The significance of the main effects (either the classes and the time periods or the habitat divisions and the time periods) on these activities appears in Table 9 (Appendix D contains all ANOVA tables used for the F-values).

Table 9. F-values of the main effects, the classes and time periods or habitat divisions and time periods, for the three different activities: grazing, resting, and other.

Activity	Main effect	F-value	DF	P-value
	Class X Time Period			
grazing	classes	1.6	6,31	0.17
grazing	time period	3.4	10,31	0.04
resting	classes	3.1	6,31	0.01
resting	time period	1.1	10,31	0.39
other	classes	3.3	6,32	0.01
other	time period	6.8	10,31	0.00
	Habitat division X Time Period			
grazing	habitat division	3.1	9,36	0.01
grazing	time period	4.9	10,36	0.00
resting	habitat division	2.5	9,36	0.02
resting	time period	2.1	10,36	0.05
other	habitat division	5.2	9,36	0.00
other	time period	8.0	10,36	0.00

Table 10 contains the separation of means for all three activities among the classes. Table 11 contains the same for the habitat divisions.

Table 10. Means[1] of the average percent of a herd engaged in grazing, resting, and other activity for each class.

Class	grazing[3]	resting	other[2]
Sagebrush bottoms	38.4[A]	14.7[A]	46.9[A]
Ridge & Ravine	41.8[A]	17.8[A]	40.3[A]
Grassed flats	35.3[A]	22.4[A]	42.3[AB]
Upland grassland	30.7[A]	27.4[A]	41.8[AB]
Old river terrace	37.5[A]	27.5[A]	34.4[AB]
Scoria hills	34.0[A]	28.2[A]	38.8[AB]
Prairie dog town	34.8[A]	29.4[A]	36.2 [B]

[1]Means followed by the same letter are not significantly different at p>0.05.

[2]Means have been adjusted to reduce the affect of the time periods.

[3]Grazing was not found to be significantly different over the classes.

Table 11. Means[1] of the average percent of a herd engaged in grazing, resting, and other activities for each habitat division.

Habitat Division	grazing[2]	resting	other[2]
Stipa comata-Bouteloua gracilis	36.0[A]	34.4[A]	29.8[A]
Introduced grass	30.9[A]	37.3[A]	31.8[A]
Prairie dog town	34.7[AB]	29.4[A]	35.8[A]
Artemisia cana	43.2 [B]	26.3[A]	30.4[A]
Agropyron smithii-Stipa comata	33.8[A]	29.6[A]	36.6[A]
Agropyron smithii-Stipa viridula	37.8[AB]	24.0[A]	38.0[A]
Rolling scoria complex	34.7[A]	30.7[A]	34.4[A]
Andropogon scoparius	42.9[AB]	21.2[A]	35.9[A]
Artemisia tridentata-Atriplex confertifolia	38.6[AB]	21.9[A]	39.5[AB]
River bottom	25.6[A]	17.2[A]	59.5 [B]

[1]Means followed by the same letter are not significantly different at p>0.05.

[2]Means have been adjusted to reduce the effect of time periods.

Trends in activities levels over time can be examined in Table 12 and Appendix E.

Table 12. Means of the average percent of a herd engaged in grazing activity in the classes over the 11 time periods.

Time period	means[1]
August 1	27.2A
August 2	30.3AB
September 2	32.2AB
September 1	33.7AB
October 2	37.4AB
November	37.4AB
June	37.5AB
April	40.9AB
October 1	41.0AB
December	41.8B
May	46.9B

[1]Means followed by the same letter are not significantly different at the $p>0.05$.

Grazing activity varied significantly among the time periods in both the classes and the habitat divisions. Grazing was significantly lower during the summer and higher during the winter and spring (Table 12, and Figures 48 and 51). The low summer grazing activity could have resulted from long days which allow grazing to be stretched out over many daylight hours, and high daytime temperatures which could have inhibited diurnal activity. Higher grazing activity in the winter could have been the result of shorter daylight hours giving bison less time to graze in and the least stressful environmental conditions occurring in the daylight hours. Higher activity in the spring may have been a result of the best environmental conditions for grazing occurring mostly during the daylight hours, and bison may have been raising their intake to meet higher physiological needs for gestation and calving (Reynolds et al 1982).

Resting activity did not vary significantly among the time periods (Figures 49 and 52). This can be attributed to the wide variance of resting activity among the classes and habitat divisions within a time period.

Other activity varied significantly among the time periods in both the classes and habitat divisions. Other activity was highest during the late summer and lower in the spring, late fall, and winter (Figures 50 and 53). Summer was high because this was the time when grazing was lowest and rutting activities were occurring.

Grazing activity did not significantly vary among the classes, but did vary significantly among the habitat divisions. Habitat divisions occurred in much smaller patches than did classes and were evenly distributed throughout the Park. As bison travelled during a day they differentiate their activity among the habitat divisions. Because the classes occupied large contiguous areas, travel to another class was sometimes impossible, so the bison ended up grazing where they were.

Resting and other activity did vary significantly among both the classes and habitat divisions. Because resting activity varied so widely, significant differences were undetectable between the levels of resting activity among the classes and habitat divisions. Probable reasons for the different levels of activity in the classes and habitat divisions follow:

1. River bottoms MU had higher other activity because bison mainly loafed on the site, and rutting activity did occur on the site. Low grazing activity was due to the low amount of available forage.

2. Artemisia cana HT had high grazing activity because bison would forage in the HT but evidently avoided resting or doing other activity. The avoidance was probably related to the high density of Artemisia cana which could prevent visual contact in herds in the HT and create microclimate conditions uncondusive to resting.

3. Introduced grass MU had low grazing activity because the dominant species Agropyron cristatum was only preferred or palatable during a short period of time in the early spring. With such low use the MU had a large buildup of litter and standing dead material which is detrimental to grazing activity (Norton et al. 1982). Resting and other activities were higher because of the low grazing level and lack of unfavorable conditions for these activities.

4. Sagebrush bottoms class had high other activity because it included the river bottoms MU which had a high level of other activity.

5. Prairie dog town class had low levels of other activity because the class was favored for resting and grazing.

Daily Activities

Daily activity of herds within each time period was analyzed by taking the percent of the herd doing each activity for an observation point and plotting these by time of day. Each period then had three graphs representing each of the three activities (Appendix F). Grazing activity in the spring peaked in the morning and evening, but substantial amounts of grazing activity occurred throughout the day. As the days became longer the peaks in the morning and evening remained, but grazing dropped during the rest of the day except for a peak at midday. The August 2 time period best exemplifies this. The fall and winter had the same pattern as the spring.

Resting activity in the spring was concentrated in the middle of the day. As days became longer the resting activity spread out with peaks occurring during mid-morning and mid-afternoon. The midday drop in resting activity was the result of the midday grazing. As the days grew shorter the resting activity again was concentrated during the middle of the day.

Other activity did not exhibit well defined peaks. There was a slight trend towards highest levels occurring after the major grazing peaks. The level of other activity did not noticeably change as day length changes.

Movement

The movement patterns of herds and individual bison were determined from direct observations of herds and locations of marked animals. The average distance moved per day for a herd was 1.65 km (SE=1.58). Table 13 shows the average distance moved by the herds in each time period. The distance a bison herd moved during a day was the same for all periods ($p>0.10$) (Table 14) even though the portion of the Park used did vary.

The number of days between locations of marked bison was noted and the average distance between the initial location and relocation found. Figure 8 contains the average distance between the initial location and subsequent relocation for varying numbers of days after initial location. The average distance moved by bison by the second day after an initial location was 2.8 km. By the third day after an

Table 13. Means of the daily distances in kilometers (km) moved by bison herds in the 11 different time periods.

Time period	Mean distance (km)
April	2.1
May	2.0
June	1.2
August 1	2.5
August 2	2.2
September 1	1.8
September 2	2.0
October 1	1.4
October 2	1.1
November	1.1
December	0.7

Table 14. ANOVA table of the logarithmically transformed values of the daily distance moved by bison herds over the 11 time periods.

Source	DF	S.S.	M.S.	F-value	P-value
Time periods	10	3.91	.391	1.57	.12
Residual	119	29.63	.249		

initial location, the distance was 4 km. The constant movement by bison in the first few days after the initial location resulted in bison rarely staying in the same locality for more than 48 hours. Bison showed no propensity to use the same site, class, or habitat division for any extended period of time.

The distance from the initial location increased as the number of days between the initial location and relocation increased. A peak was reached by the 10th day at a distance of 7.6 km. The distances

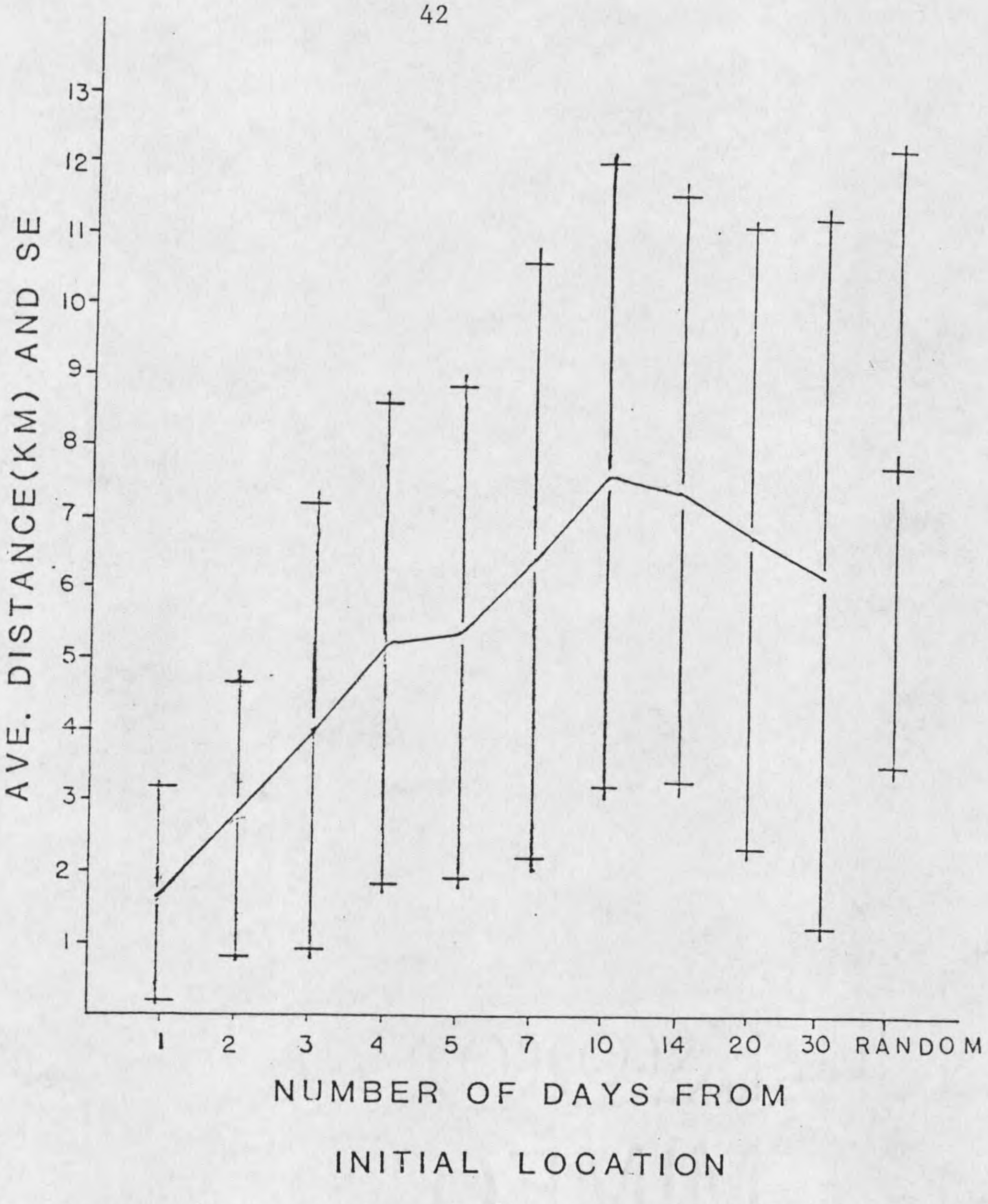

Figure 8. Average distance and standard error between the initial location and relocation of marked animals after various number of days, along with the average distance and standard error between two random points.

then declined after the 10th day, but not to the level of the first 2 or 3 days after the initial location. Table 15 shows the results from tests of independence between the distances found for various numbers of days after initial location to that of the distances found between two randomly generated points. No significant differences were found between the distances at the 7th, 10th, 14th, and 20th days after initial location and the random distances. Apparently the distances moved by bison after the second and third weeks were not influenced by where the bison were a week or two before. This trend may not hold true for dates beyond the 30th day after initial location because at the 30th day the distances were no longer random and bison were starting to clump their locations around the initial location.

Table 15. G-tests of the distances between two random points against relocation a number of days later.

Days after intial location	G-statistic	P-value	DF
5	22.1	0.00	7
7	11.9	0.10	8
10	5.9	0.66	7
14	3.5	0.89	8
20	4.8	0.84	9
30	22.1	0.00	7

The shortest distance to permanent water was recorded for each day a bison herd was observed. Permanent water sources were defined as all developed springs and the Little Missouri River. The average distance to permanent water was 1 km (SE=1.1 km) for the study period. The average distance to permanent water for a randomly placed transect of 1.6 km was 1.8 km (SE=1.3 km). In a comparison between the observed distances to water and the random distances the observed was significantly different ($p<.05$). The observed distances were closer or more clumped around the permanent water sources, suggesting that bison were dependent on permanent water sources. Because most permanent water sources were situated in or around preferred habitats, determining whether bison were selecting for water or for some other attribute of the habitat was not possible. Other observations which may support the argument that bison were not selecting for permanent water sources are:

1. Bison were seen eating snow when available and not seen drinking water at those times.

2. Bison, because of their high mobility, were able to utilize different water sources each day.

3. Bison used temporary water sources when available.

4. Bison were observed going without water for at least one day.

5. Bison would go to water once a day,and the length of stay at watering areas was of short duration--one hour or less for even the largest herd.

CONCLUSIONS AND SUMMARY

Many aspects of bison habitat use and distribution found in this study have been reported in other studies. These being:

1. The preference for grasslands.

2. The home ranges being large and significantly overlapping with the rest of the population.

3. The social structure being fluid with no long term individual or herd association.

4. The mature bulls using areas not normally frequented by herds.

5. The constant movement of bison into new areas.

6. The seasonal changes in distribution and habitat use.

The average daily distance moved in this study was lower than the distances reported in the other studies. This may have been due to the methods of measuring the distances moved and/or differences between study areas. Habitat use by bulls was only recorded in the the whole population habitat use which also included the cow herd use. Because the whole population habitat use was similar to the cow herd habitat use, there was probably little difference in overall bull use when compared to cow herd use. The other studies found differences in bull and cow herd use. It is possible that if mature bull use had been measured more intensively more differences might have been found.

The daily activity patterns of bison in the study were similar to those recorded for many other ungulates (Leuthold 1977, Mloszewski 1983). The bison had a definite crepuscular behavior pattern with grazing being the deterministic factor.

grazing being the deterministic factor.

The behavior of bison in the Park was a combination of nomadism and the preference for certain components of the environment. The nomadic behavior of the bison was based on:

1. Bison being highly mobile, moving to new localities and habitats almost daily.

2. The distances moved by bison apparently not being influenced by where they were located the week before.

3. The distribution of bison herds resembling a random pattern.

4. The uniform distribution of locations over the area used during a single time period.

5. Home ranges of individual bison being as large as that for the whole population.

6. The constantly changing associations between individuals and the lack of fidelity to any one herd.

7. The grazing activity not being significantly different over the classes.

8. The bison's ability to use different watering sources each day.

The preferential behavior of the bison was based on:

1. The bison's preference for certain habitats.

2. The change in use of habitats and areas of the park as changes in the environment occurred.

3. The clumped locations for individual bison.

4. The significant differences in activity patterns among habitat components.

5. The clumped locations of herds around water sources.

Both nomadism and the action of preference had adaptive significance for the bison. Nomadism is adaptive in that it allowed the bison to cope with the fluctuating forage production found on the grasslands. Bison require large amounts of forage to sustain their large size and energy needs. Because grasslands vary widely in forage production between locations and years, a nomadic bison was more capable of finding those areas of favorable forage production which would satisfy its forage needs.

The consequence of nomadism, especially with constant movement and random dispersal over time, was that plants were potentially grazed only once, if at all, in a 3-4 week period. New theories on the relationship between herbivory and plant physiology, ecology (Grunow 1980) suggest that plants are better able to cope with herbivory when it occurred only once, rather than occurring as several regrazings during the growing season. Grassland plants then are better able to cope with herbivory by a nomadic animal rather than one which is sedentary and regrazes the same plant regularily.

Preference for certain environmental factors is adaptive because, even though bison were nomadic, no animal can afford to leave all aspects of its behavior to chance and expect to survive (Alcock 1984). Bison were well adapted to a graminiod diet, and so as they travelled they chose for those areas dominated by graminiods, the grasslands. Preference for other habitats was based on the habitats being well suited to the other non-grazing activities of bison.

Together these behaviors result in the bison being well suited to the grassland environment. These behavioral traits were also found in other large, herding bovids, especially the African buffalo (Syncerus caffer) (Leuthold 1977, Owen-Smith 1982, Mloszewski 1983). It appears that large bovids in an environment dominated by large grasslands will develop these behaviors, even when the grasslands and animals have a different evolutionary history.

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LITERATURE CITED

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APPENDICES

APPENDIX A

Area Covered by the Habitat Divisions

Table 16. Hecterage of habitat types, mapping units, and complexes as they occur in each physiographic/vegetational class in the North Unit.

Breaks	
1. Stipa comata - Bouteloua gracilis	2.4
2. Hardwood Draws	3.5
3. Populus tremuloides - Betula occidentalis	10.1
4. Andropogon scoparius - Juniperus horizontalis	7.6
5. Juniperus scopulorum - Oryzopsis mircantha	242.4
6. Artemisia tridentata - Atriplex confertifolia	123.6
7. Andropogon scoparius	8.3
8. Unvegetated	2519.7
Sagebrush Bottom	
1. Hardwood Draws	6.3
2. Artemisia cana	748.7
3. River Bottom	16.9
4. Willows	30.8
5. Marsh	18.8
6. Man-Managed	7.0
7. Brush	1.3
8. Grassed Sand Floodplains	72.8
9. Unvegetated	15.1
Wooded Draws	
Included in the other classes as Hardwood Draw and Populus tremuloides - Betula occidentalis	
Upland Grasslands	
1. Agropyron smithii - Stipa comata	172.1
2. Agropyron smithii - Stipa viridula	115.1
3. Stipa comata - Bouteloua gracilis	97.6
4. Hardwood Draw	0.6
5. Andropogon scoparius - Juniperus horizontalis	7.8
6. Artemisia tridentata - Atriplex confertifolia	1.9
7. Andropogon scoparius	15.7
8. Brush	0.2
9. Unvegetated	9.1
Prairie Dog Town	
1. Prairie Dog Town	48.1

Table 16. Continued

Toe Slopes		
1.	Agropyron smithii - Stipa comata	122.7
2.	Agropyron smithii - Stipa viridula	609.6
3.	Stipa comata - Bouteloua gracilis	13.7
4.	Hardwood Draw	311.2
5.	Populus tremuloides - Betula occidentalis	13.7
6.	Artemisia cana	6.3
7.	Andropogon scoparius - Juniperus horizontalis	135.0
8.	Juniperus scopulorum - Oryzopsis mircantha	116.0
9.	Artemisia tridentata - Atriplex confertifolia	310.0
10.	Andropogon scoparius	266.1
11.	Brush	3.7
12.	Unvegetated	380.4
Rolling Grassland		
1.	Agropyron smithii - Stipa comata	22.7
2.	Agropyron smithii - Stipa viridula	737.9
3.	Stipa comata - Bouteloua gracilis	7.5
4.	Hardwood Draw	51.9
5.	Populus tremuloides - Betula occidentalis	0.8
6.	Andropogon scoparius - Juniperus horizontalis	26.6
7.	Artemisia tridentata - Atriplex confertifolia	5.3
8.	Andropogon scoparius	48.6
9.	Introduced Grasses	14.1
10.	Brush	9.0
11.	Unvegetated	76.8
Achenbach Hills		
1.	Achenbach Hills Complex	77.6
2.	Populus tremuloides - Betula occidentalis	1.4
Bottom Grasslands		
1.	Agropyron smithii - Stipa viridula	210.0
2.	Hardwood Draw	0.1
3.	Juniperus scopulorum - Oryzopsis mircantha	0.2
4.	Brush	1.5
5.	Grassed Sand Floodplains	60.7
6.	Unvegetated	5.0
Cottonwood Forests		
1.	Populus deltoides - Juniperus scopulorum	88.6

Table 17. Hecterage of habitat types, mapping units, and complexes as they occur in each physiographic/vegetational class in the South Unit.

Breaks		
1.	Agropyron smithii - Stipa comata	8.4
2.	Agropyron smithii - Stipa viridula	30.4
3.	Stipa comata - Bouteloua gracilis	12.3
4.	Hardwood Draw	93.4
5.	Populus tremuloides - Betula occidentalis	1.0
6.	Andropogon scoparius - Juniperus horizontalis	72.8
7.	Juniperus scopulorum - Oryzopsis mircantha	234.6
8.	Artemisia tridentata - Atriplex confertifolia	302.7
9.	Andropogon scoparius	134.2
10.	Man-Managed	6.8
11.	Artemisia tridentata - Bouteloua gracilis	63.5
12.	Steep Scoria	30.4
13.	Rolling Scoria	3.5
14.	Brush	1.9
15.	Unvegetated	2701.2
Sagebrush Bottoms		
1.	Agropyron smithii - Stipa viridula	46.9
2.	Hardwood Draws	14.5
3.	Artemisia cana	978.9
4.	Andropogon scoparius	1.6
5.	River Bottom	93.2
6.	Man-Managed	18.6
7.	Unvegetated	35.6
Wooded Draws		
	Included in the other classes as Hardwood Draws.	
Upland Grassland		
1.	Agropyron smithii - Stipa comata	77.2
2.	Agropyron smithii- Stipa viridula	513.5
3.	Stipa comata - Bouteloua gracilis	192.3
4.	Hardwood Draw	0.3
5.	Artemisia tridentata - Atriplex confertifolia	0.7
6.	Andropogon scoparius	25.7
7.	Introduced Grasses	155.7
8.	Brush	2.6
9.	Unvegetated	42.6
Prairie Dog Towns		
1.	Prairie Dog Town	168.4

Table 17. Continued

Old River Terrace		
1.	Agropyron smithii - Stipa comata	608.6
2.	Agropyron smithii - Stipa viridula	184.0
3.	Stipa comata - Bouteloua gracilis	159.4
4.	Hardwood Draw	2.9
5.	Andropogon scoparius	7.7
6.	Introduced Grasses	25.9
7.	Man-Managed	5.2
8.	Petrified Forest Complex	22.0
9.	Unvegetated	--
Grassland Flats		
1.	Agropyron smithii - Stipa comata	2.3
2.	Agropyron smithii - Stipa viridula	1347.3
3.	Hardwood Draw	13.8
4.	Artemisia cana	13.6
5.	Andropogon scoparius - Juniperus horizontalis	7.1
6.	Juniperus scopulorum - Oryzopsis mircantha	5.4
7.	Artemisia tridentata - Atriplex confertifolia	9.4
8.	Andropogon scoparius	47.4
9.	Introduced Grasses	2.9
10.	Man-Managed	2.6
11.	Artemisia tridentata - Bouteloua gracilis	32.7
12.	Rolling Scoria Complex	12.8
13.	Brush	2.9
14.	Unvegetated	462.6
Ridge & Ravine		
1.	Agropyron smithii - Stipa comata	103.6
2.	Agropyron smithii - Stipa viridula	372.3
3.	Stipa comata - Bouteloua gracilis	14.5
4.	Hardwood Draw	276.0
5.	Populus tremuloides - Betula occidentalis	2.4
6.	Artemisia cana	21.0
7.	Andropogon scoparius - Juniperus horizontalis	589.8
8.	Juniperus scopulorum - Oryzopsis mircantha	77.5
9.	Artemisia tridentata - Atriplex confertifolia	94.3
10.	Andropogon scoparius	1652.8
11.	Man-Managed	1.3
12.	Steep Scoria Complex	12.4
13.	Rolling Scoria Complex	18.2
14.	Brush	4.4
15.	Unvegetated	1489.2

Table 17. Continued

Scoria Hills		
1.	Agropyron smithii - Stipa viridula	81.7
2.	Hardwood Draws	23.1
3.	Artemisia cana	8.3
4.	Andropogon scoparius - Juniperus horizontalis	4.6
5.	Juniperus scopulorum - Oryzopsis mircantha	63.0
6.	Artemisia tridentata - Atriplex confertifolia	35.7
7.	Andropogon scoparius	10.6
8.	Artemisia tridentata - Bouteloua gracilis	14.2
9.	Steep Scoria Complex	2360.9
10.	Rolling Scoria Complex	1406.0
11.	Unvegetated	524.4
Cottonwood Forests		
1.	Populus deltoides - Juniperus scopulorum	88.6

APPENDIX B

Percent Use by Bison of the Classes and Habitat Divisions

Figures showing the percent use determined from direct observations of bison in each class and habitat division by time period (Table 1). Non-parametric confidence intervals are shown (Hollander and Wolfe 1973).

denotes limits of non-parametric confidence interval

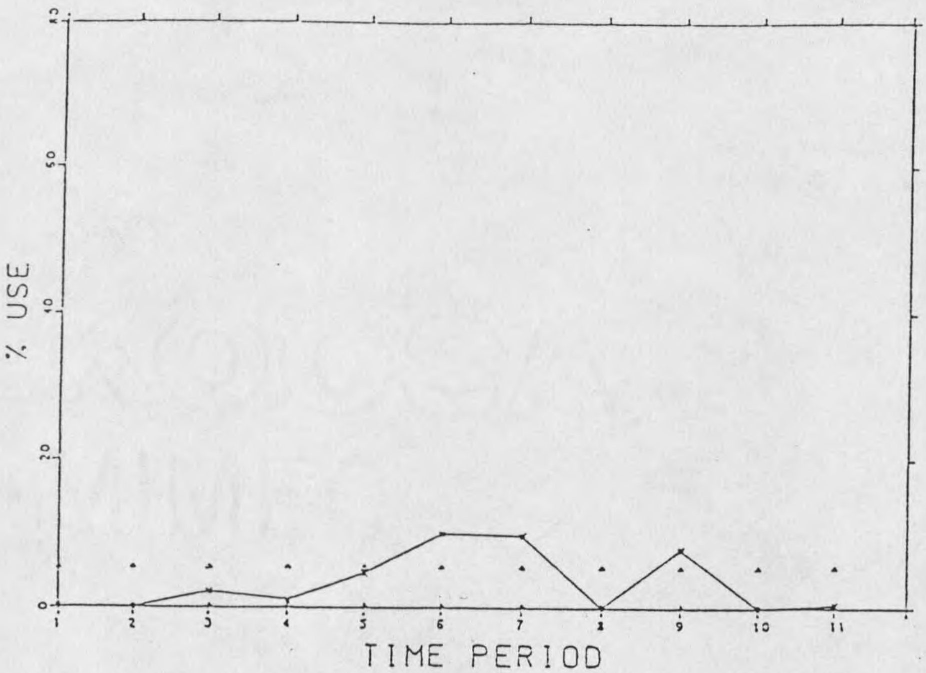

Figure 9. Cottonwood forests class.

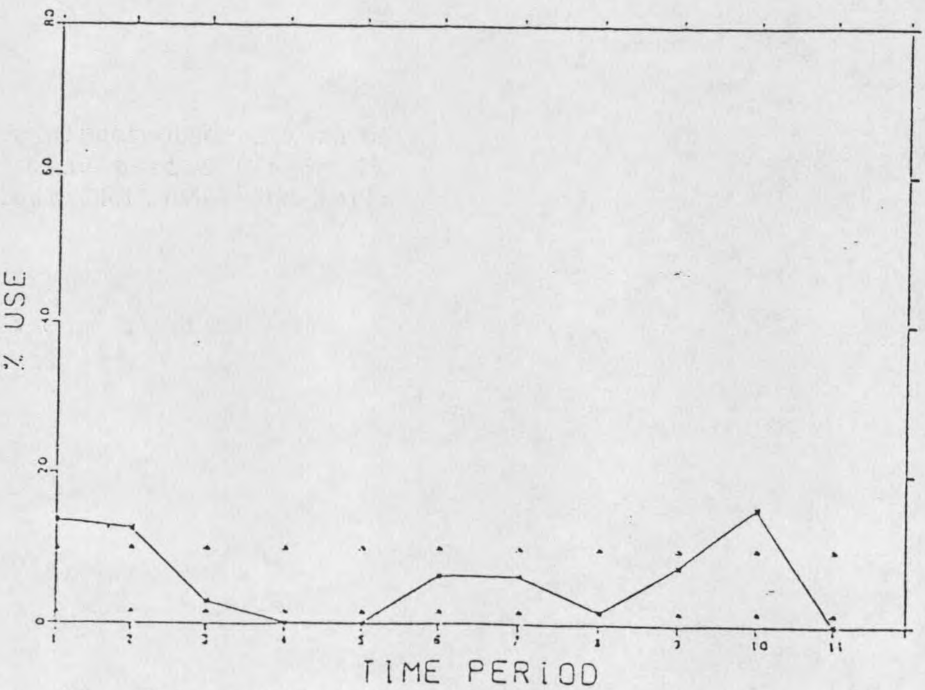

Figure 10. Ridge & Ravine class.

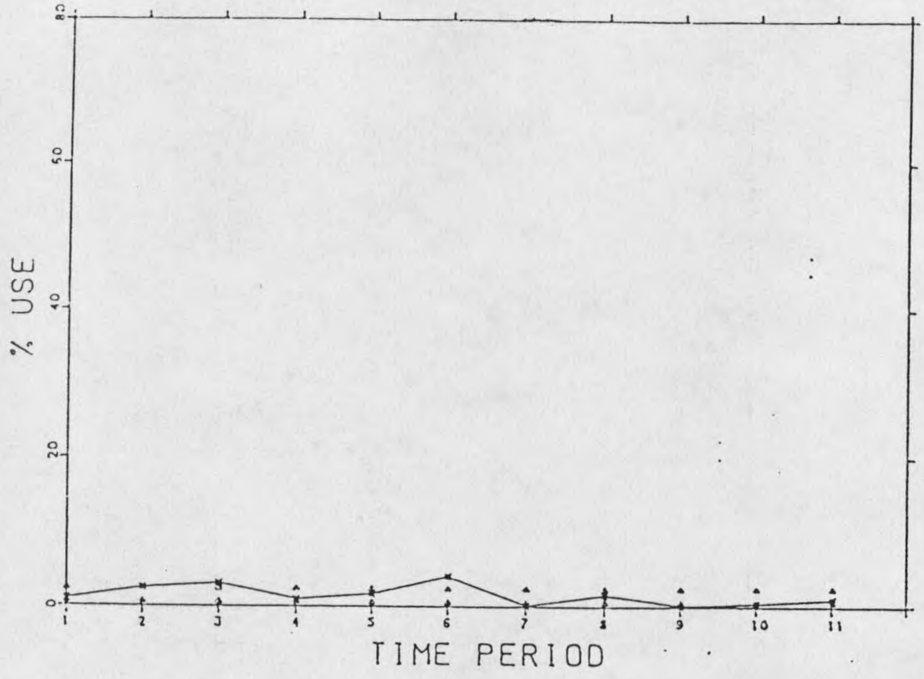

Figure 11. Breaks class.

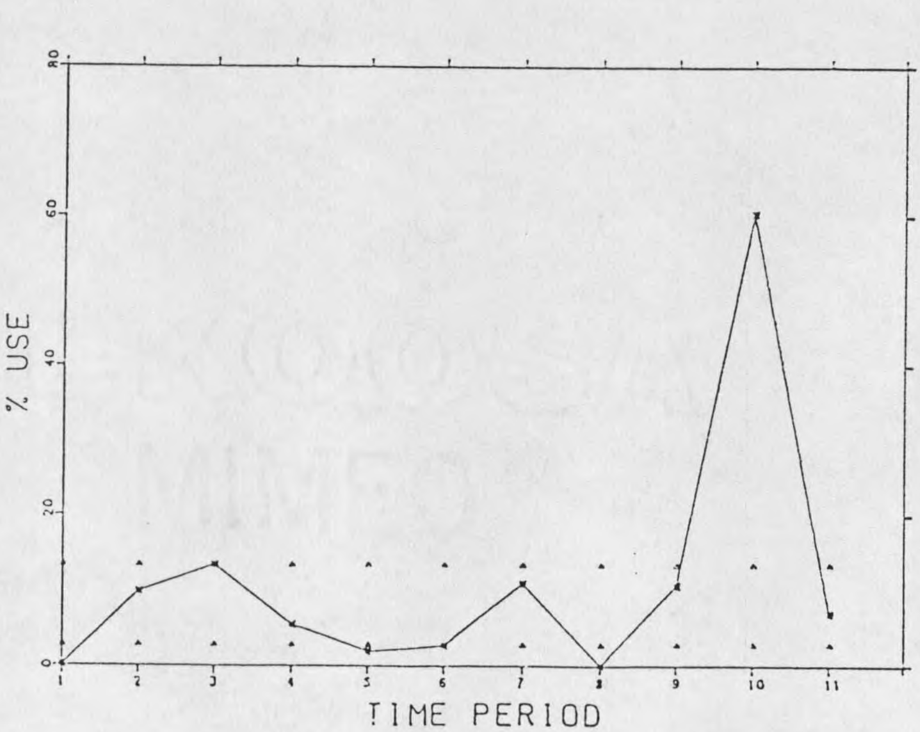

Figure 12. Scoria hills class.

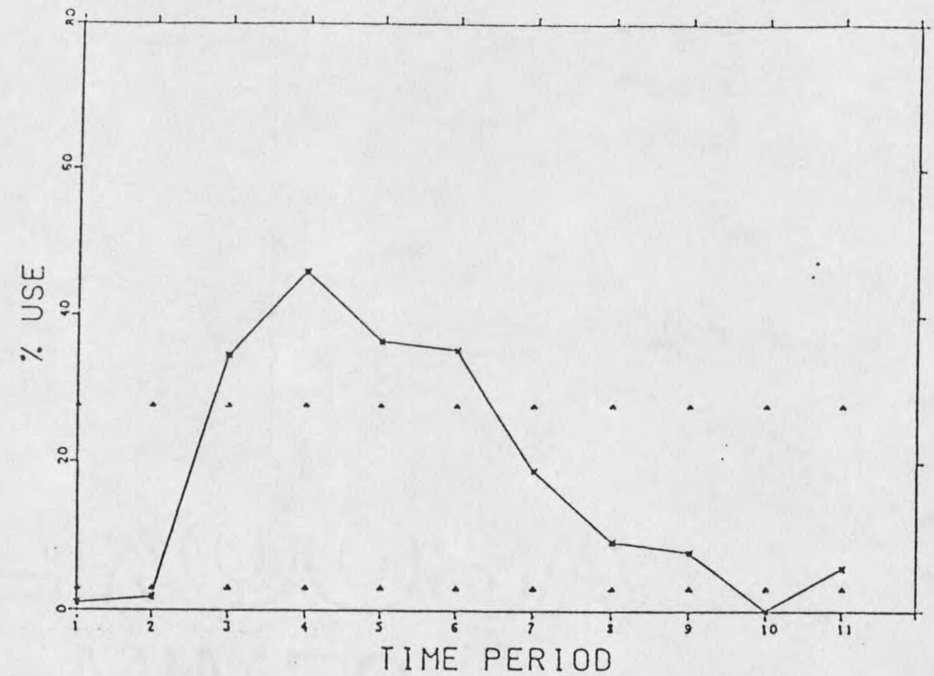

Figure 13. Prairie dog town class.

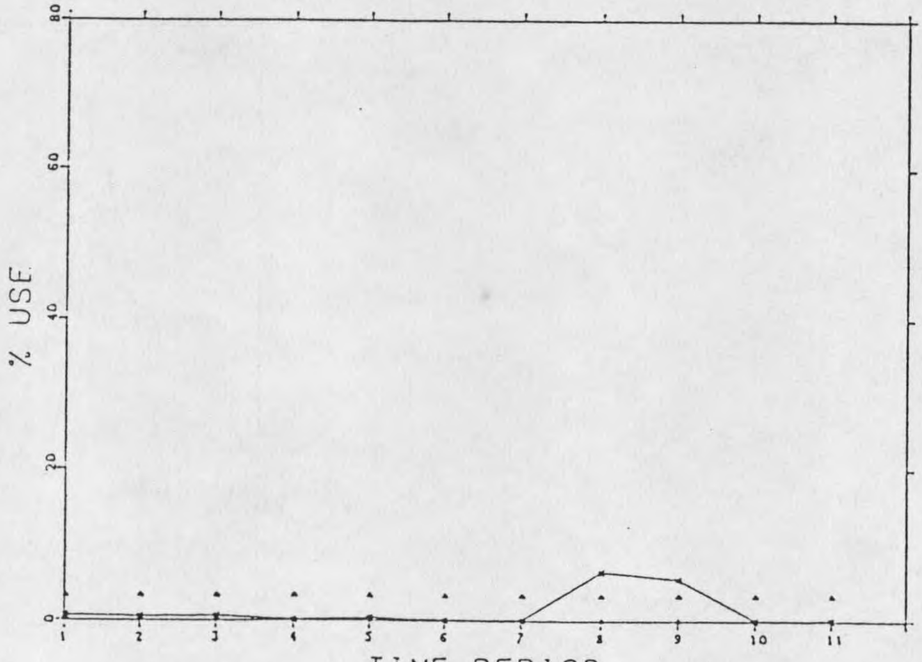

Figure 14. Wooded draw class.

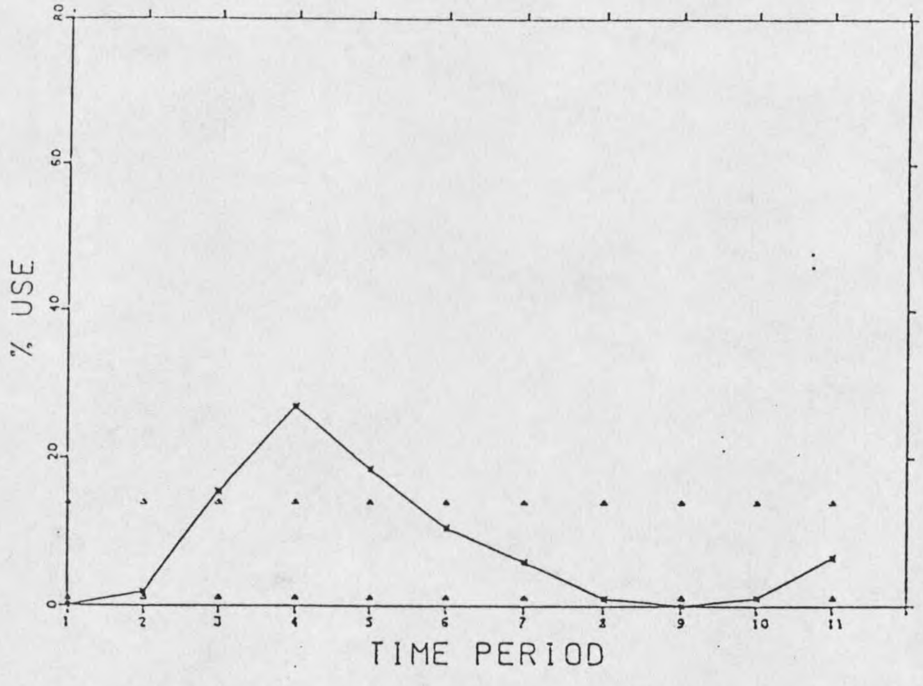

Figure 15. Grassland flats class.

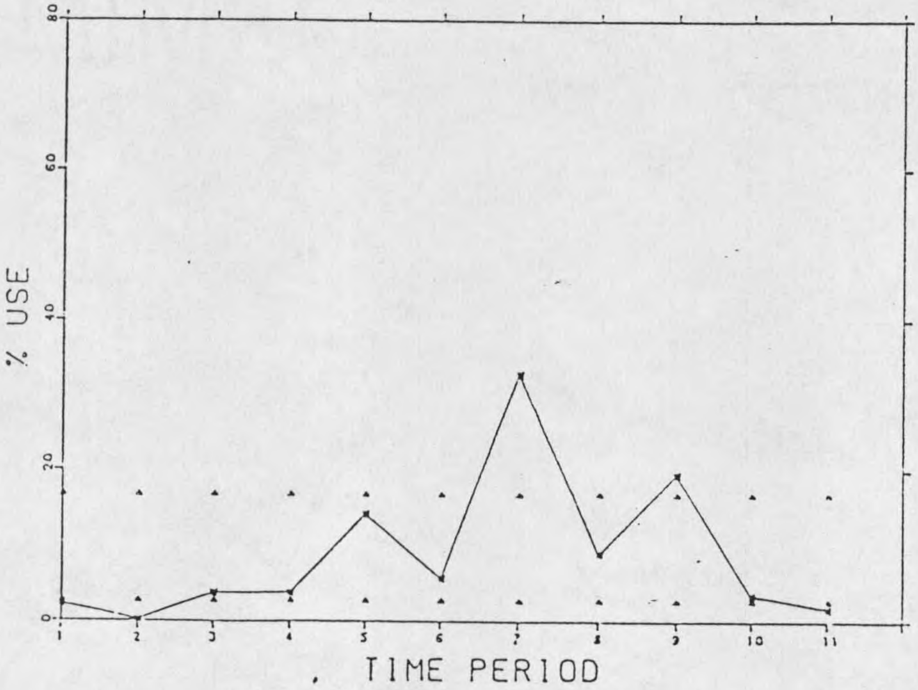

Figure 16. Sagebrush bottoms class.

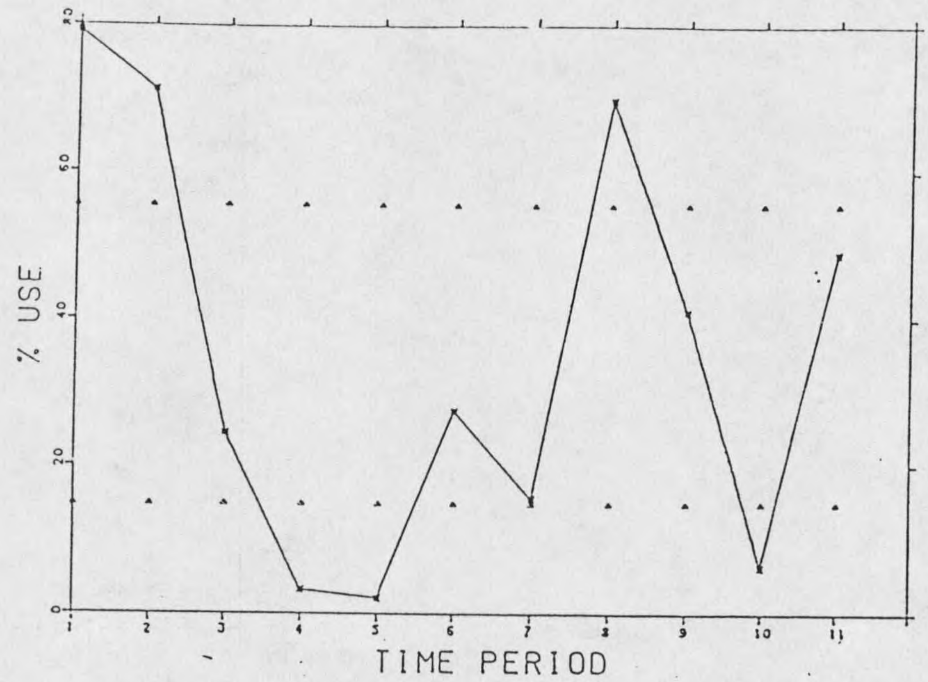

Figure 17. Old river terrace class.

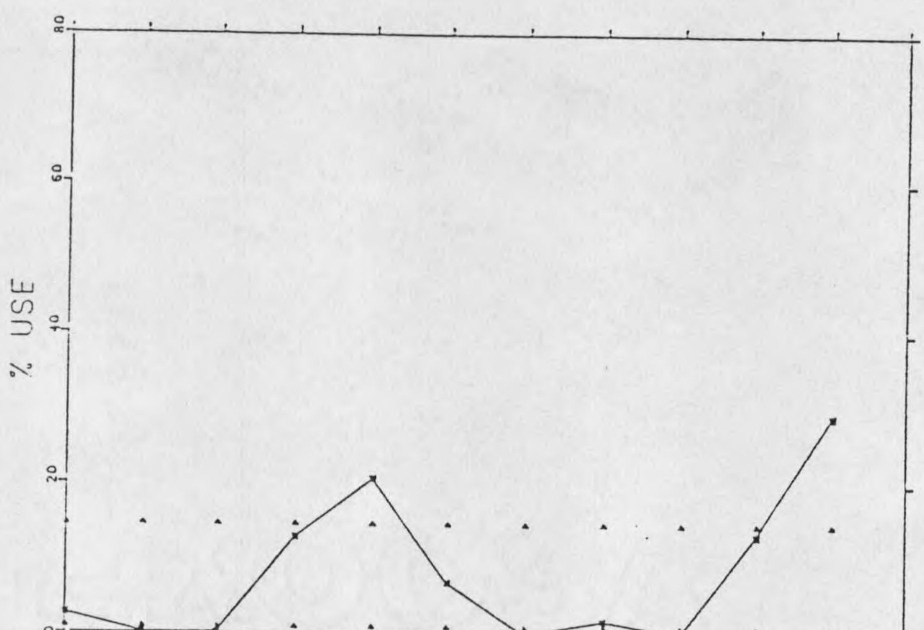

Figure 18. Upland grassland class.

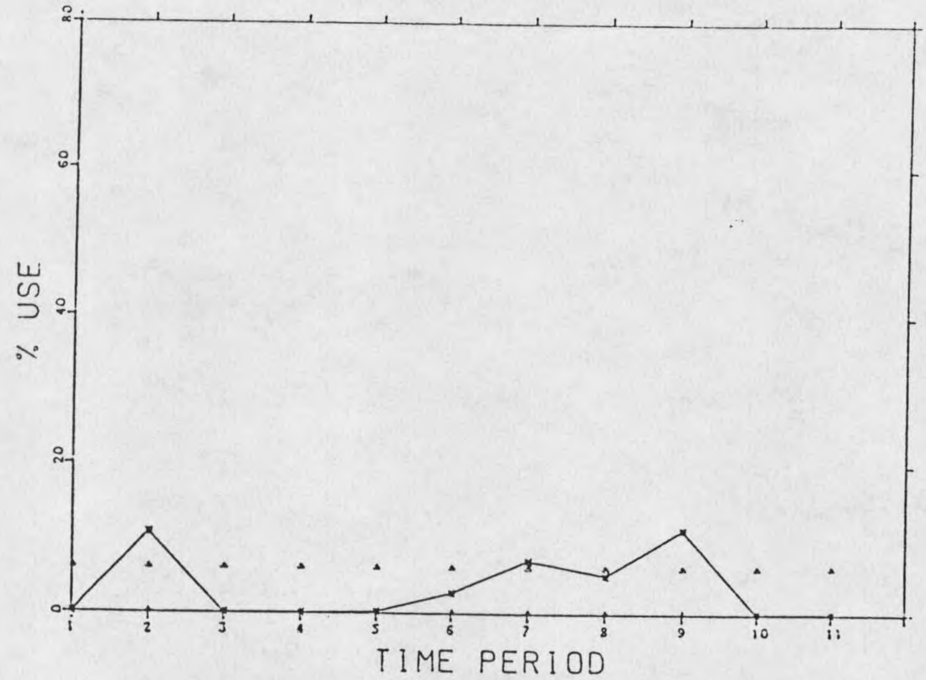

Figure 19. Man-managed MU.

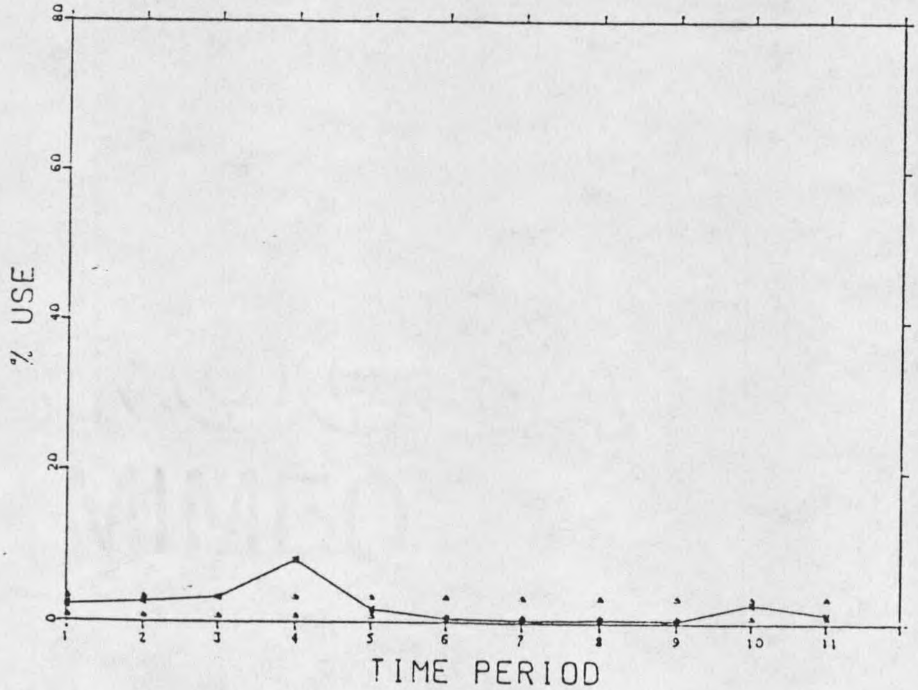

Figure 20. Artemisia tridentata - Atriplex confertifolia.

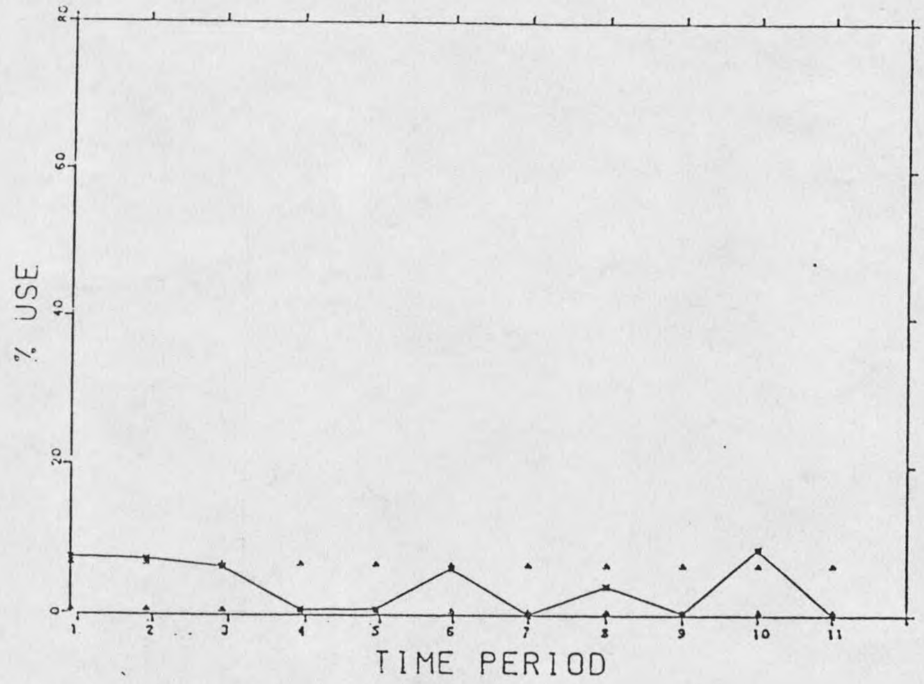

Figure 21. Stipa comata - Bouteloua gracilis HT.

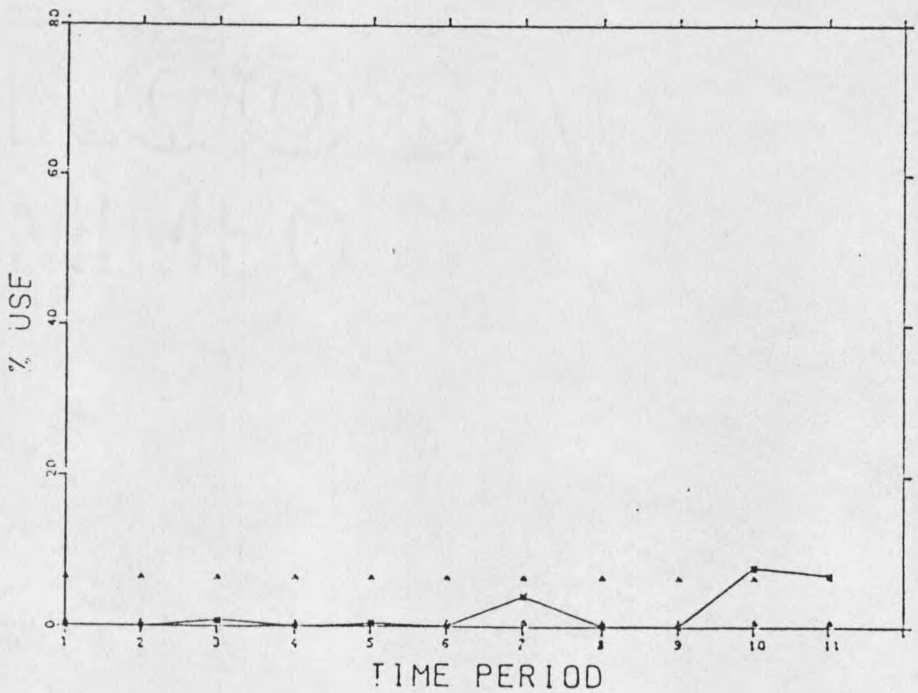

Figure 22. Steep scoria complex.

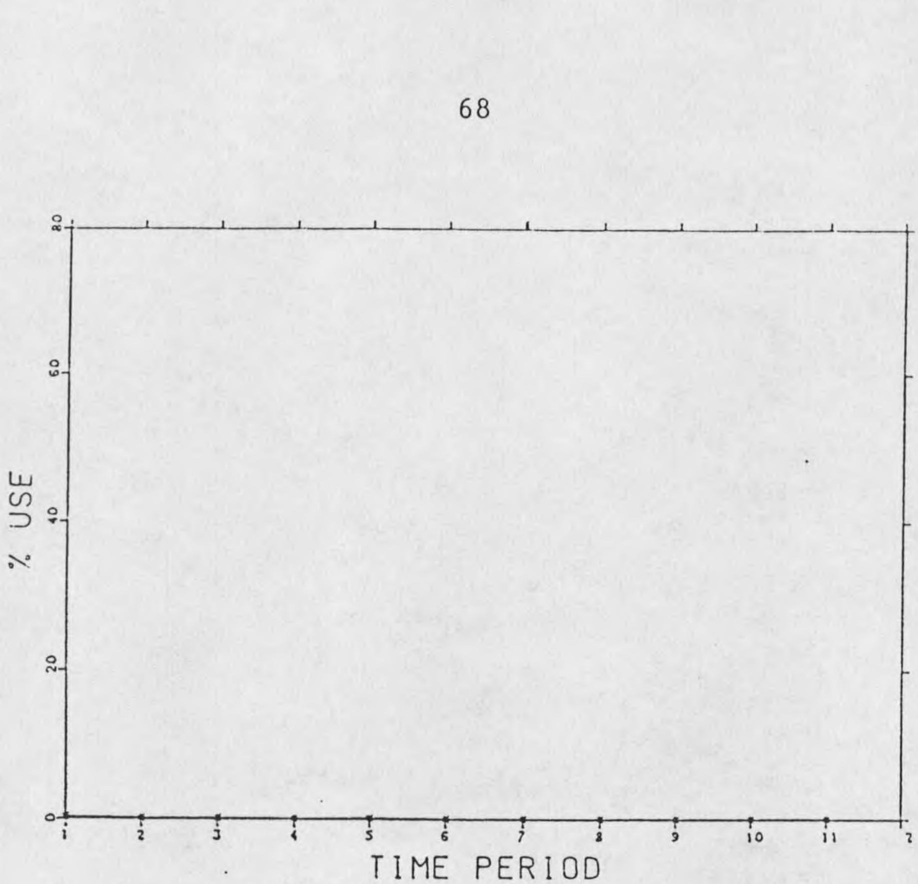

Figure 23. Unvegetated area.

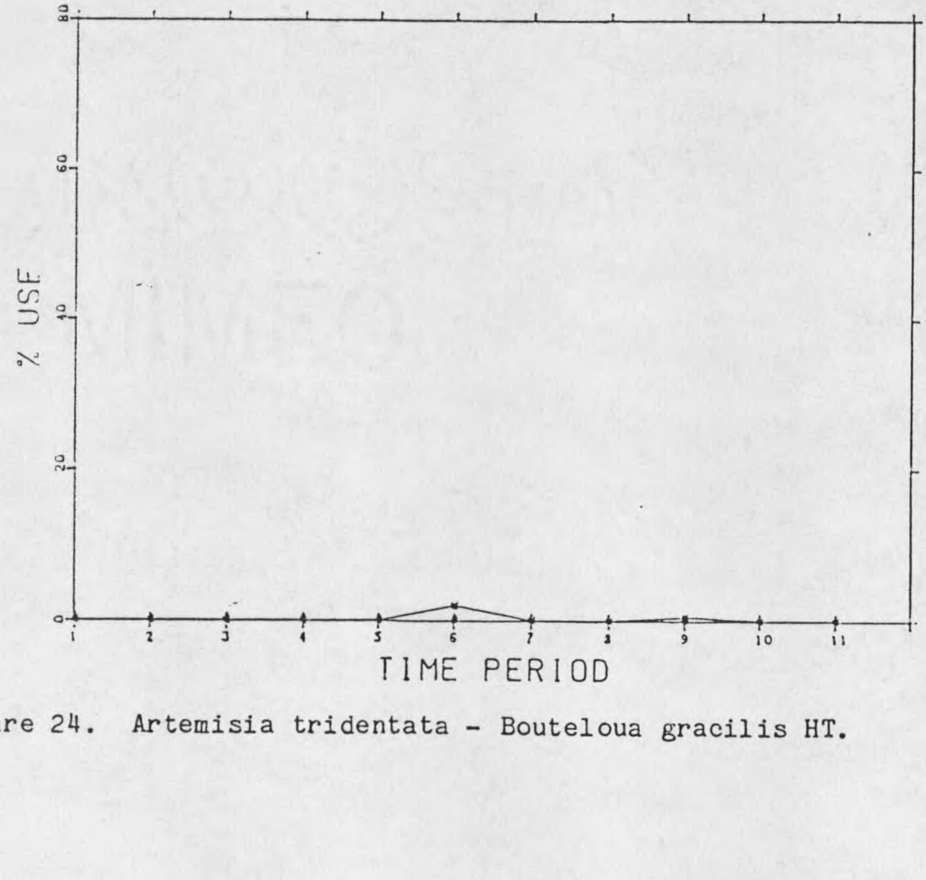

Figure 24. Artemisia tridentata - Bouteloua gracilis HT.

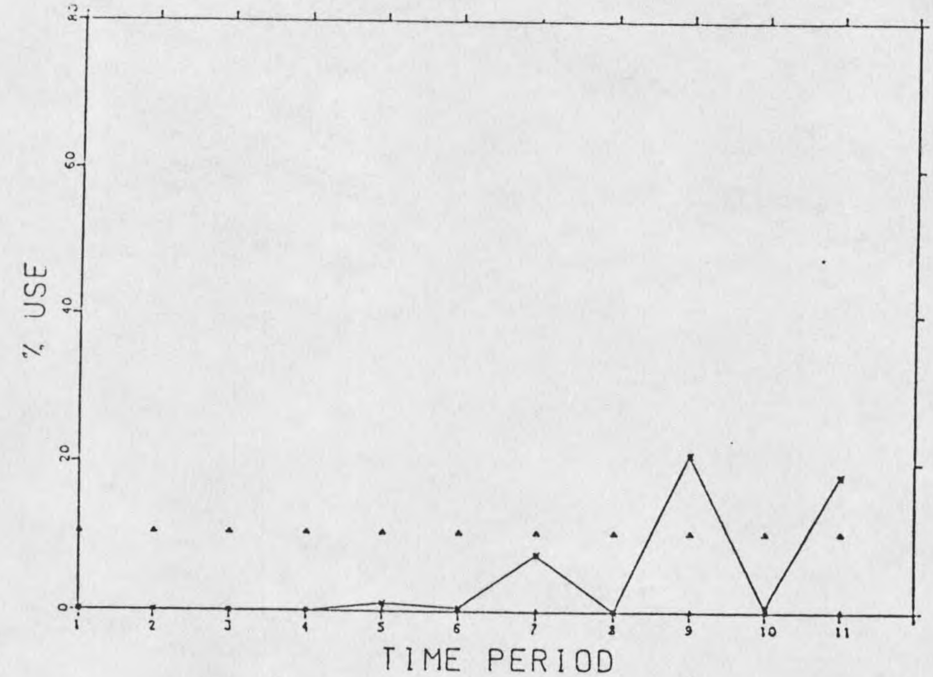

Figure 25. Introduced grasses MU.

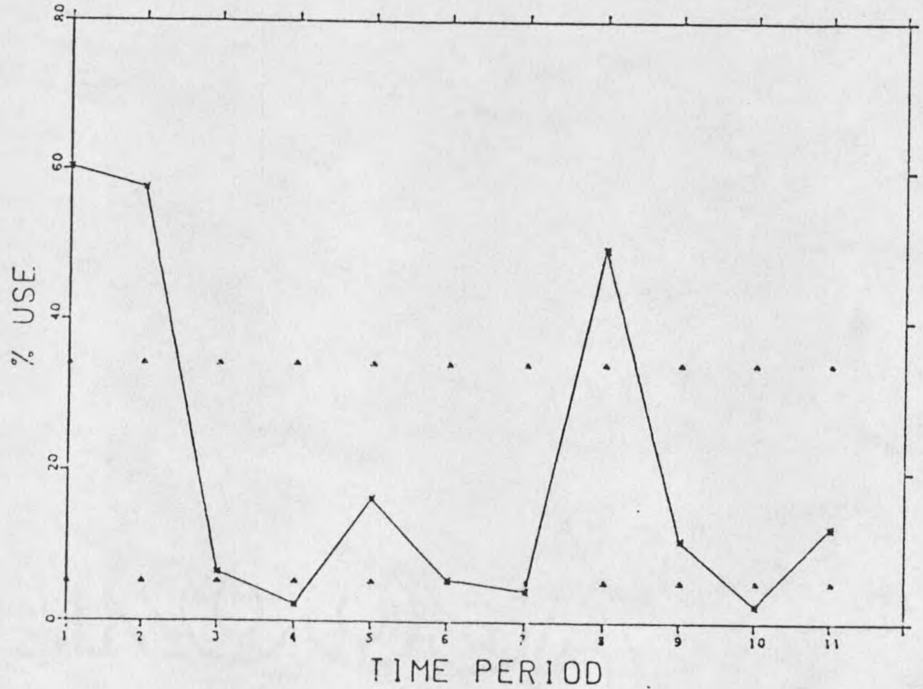

Figure 26. Agropyron smithii - Stipa comata HT.

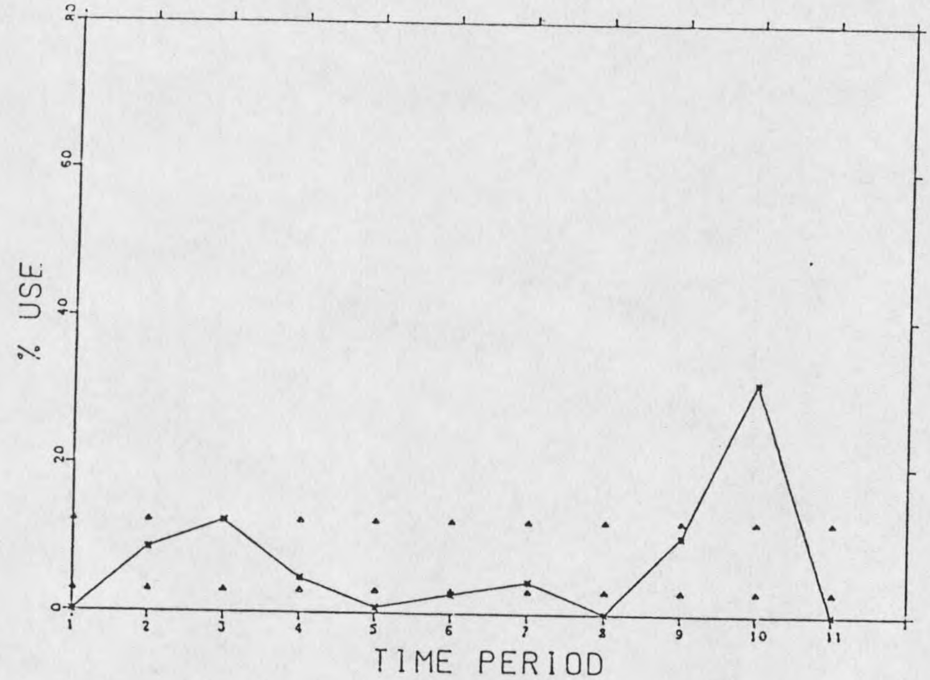

Figure 27. Rolling scoria complex.

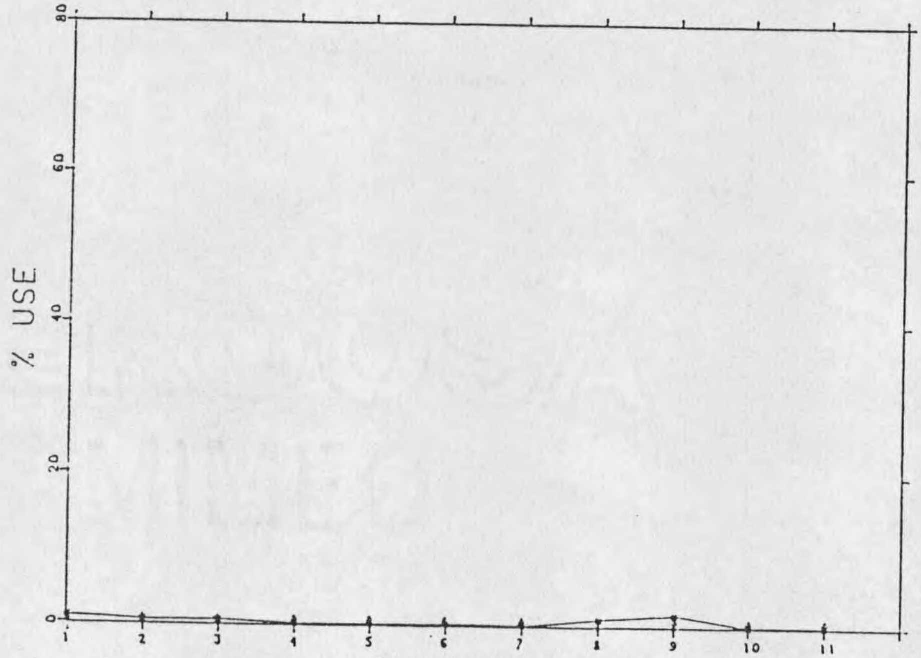

Figure 28. Hardwood draw HT.

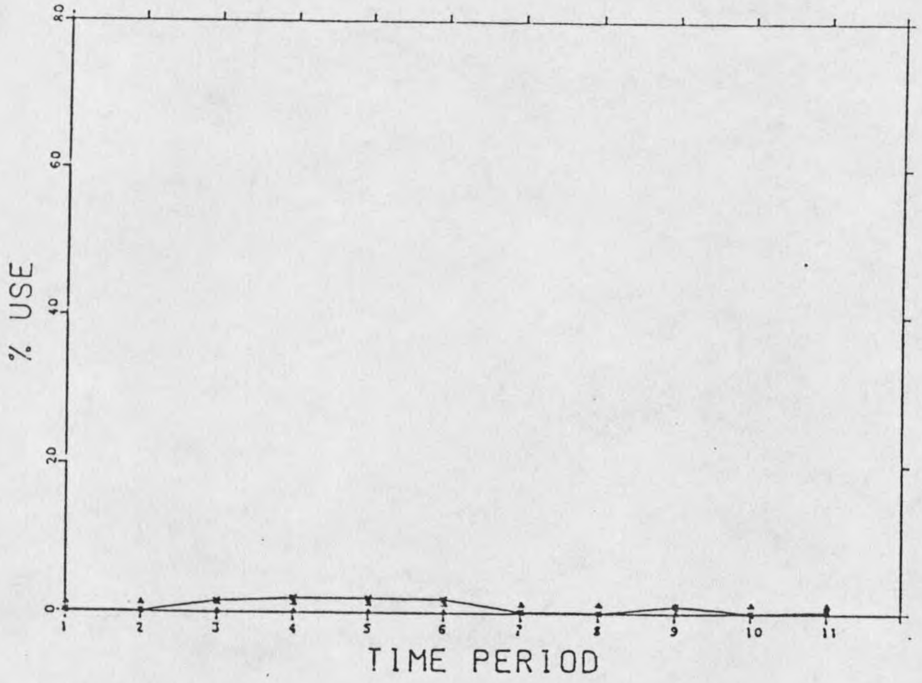

Figure 29. Andropogon scoparius - Juniperus horizontalis HT.

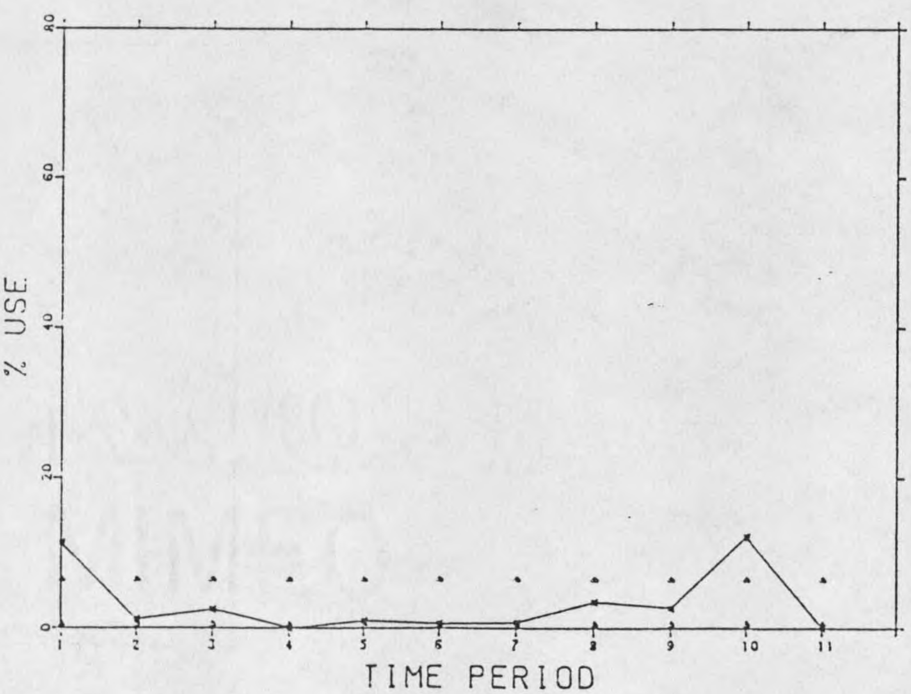

Figure 30. River bottoms MU.

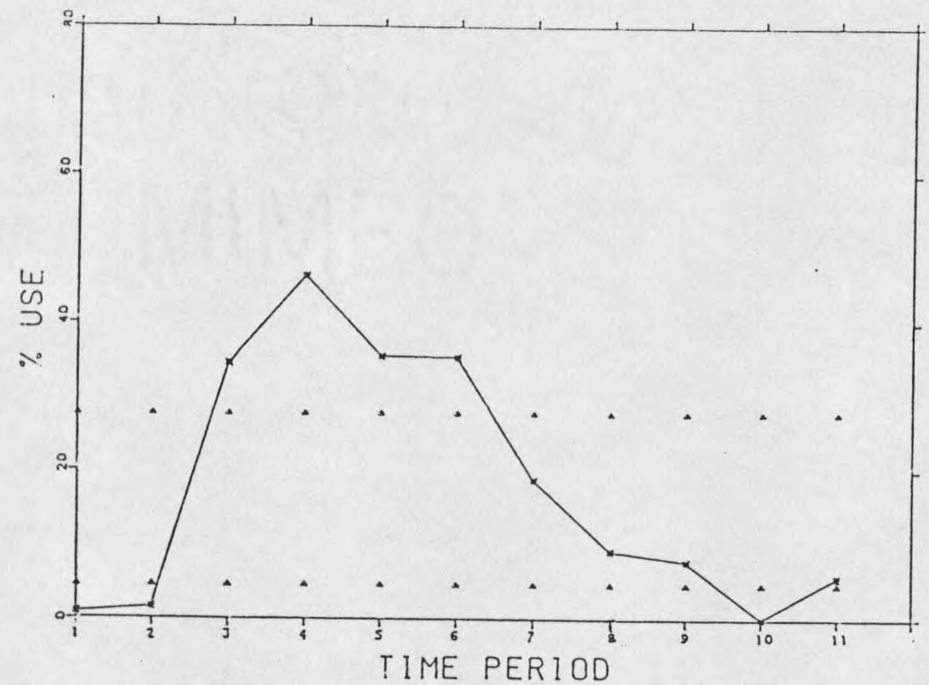

Figure 31. Prairie dog town MU.

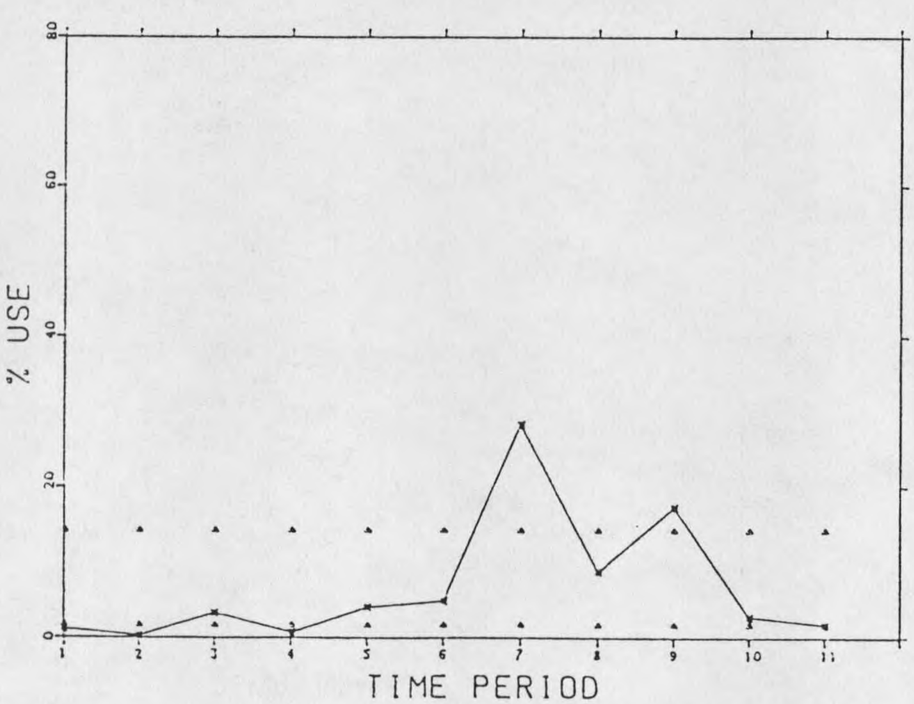

Figure 32. Artemisia cana HT.

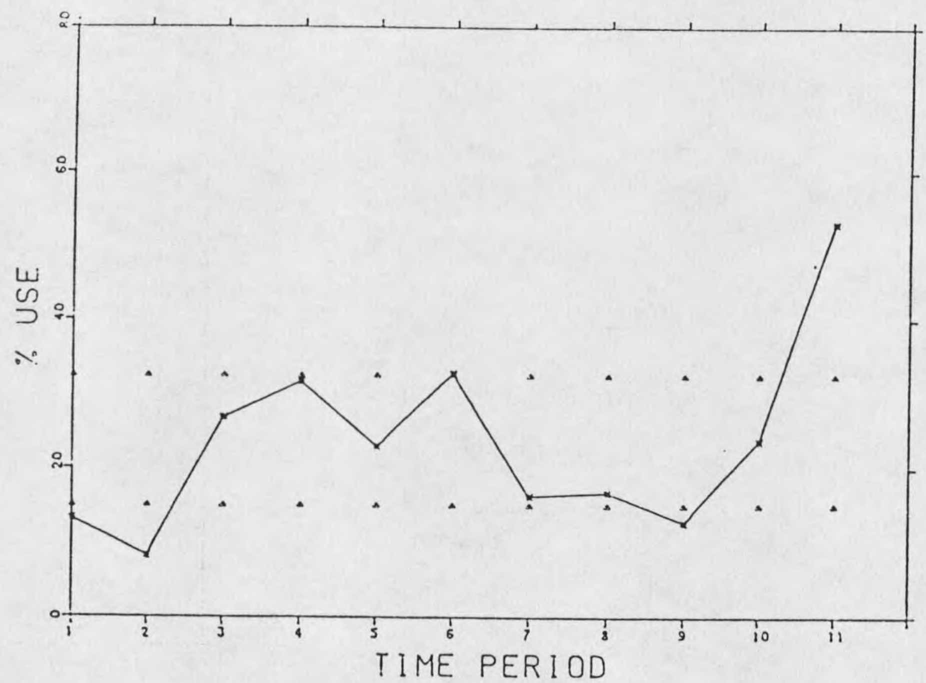

Figure 33. Agropyron smithii - Stipa viridula HT.

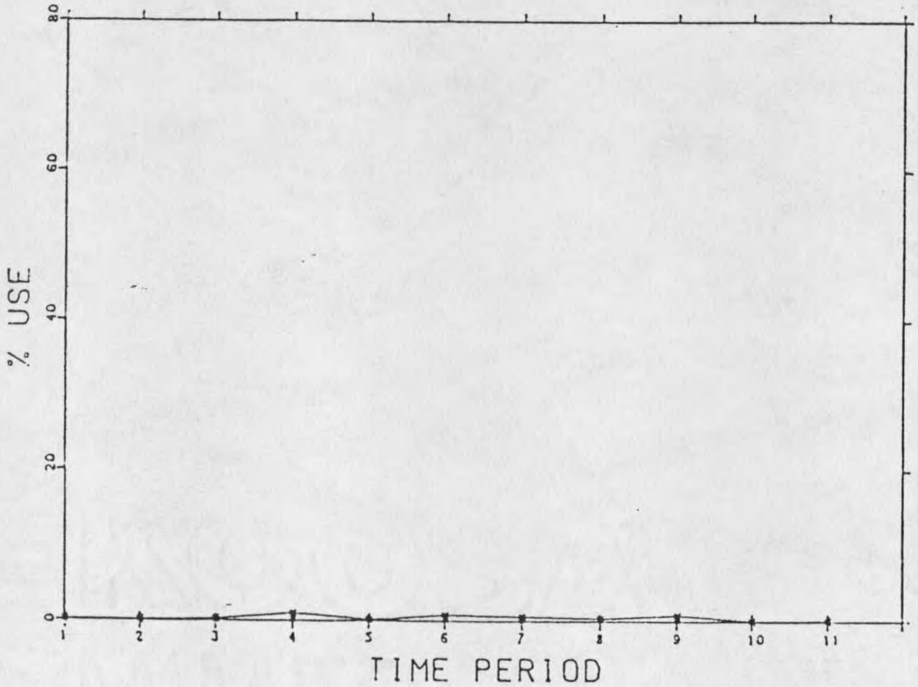

Figure 34. Watering area MU.

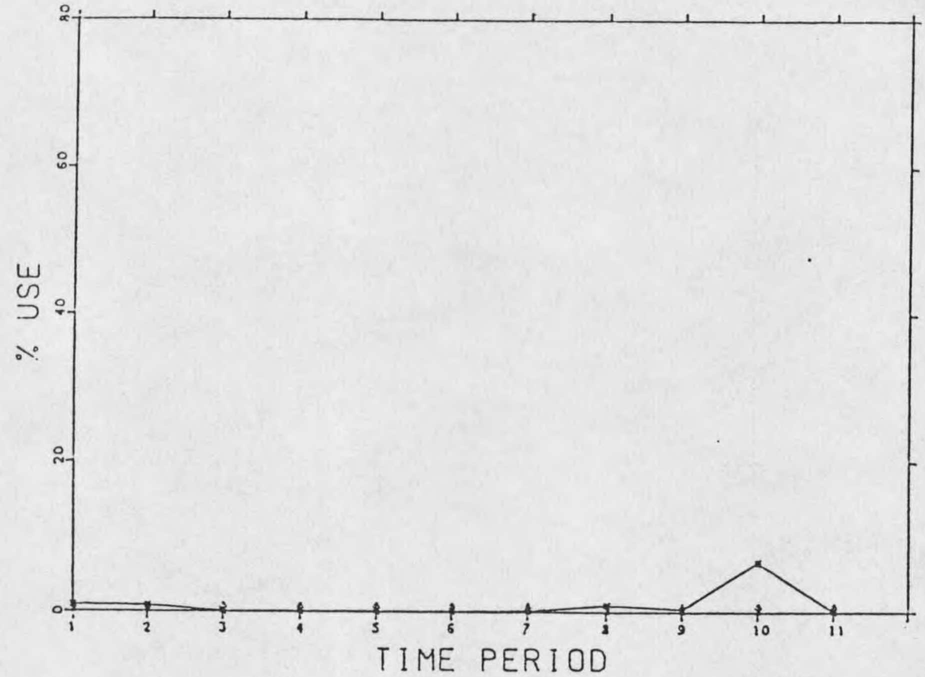

Figure 35. Populus deltoides - Juniperus scopulorum HT.

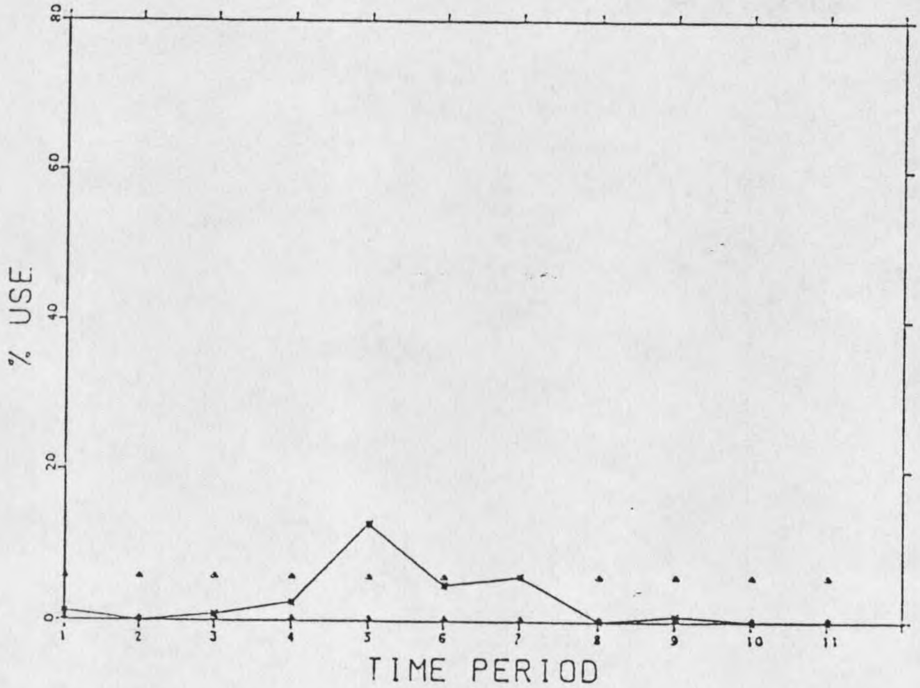

Figure 36. Andropogon scoparius HT.

APPENDIX C

Daily Movement of Herds in Each Time Period

Figures of the daily movement of all herds observed for each time period. - denotes starting location. Letters denote ending location. Those daily movements ending in the same letter were herds followed in consecutive days.

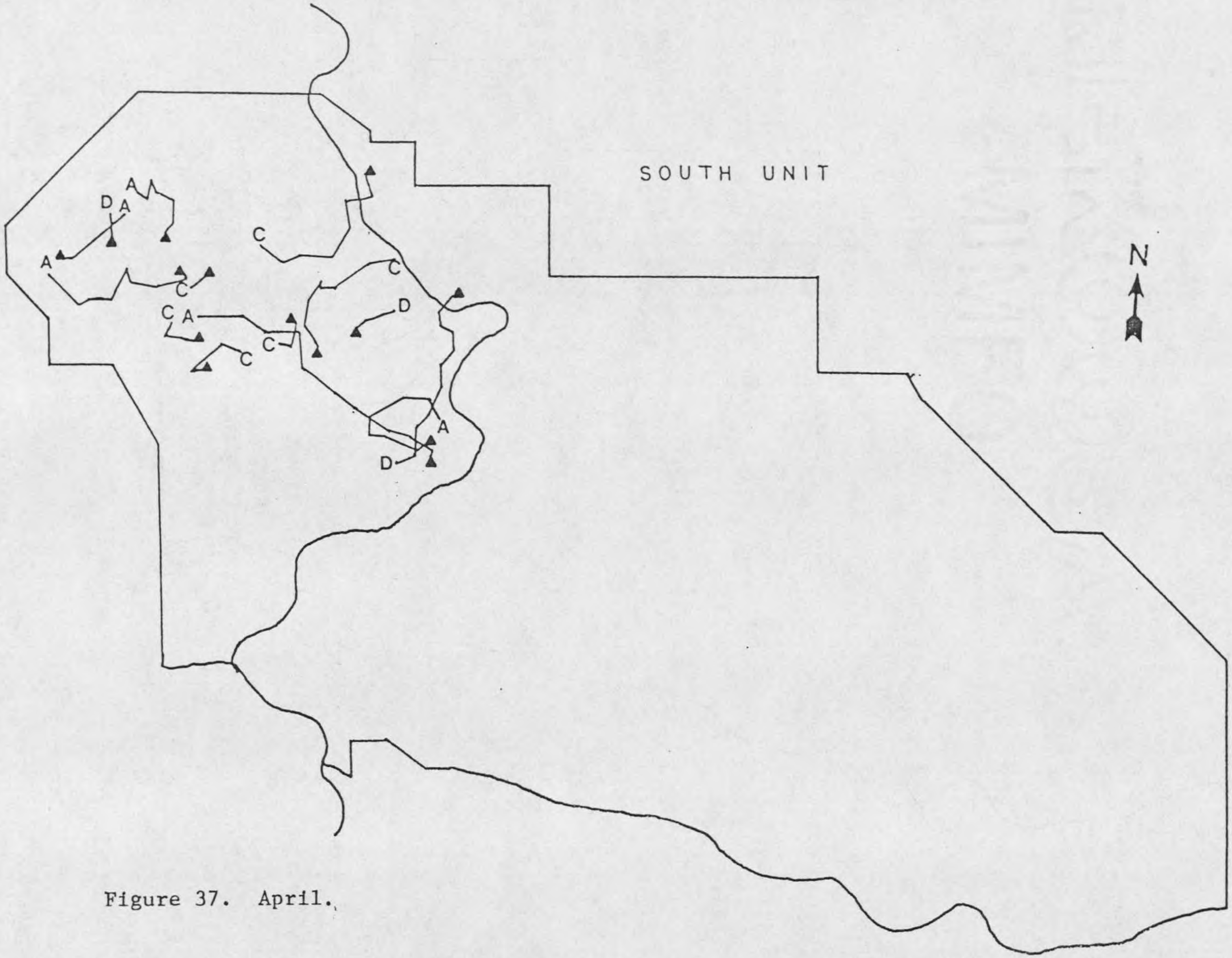

Figure 37. April.

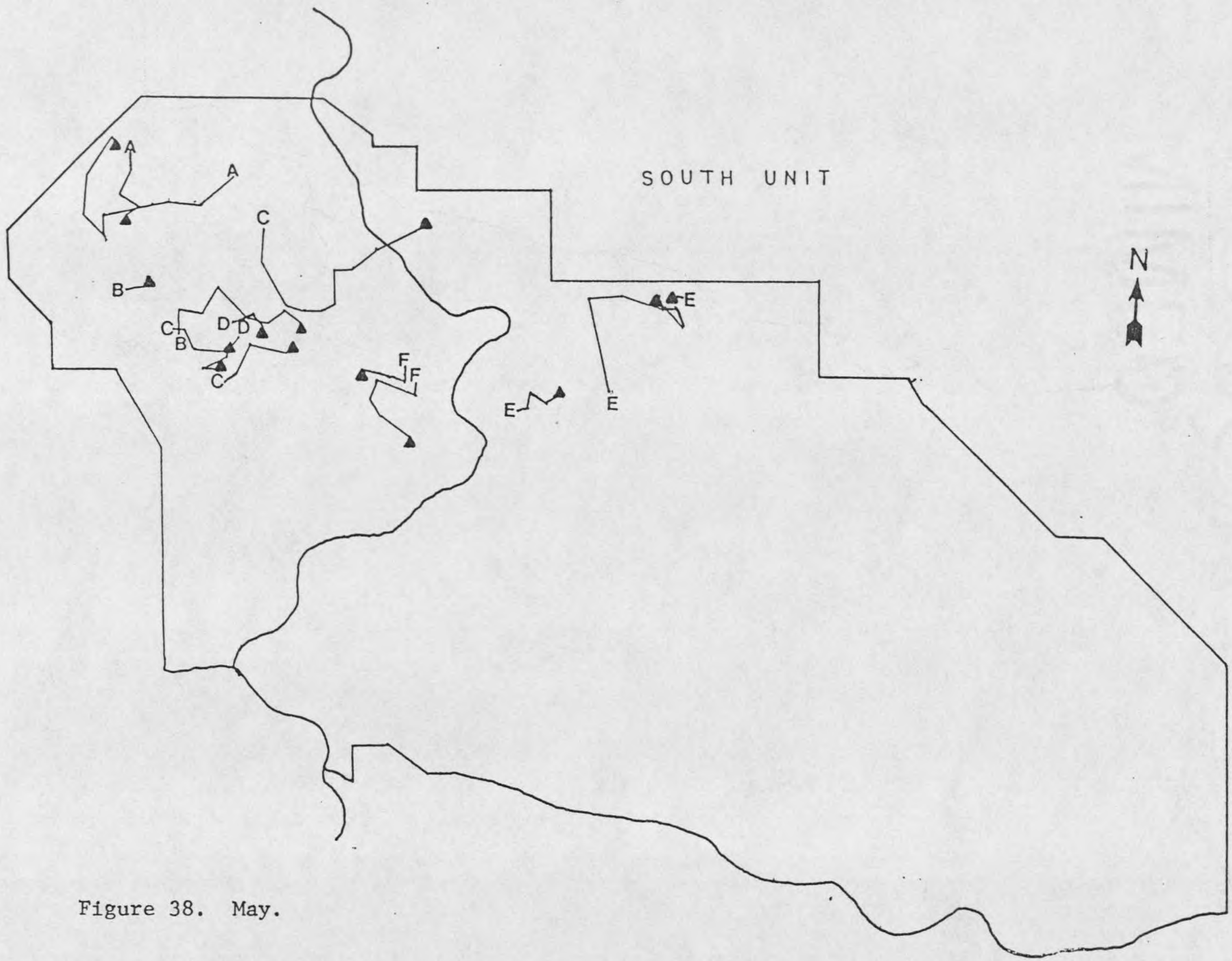

Figure 38. May.

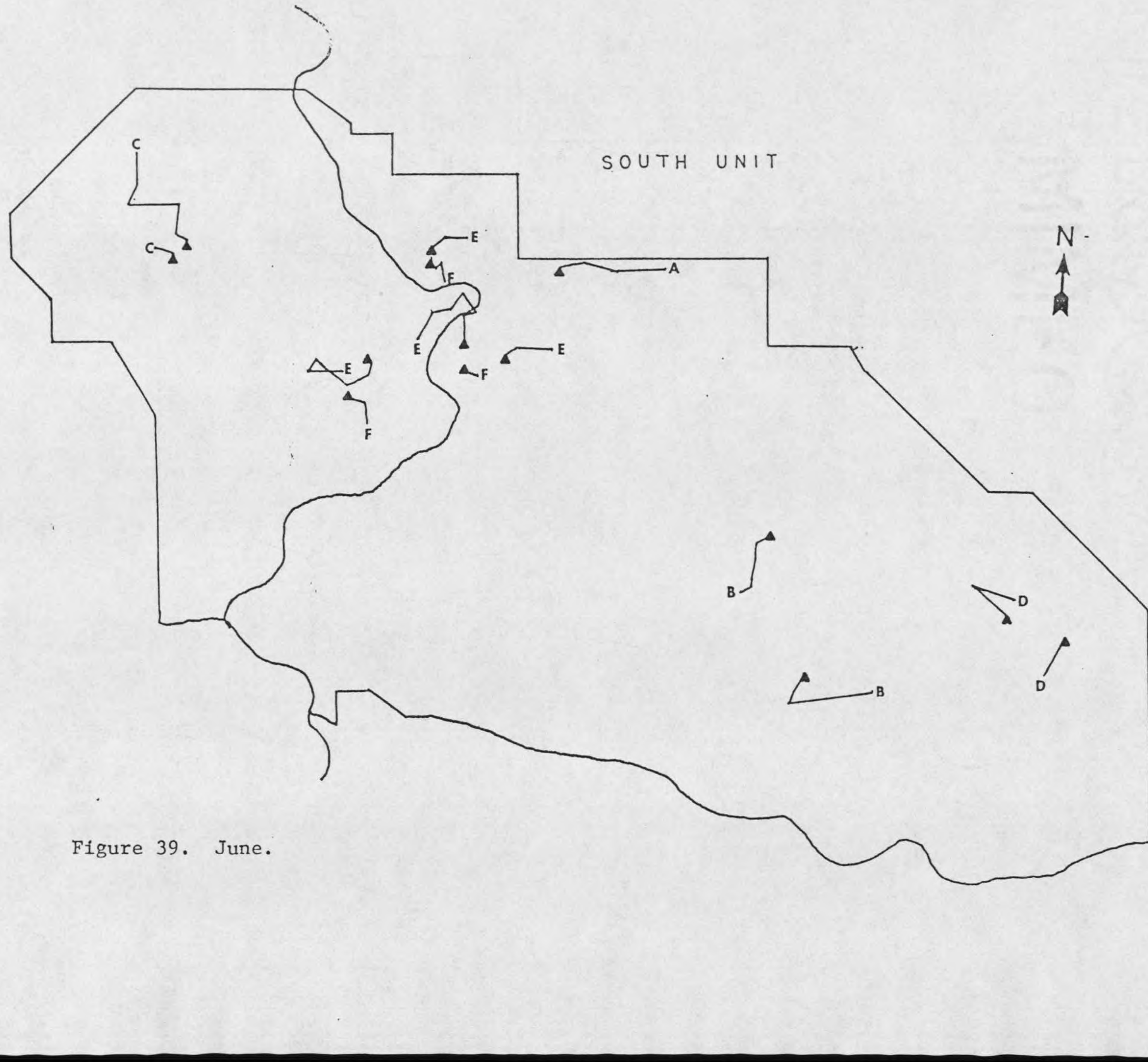

Figure 39. June.

Figure 40. August 1.

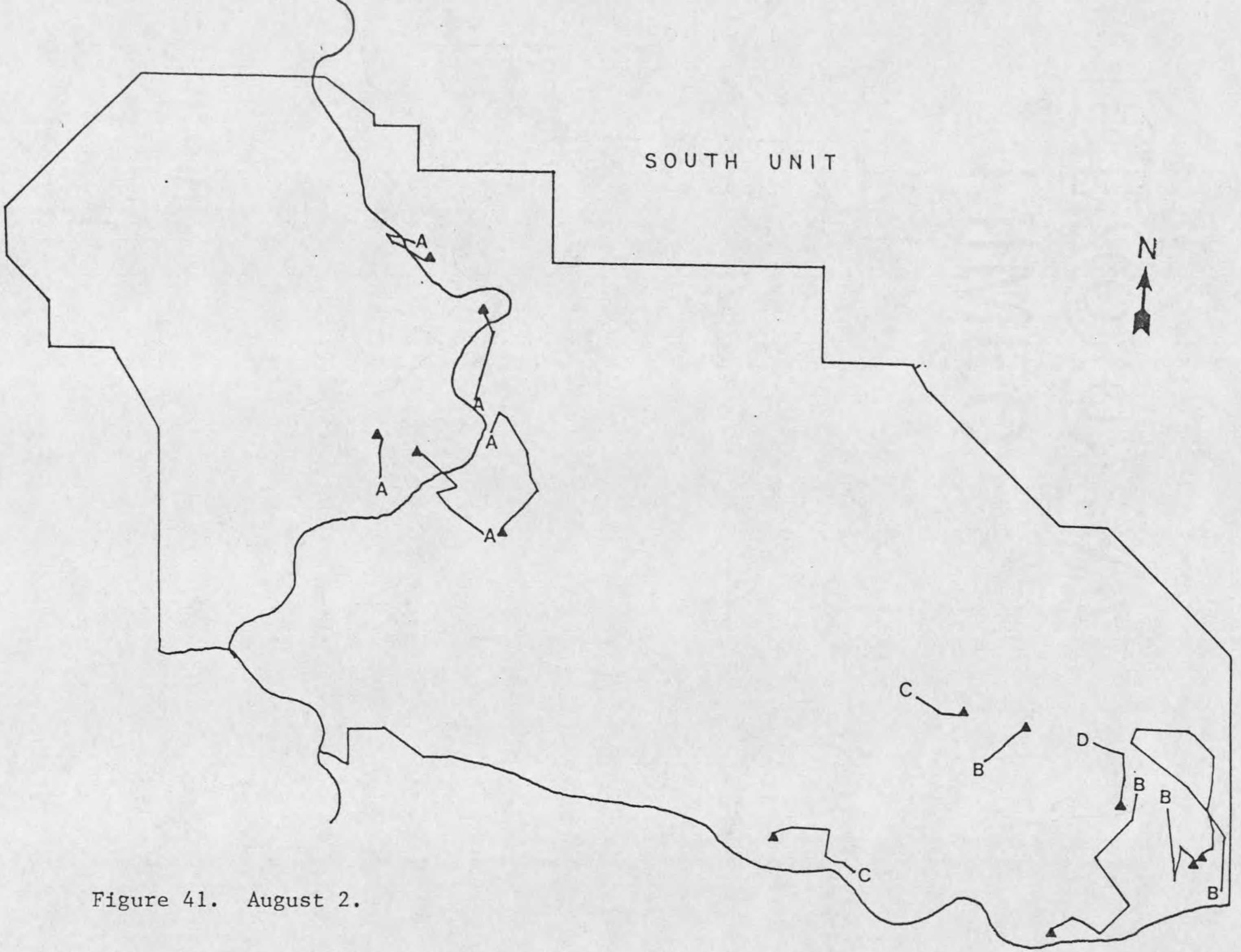

Figure 41. August 2.

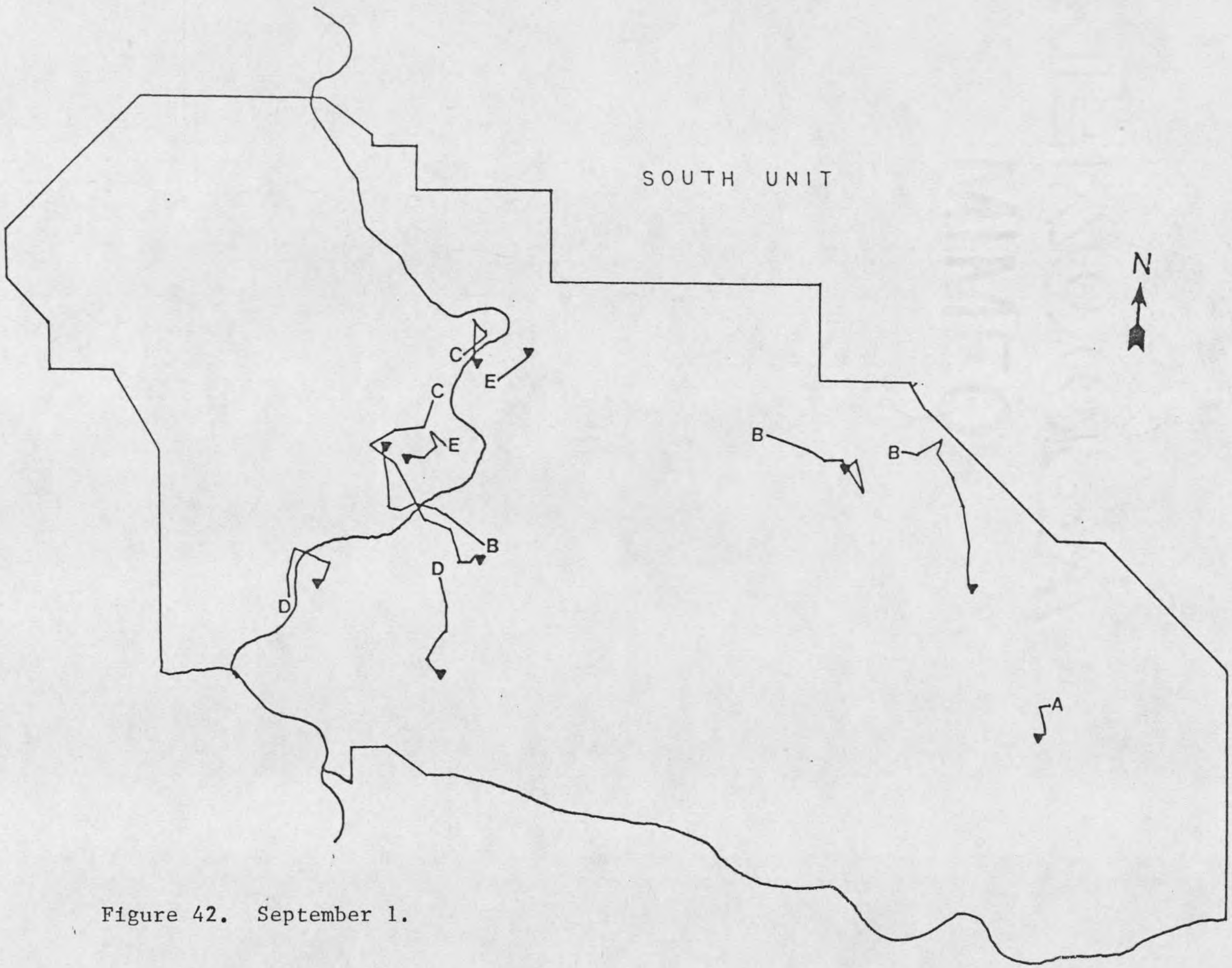

Figure 42. September 1.

Figure 43. September 2.

Figure 44. October 1.

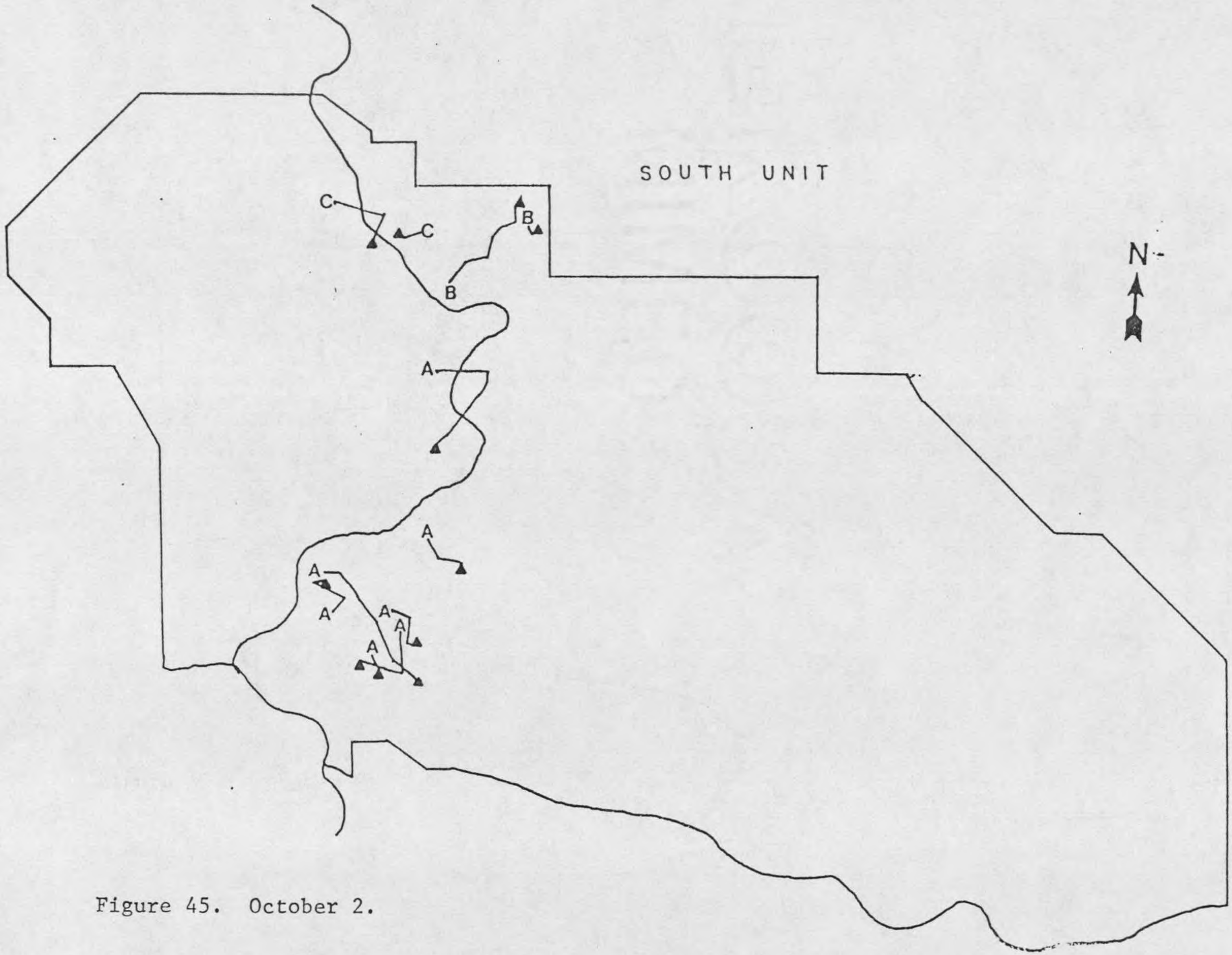

Figure 45. October 2.

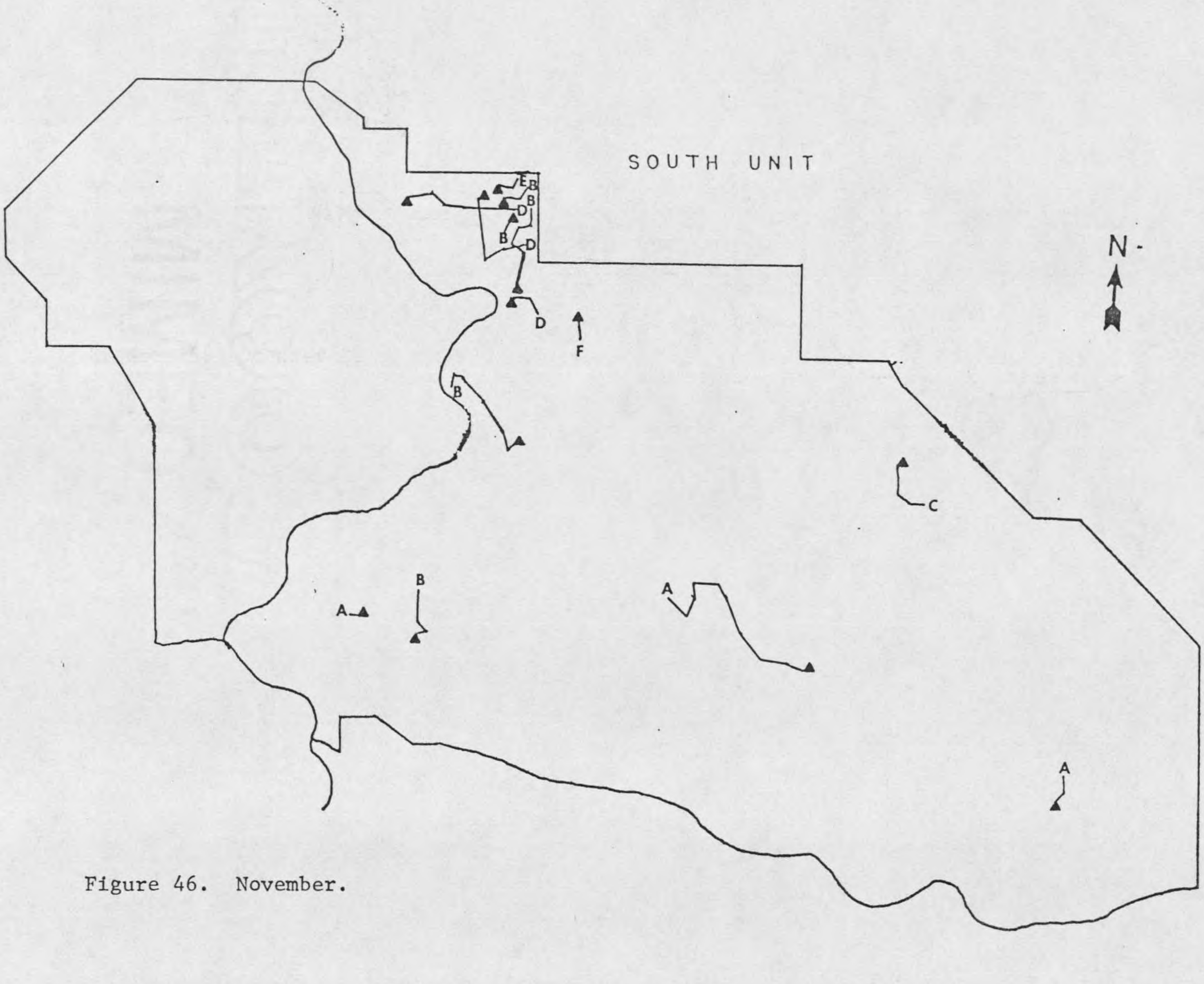

Figure 46. November.

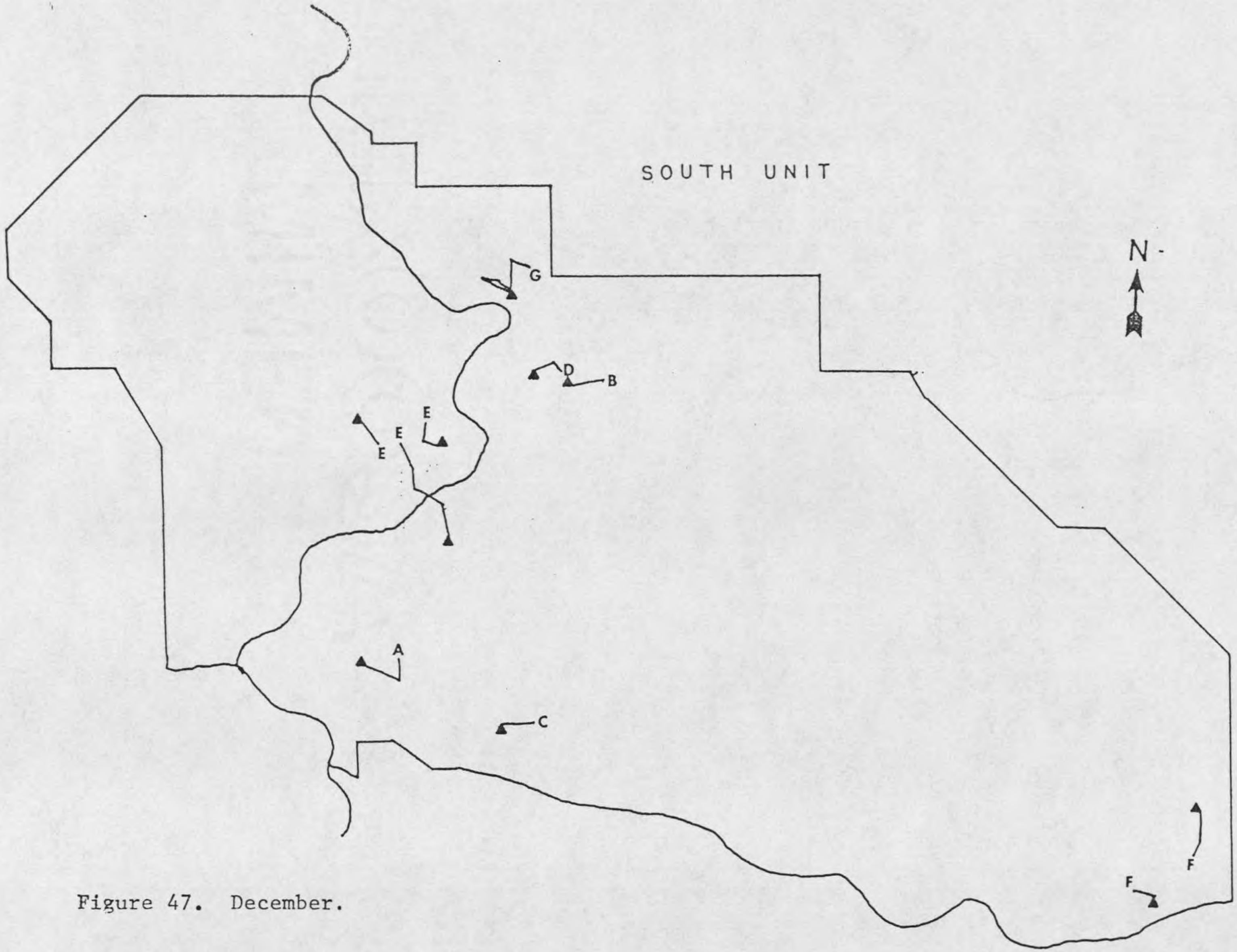

Figure 47. December.

APPENDIX D

Activity Analysis of Variance Tables

ANOVA tables from the analysis of grazing, resting, and other activity among the classes and time periods or the habitat divisions and time periods.

Table 18. ANOVA tables of grazing activity among the classes and time periods.

Full model

Source	DF	SS	MS
regression	16	0.180	0.0113
residual	31	0.120	0.0038
total	47	0.301	

Reduced model of the classes

Source	DF	SS	MS
regression	10	0.142	0.0142
residual	37	0.158	0.0042
total	47	0.301	

Reduced model of the time periods

Source	DF	SS	MS
regression	6	0.047	0.0079
residual	41	0.253	0.0061
total	47	0.301	

Table 19. ANOVA tables of resting activity among the classes and time periods

Full model

Source	DF	SS	MS
regression	16	0.436	0.0212
residual	31	0.516	0.0166
total	47	0.952	

Reduced model of the classes

Source	DF	SS	MS
regression	10	0.131	0.0131
residual	37	0.821	0.0221
total	47	0.952	

Reduced model of the time periods

Source	DF	SS	MS
regression	6	0.252	0.0420
residual	41	0.700	0.0170
total	47	0.952	

Table 20. ANOVA tables of other activity among the classes and time periods.

Full model

Source	DF	SS	MS
regression	16	0.341	0.0213
residual	31	0.117	0.0037
total	47	0.458	

Reduced model of the classes

Source	DF	SS	MS
regression	10	0.265	0.0265
residual	37	0.193	0.0052
total	47	0.458	

Reduced model of the time periods

Source	DF	SS	MS
regression	6	0.084	0.0140
residual	41	0.374	0.0091
total	47	0.458	

Table 21. ANOVA tables of grazing activity among the habitat divisions and time periods.

Full model

Source	DF	SS	MS
regression	19	0.253	0.0133
residual	36	0.109	0.0030
total	55	0.362	

Reduced model of the habitat divisions

Source	DF	SS	MS
regression	10	0.170	0.0170
residual	45	0.192	0.0042
total	55	0.362	

Reduced model of the time periods

Source	DF	SS	MS
regression	9	0.103	0.0115
residual	46	0.259	0.0056
total	55	0.362	

Table 22. ANOVA tables of resting activity among the habitat divisions and time periods.

Full model

Source	DF	SS	MS
regression	19	0.360	0.0189
residual	36	0.296	0.0082
total	55	0.656	

Reduced model of the habitat divisions

Source	DF	SS	MS
regression	10	0.172	0.0172
residual	45	0.484	0.0107
total	55	0.656	

Reduced model of the time periods

Source	DF	SS	MS
regression	9	0.186	0.0207
residual	46	0.470	0.0102
total	55	0.656	

Table 23. ANOVA tables of other activity among the habitat divisions and time periods.

Full model

Source	DF	SS	MS
regression	19	0.400	0.0211
residual	36	0.086	0.0241
total	55	0.487	

Reduced model of the habitat division

Source	DF	SS	MS
regression	10	0.287	0.0287
residual	45	0.200	0.0044
total	55	0.487	

Reduced model of the time periods

Source	DF	SS	MS
regression	9	0.207	0.0230
residual	46	0.280	0.0060
total	55	0.487	

APPENDIX E

Average Percent of the Herds Engaged in the Different Activities Among the Time Periods

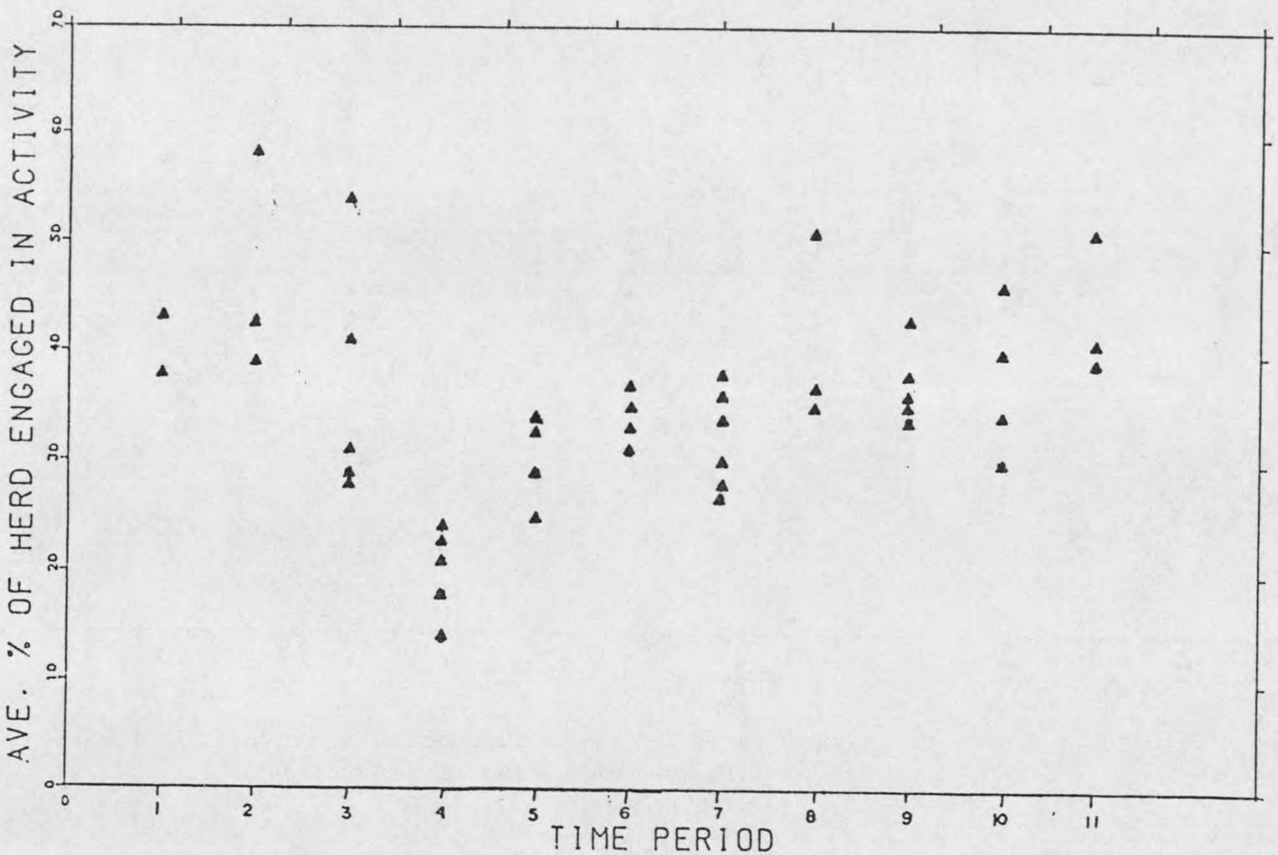

Figure 48. Average percent of observed herds engaged in grazing activity among the classes in each time period.

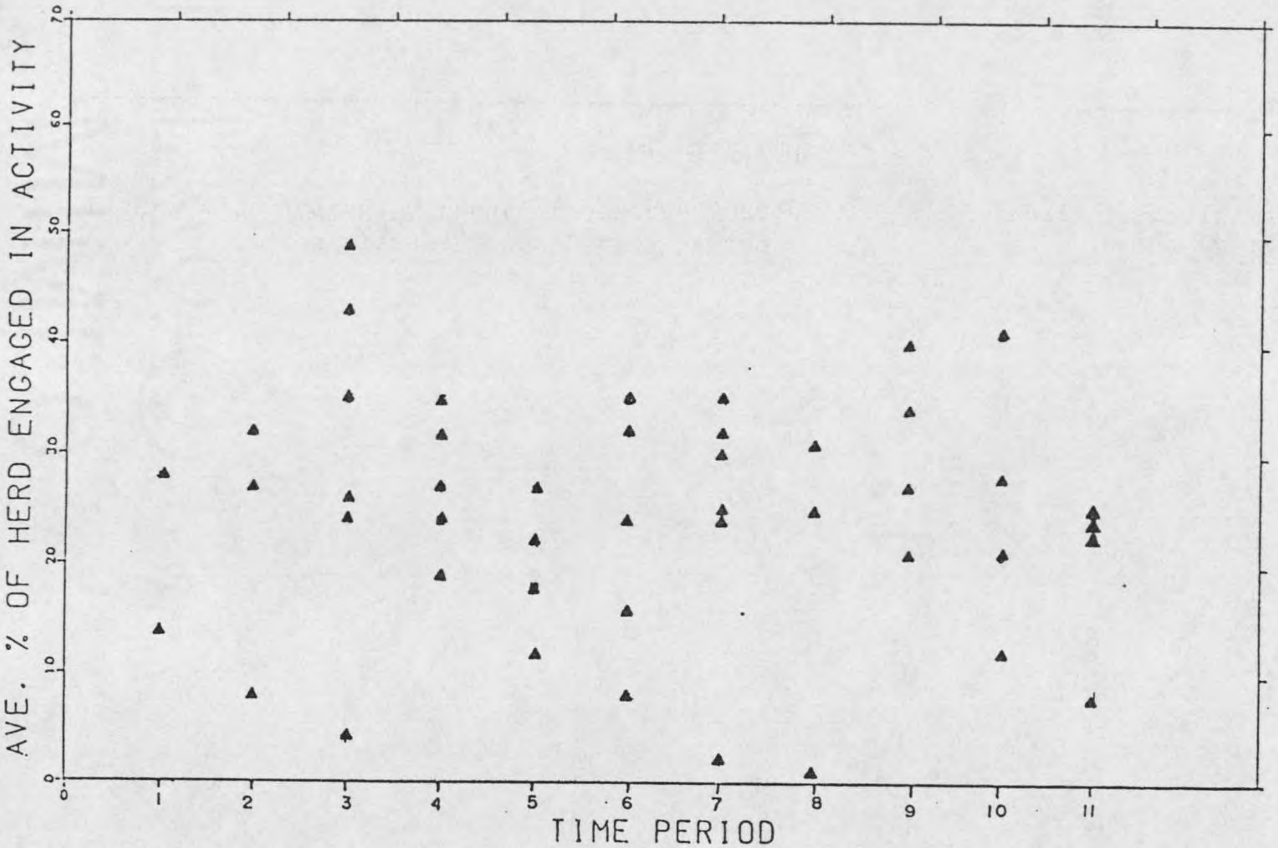

Figure 49. Average percent of observed herds engaged in resting activity among the classes in each time period.

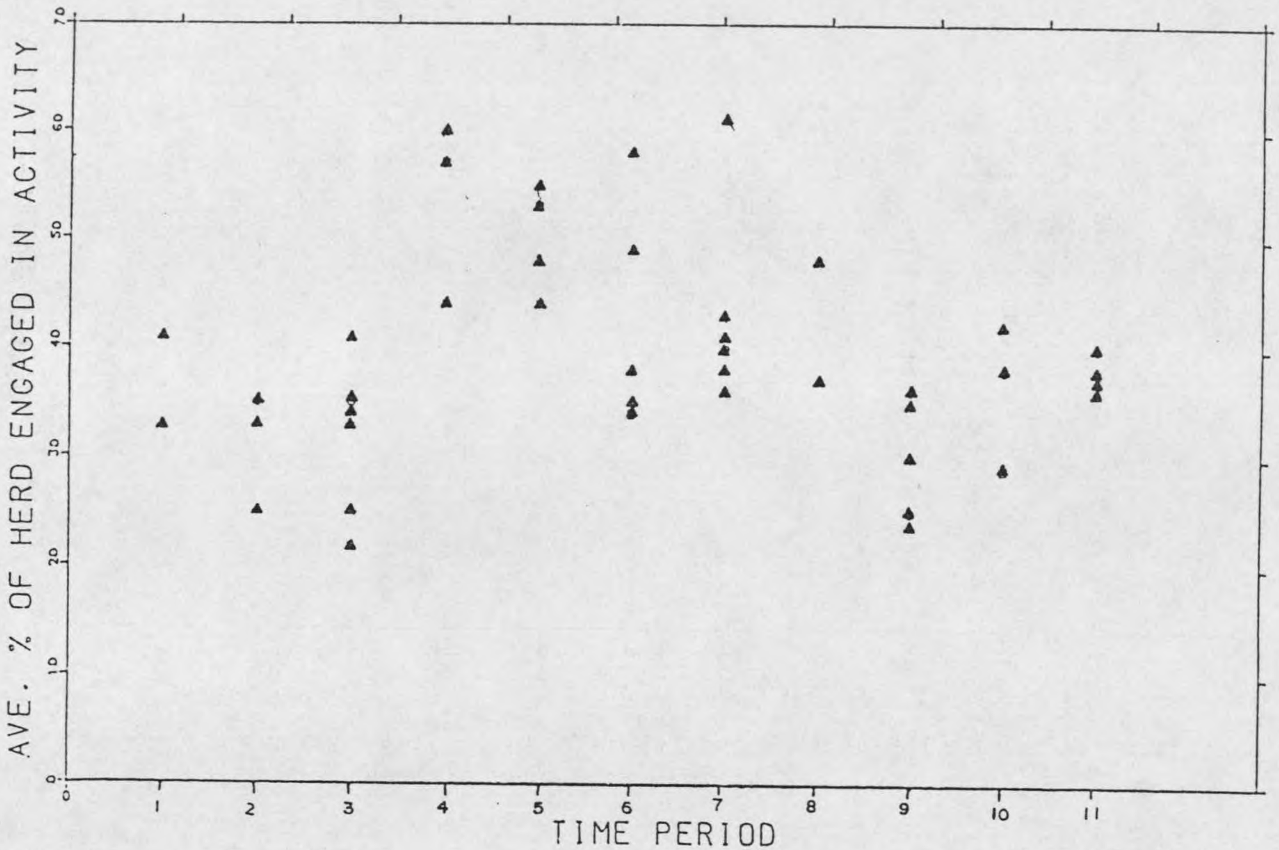

Figure 50. Average percent of observed herds engaged in other activity among the classes in each time period.

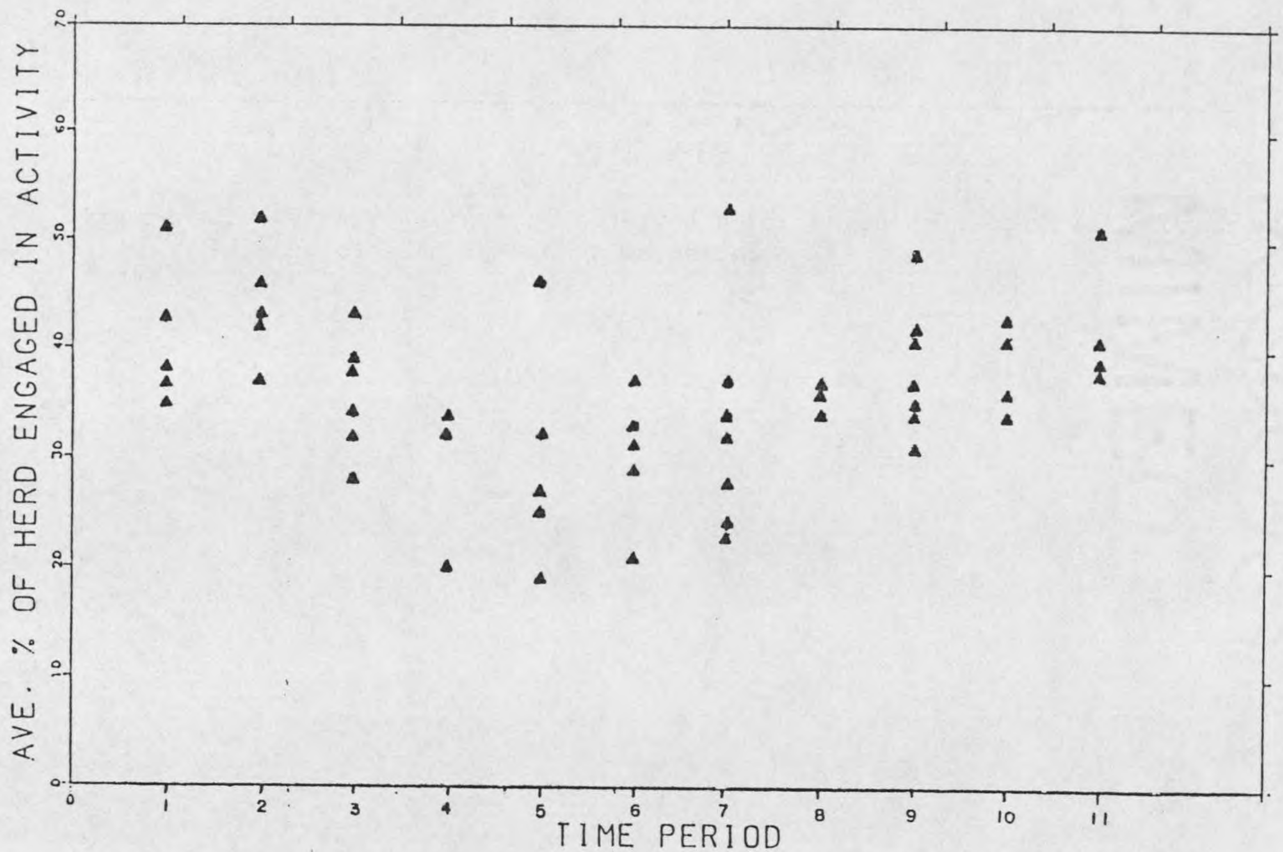

Figure 51. Average percent of observed herds engaged in grazing activity among the habitat divisions in each time period.

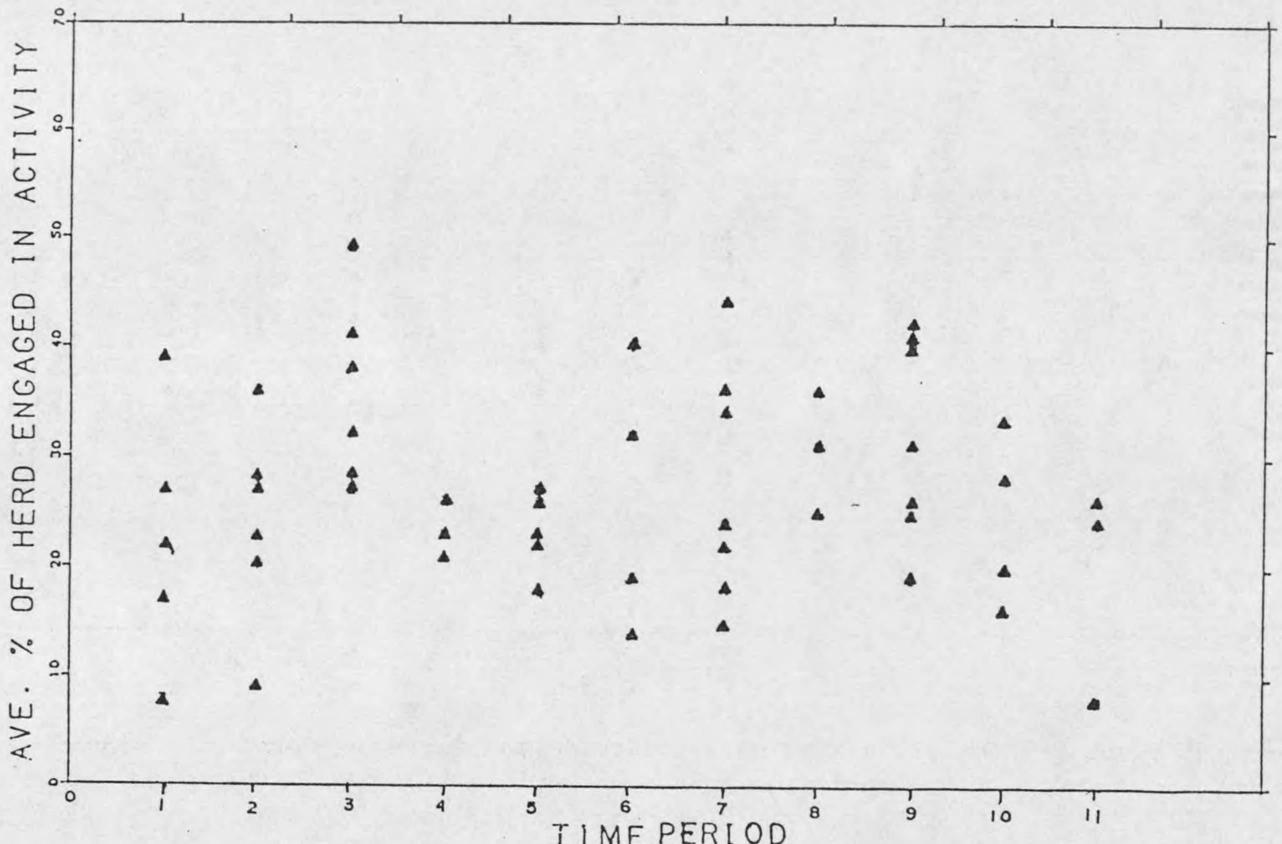

Figure 52. Average percent of observed herds engaged in resting activity among the habitat divisions in each time period.

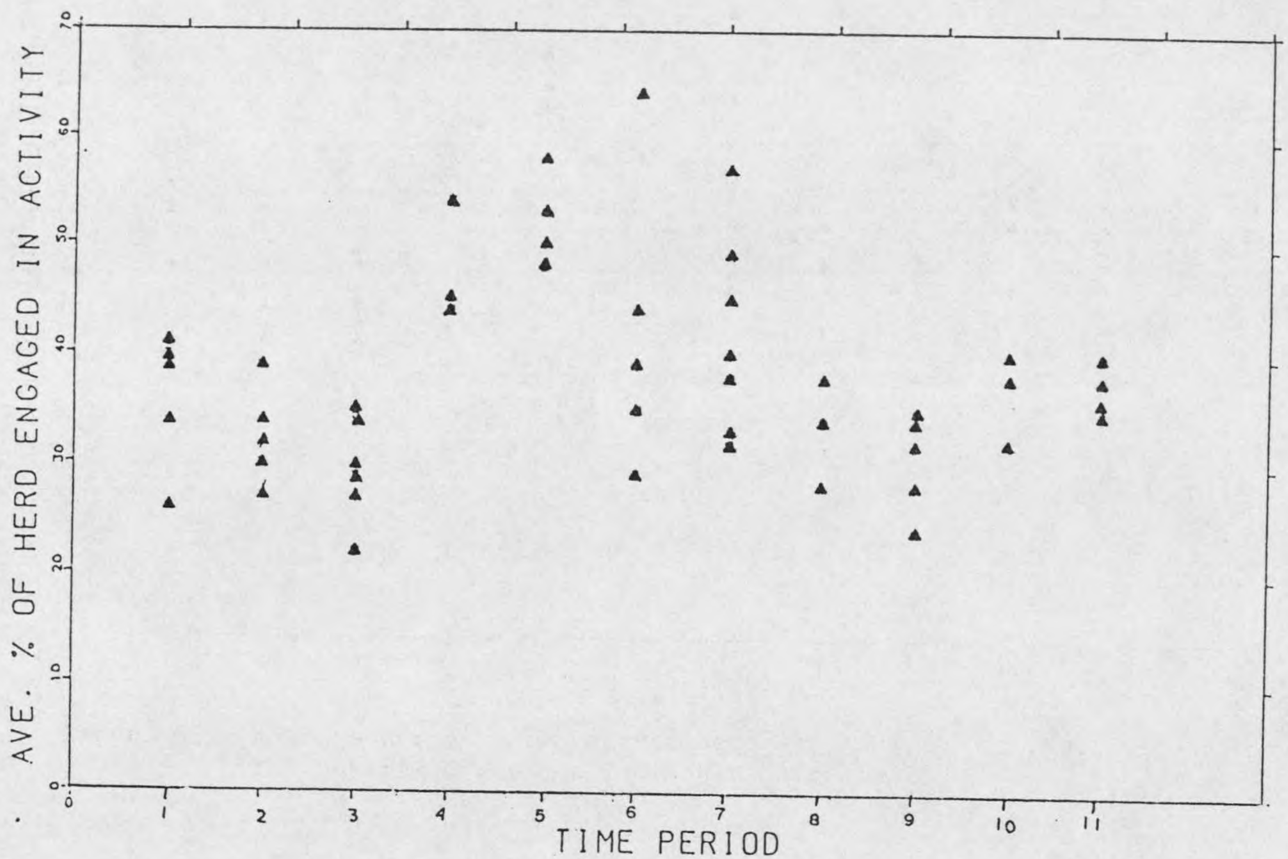

Figure 53. Average percent of observed herds engaged in other activity among the habitat divisions in each time period.

APPENDIX F

Percent of the Herds Engaged in the Different Activities During the Daylight Hours for Each Time Period

Figures showing the percent of observed herds engaged in grazing, resting, or other activity during daylight hours for each time period.

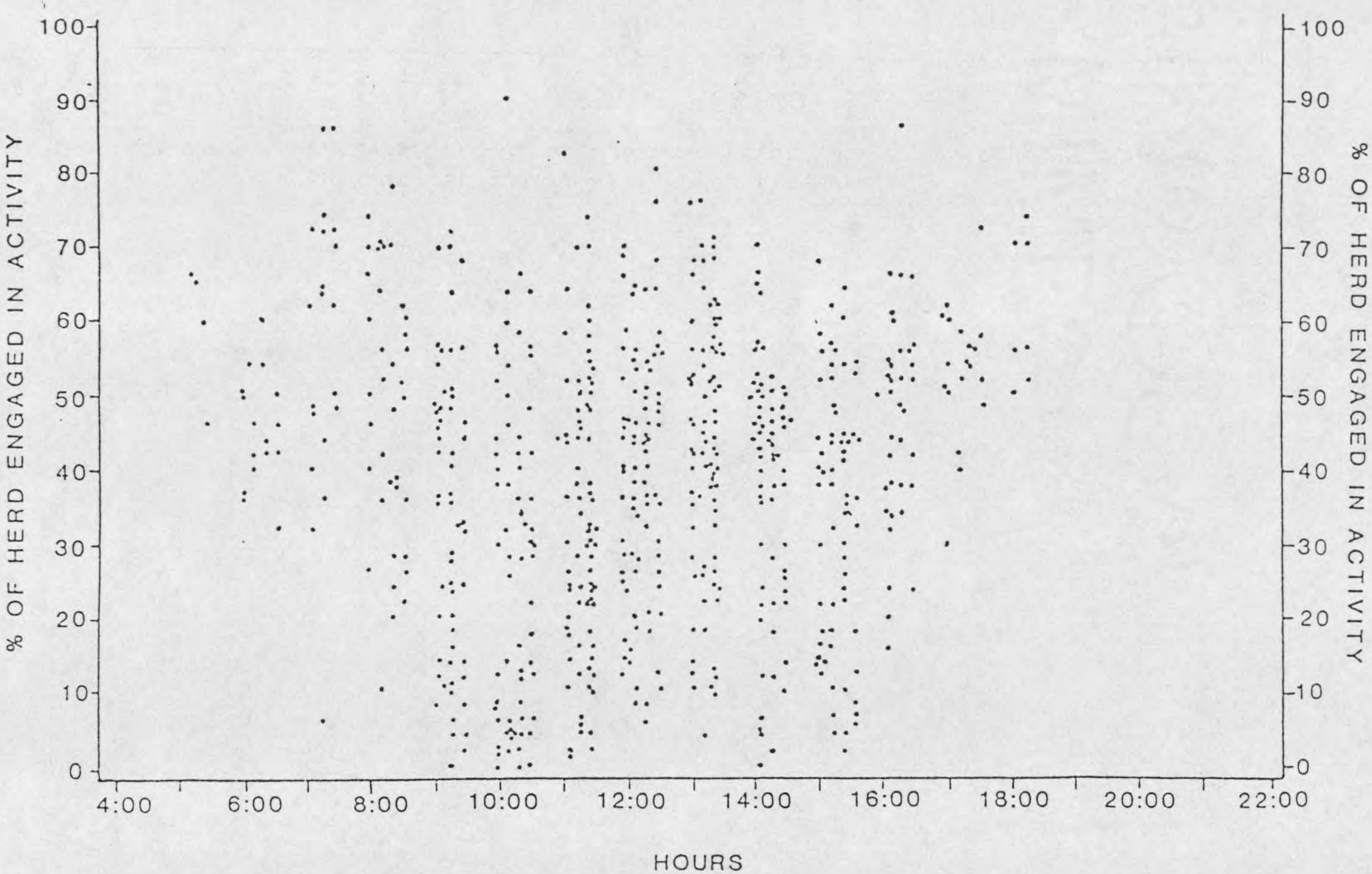

Figure 54. Grazing activity for April.

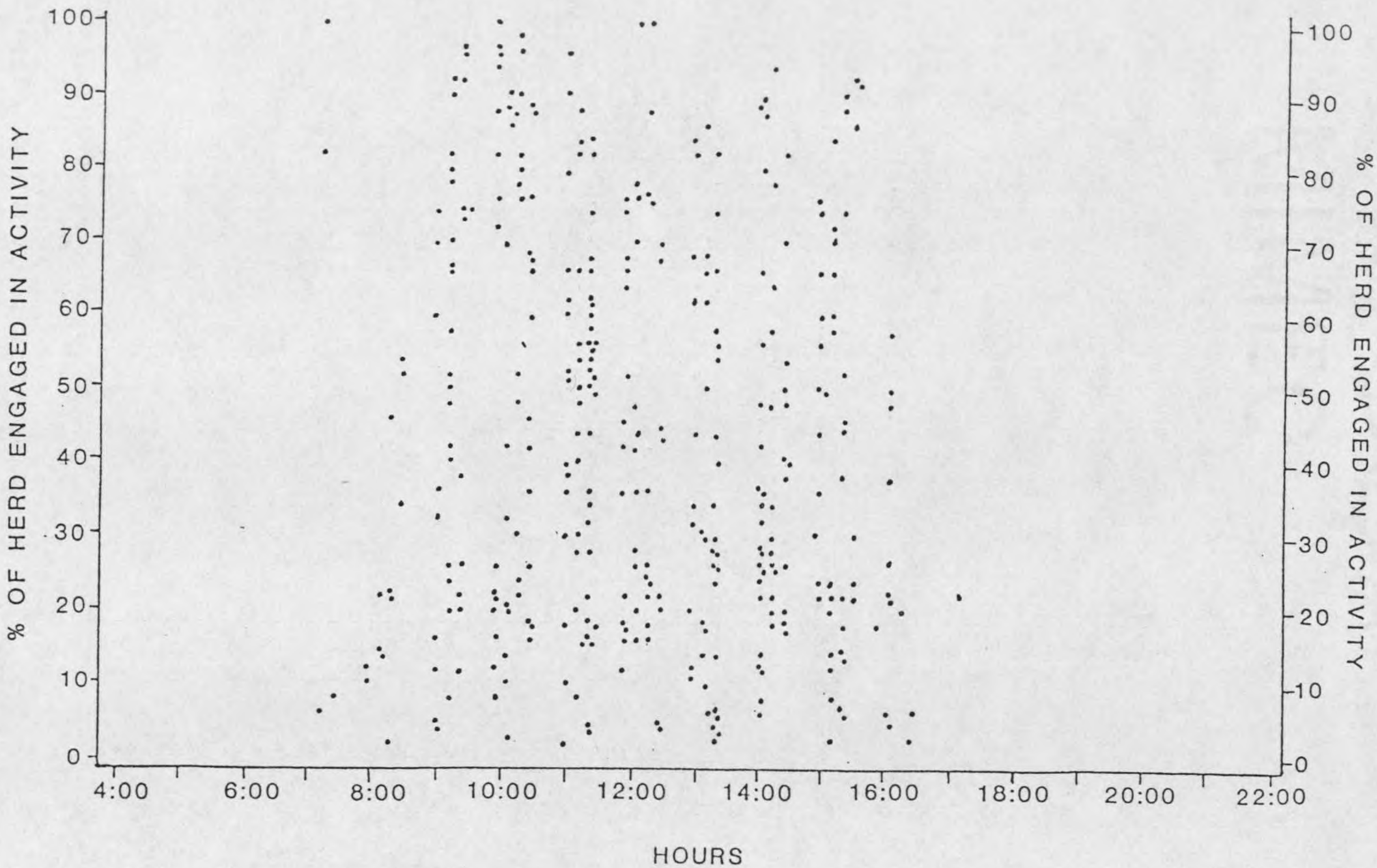

Figure 55. Resting activity for April.

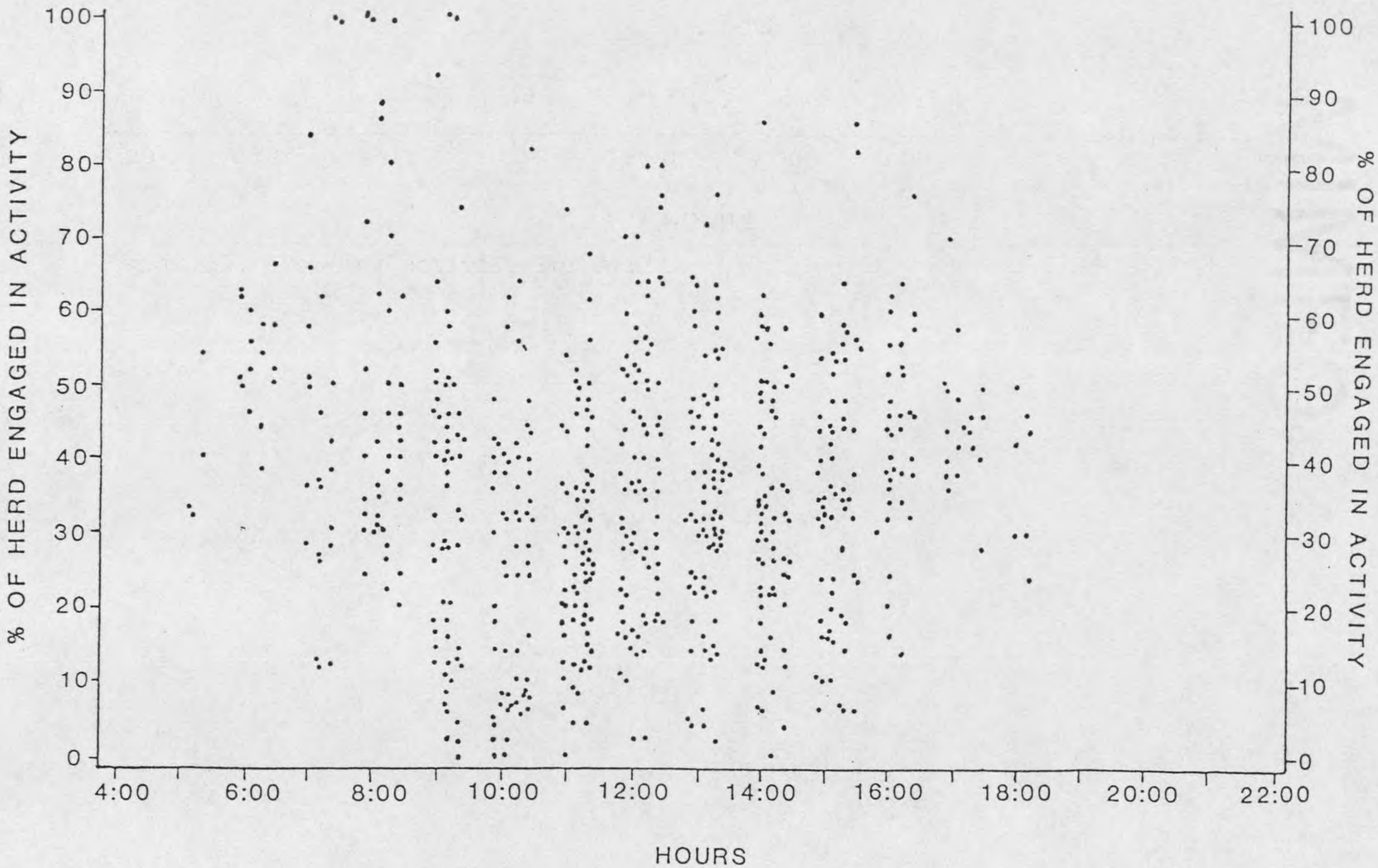

Figure 56. Other activity for April.

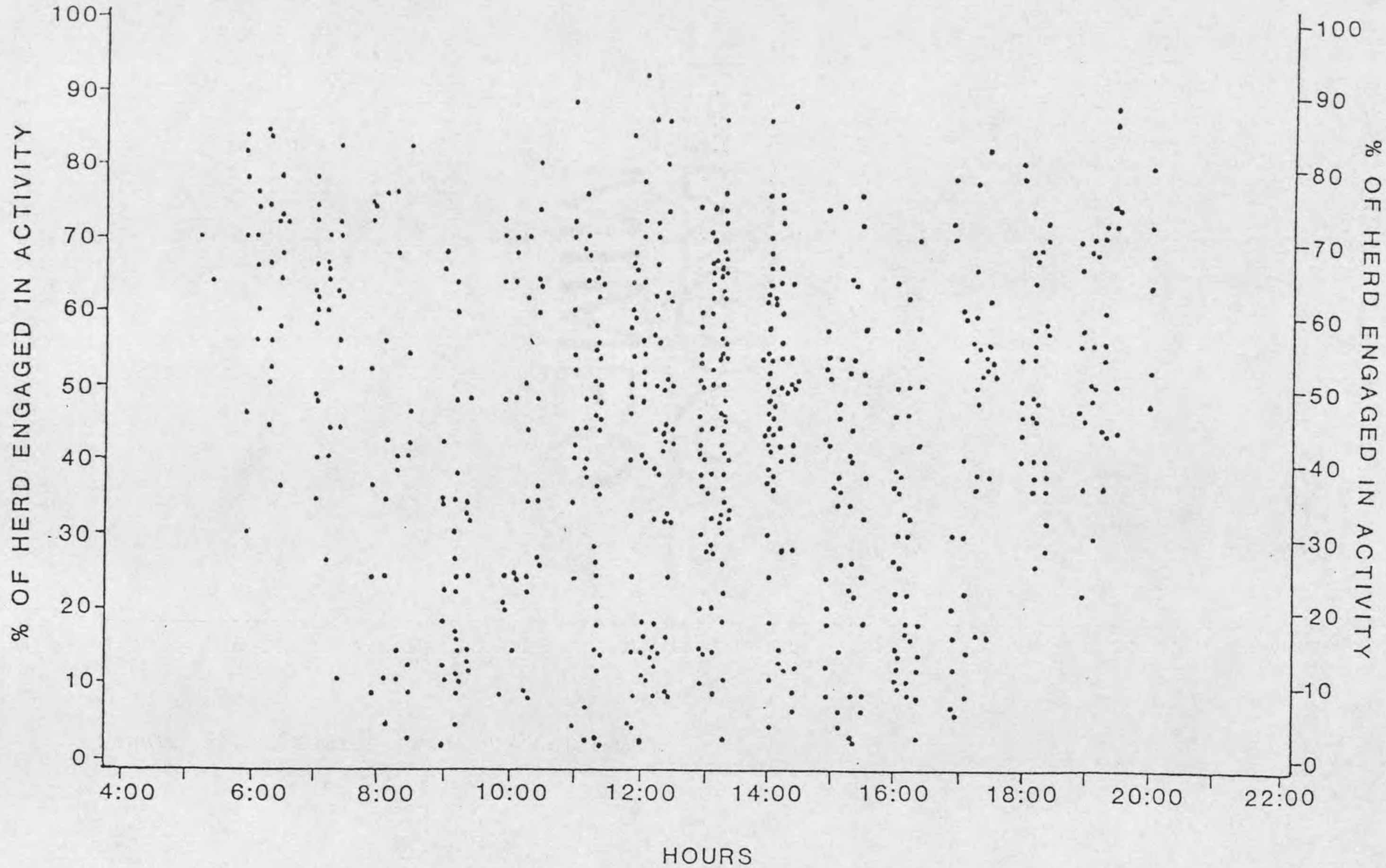

Figure 57. Grazing activity for May.

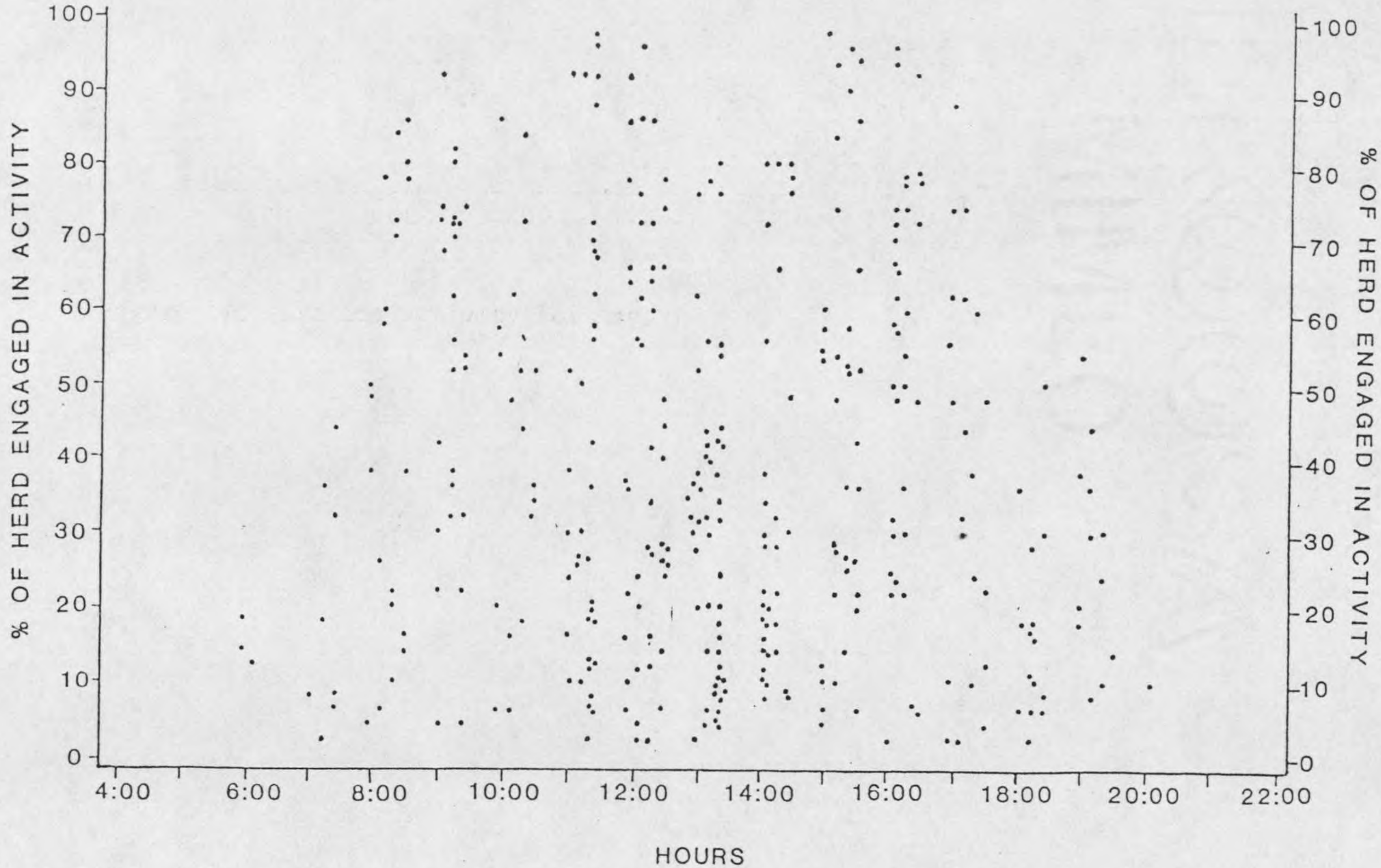

Figure 58. Resting activity for May.

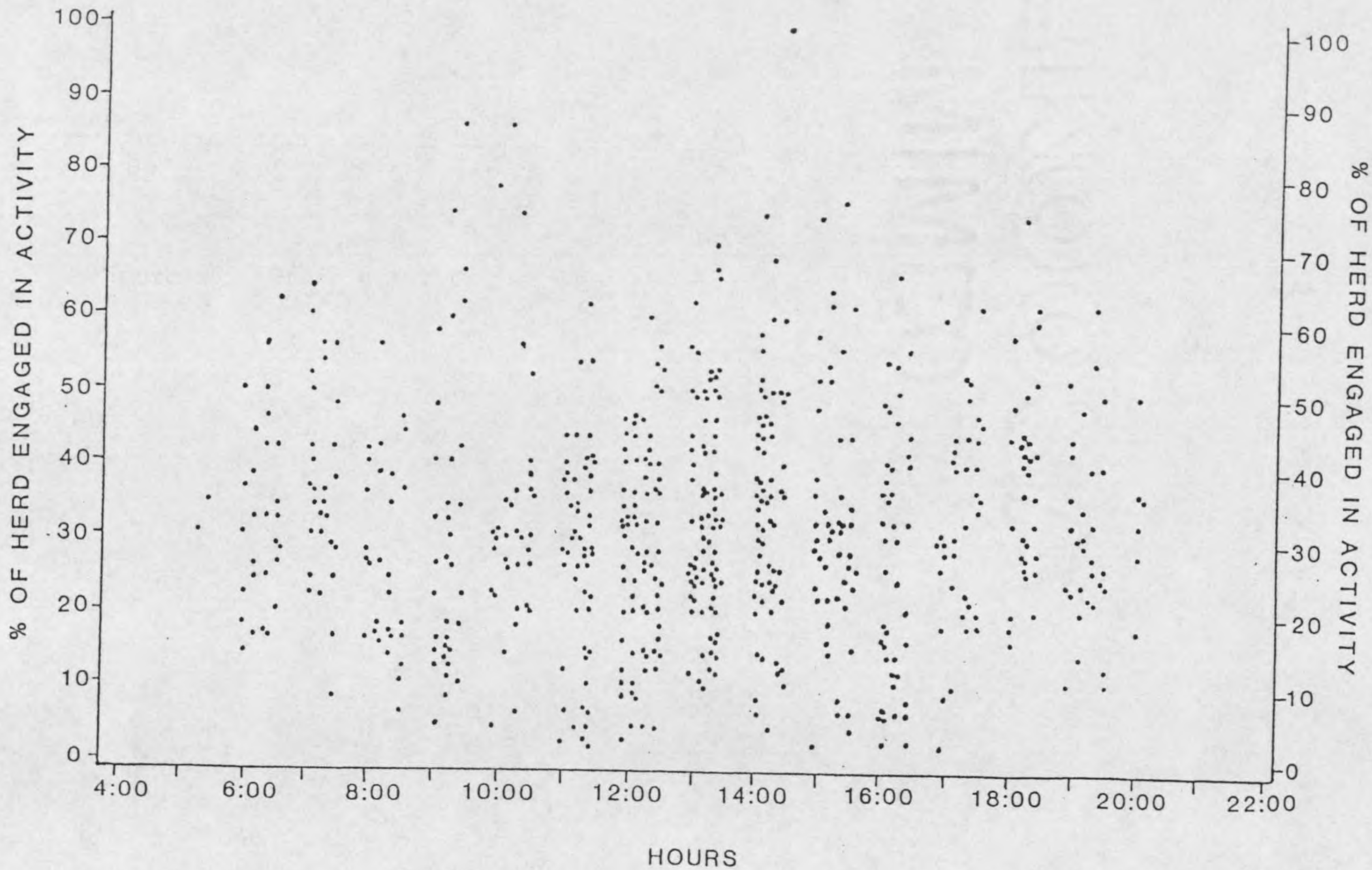

Figure 59. Other activity for May.

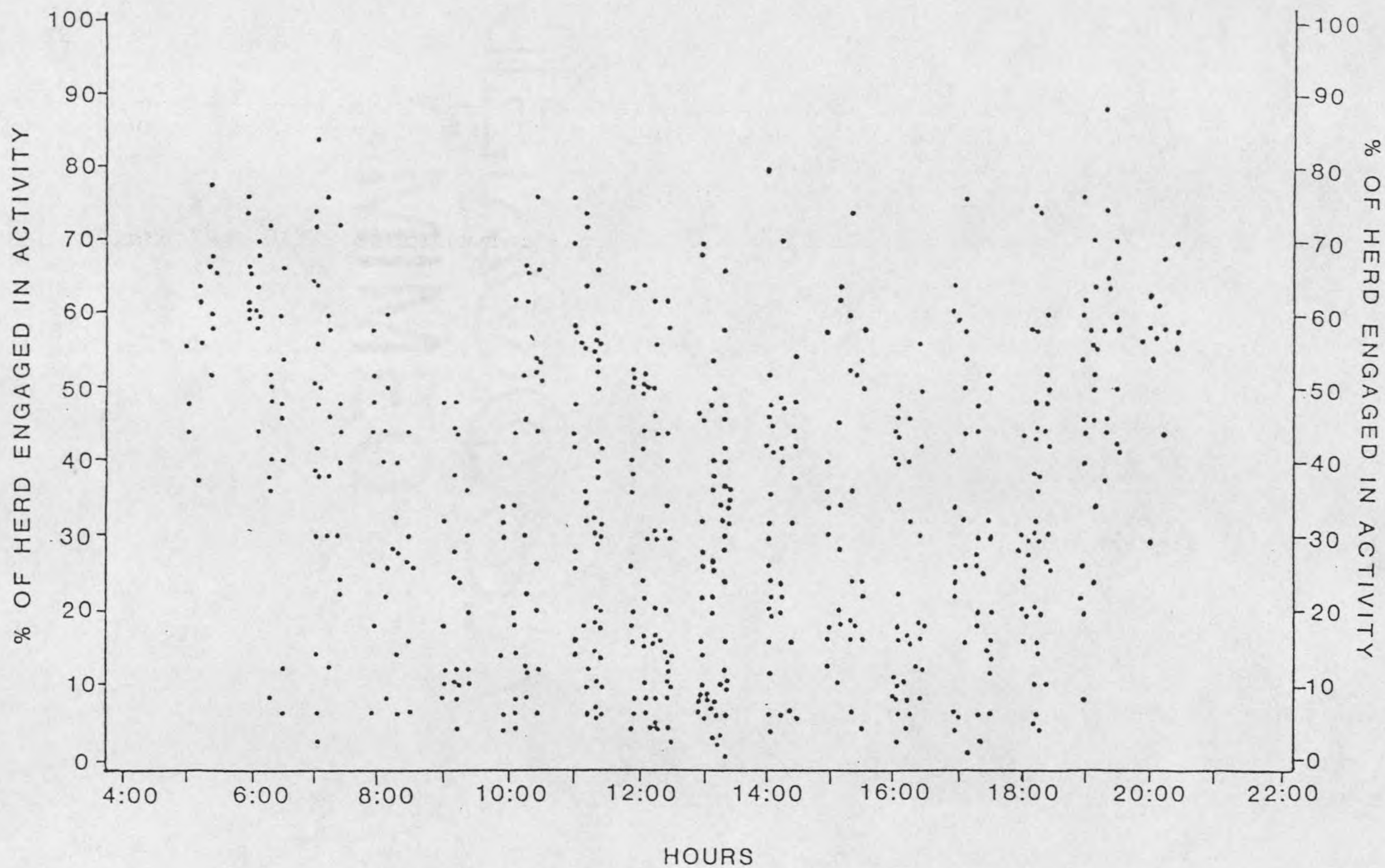

Figure 60. Grazing activity for June.

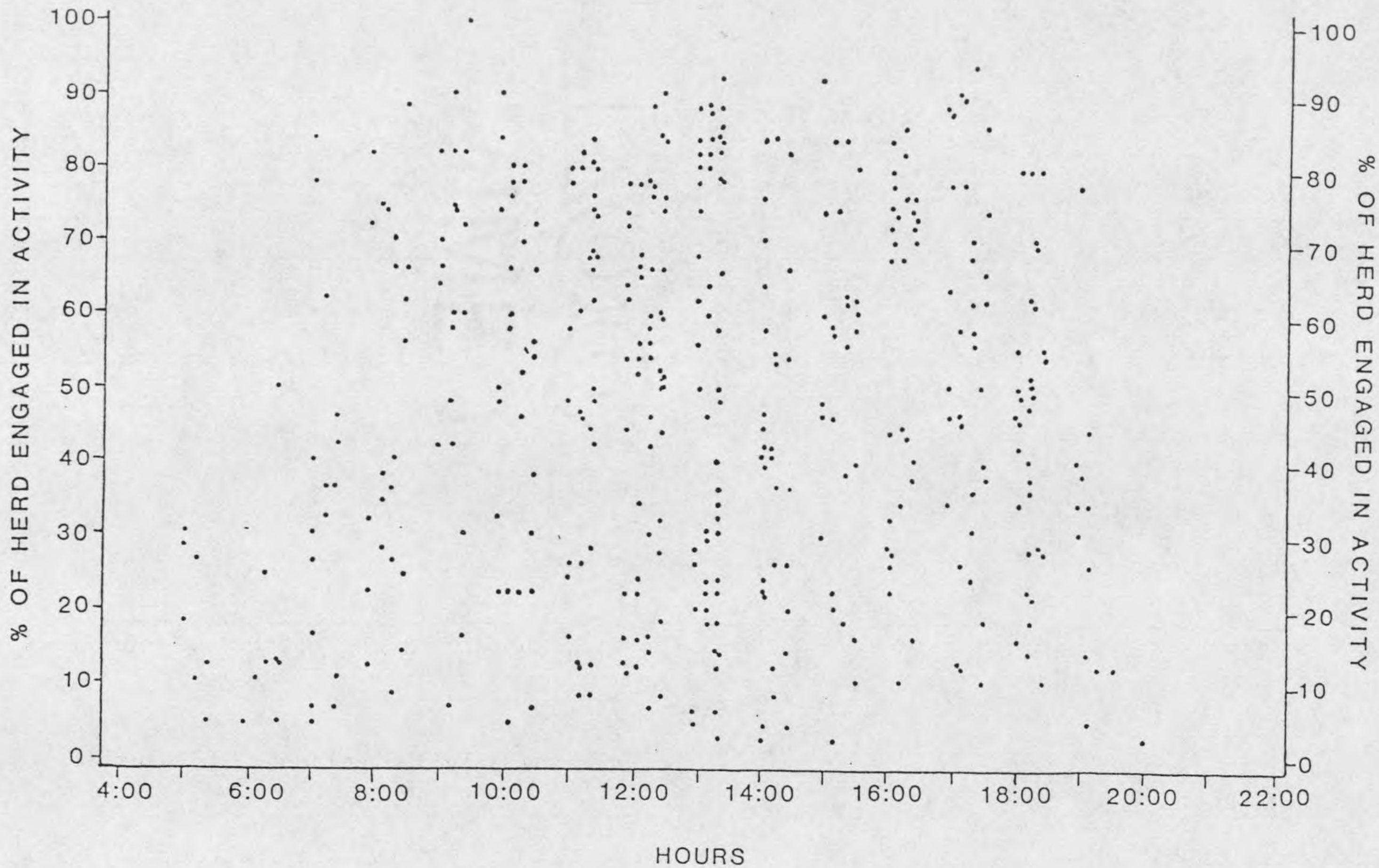

Figure 61. Resting activity for June.

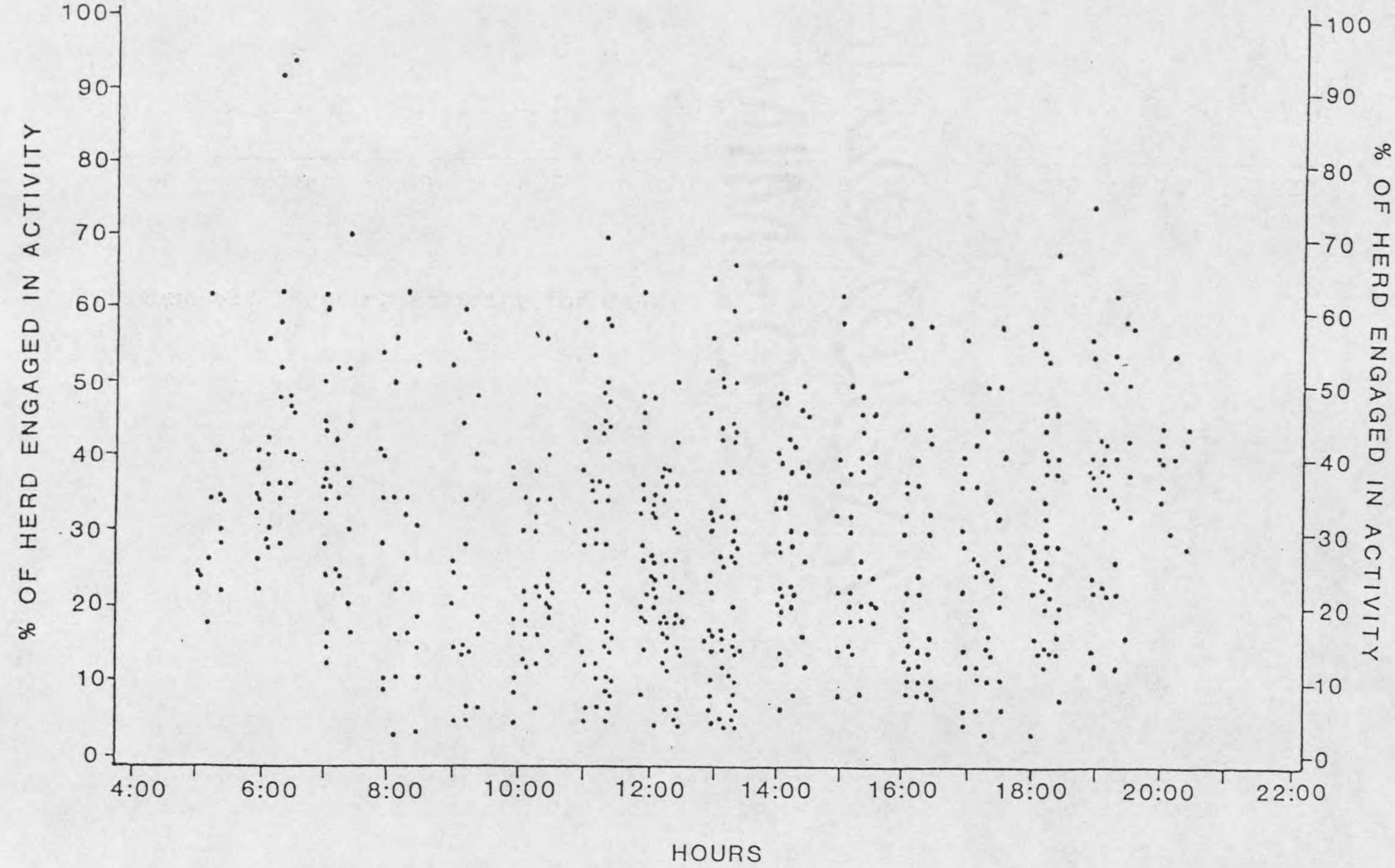

Figure 62. Other activity for June.

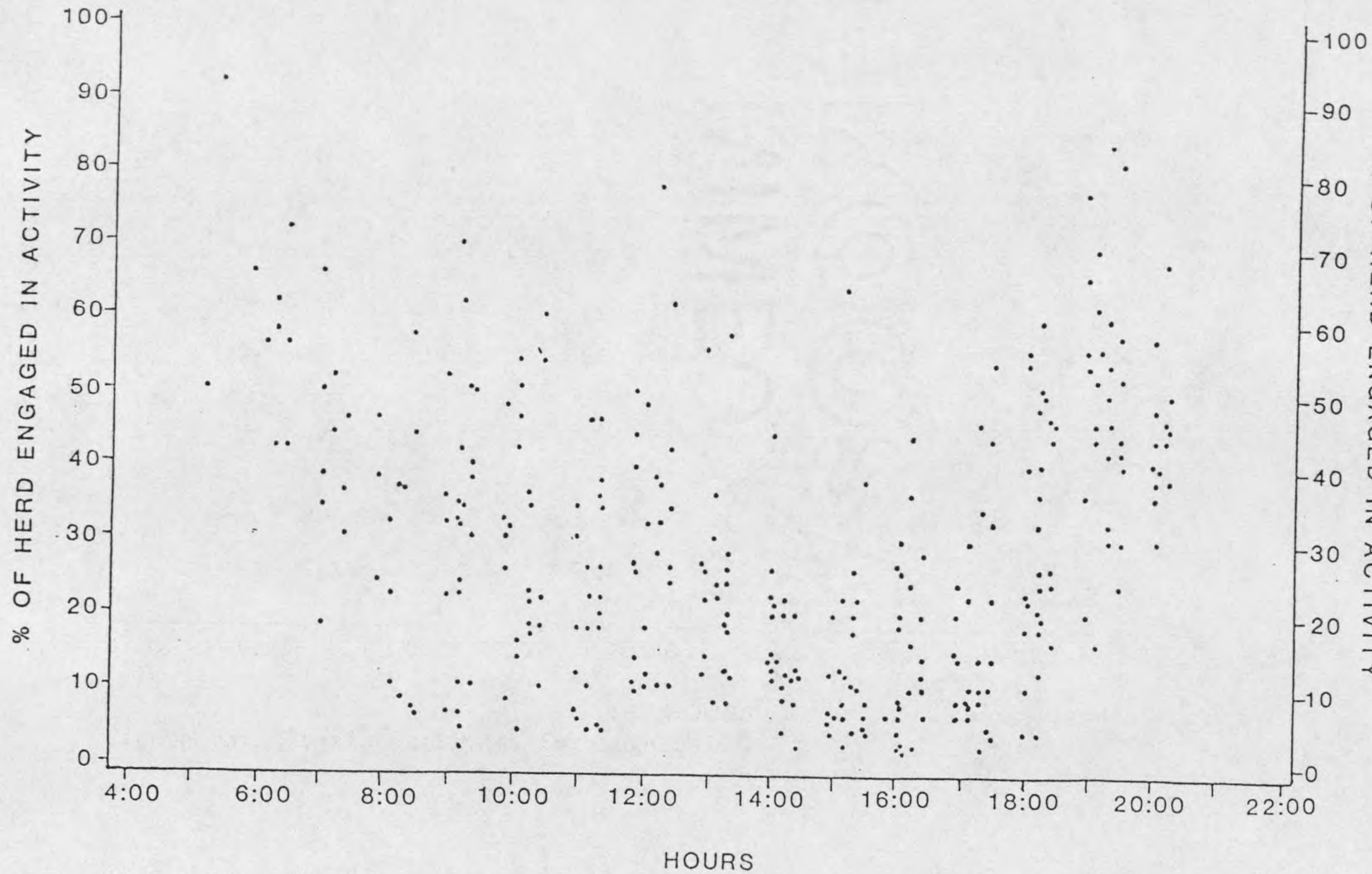

Figure 63. Grazing activity for August 1.

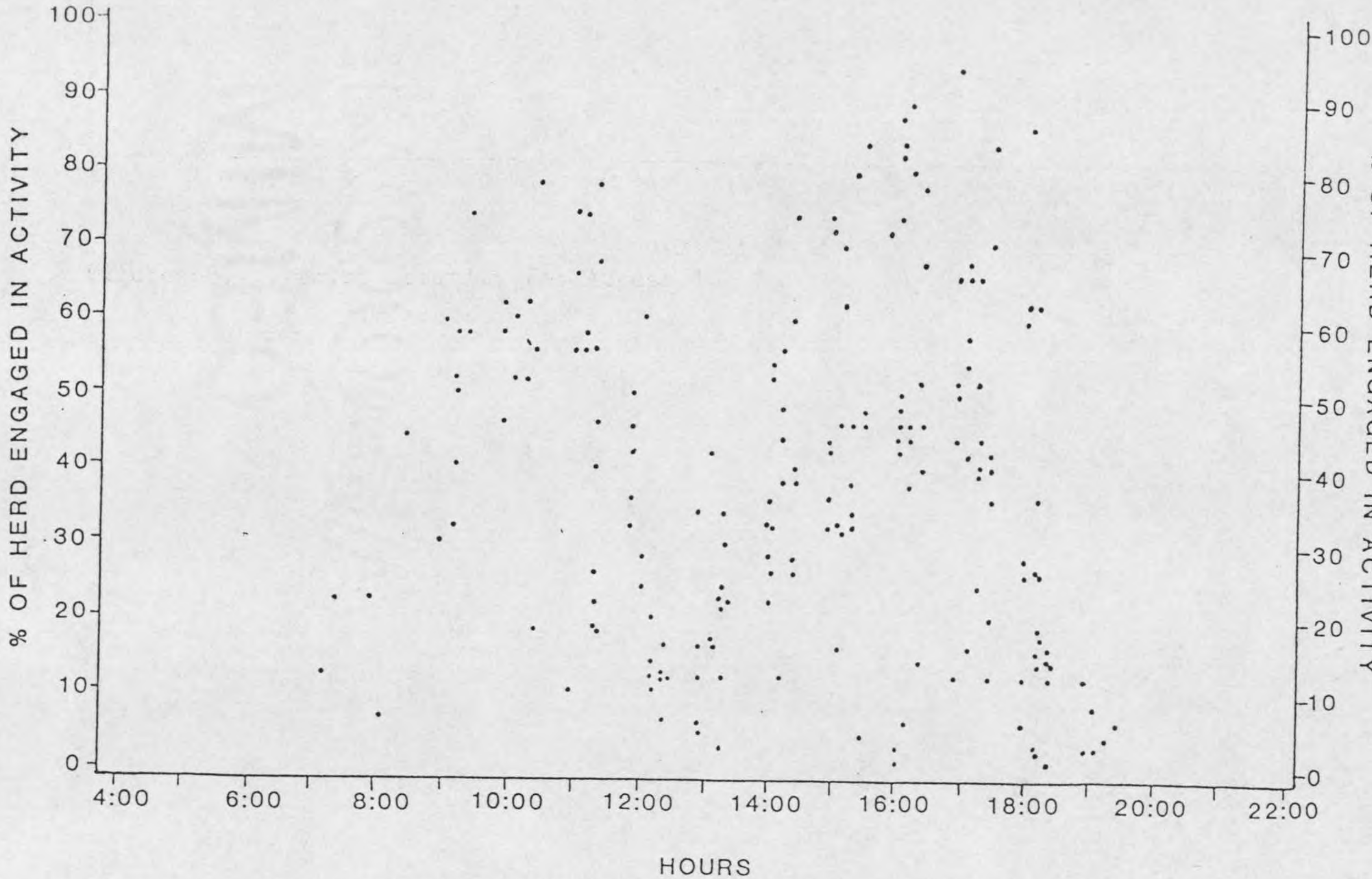

Figure 64. Resting activity for August 1.

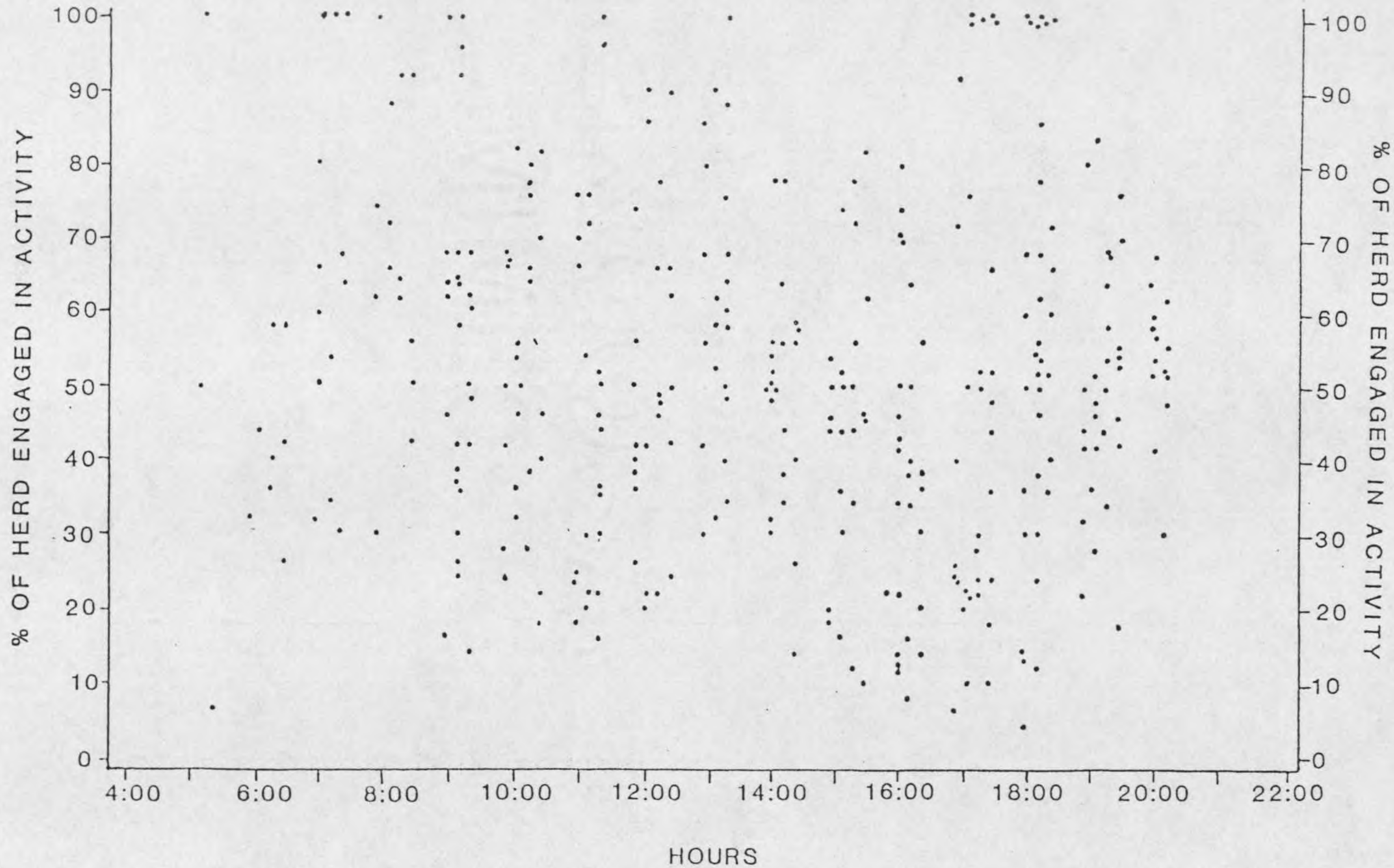

Figure 65. Other activity for August 1.

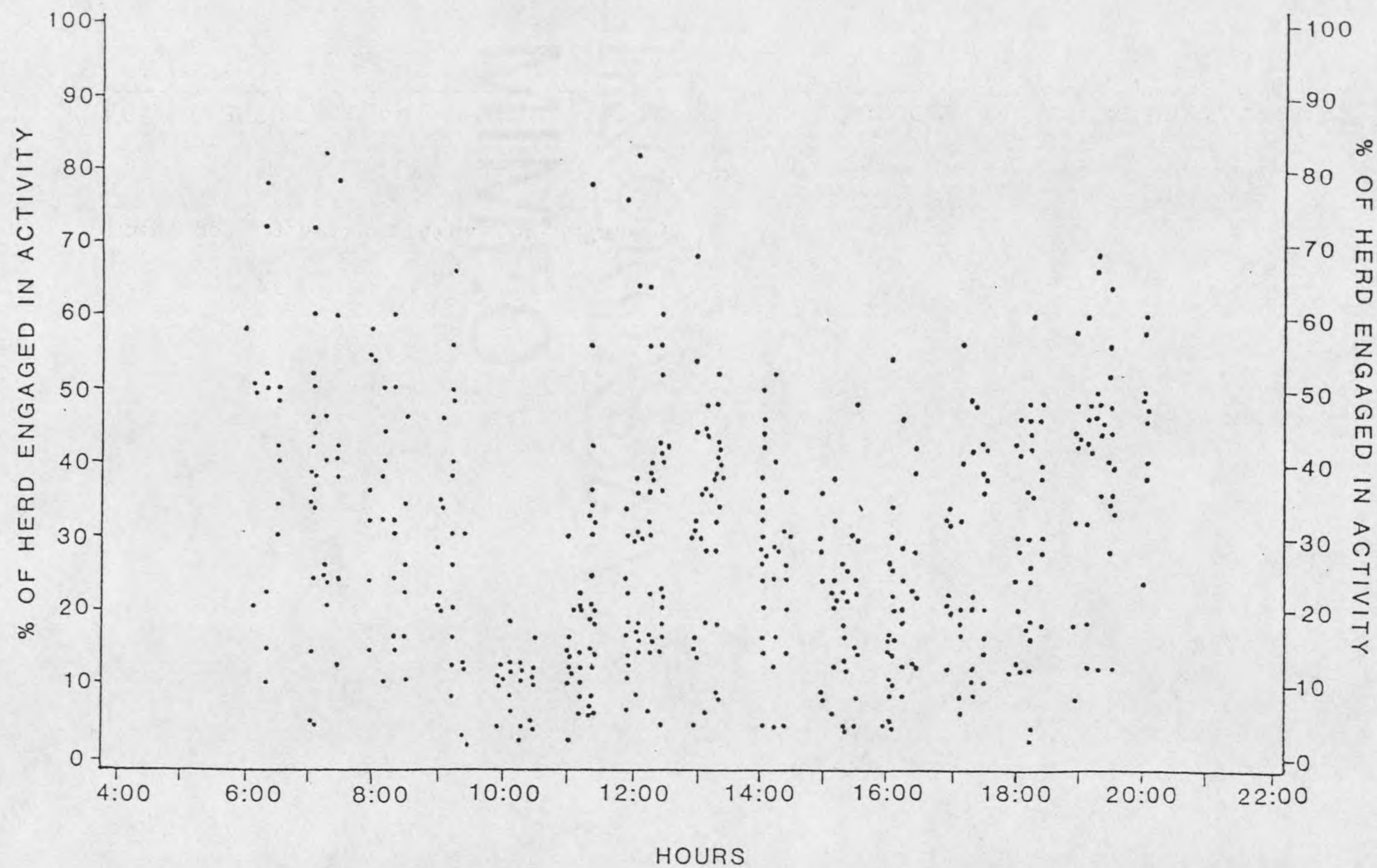

Figure 66. Grazing activity for August 2.

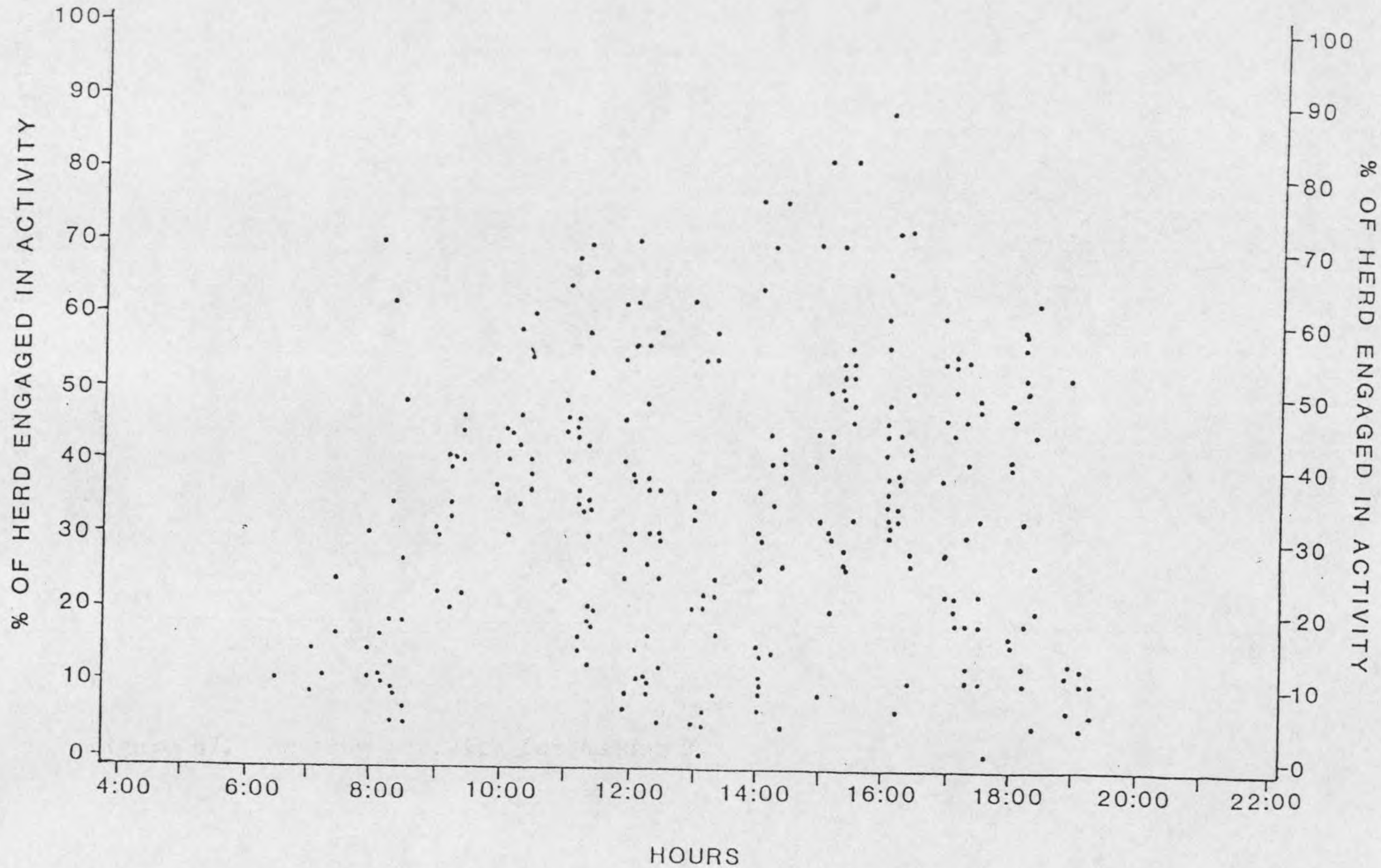

Figure 67. Resting activity for August 2.

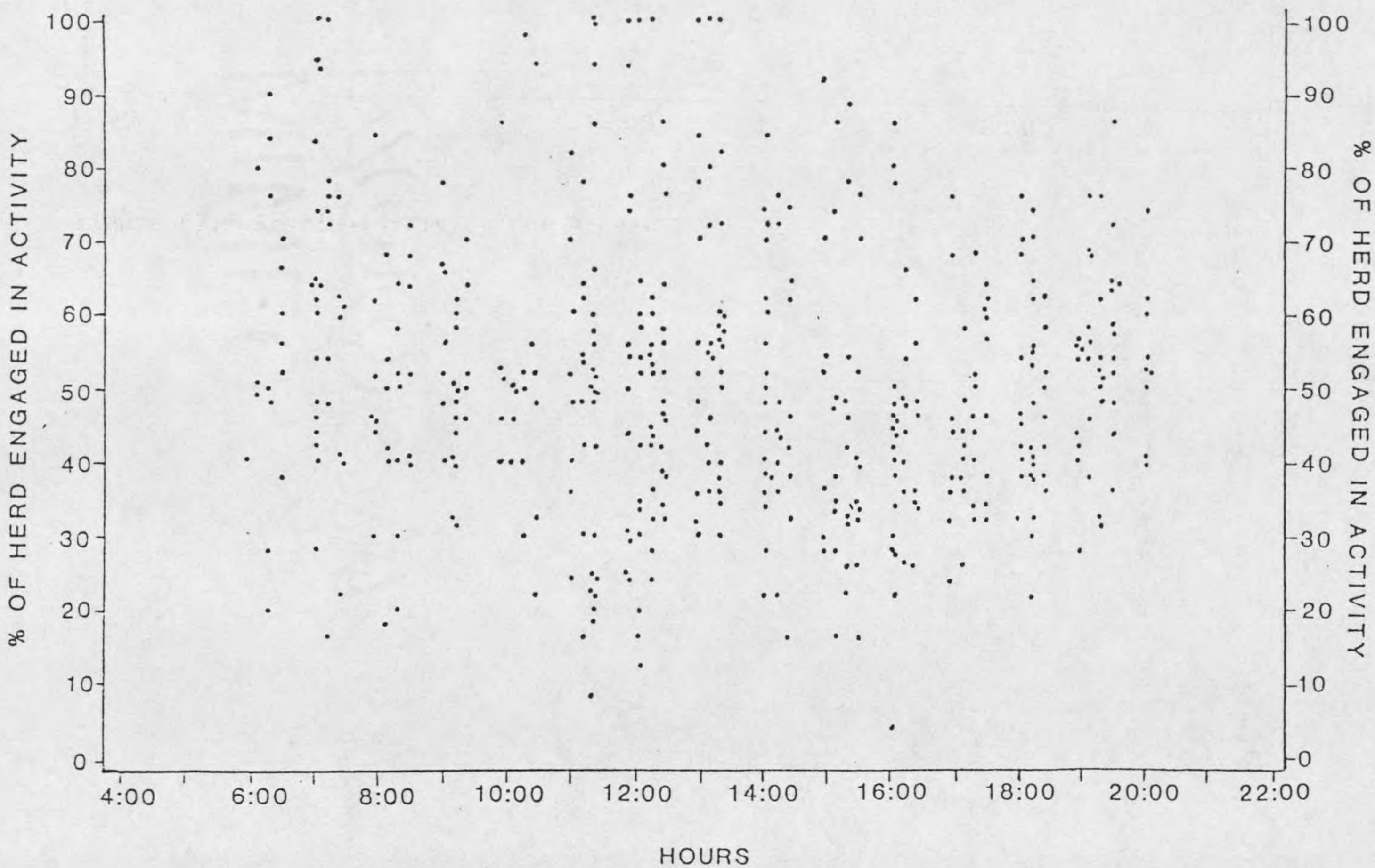

Figure 68. Other activity for August 2.

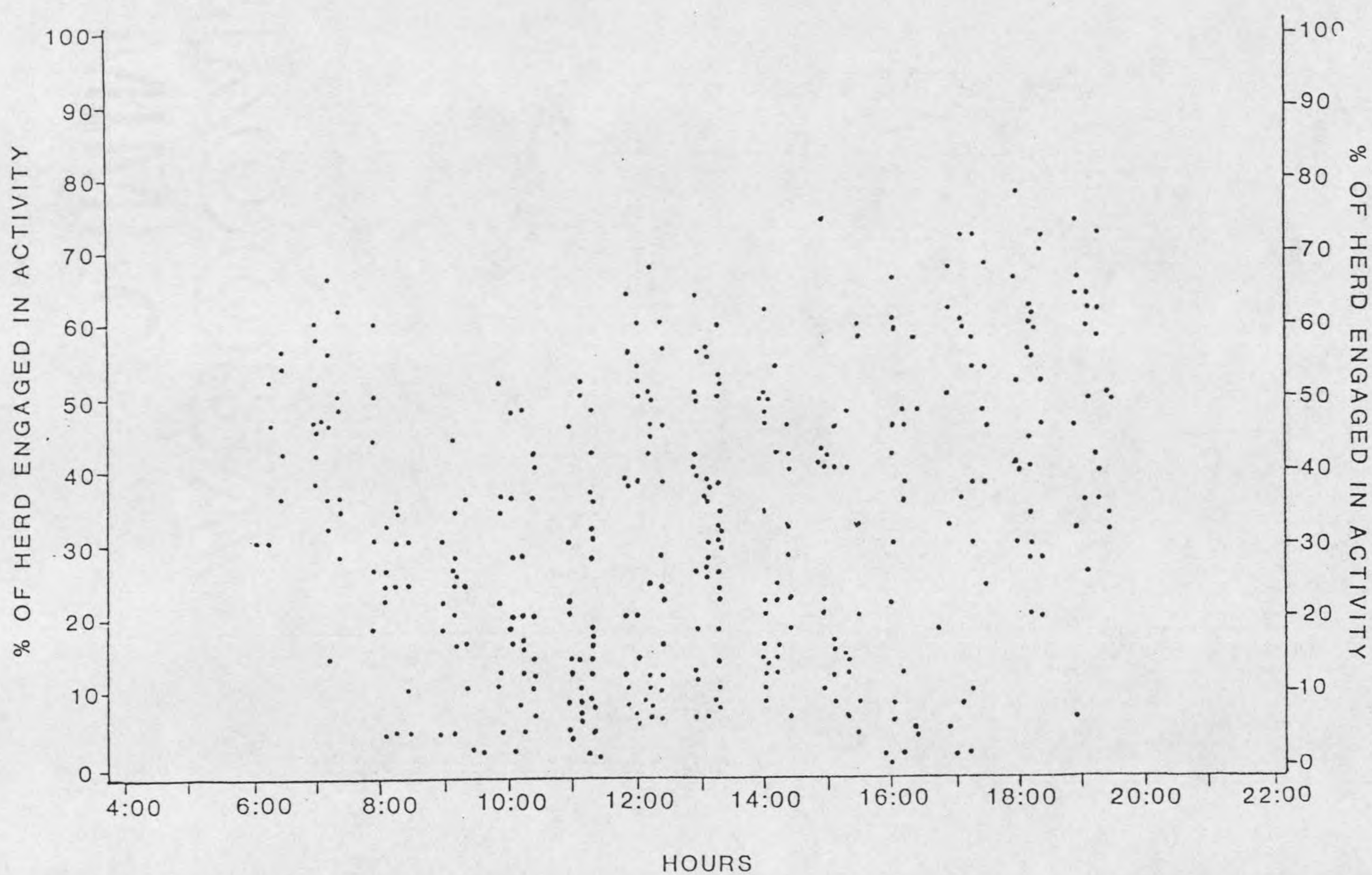

Figure 69. Grazing activity for September 1.

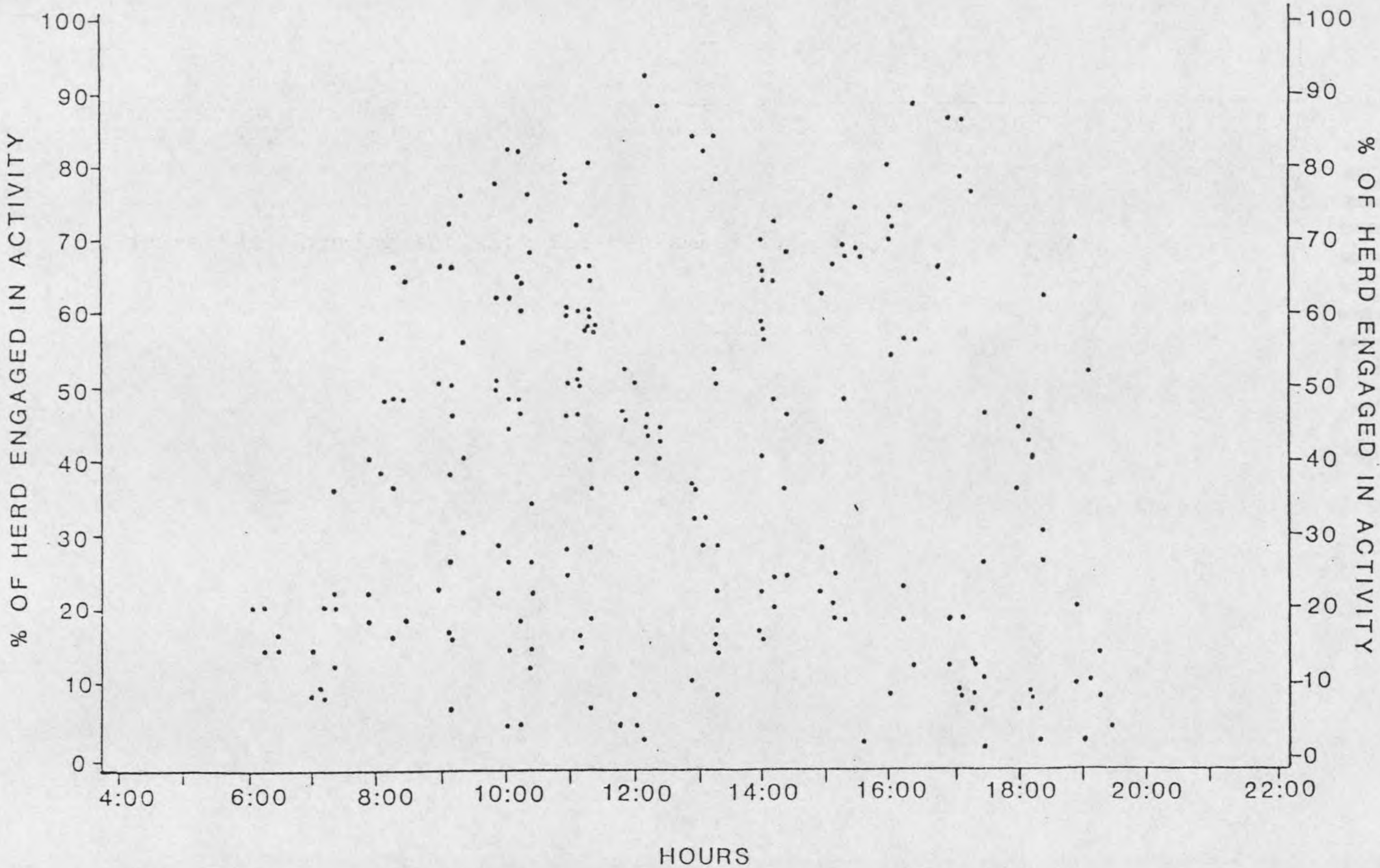

Figure 70. Resting activity for September 1.

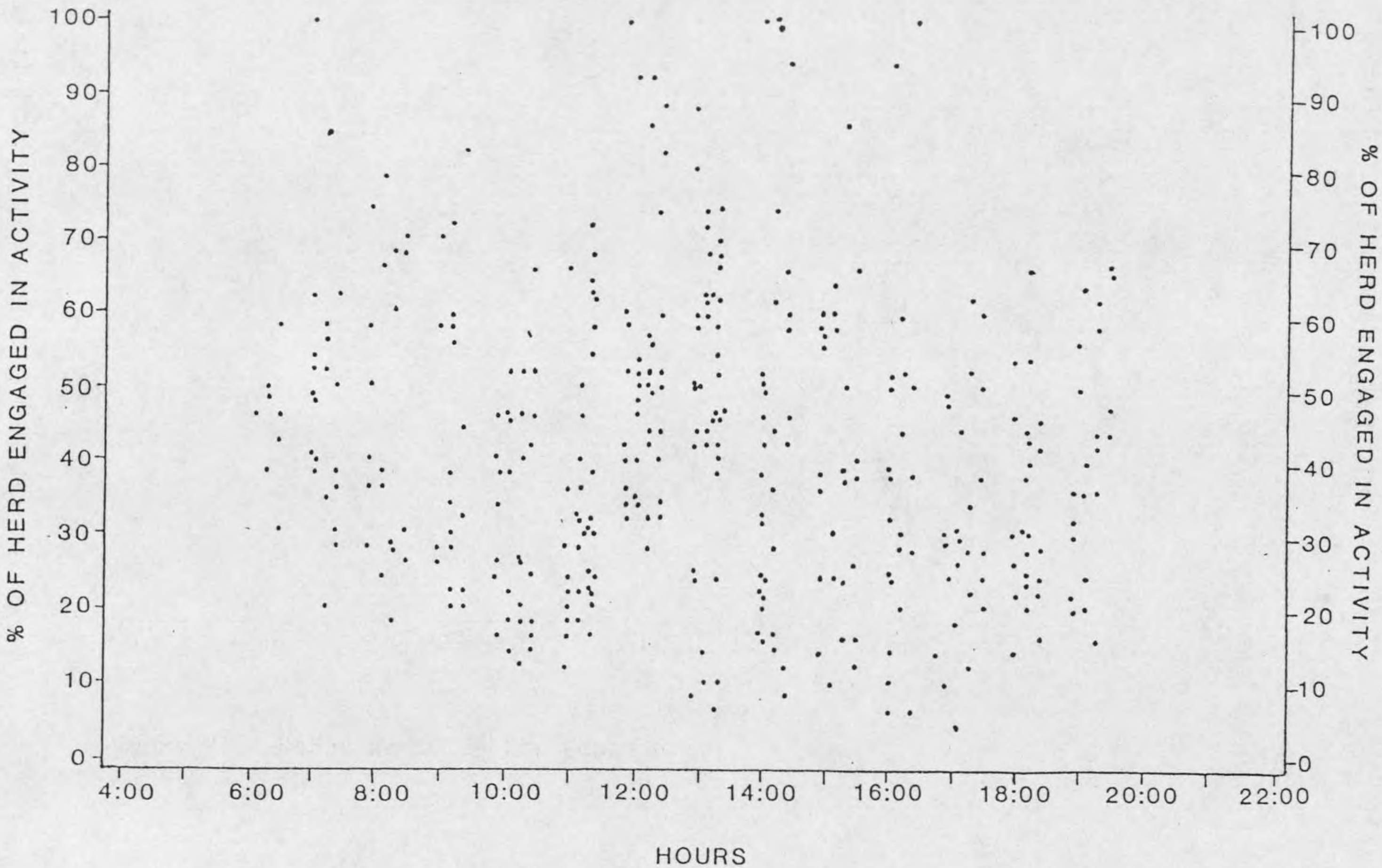

Figure 71. Other activity for September 1.

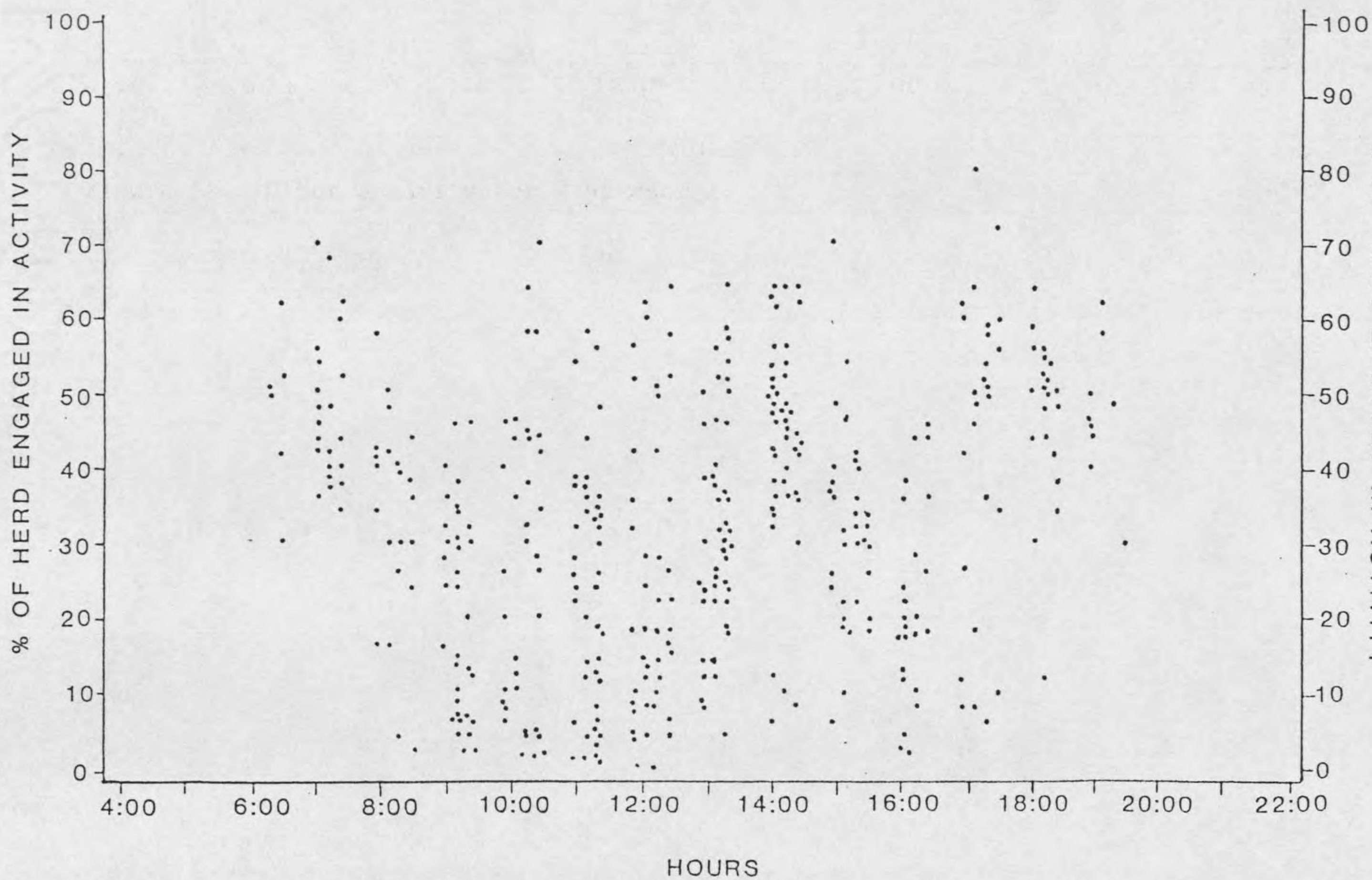

Figure 72. Grazing activity for September 2.

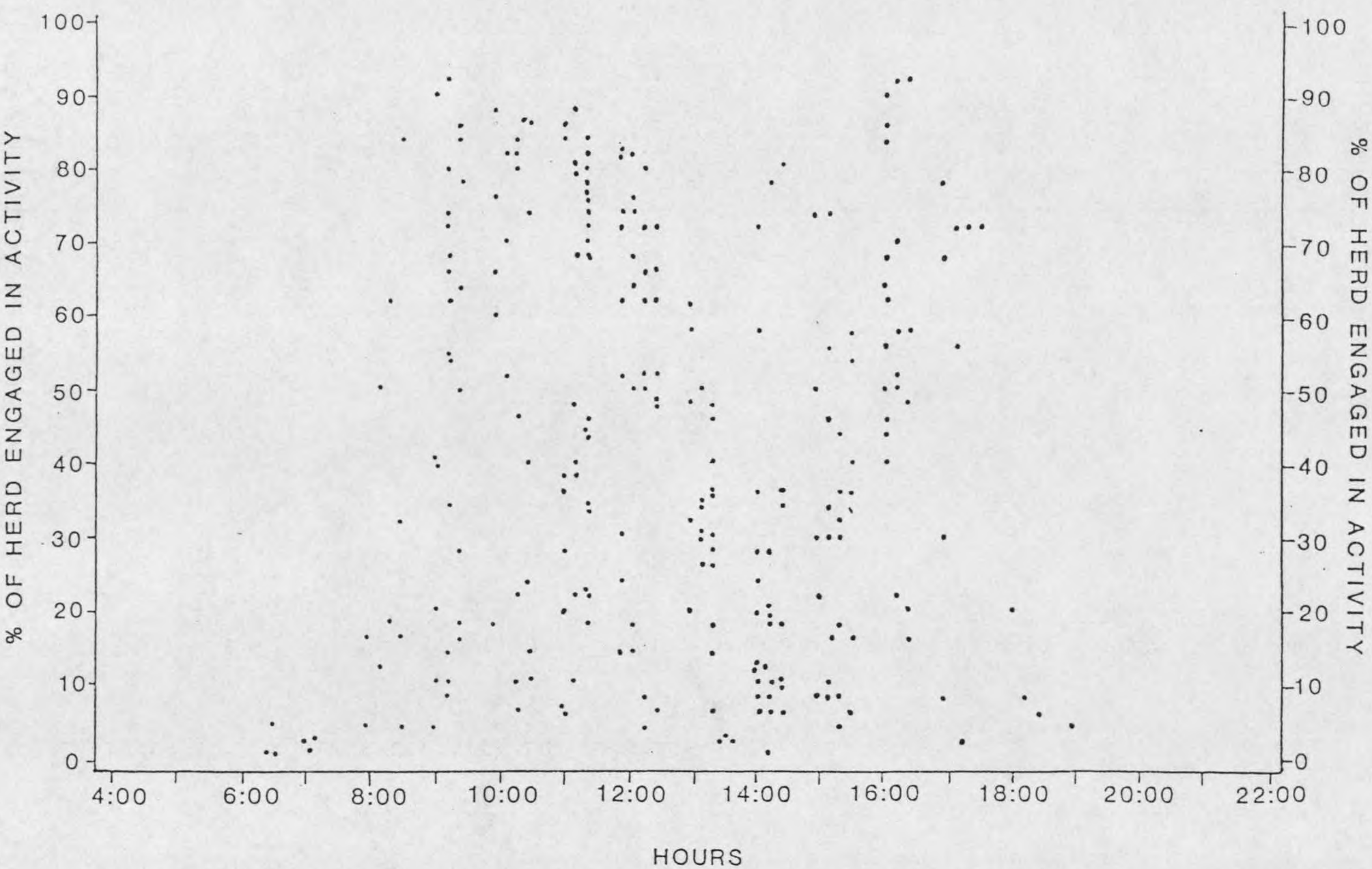

Figure 73. Resting activity for September 2.

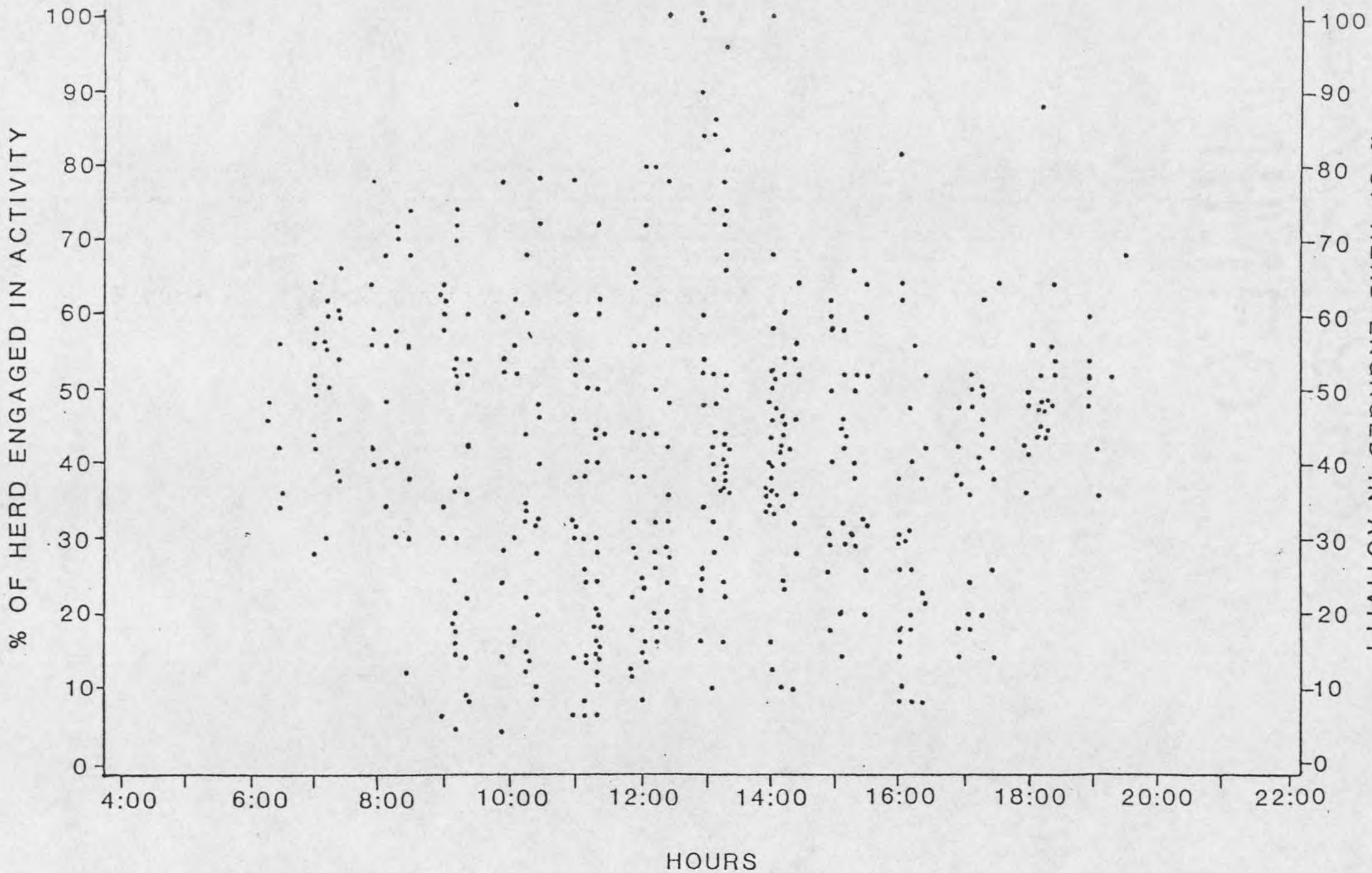

Figure 74. Other activity for September 2.

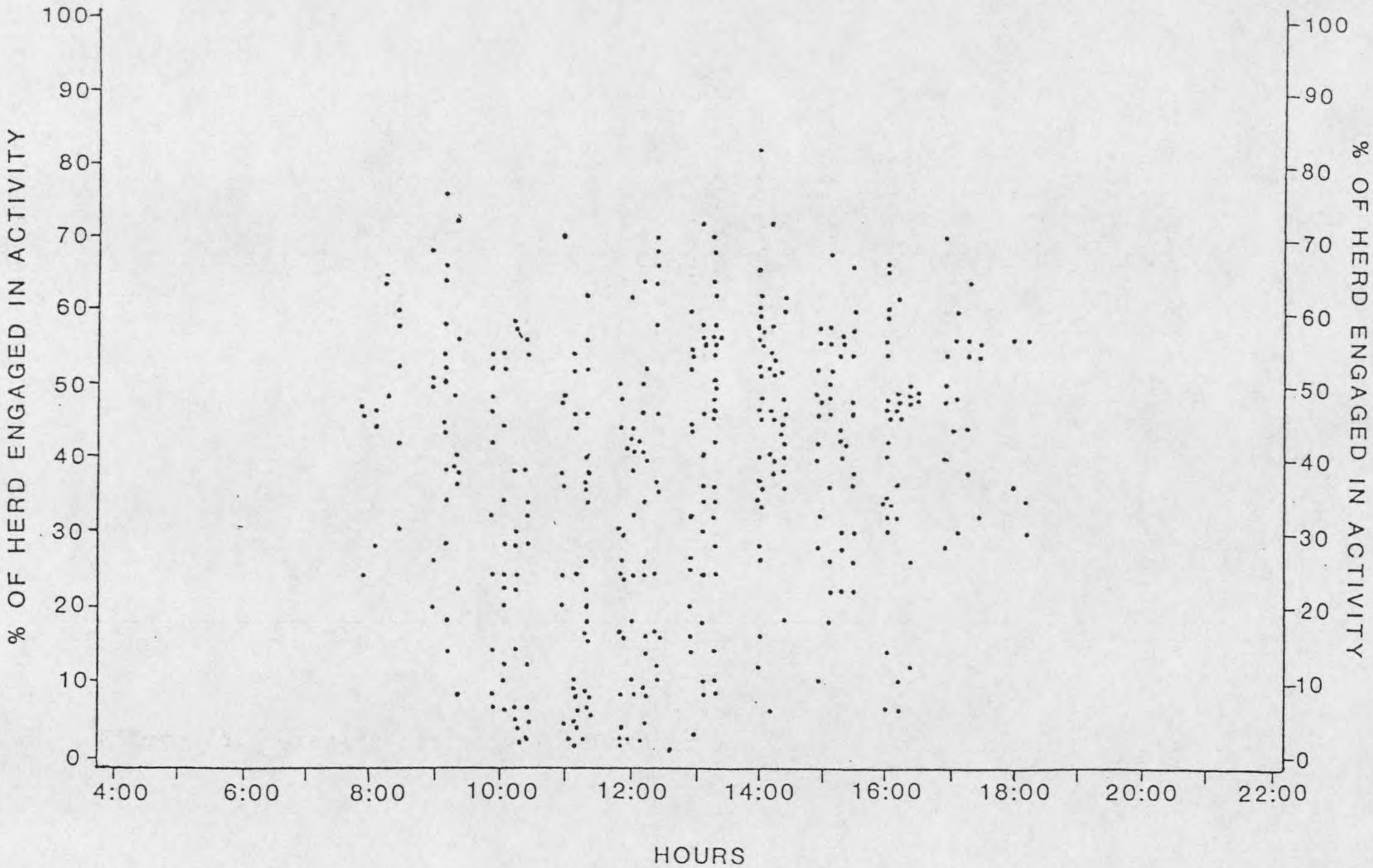

Figure 75. Grazing activity for October 1.

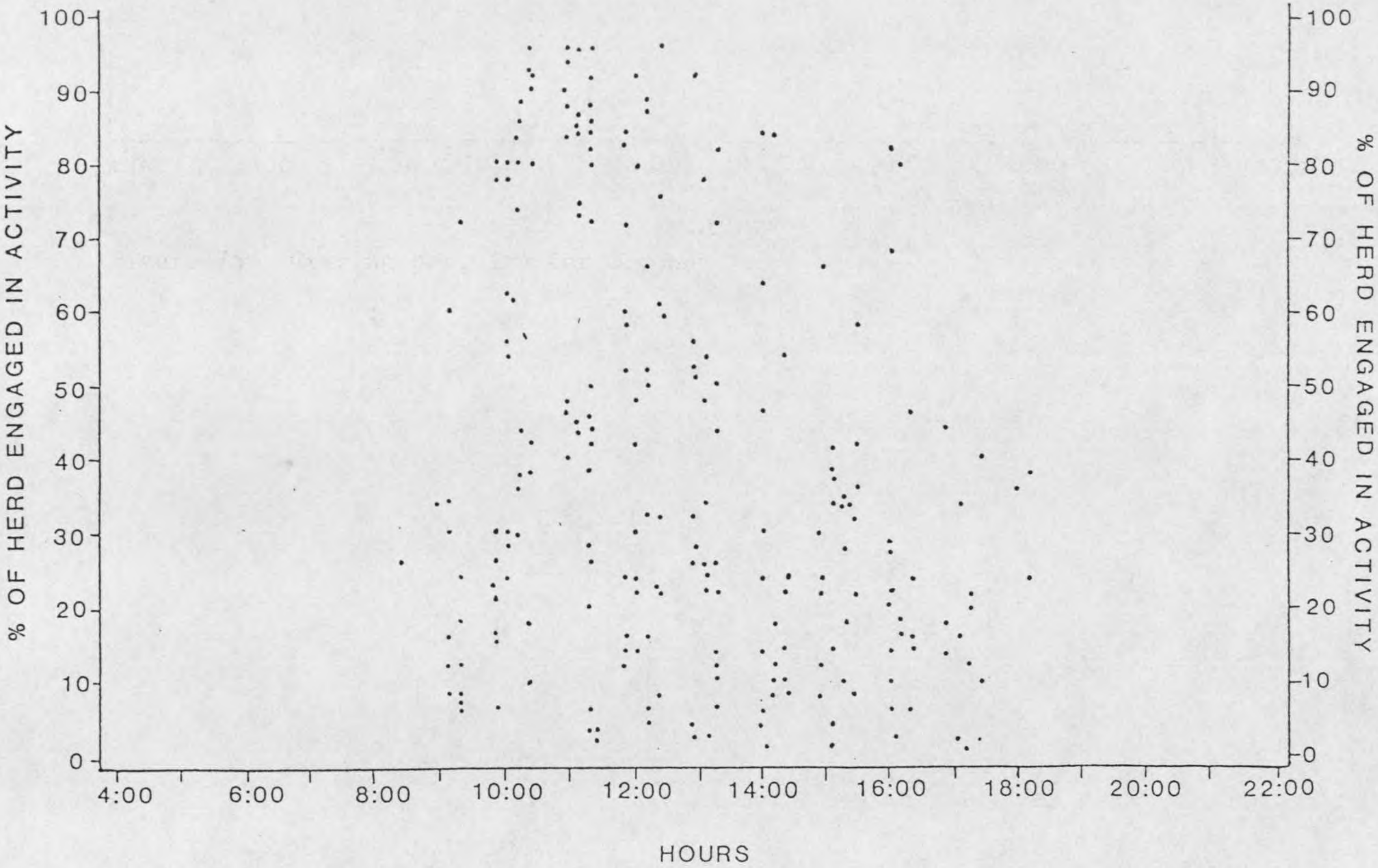

Figure 76. Resting activity for October 1.

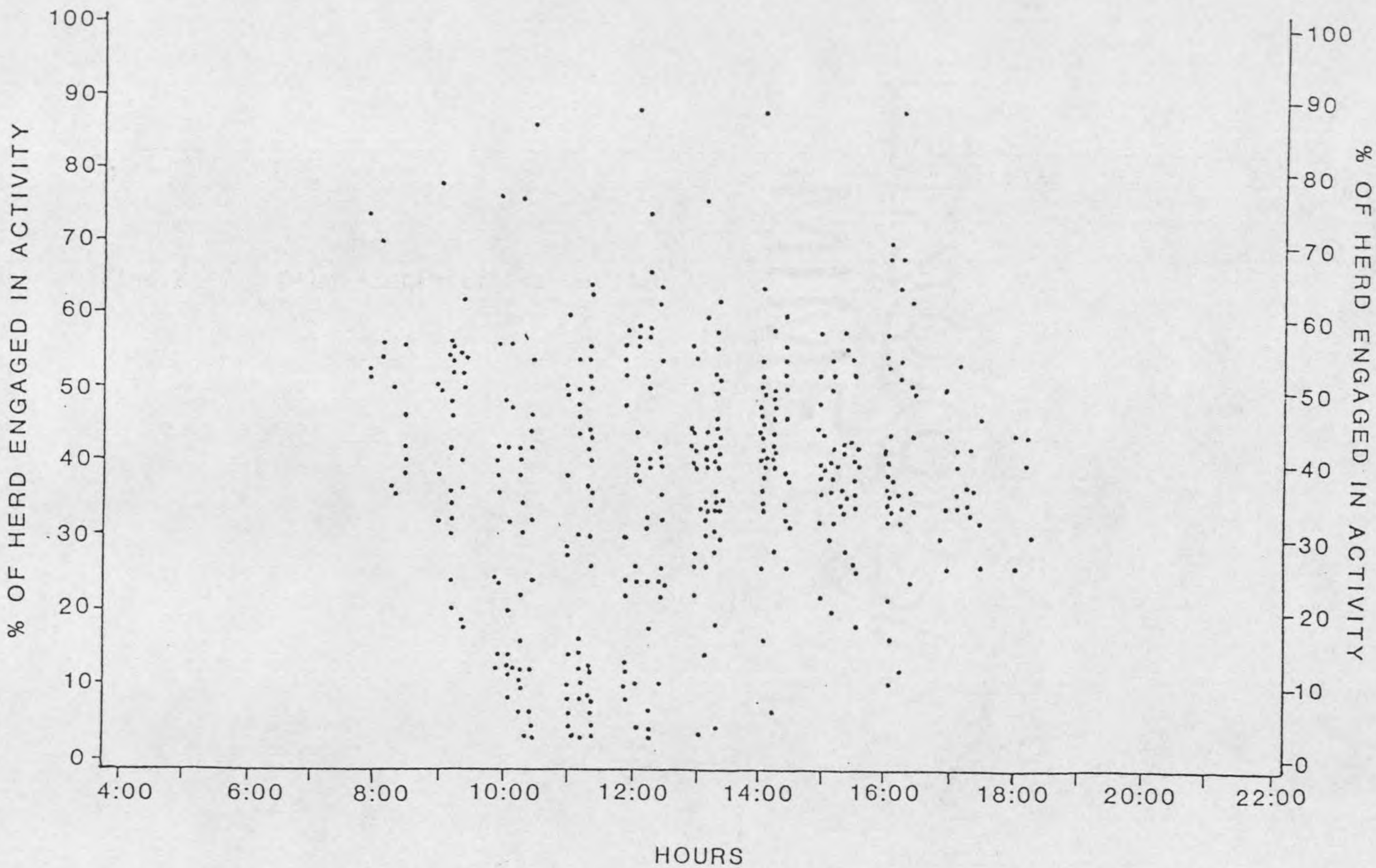

Figure 77. Other activity for October 1.

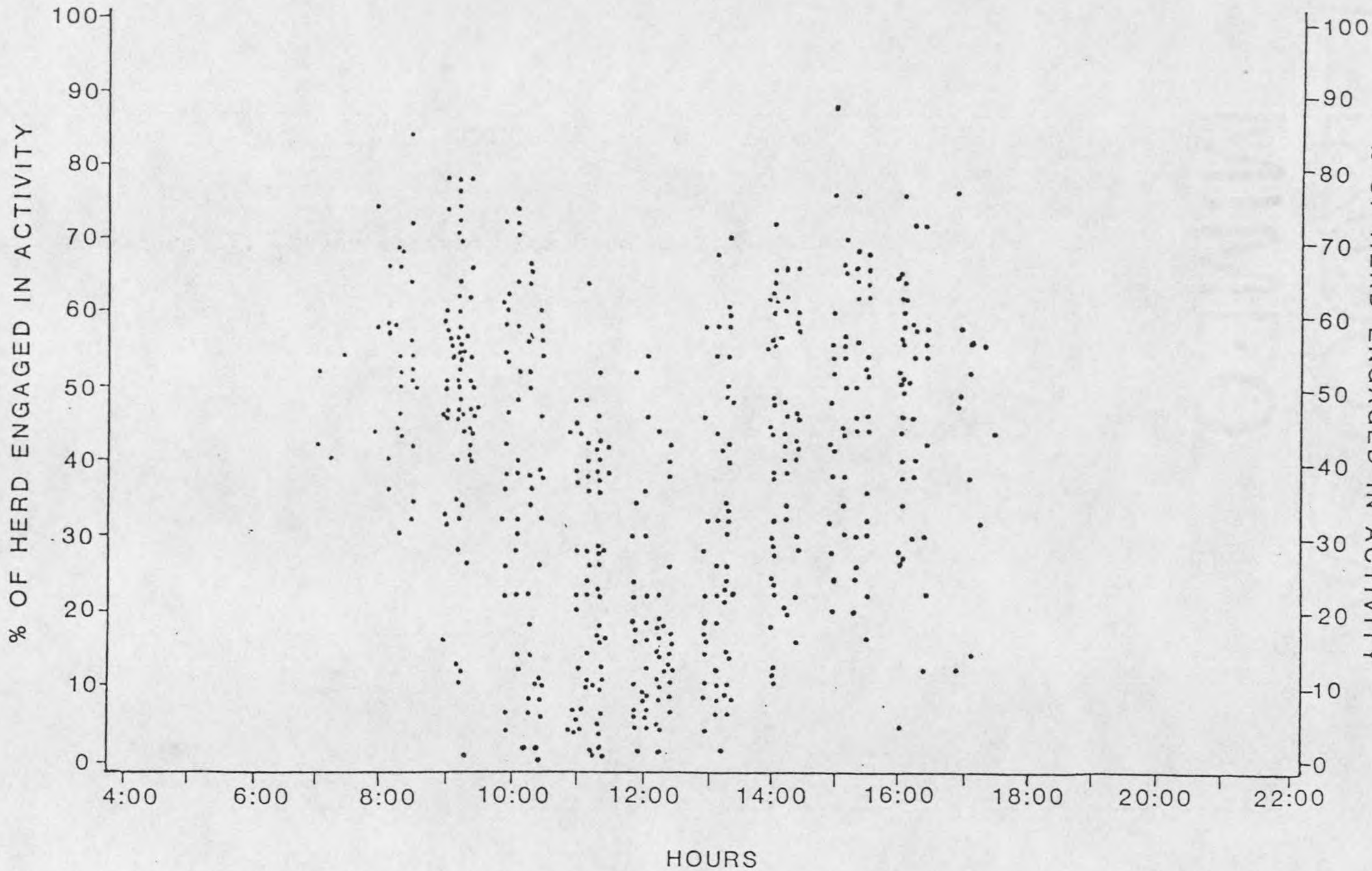

Figure 78. Grazing activity for October 2.

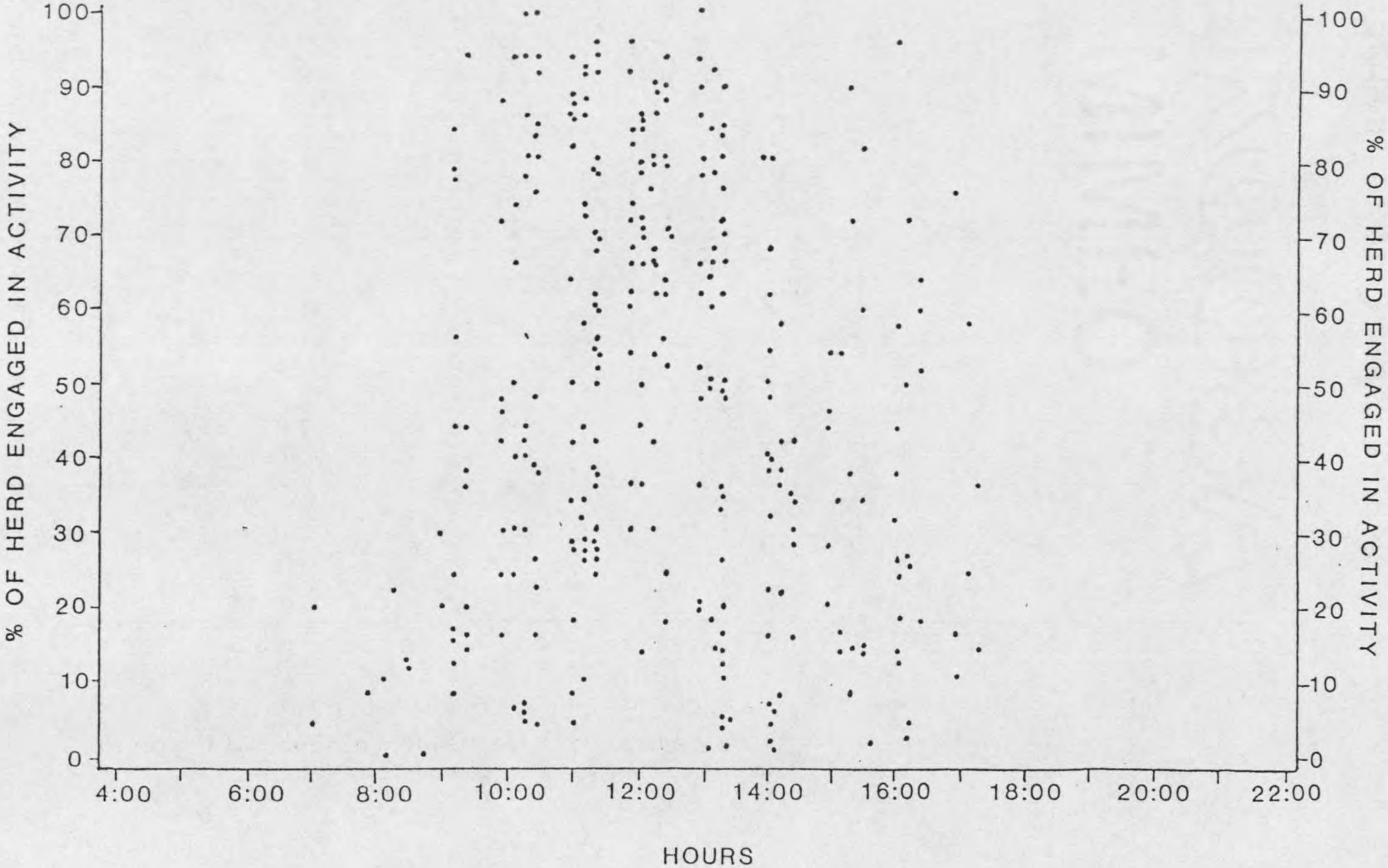

Figure 79. Resting activity for October 2.

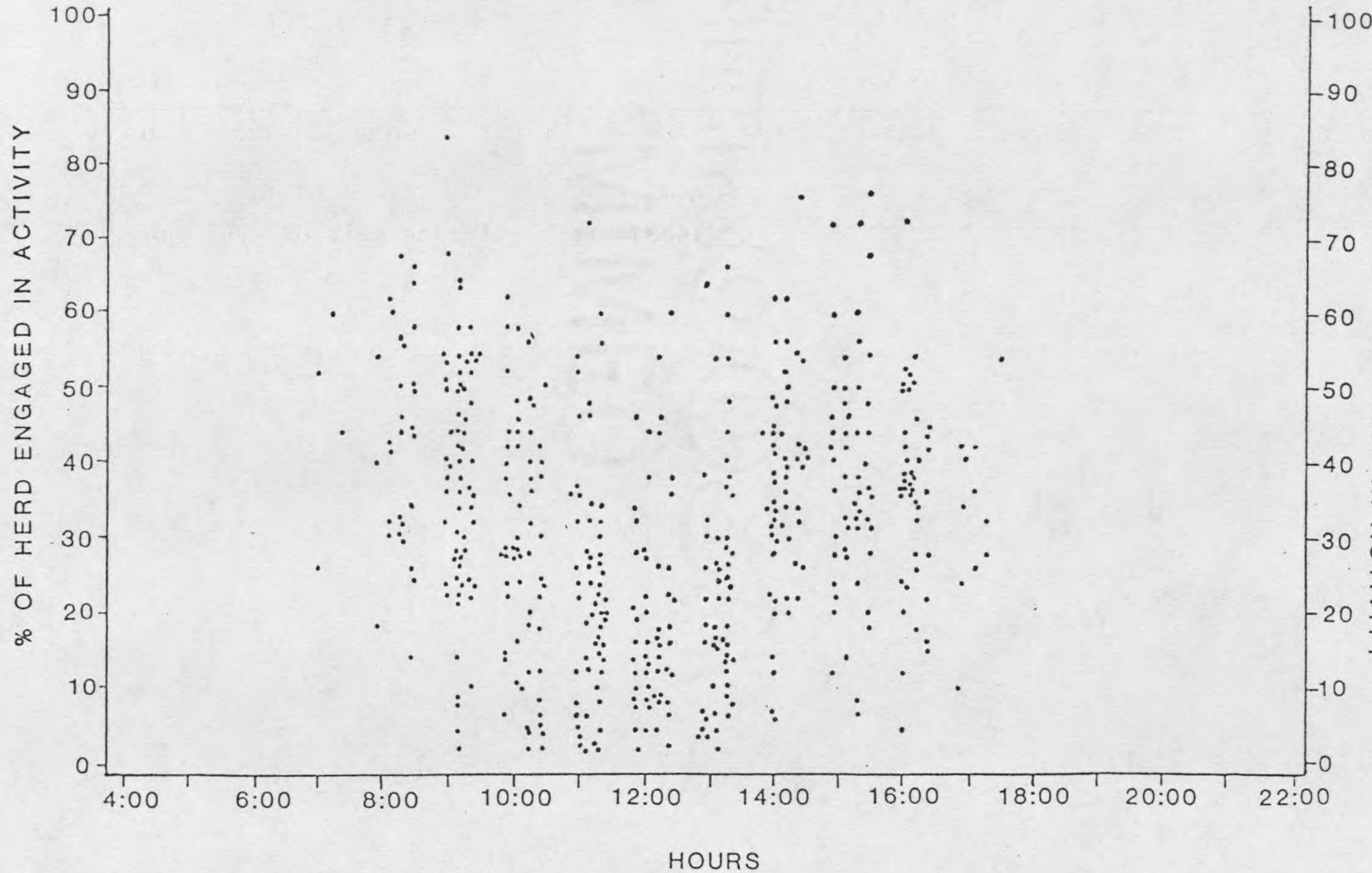

Figure 80. Other activity for October 2.

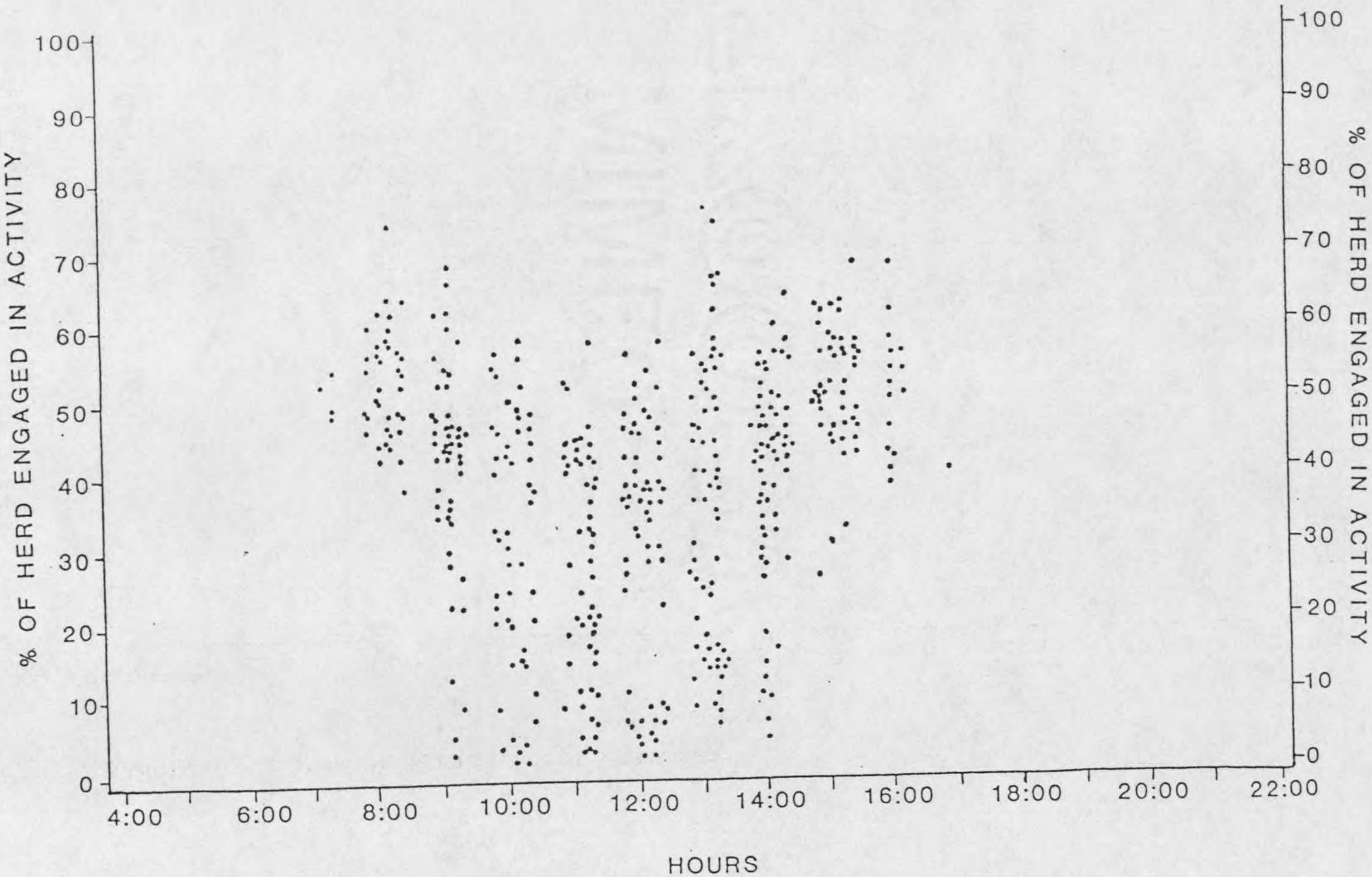

Figure 81. Grazing activity for November.

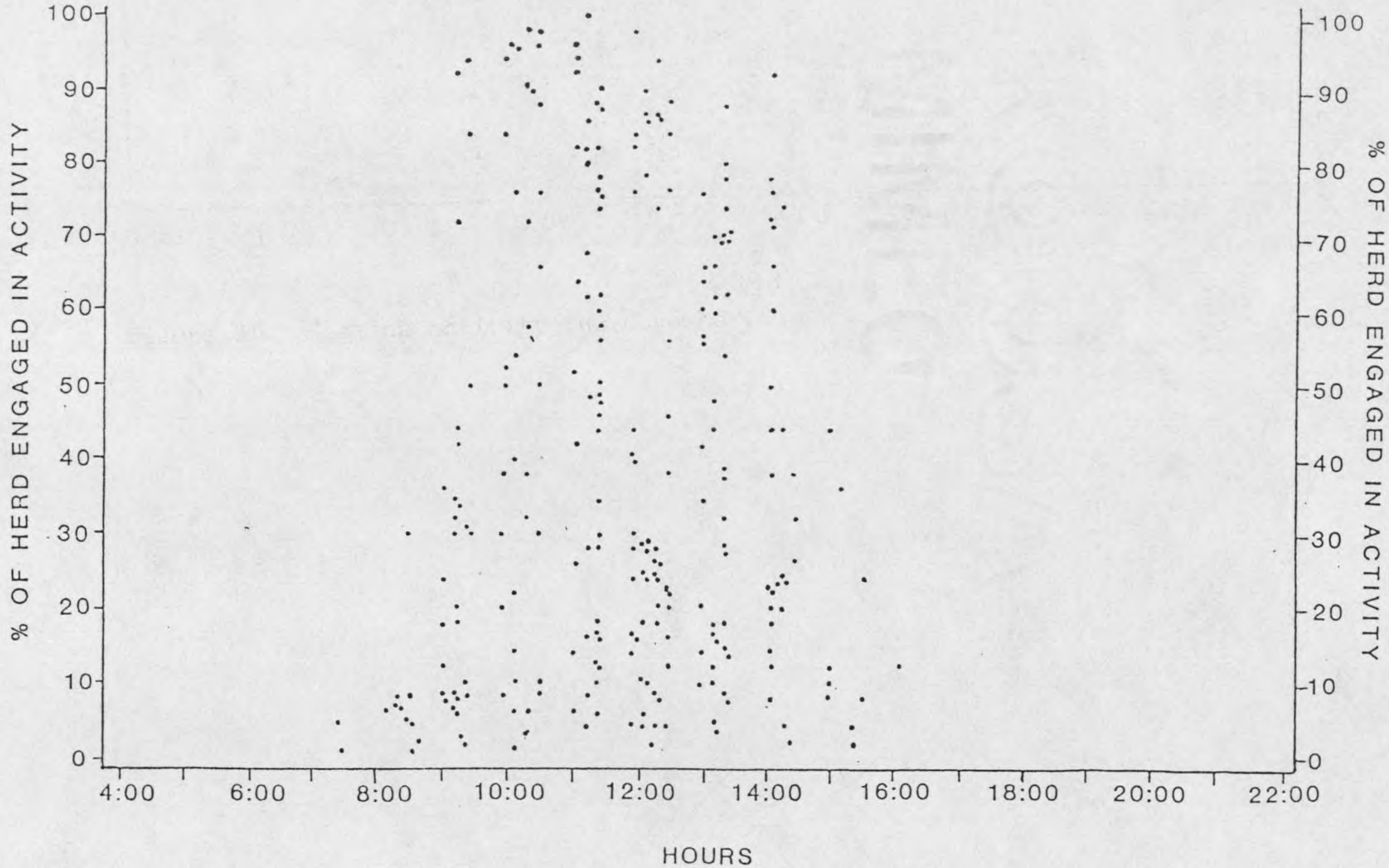

Figure 82. Resting activity for November.

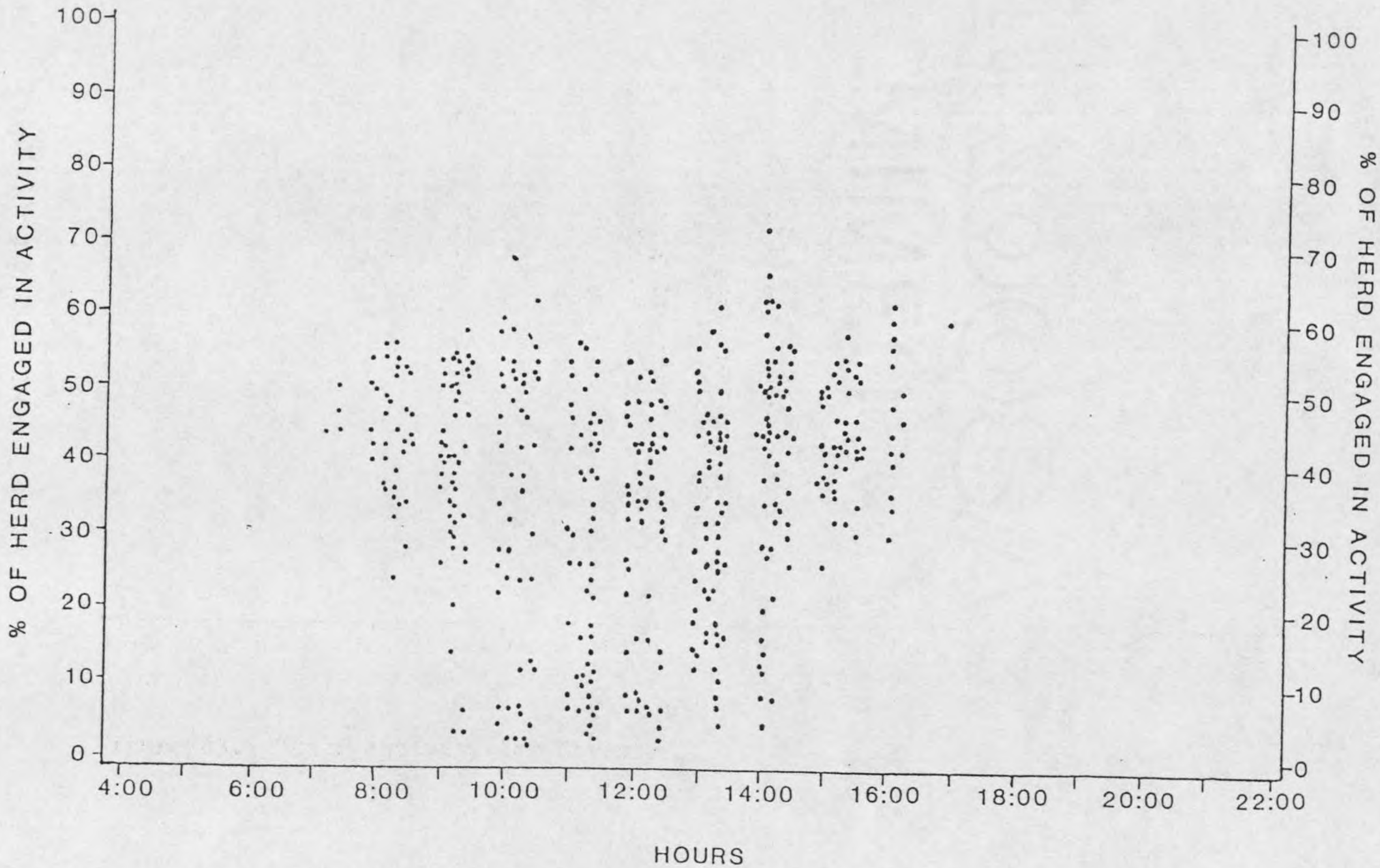

Figure 83. Other activity for November.

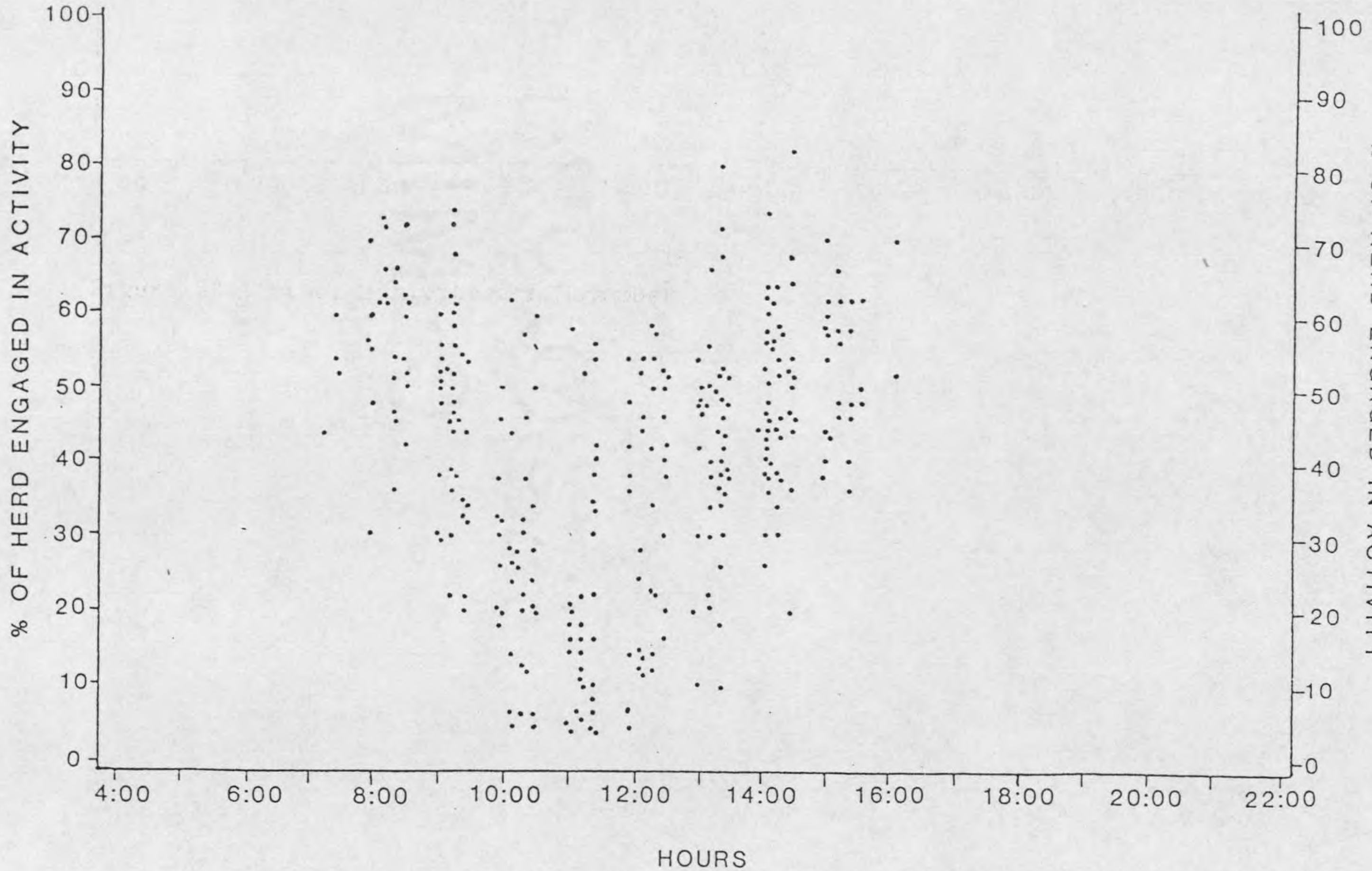

Figure 84. Grazing activity for December.

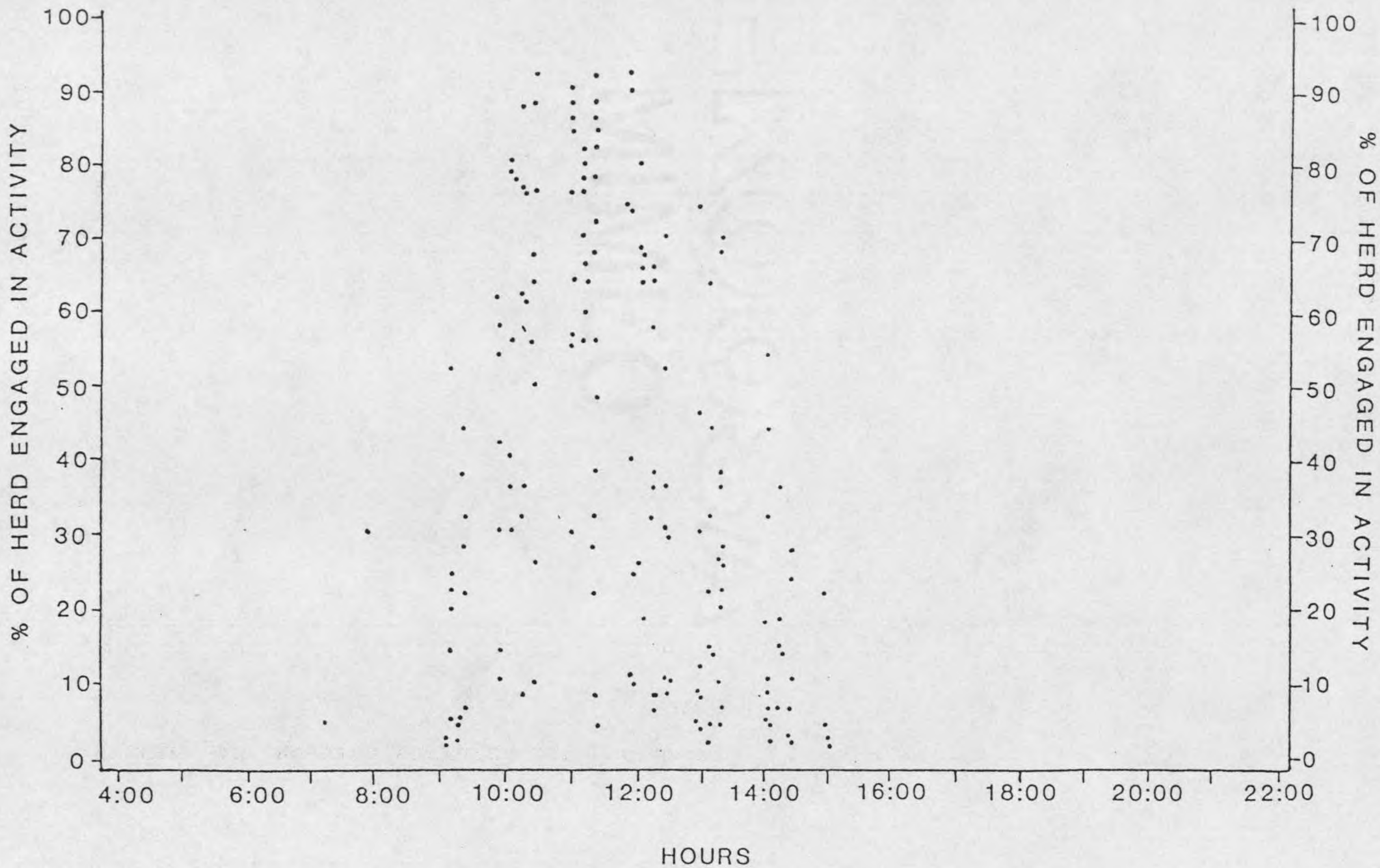

Figure 85. Resting activity for December.

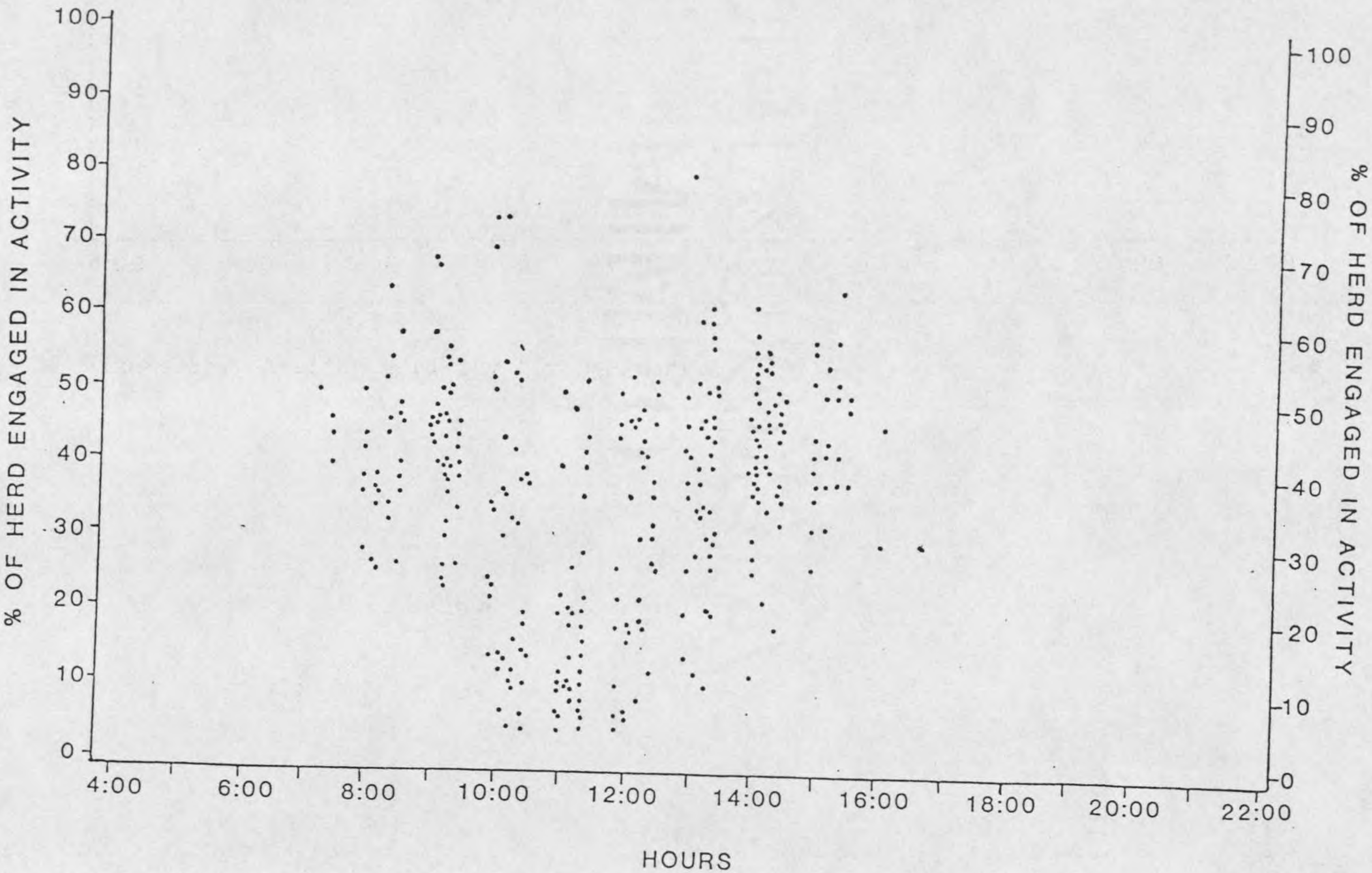

Figure 86. Other activity for December.