

SOCIAL STRUCTURE OF ANDEAN DEER (HIPPOCAMELUS ANTISENSIS) IN
SOUTHERN PERU

by

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ABSTRACT

The taruca (Hippocamelus antisensis) is the only deer species found permanently in rugged mountainous habitat above the tree line. I studied the social organization of this deer in relation to its reproductive cycle and habitat use in the high Andes of southern Peru. Tarucas bred seasonally. Most fawns were observed towards the end of the rainy season between February and April. Mating was most common in June, during the dry season, and antler-shedding in males occurred in September/October, at the onset of the rainy season. The deer lived in social groups and, unlike most seasonally breeding cervids, formed large mixed-sex groups nearly all year. During the birth season, however, all pregnant females segregated to form female associations. At this time, adult males were found equally in mixed-sex groups or in small all-male groups. These groups differed in their habitat use. Female groups used areas of higher elevation, steeper slopes, and greater rock-cover than either male or mixed-sex groups. I suggest that selection of more rugged and concealed habitats by lactating females is primarily an antipredator strategy to reduce risk of predation on fawns. Tarucas are compared with other social Cervidae and with their ecological counterpart: the mountain Caprinae. The social structure of Hippocamelus resembles that of wild goats (Capra spp) and other Caprinae of similar ecology but it differs from that of wild sheep (Ovis spp).

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GENERAL INTRODUCTION

Most of our knowledge on relationships between social organization and habitat among the Cervidae comes from studies of species in temperate and sub-tropical habitats in the Northern hemisphere (Clutton-Brock et al., 1982; Eisenberg, 1981; Hirth, 1977; LaGory, 1985; Maublanc et al., 1985; Schaller, 1967; Takatsuki, 1983). An important group of neotropical species has been largely neglected (Roe, 1974). Of the 16 genera of cervids in the world, 6 (11 extant species) are found in South America (Hershkovitz, 1982). Neotropical deer represent one of the most diversified assemblies of cervids, both in terms of external characteristics and range of habitats occupied. Information on their behavior and ecology should therefore aid our general understanding of social systems among the Cervidae.

This study focuses on a neotropical species, the Andean deer or taruca (Hippocamelus antisensis). The taruca is a medium-sized deer that inhabits the high Andes between northern Argentina and Chile and northern Peru (Cabrera, 1961; Grimwood, 1969; IUCN, 1982). Descriptions of its external characteristics are found in Fradrich (1978), Pearson (1951), Roe (1974), Roe and Rees (1976), and Whitehead (1972). Found at elevations of up to 5,200 m, the taruca is the only deer that lives permanently in high mountainous habitat above the treeline. Its ecological range does not overlap that of other cervids. Its closest relative, the huemul, Hippocamelus bisulcus, is found at lower elevations in central Chile and

neighboring areas of Argentina (Povilitis, 1978). Thus, H. bisulcus and H. antisensis have allopatric distributions. Only in some areas does the lower limit of taruca habitat appear to be contiguous with that of white-tailed deer, Odocoileus virginianus (Jungius, 1974; R. Marin, pers. comm.). The taruca is thus ecologically unique among cervids, inhabiting a niche usually occupied by mountain sheep and goats in other parts of the world (Geist, 1971; Schaller, 1977). Its unusual habitat may reflect the fact that mountain Caprinae have never become established in the neotropics. Indeed, tarucas seem superbly adapted to rugged mountainous terrain. The animals are stockily built and have short legs and very short hooves (Fradrich, 1978; Roe and Rees, 1976). Some observers have noted the deer's agility on rocky terrain (Roe and Rees, 1976) and others have remarked on the physical resemblance of Hippocamelus to wild mountain sheep (Fradrich, 1978). These characteristics suggest that Hippocamelus is the ecological counterpart of Caprinae. Despite the unusual niche of the taruca, no detailed studies of the social organization of the species have ever been made.

In this study I describe some aspects of the social organization of a population of Hippocamelus antisensis in the Andes of southern Peru and examine ecological factors influencing its grouping patterns. I consider taruca group dynamics in relation to (1) reproductive phenology (Chapter 1), and (2) habitat use (Chapter 2).

CHAPTER 1. REPRODUCTIVE CYCLE AND GROUPING PATTERNS

1.1 INTRODUCTION

This study deals with some aspects of the social organization of Hippocamelus antisensis. For the purposes of this study, the term social organization refers to the manner in which members of a single-species population are positioned in time and space in relation to one another (Hirth, 1977; Leuthold, 1977). Thus, social organization includes group sizes, sex-age group compositions (group types), and temporal and spatial arrangements among the different individuals or groups. I specifically do not emphasize the behavioral mechanisms underlying social organization. Therefore, I will be concerned with the consequences of social or individual-habitat interactions.

Among ungulates, seasonal changes in social organization are greatly influenced by the reproductive cycle, which in turn is determined by seasonal fluctuations of the environment (Bunnell, 1982; Clutton-Brock et al. 1982; Hirth, 1977; Leuthold, 1977; Nievergelt, 1974; Schaller, 1977; Thompson and Turner, 1982).

Although there is information on seasonal fluctuations of the environment in neotropical highlands (Carpenter, 1976; Franklin, 1983; O.N.E.R.N., 1965; Pearson, 1951; Troll, 1968), little is known about annual reproductive or social patterns of Hippocamelus antisensis (Roe, 1974; Roe and Rees, 1976).

In this chapter I first present basic information on the annual reproductive cycle of the deer. Three aspects are examined: (1) the time and spread of the birth season; (2) the mating period; and (3) the antler cycle in males. Second, I examine the grouping patterns of Hippocamelus associated with the reproductive cycle. Four grouping features are considered: (1) group sizes; (2) types of grouping; (3) distribution of sex-age classes among the different groups; and (4) stability of the groups encountered during the study.

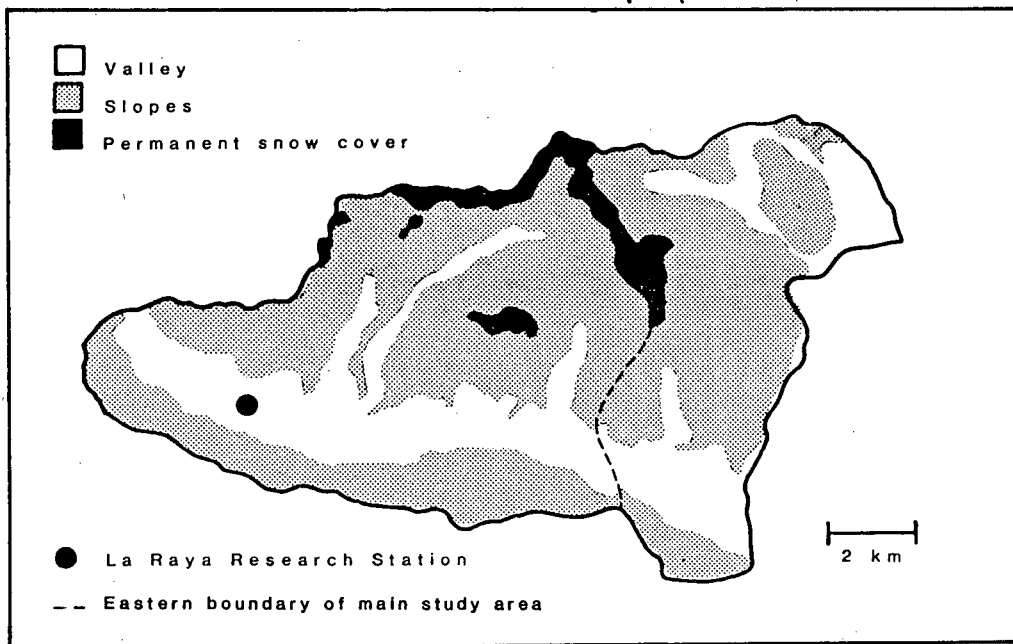
1.2 MATERIALS AND METHODS

1.2.1 Study Area

This study was carried out at La Raya (about 14° 30'S, 70° 58'W) in southern Peru (Fig. 1). This site is accessible, has a relatively large deer population, and has a large and well equipped research and range management station, the Centro Nacional de Camelidos Sudamericanos. In contrast to other areas that I visited, La Raya shows almost no signs of overgrazing by domestic stock. My observations were made within the station's 120 km² area, on a main study area of 79 km². The region is part of the Puna, a treeless, high Andean formation dominated by perennial bunch grasses. Here, the Eastern and Central Cordilleras of the Andes come together, forming a knot at the divide between the Amazon and Lake Titicaca Basin drainages. The terrain is very rugged with steep-sided mountains surrounding a broad main valley and smaller side valleys. Rocky outcrops or permanent ice fields cover most of the upper slopes and mountain tops. Mean elevation of the main study area is 4,630 m and within its altitudinal range (4,070 to 5,470 m) three ecological zones occur: subalpine meadow, alpine tundra, and glacial (O.N.E.R.N., 1965).

The vegetation consists mainly of tall bunch-grasses (Festuca, Stipa, and Calamagrostis spp) which give cover to smaller graminoids, forbs, mosses, and lichens. Marshy vegetation, dominated by Distichia muscoides, is common along the moist valley bottoms and on some slopes where water filters

Figure 1. Map of Peru and the study area at La Raya.



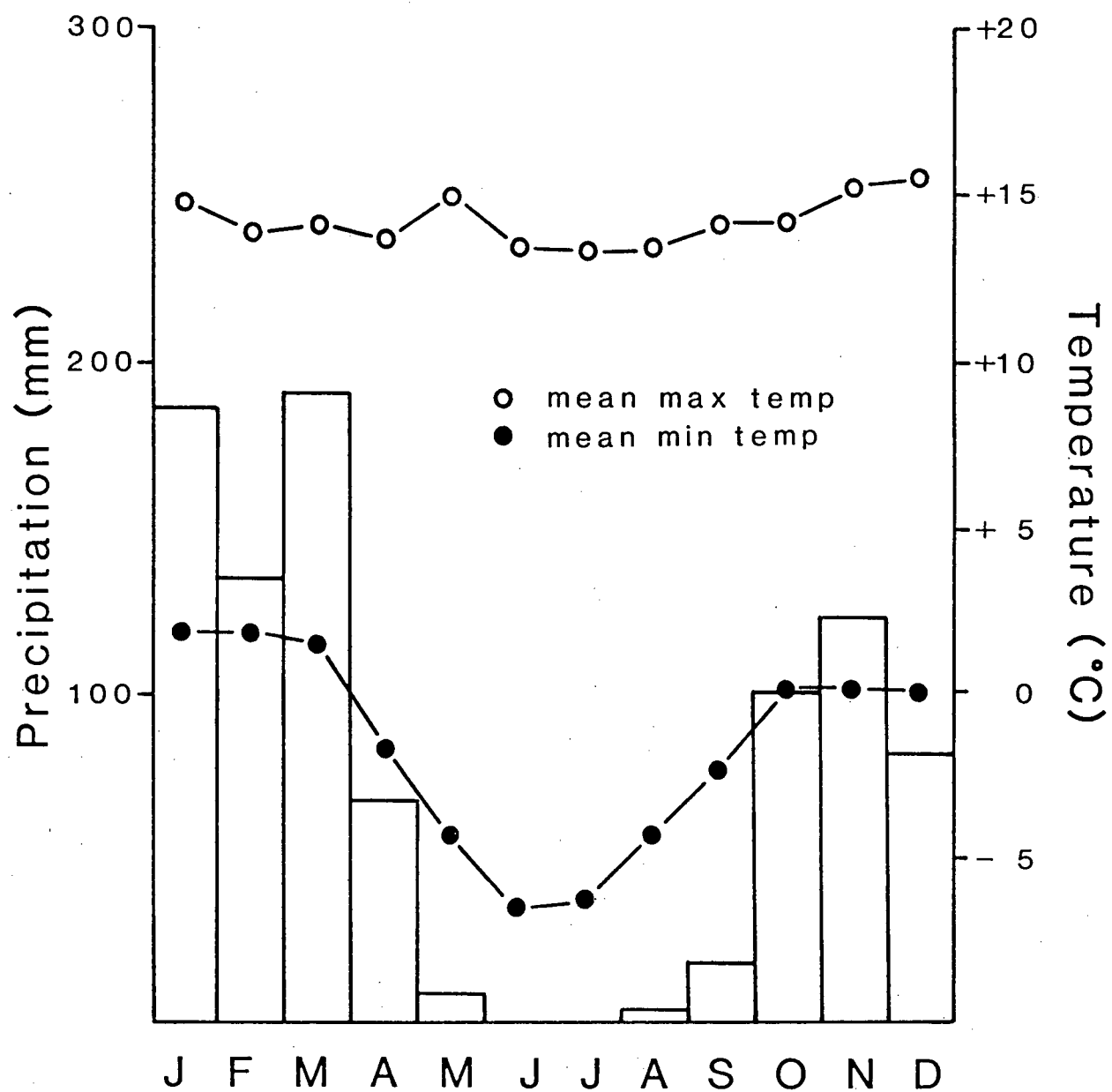
out from the melting glaciers. Short shrubs (Senecio, Baccharis spp) are found only in a few sites along the upper limit of the vegetation.

A more detailed description of the study area is given in Section 2.3.1 where the results of habitat analysis are presented.

The climate in the highlands of southern Peru has been described by Carpenter (1976), Franklin (1983), O.N.E.R.N. (1965), Pearson (1951), and Troll (1968). Annual precipitation of about 900 mm is strongly seasonal, with a wet season in October through April and a dry season in May through September (Fig. 2). Most of this precipitation is in the form of rain or hail (below 4,800 m) and snow or hail (above 4,800 m).

Both the altitude and the precipitation regime greatly influence temperature patterns in these tropical highlands. Mean annual temperature ranges from 6° C at 4,100 m to 0° C above 4,800 m (O.N.E.R.N., 1965) but fluctuates little with season. Large diurnal fluctuations do occur. The intense solar radiation at these elevations results in relatively warm days and cold nights. This is especially true during the dry season from May through September, a time of clear skies and heavy night frosts (Table 1). During the rainy season, diurnal fluctuations in temperature are less marked. Night temperatures are usually above freezing, but days tend to be cold because of overcast skies. Figure 2 shows mean monthly maximum and minimum temperatures at La Raya.

Figure 2. Mean monthly precipitation, and minimum and maximum temperatures at La Raya. Means were estimated from 1980 and 1981 daily records. Precipitation is shown by bars.



The main human activity at La Raya involves research

Table 1. Mean number of days with freezing night temperatures (≤ 0 C) at La Raya, Peru. Means were calculated from 1980 and 1981 daily records.

MONTH	NUMBER OF DAYS WITH NIGHT FROSTS
January	5
February	4
March	5
April	26
May	31
June	30
July	31
August	30
September	23
October	17
November	13
December	16

and management of the alpaca (Lama pacos) . Some 5,000 alpacas are maintained in herds averaging 340 animals. The station also supports about 400 llamas (Lama glama) and a few domestic sheep, cattle, and horses. Most of the highland pastures of Peru are used for extensive alpaca grazing, but unlike La Raya, these lands are community owned and in some areas domestic sheep

outnumber alpacas.

Beside Hippocamelus , the only other wild ungulate in the area is the vicuna (Lama vicugna). Potential predators of tarucas include the cougar (Felis concolor) , semi-feral dogs, and Andean foxes (Dusicyon culpaeus) . More will be said about predators in Chapter 2.

1.2.2 Study Animals and Data Acquisition

Most field work was done from November 1980 to December 1981, although some preliminary observations were made between August and October 1980. I covered the area on horseback, and observed tarucas mainly from regular search paths and look-out points. When weather and time permitted, groups were observed for as long as they remained in sight with the aid of binoculars and a 20-45X spotting scope. All observations were made in daylight between 0500 and 1800 h. Tarucas were observed at distances of 30 to 1,500 m, though most observations were within a range of 100 - 1,000 m.

Animals were classified into 5 broad age/sex classes: adult males, adult females, yearling males, yearling females, and fawns. Adult males were distinguished by their large body size, large antlers (rear tine up to twice the ear length), long rostrum, and thick neck. Adult females were smaller than adult males, lacked antlers, and had long rostra but thin necks. Yearlings, with short rostra and thin necks, were smaller than adult males and females. Though most yearling males had only a

pair of short spikes, some had small forked antlers. Fawns were distinguished by their small size and their dark-grey coats. About a month after they were first observed, fawns started to acquire the sandy-brown pelage characteristic of older animals.

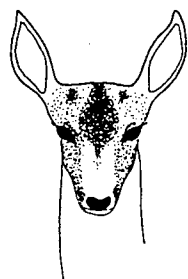
I was eventually able to identify specific individuals by the markings on their heads, and in the case of males, also by the size and shape of their antlers. Figure 3 illustrates the facial patterns and antlers of selected known individuals.

Once a group was located, I recorded the presence of any known individual, the number and classes of deer within the group, their activities at 5-min intervals, any behavioral interaction between two animals, and a range of environmental variables at the beginning, end, and every hour during the observation period. A detailed account of habitat data recorded is given in Section 2.2.

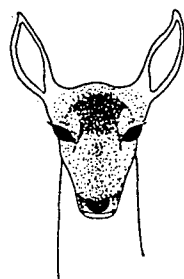
Throughout the study I conducted 175 observation periods ranging from less than 5-min to 8-hrs in duration. On average observations lasted approximately 1 hour. Since deer density was relatively low (about 1.2 animals/km²) groups were found widely spaced, and it was rare to have more than one group in sight. However, if a group being monitored changed in size and/or composition (because of animals joining or leaving the group) it was treated as a new group. Thus, I had 208 group sightings which included 310 observations of adult males, 500 of adult females, 264 of yearlings, and 112 of fawns. In addition, I observed 19 groups whose age/sex composition could not be determined.

Figure 3. Facial markings of eight known individuals. Also note antler shapes in adult males.

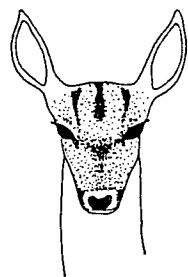
Females



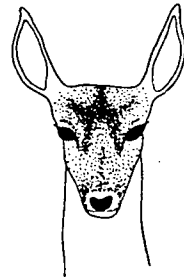
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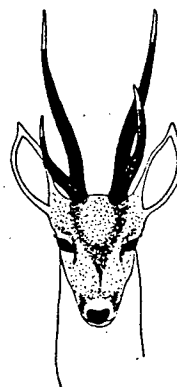


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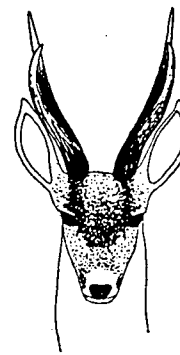


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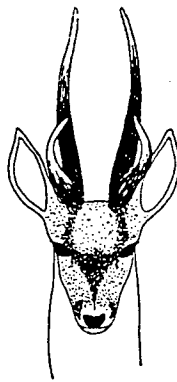
Males



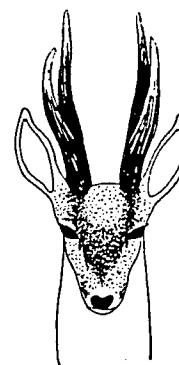
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1.2.3 Data Analysis

Data from 1980 and 1981 showed similar patterns and, unless otherwise specified, have been combined. Sample sizes were small in some months, and all group data have been pooled into 2-month periods. From July 1981 on, I could not distinguish yearling females born in 1980 from adult females. Yearling males, however, remained distinct until the end of the study in December 1981. Fawns born in early 1981 were considered yearlings from September 1981 or, if males, when they grew their first set of antlers.

1.3 RESULTS

1.3.1 Reproduction

Here, I consider three events related to reproduction: 1) fawning (births), determined by the relative number of fawn sightings; 2) mating activity, defined by the frequency and nature of male/female interactions; and 3) the antler cycle in males.

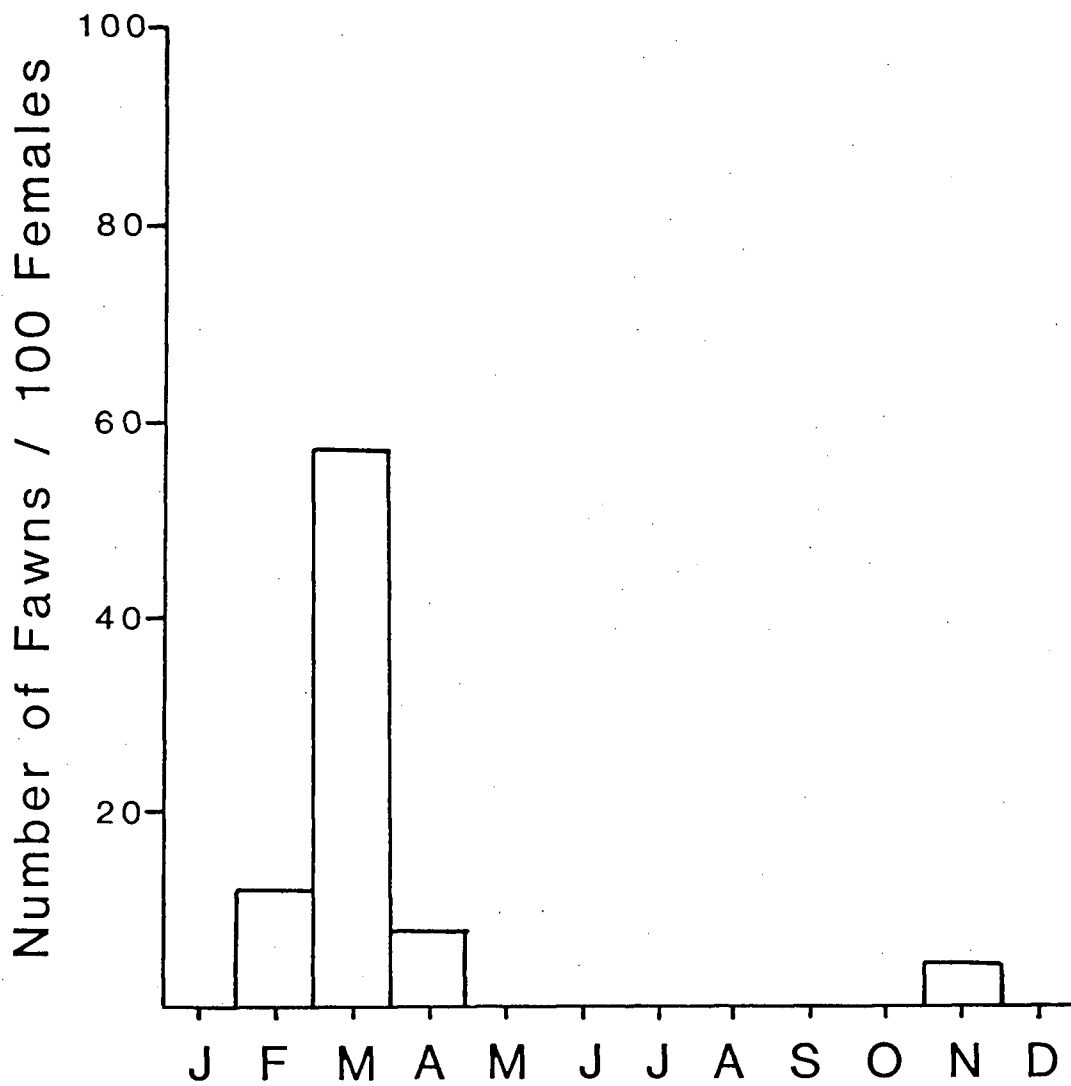
Fawning

To estimate the relative number of fawns born per month I used the number of fawn sightings/100 adult females. I distinguished small fawns from older fawns by pelage color and size relative to their mothers'. In 1981, fawns appeared between February and April, with a sharp peak in March, late in the rainy season (Fig. 4). Of all small fawn sightings, 83% (29/35) occurred between 20 February and 31 March. These "birth" dates, however, are likely to be biased, and peak number of births may have occurred earlier in February (see below). Only 2 fawns were observed outside the main fawning season in November 1980.

Mating activity

In the analysis of male/female interactions, only observations of 5-min or longer were used. I defined a

Figure 4. Relative number of young fawns expressed as fawn sightings per 100 adult females. November sightings correspond to 1980 only, the remainder to 1981.



male/female interaction as any sequence of behavioral displays or contact behaviors between adults of different sex. They usually were initiated by a male approaching a female and were often ended by the female moving away or by the male mounting the female. I recorded 70 interactions during 64 observation periods totalling 107 h 51 min.

The highest number of interactions took place in June in the middle of the dry season (Fig. 5). The number of interactions was lowest in March and April when the sexes were most segregated. Male/female interactions were also rare in October and November when males had dropped their antlers (see below).

The proportion of male/female interactions that led to mounting was also highest in June (Fig. 6). Most of the time I could not distinguish between successful and attempted mounts. The former might also have been relatively more frequent in June. I did not observe any male/female interactions in July. However, none of my observations of mixed-sex groups during this month lasted more than 5 minutes. Thus breeding may have continued into July.

Extrapolation from peak of mating activity in June to peak of relative number of sightings of small-fawns in March gives an approximate gestation period of 270 days. This figure is higher than that for any other cervid species (Eisenberg, 1981: Appendix 4). The most likely explanation is that births actually occurred before taruca fawns were first observed. In most cervids, young remain hidden for some time after birth (De

Figure 5. Number of adult male/female interactions /hr of observ. Only obs. of 5-min or longer are included. Ratios represent num. of interactions/total monthly obs. time (min.). No data were obtained in July and no interactions occurred in November. 1980/1981 data are combined.

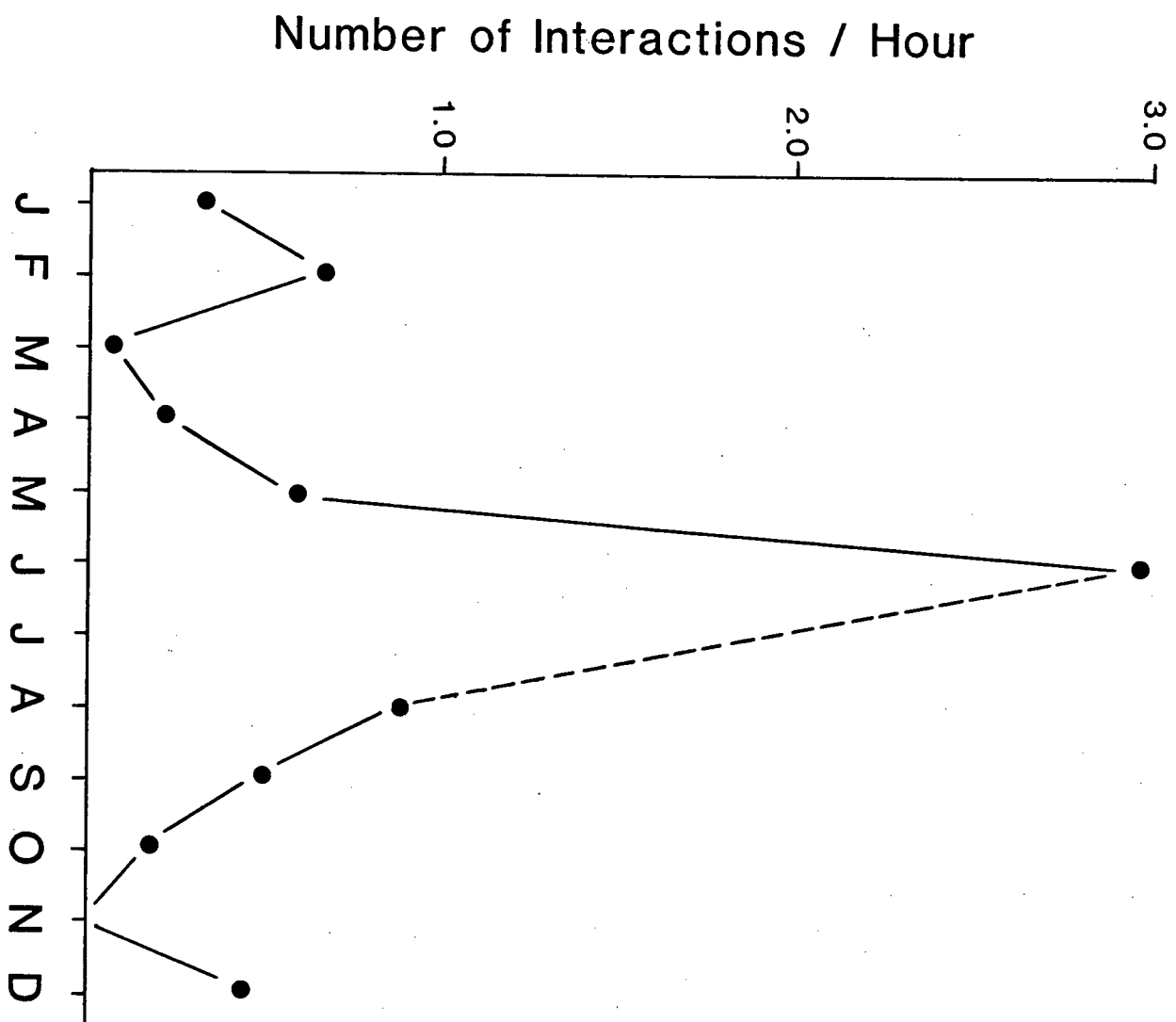


Figure 6. Percentage of interactions leading to mounting of adult females by adult males. No data were obtained in July and no interactions occurred in November. 1980/1981 data have been combined.

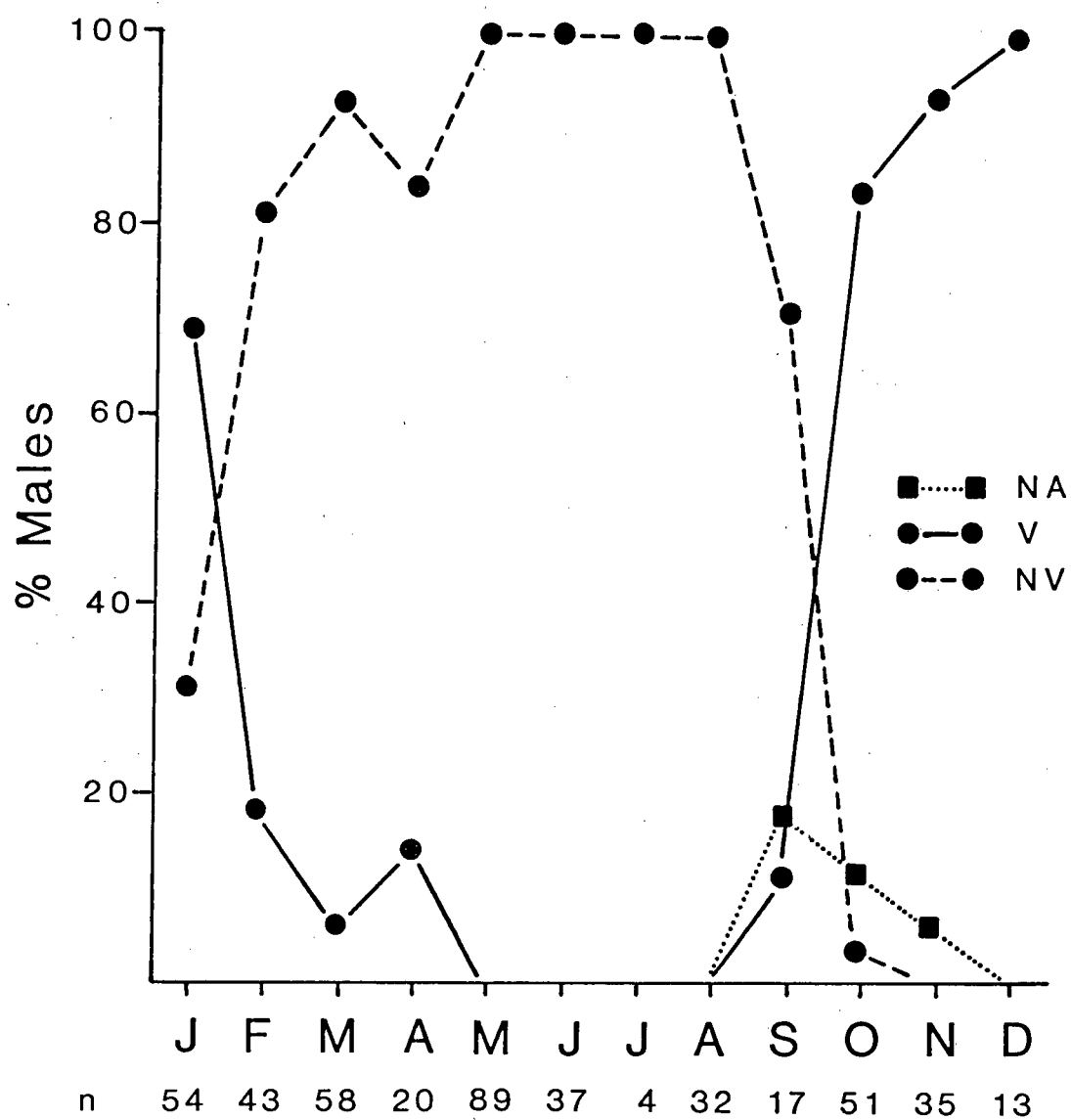
Vos, 1967; Lent, 1974). From evidence presented later (sections 1.3.2 and 2.3.5), I estimate peak number of births in February, with the birth season extending from January to March. This correction yields an approximate gestation period of 240 days, a figure more compatible with those known for other deer (Eisenberg, 1981).

Antler cycle

Data on antler condition was based on 453 sightings of males (adults and yearlings pooled together). The antler cycle was highly synchronized and seasonal (Fig. 7). The proportion of males with clean antlers increased from 30% in January to 100% in May. All adult males, however, had shed their velvet as early as February. During the dry season, when mating activity was most intense (Figs. 5 and 6), all males had clean antlers (Fig. 7). By September males were dropping antlers, and some new antlers were in velvet. By December all males were in velvet (Fig. 7).

In summary, 94% of births occurred towards the end of the rainy season; mating took place during the driest months; and antler shedding in males was observed during the onset of the rainy season. Therefore, the reproductive cycle in Hippocamelus antisensis is markedly associated with seasonal climatic patterns.

Figure 7. Antler cycle of males. Percentage of males (adults and yearlings pooled) with no antlers (NA), antlers in velvet (V), or free of velvet (NV). N= number of male sightings. 1980/1981 data have been combined.



1.3.2 Grouping Patterns

Mean group size for the entire study was 6.4 (\pm 0.36 SE) deer, and groups ranged from 1 to 31 animals. Mean size varied little seasonally but was smaller (5.0-5.3) just prior to and during fawning (January-April) and larger (7.3-7.6) during the rest of the year (Table 2).

Table 2. Mean group size throughout the year. Data from 1980 and 1981 have been combined and pooled into 2-month periods.

MONTH	MEAN SIZE (\pm SE)	No. GROUPS
JAN/FEB	5.3 (\pm 0.60)	61
MAR/APR	5.0 (\pm 0.59)	43
MAY/JUN	7.4 (\pm 0.89)	57
JUL/AUG	7.3 (\pm 1.50)	20
SEP/OCT	7.3 (\pm 1.01)	21
NOV/DEC	7.6 (\pm 1.16)	26

Groups were classed into 3 group types of various age/sex compositions (Table 3). Mixed groups contained both adult males and adult females and also included yearlings and/or fawns most of the time (Table 4). Male groups consisted of one or more adult males and rarely included yearlings of either sex. Fawns never occurred in male groups (Table 4). Female groups

contained one or more adult females and often included fawns and/or yearlings (Table 4). Yearlings never associated to form all-yearling groups. Lone yearlings were observed on only 4 occasions during the entire study and were probably animals briefly separated from other groups.

Table 3. Group types encountered at La Raya during entire study.

GROUP TYPE	MEAN SIZE (\pm SE)	% (n)
MIXED-SEX	9.5 (\pm 0.54)	52.9 (108)
MALE	1.8 (\pm 0.21)	22.5 (46)
FEMALE	4.2 (\pm 0.46)	24.5 (50)

I consider four aspects of grouping patterns: 1) the mean size of the three types of groups during the year; 2) changes in the proportion of types of groups over the year; 3) the distribution of individual deer classes among the different groups; and 4) the temporal stability of these groups.

Table 4. Total number of groups with and without young (yearlings and fawns pooled together) for the entire study.

GROUP TYPE	WITH YOUNG	WITHOUT YOUNG
MIXED-SEX	81	26
MALE	4 *	42
FEMALE	28	22

* These groups contained no fawns.

Mean group size

Mixed groups were by far the largest throughout the year though they were relatively smaller (mean = 7.7-8.8) before and during fawning (January-April) than (mean = 10.4-11.7) during the dry season when mating took place (Fig. 8). On average mixed groups consisted of 2.4 adult males, 3.9 adult females, and, if present, 2.8 young (fawns and yearlings pooled together). Table 5 presents the detailed composition of mixed groups throughout the year.

Male groups were very stable in size and consisted mainly of one or two adult males (Fig. 8). The largest male group contained 5 adults and 2 yearlings. Yearlings of either sex occurred with adult males on only four occasions between January and April. Female groups were larger (mean = 5.4) during and after fawning (March-June) and smaller (mean = 2.5-4.5) during the rest of the year (Fig. 8). On average they

Figure 8. Mean size of deer groups : mixed-sex (MX), female (F), and male (M). Vertical lines represent \pm SE. 1980/1981 data have been combined and pooled into 2-month periods.

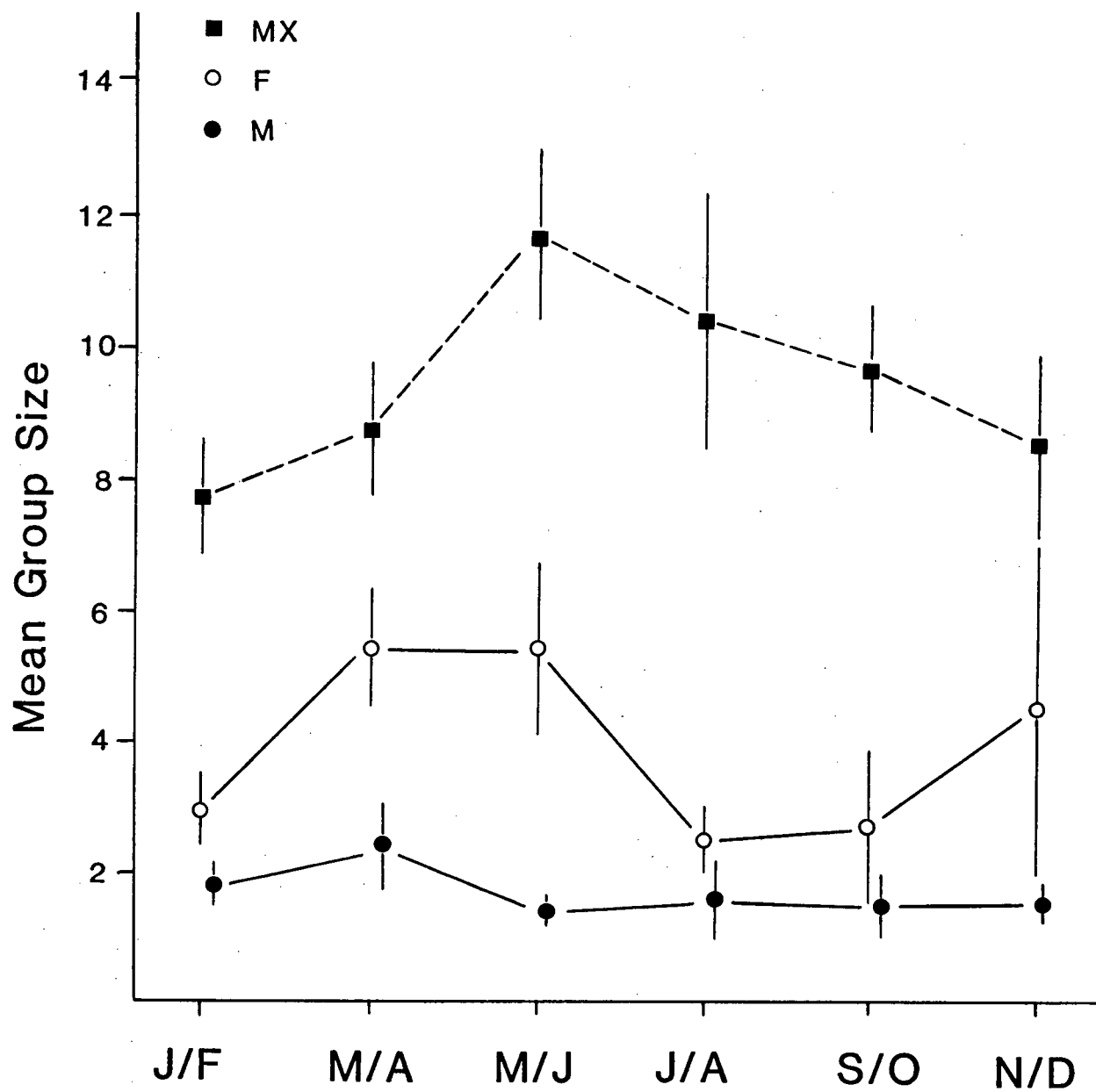


Table 5. Structure of mixed-sex groups during entire study. Only groups for which all individuals were classed are included. For each class, the mean number of individuals per group (\pm SE) was obtained by pooling data for 1980 and 1981 into 2-month periods.

MONTH	No.GROUPS	AD.MALES	AD.FEMALES	YEARLINGS	FAWNS
JAN/FEB	22	2.3 (± 0.28)	2.7 (± 0.32)	2.1 (± 0.49)	0.0
MAR/APR	12	2.0 (± 0.33)	2.9 (± 0.47)	3.5 (± 0.51)	0.3 (± 0.22)
MAY/JUN	27	2.6 (± 0.23)	5.1 (± 0.64)	2.2 (± 0.36)	1.8 (± 0.42)
JUL/AUG	9	2.7 (± 0.53)	5.0 (± 1.47)	0.3 (± 0.17)	0.0
SEP/OCT	13	2.6 (± 0.31)	3.9 (± 0.47)	3.2 (± 0.44)	*
NOV/DEC	13	1.8 (± 0.25)	3.0 (± 0.45)	1.1 (± 0.33)	*

* Yearlings and older fawns pooled together.

consisted of 2.5 adult females, and if present, 3.2 young (fawns and yearlings pooled). Table 6 gives the composition of female groups throughout the year.

Proportion of types of groups

Mixed groups were present year-round and, with the exception of January-April, were the most common group-type observed (Fig. 9). The low proportion of mixed groups in the sample before and during fawning was associated with a slight

Table 6. Structure of female groups during entire study. Only groups for which all individuals were classed are included. For each class, mean number of individuals per group (\pm SE) was obtained by pooling data for 1980 and 1981 into 2-month periods.

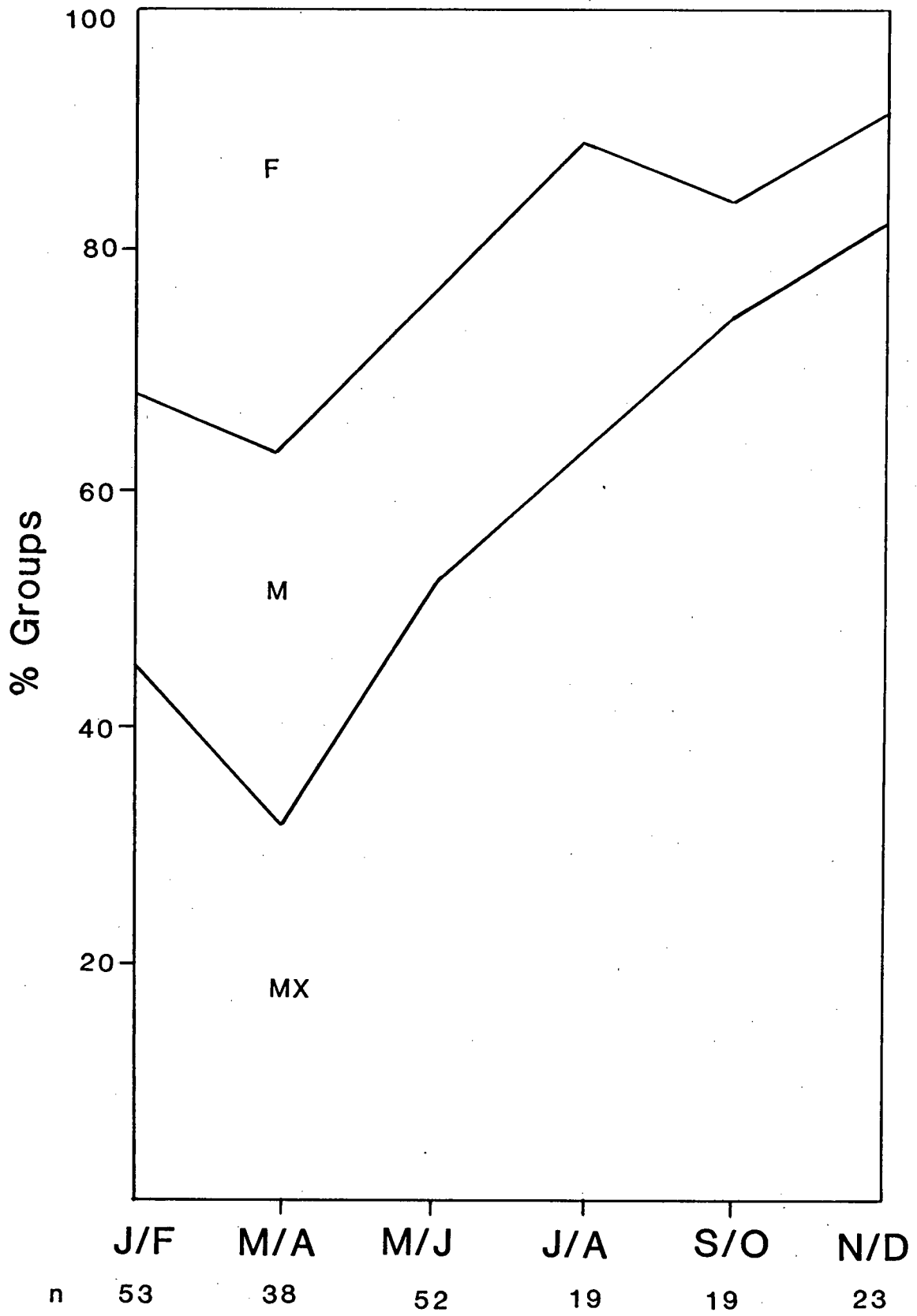
MONTH	NO.GROUPS	AD.FEMALES	YEARLINGS	FAWNS
JAN/FEB	17	1.8 (± 0.22)	0.9 (± 0.44)	0.2 (± 0.14)
MAR/APR	14	2.6 (± 0.33)	0.7 (± 0.27)	2.1 (± 0.44)
MAY/JUN	12	3.1 (± 0.51)	1.2 (± 0.49)	1.2 (± 0.68)
JUL/AUG	2	2.5 (± 0.50)	0.0	0.0
SEP/OCT	3	2.3 (± 0.88)	0.3 (± 0.33)	0.0
NOV/DEC	2	4.0 (± 3.00)	0.0	0.5 (± 0.50)

increase in the proportion of male groups and a marked increase in the proportion of female groups. After fawning, mixed groups became progressively more common and by November/December, when all males had dropped their antlers or were in velvet, 80% of all groups were mixed.

Distribution of deer classes among groups

The manner in which different sex/age classes associated with different types of groups varied seasonally (Figs. 10-14). Adult males spent most of the time in mixed groups, except during fawning, when more than 50% of them were found in male groups. The pattern for adult females was similar to that of adult males. They spent most of the time in mixed

Figure 9. Proportion of different types of groups: : mixed-sex (MX), male (M), and female (F). N= number of groups sighted. 1980/1981 data have been combined and pooled into 2-month periods.



groups, except during fawning, when 50% of them were associated with their fawns, yearlings, or other females.

Both adult males and females were associated in mixed groups or with animals of their own sex throughout the year. Solitary animals were infrequently observed. Adult males, however, were solitary more often than adult females (Fig. 12). The proportion of single males was above 9% between January and August, and reached a peak of 14% in March/April during fawning. Only 3% of all adult males were found alone between September and December, during antler shedding and growth. During most of the year single females were extremely rare. Only immediately before fawning did the proportion of lone females increase to 8%.

Most yearlings remained in mixed groups throughout the year (Fig. 13). Young fawns were observed exclusively in female groups between February and April (Fig. 14). A few older fawns were found in mixed groups in April when some lactating females began to return to mixed groups. By May/June almost all fawns were with their mothers in the large mixed groups.

Segregation of pregnant females and adult males

The occurrence of small fawns only in female groups from February to April, clearly indicates that all pregnant females segregated from mixed groups and thus from adult males. No female groups were observed in December 1980 or 1981. Females began to segregate in mid January, when 6 (29% of all

Figure 10. Relative number of adult males in mixed-sex and male groups. MX= mixed-sex groups; M= male groups; n= number of adult male sightings. 1980/1981 data have been combined and pooled into 2-month periods.

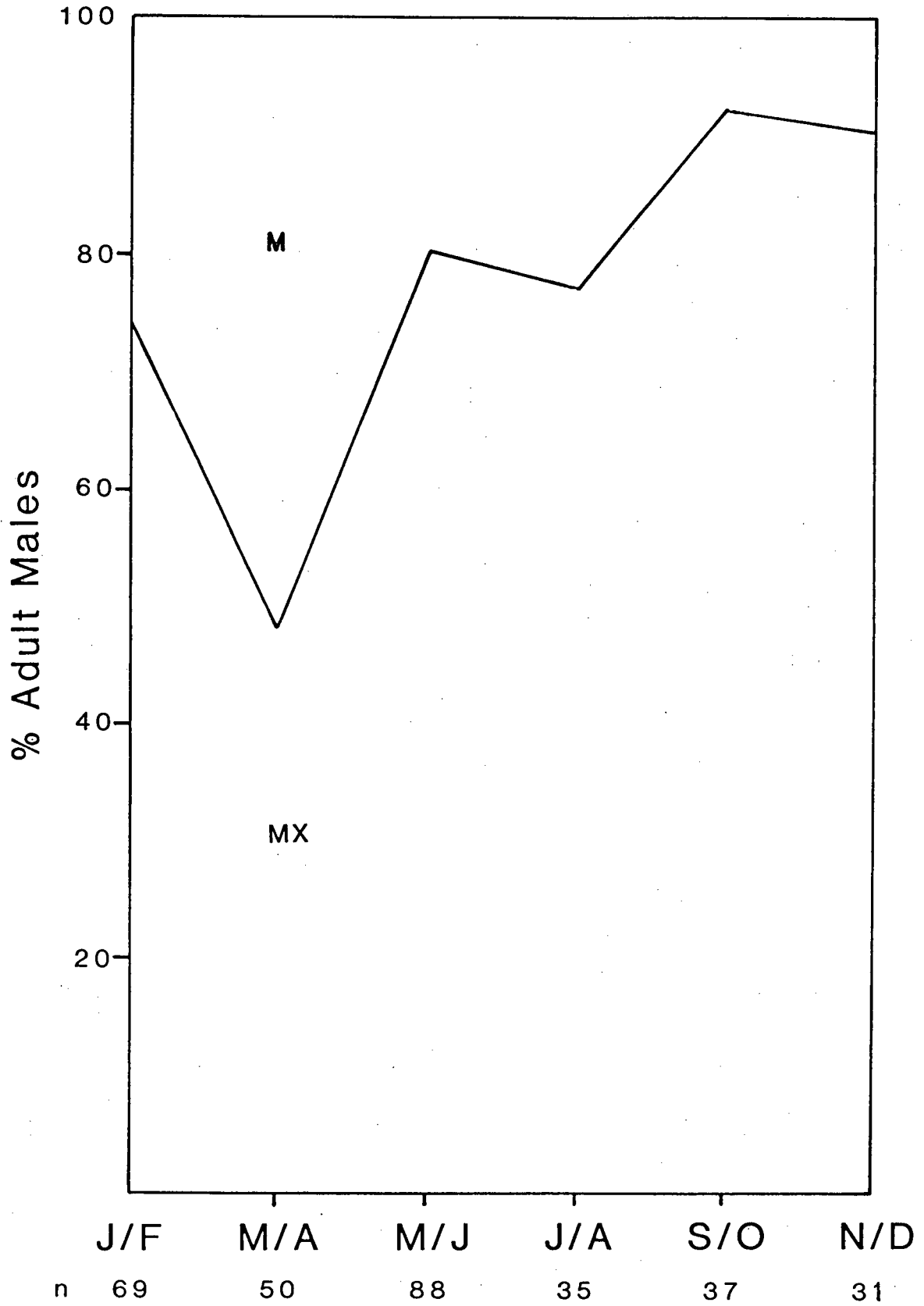


Figure 11. Relative number of adult females in mixed-sex and female groups. MX= mixed-sex groups; F= female groups; n= number of adult female sightings. 1980/1981 data have been combined and pooled into 2-month periods.

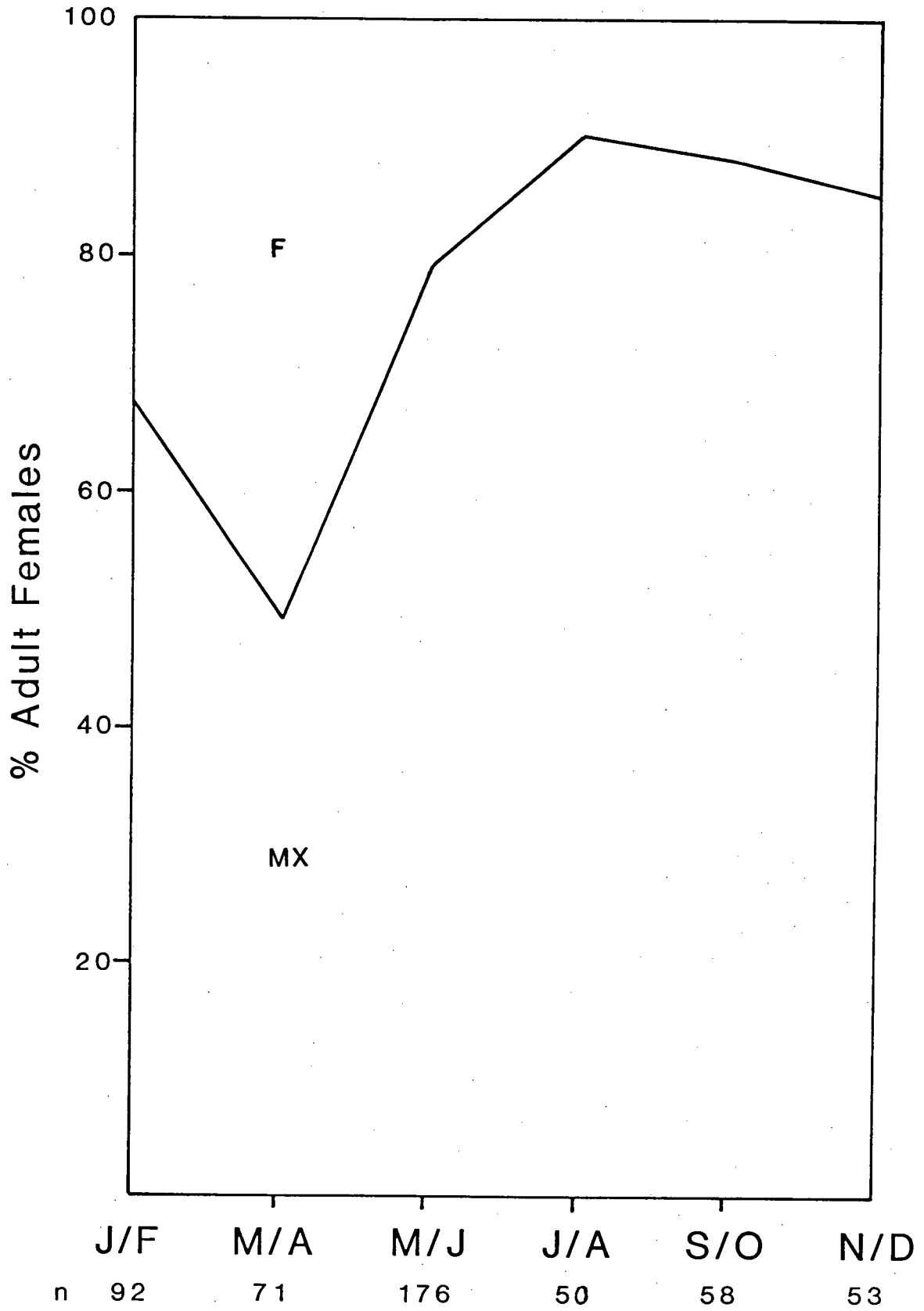


Figure 12. Percentage of adult males and females observed as solitary individuals. Single females accompanied by fawns have been included. SM= solitary males; SF= solitary females. 1980/1981 data have been combined and pooled into 2-month periods.

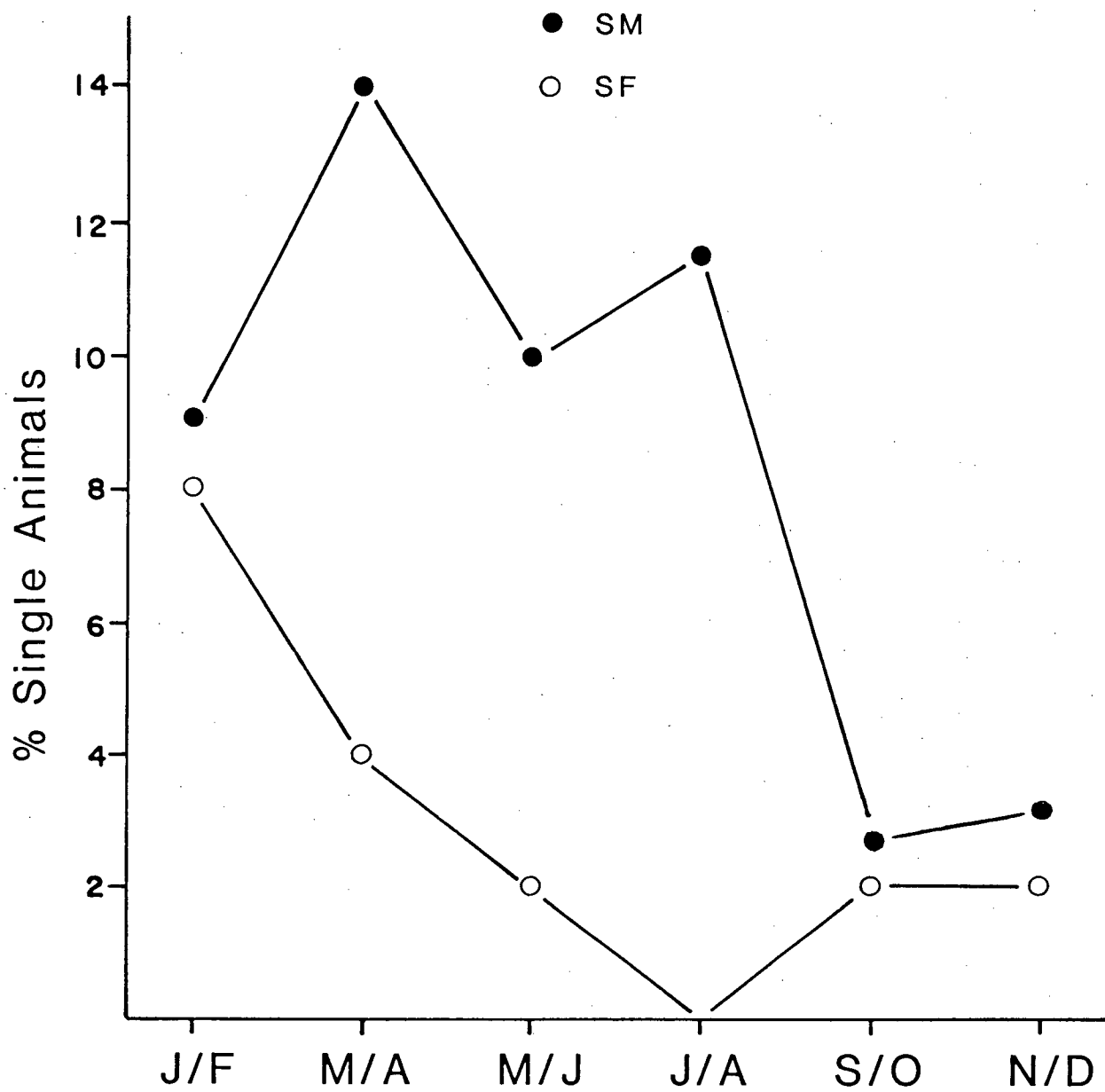


Figure 13. Relative number of yearlings in mixed-sex, male, and female groups. MX= mixed-sex groups; M= male groups; F= female groups; Y= lone yearlings; n= number of yearling sightings. 1980/1981 data have been combined and pooled into 2-month periods.

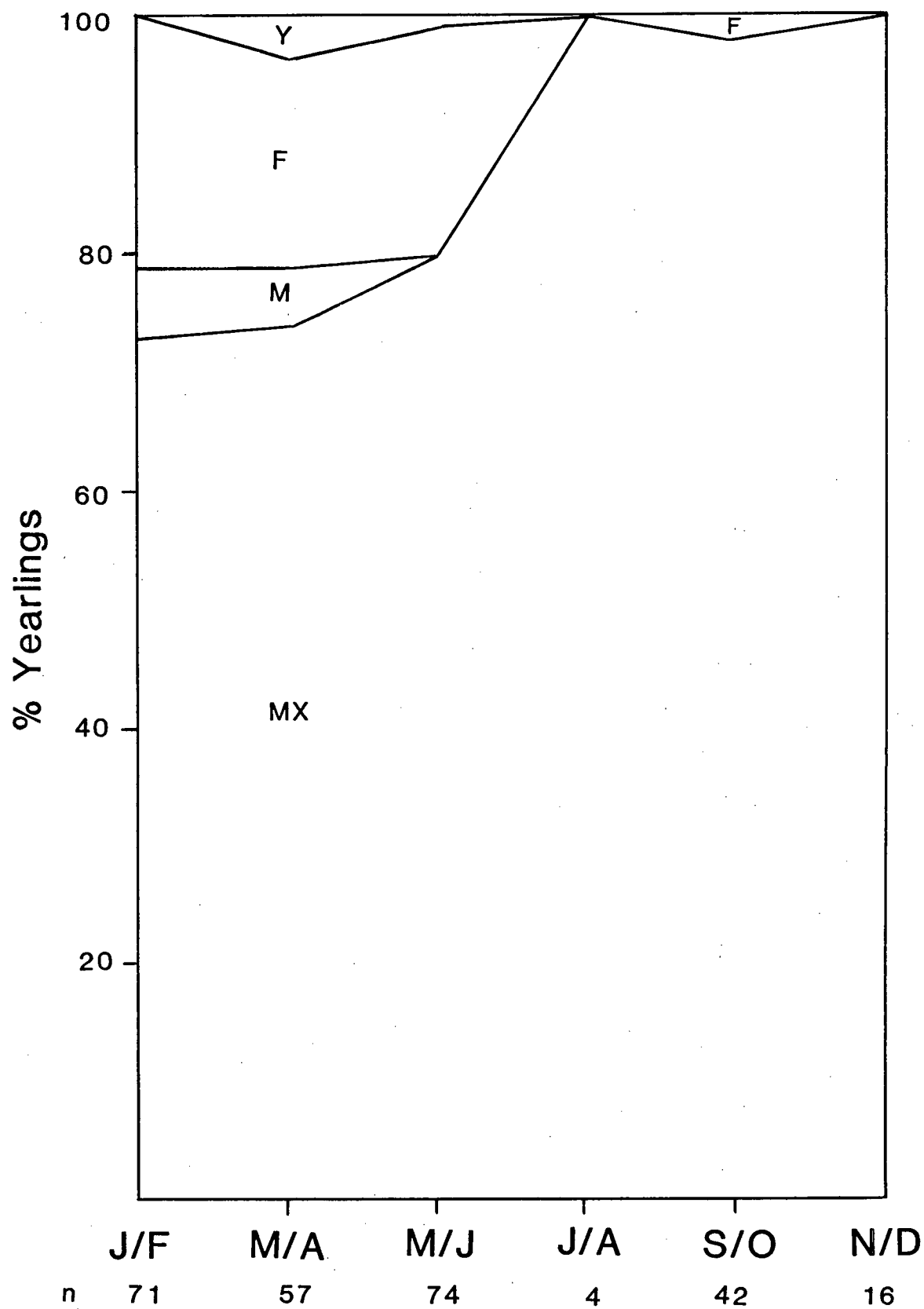
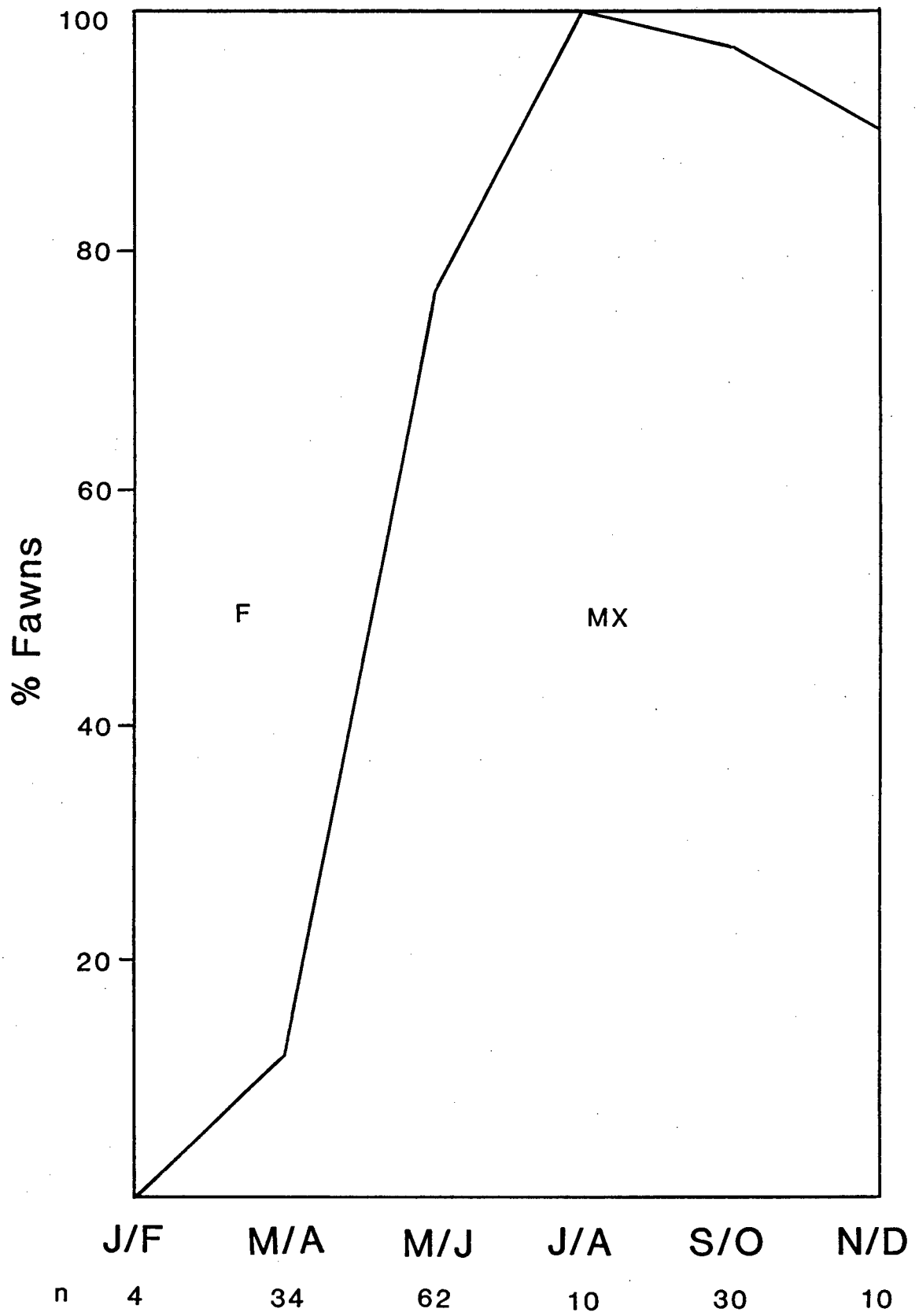


Figure 14. Relative number of fawns in female and mixed-sex groups. MX= mixed-sex groups; F= female groups; n= number of fawn sightings. For this figure, fawns born in 1981 have been considered as such until the end of the study (December 1981) to show their yearly association pattern.



groups in this month) female groups were encountered. Some lactating females were first seen in mixed groups in early April. These group observations and the records of two known pregnant females indicate that the sexual segregation may have lasted from 5 to 10 weeks. My observations also suggest that once adult females became segregated, they may also avoid contact with male or mixed groups.

A different pattern was found among adult males. Records of known adult males (5 of which were the largest males during the study) indicate that although up to 50% of adult male sightings during fawning were in male groups, some rejoined mixed groups several times while others rarely left mixed groups. This finding indicates that adult males do not move away from mixed-sex groups; rather, females segregate themselves.

Group stability

From the analysis so far, it is not clear how stable or "cohesive" the various types of groups described were at different times of the year. A measure of relative stability can be obtained by comparing changes in group size and composition within observation periods with longer-term changes obtained from data on known individuals.

On the whole, all group-types remained very stable in size and composition within observation periods (Table 7) both during and outside the fawning season. Even large groups (9-18

animals) retained their identity during observations that lasted up to 6 hours. This suggests that tarucas formed cohesive social aggregations at least during daily activities.

Table 7. Changes in group size/composition within observation periods. Only observations of 30 min or longer have been included.

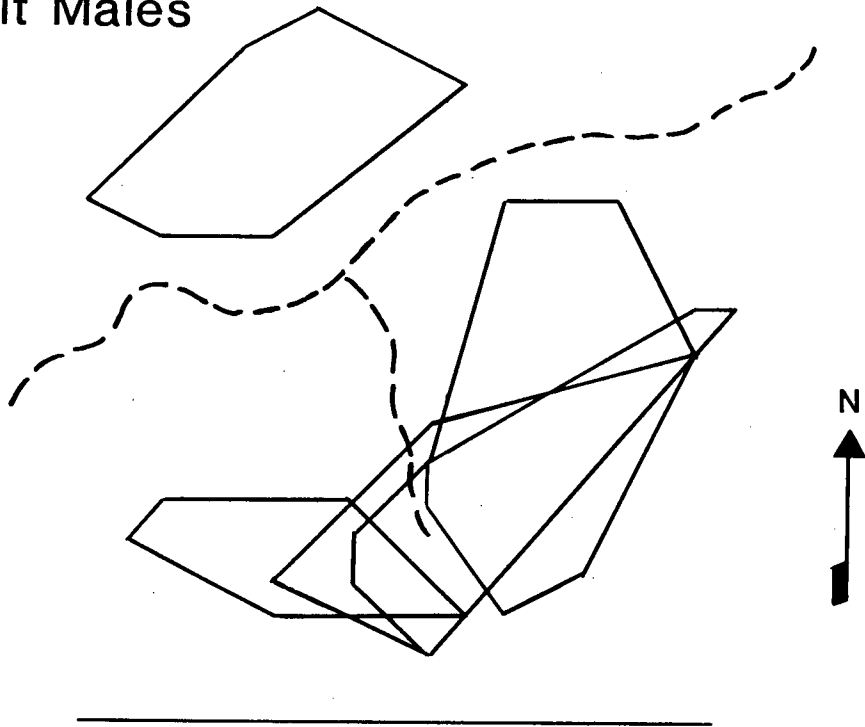
GROUP-TYPE	TOTAL NUMBER OBSERVATIONS	NUMBER OF CHANGES PER OBSERVATION/HOUR
FEMALE	10	0.02
MALE	12	0.02
MIXED-SEX	43	0.01

Data on known individuals, however, indicate that specific groups did not remain stable over several days. Known adult males and females were both observed to be in groups of different size or composition on almost all occasions in which these individuals were identified (Table 8).

Locational data from these known animals indicate that both sexes remained in particular areas during the study (Fig. 15) and strongly suggest that adults have year-round home ranges, though seasonal shifts in habitat use are marked (see

Figure 15. Locations of known adult males and females.
Only individuals with 5 or more sightings and with more than 30 days between first and last sighting have been included.

Adult Males



Adult Females

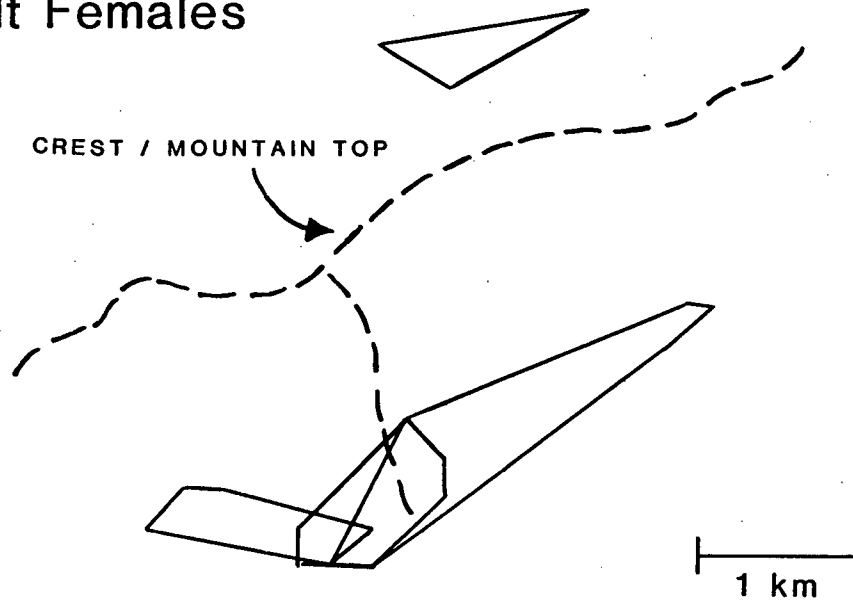


Table 8. Number of sightings of known individuals and number of different groups in which the former were found. Only animals with 5 or more sightings are included. Mean time-span between sightings was 15 days. Mean time-span between first and last sighting was 135 days.

CLASS	NO. ANIMALS	TOTAL SIGHTINGS	TOTAL NO. OF DIFFERENT GROUPS
ADULT MALES	8	80	74
ADULT FEMALES	4	27	27

Chapter 2). This resulted in different animals associating with particular individuals or groups but not with others within the study area. It appears that although particular groups were not stable on a long-term basis, different individuals seemed to be part of larger "sub-population" units.

To summarize, tarucas displayed a strong tendency to form social aggregations throughout the year. Solitary animals were infrequent. Group size and structure, however, changed seasonally and these changes were highly correlated with the reproductive cycle of the deer. Mixed-sex groups were the largest and most common, except during the fawning season when smaller single-sex groups were more frequent. At this time, all pregnant females (and perhaps some barren females as well) were completely segregated from mixed-sex groups. Although adult males were frequently seen in male groups during this period, data on known individuals indicate that male groups are

transient. My observations strongly suggest that pregnant females move away from and subsequently avoid contact with male or mixed groups. Finally, the seasonal groupings of tarucas are neither random aggregations of individuals nor stable social units. Both sexes formed short-term cohesive social groups while foraging and engaging in other activities during the day but did not aggregate always with the same individuals on a longer-term basis. Although unstable, these groups were comprised of individuals who remained in restricted areas year-round. Thus, these "open" groups appeared to be subsets of larger and perhaps more stable sub-population units.

1.4 DISCUSSION

Reproductive Cycle

Tarucas breed seasonally in an area characterized by marked seasonal fluctuations in the environment. Mating occurs in winter during the driest months, antler shedding in males occurs in spring during the onset of the rainy season, and fawning towards the end of the rainy season in late summer.

The sparse information available for this species in other locations in southern Peru agrees with my findings. Pearson (1951) examined six specimens from Arequipa and Puno in December. Three adult males had their antlers in velvet and one young male had short spike antlers and lacked the last molars. The remaining two were pregnant females. From the size of one fetus (410 mm), he estimated birth in February or March. Whitehead (1972) stated that the rut in Peru occurs between June and August and Roe and Rees (1976) recorded instances of courtship and mounting behavior during their observations between 8 and 15 June in Puno. They noted that all adult males had antlers free of velvet. Although they observed no fawns, some older fawns may have been mistaken for yearling females. During a preliminary study of tarucas in Pampa Galeras (15° 40'S, 74° 40'W), Ayacucho, between 24 February and 20 June 1980, I observed fawns in April. I was unable, however, to find deer in March. In the course of making 20 group observations in this location, I observed only one instance of mounting behavior on 17 May 1980. I could not find any deer in June 1980. All males

had clean antlers throughout this pilot study. .

The relationship between breeding cycles and seasonal environments is well documented for many ungulates in northern latitudes (e.g. Anderson, 1981; Bunnell, 1982; Chapman and Feldhamer, 1982; Schaller, 1977; Thompson and Turner, 1982) where seasonal breeding presumably occurs in response to periodic fluctuations in food availability (Bunnell, 1982; Geist, 1974a; Thompson and Turner, 1982). The climatic patterns in northern latitudes, however, are different from those in tropical highlands (Franklin, 1983; Troll, 1968) and the differences may explain why the timing of reproductive events in Hippocamelus antisensis differs from that in northern latitude ungulates.

Temperate climates are characterized by seasonal variations in day length and temperature. This pattern results in most young being born during spring and early summer, a period of rapid plant growth. The onset and length of the birth season in any particular location is related to the duration and predictability of this plant-growing season (Bunnell, 1982; Thompson and Turner, 1982).

On the other hand, in tropical highlands climate is characterized by large diurnal fluctuations in temperature and season is influenced by summer rains. Changes in day length throughout the year are relatively small. Drought and subzero night temperatures in the winter limit the growing season to one part of the year (Franklin, 1983; Troll, 1968). During the dry winter months, most areas are devoid of green vegetation and

many annual forbs and small grasses disappear. At the onset of the wet season (in spring) increasing rains bring moisture to the dried-out soils, but the persistent night frosts (see Table 1) result in a slow recovery of the vegetation. Although I did not monitor plant phenology quantitatively, my observations indicate that plant growth at La Raya, as in other sites in southern Peru (Franklin, 1983; Menard, 1984), reaches its peak sometime in February/March. This time appears to be the optimal fawning time in Hippocamelus.

The vicuna (Lama vicugna) is the only other local wild ungulate living as high as the taruca. It too has a restricted breeding season in southern Peru and gives birth to young between February and April (Franklin, 1974), with a peak of births in March (Koford, 1957; pers. obs.). Another wild ungulate of comparable size that inhabits tropical highlands is the Walia ibex (Capra ibex walia). It is found in the Simen Mountains of Ethiopia, at about the same latitude as La Raya but north from the equator. Seasons are thus reversed. Although Walia ibexes breed throughout the year, they have distinct rutting and birth peaks (Nievergelt, 1974, 1981). Births are most common in September/October, at the end of the rainy season, and this time coincides with greater availability of fresh food (Nievergelt, 1974). The fact that Walia ibexes can breed year-round presumably reflects the more constant environmental conditions that exist in the Simen Mountains. Ibexes are found at an average elevation of 3,390 m (Nievergelt, 1974) which is lower than that for Hippocamelus at La Raya (mean = 4,661 m). Although the Simen Mountains have a well-defined

rainy season (from May to September/October) and large diurnal temperature fluctuations (mean temperature remains fairly constant throughout the year), mean minimum temperatures never drop below 0° C and even absolute minimum temperatures never fall below -2.5° C (Nievergelt, 1981: Table 1). The milder climatic conditions and the fact that numerous water sources outlast the dry season in the Simen Mountains result in green vegetation being available year-round (Nievergelt, 1974).

I conclude that the breeding cycle in Hippocamelus is strongly seasonal and is determined by the precipitation and temperature patterns characteristic of the highlands of southern Peru. A quantitative study of the effects of rainfall and temperature on plant growth and a comparison of taruca breeding cycles under different climatic conditions are needed to test this hypothesis. Differing environmental conditions seem to exist within the geographic range of Hippocamelus antisensis. Tarucas have been reported in a number of high Andean habitats ranging from more equatorial environments in La Libertad (about 8° S), Peru, to more temperate latitudes in Catamarca (about 28° S), Argentina, and from wetter and more constant climate of the eastern Andean slopes to drier and more unpredictable environments of the western slopes of the Andes (I.U.C.N., 1982). My observations of two fawns outside the main fawning season at La Raya, suggest that tarucas could breed at other times of the year and thus be able to adapt to local conditions within their entire range.

Gregariousness of Tarucas and Their "Open" Habitat

At La Raya, tarucas live in open habitat and are gregarious. The largest group I observed consisted of 31 animals although groups of over 40 deer have been reported occasionally by personnel of La Raya Research Station. Solitary deer were uncommon.

Information on the distribution of tarucas suggest that they live in open mountainous terrain throughout their range (I.U.C.N., 1982; Jungius, 1974; Pearson, 1951; Roe and Rees, 1976; Whitehead, 1972). Zooarchaeological findings indicate that natives have hunted tarucas in the high Andes since at least 6,000 b.c. (Wheeler, 1982). Grimwood's (1969) claim that the distribution of Hippocamelus antisensis is determined by the availability of Polylepis forests is thus unfounded (Roe, 1974; Roe and Rees, 1976; pers. obs.). Data on group size elsewhere are meager, but they suggest that tarucas are also gregarious in other locations. Hofmann and Ponce del Prado (1970) reported a group of 15 deer and observed a lone female taruca on high, steep slopes, in alpine tundra habitat near Abra Malaga, Cusco. In the same area, "large herds" were common in previous years (Hofmann and Ponce del Prado, 1970). Jungius (1974) observed some solitary males and groups of 3 to 13 animals in rugged terrain above the treeline in northwestern Bolivia, and Pearson (1951) found tarucas in groups of 2 to 8 animals among grassy hills interspersed by rugged rock outcroppings in southern Peru. Roe and Rees (1976) observed six groups ranging from 3 to 14 deer in the same type of habitat in

southern Peru. From their data (Table 1, p. 726) I computed a mean group size of $6.8 (\pm 1.58 \text{ SE})$ deer. In Pampa Galeras, Ayacucho, I found tarucas at very low densities (approx. 0.3 deer/km^2) occupying the same mountainous, open terrain. Group size ranged from 1 to 11 animals, but mean size was lower (mean = $2.65 \pm 0.55 \text{ SE}$) than it was at La Raya (mean = $5.8 \pm 0.49 \text{ SE}$) for the same months.

The relationship between group size and habitat structure has been extensively examined for African ungulates and has led to development of a general model. According to Estes (1974), Geist (1974b), Jarman (1974), and Leuthold (1977) ungulate species or populations occupying open habitats live in social groups, whereas those inhabiting dense bush or forest tend to live singly or in very small groups. Groups in open habitat presumably form in response to greater availability and more even distribution of food resources and to predation pressures derived from their conspicuousness in open terrain. Although this model was developed mainly for African bovids, it seems to apply to cervids as well (Clutton-Brock et al., 1982; Eisenberg, 1981; Hirth, 1977; Maublanc et al., 1985; Takatsuki, 1983).

As predicted by the above model, the social structure of Hippocamelus antisensis differs from that of its closest relative, the Chilean huemul (H. bisulcus). In the Nevados de Chillan and Rio Claro areas, Povilitis (1978, 1983) found huemuls mainly in dense shrub or forest habitats at elevations between 1,450 and 1,700 m. Mean group size was very small (mean

= 1.6 animals) and huemuls were seen singly or in adult male-female pairs with or without young. Another close relative of Hippocamelus, the white-tailed deer (Odocoileus virginianus) , lives in a variety of habitats, but tends to form large social groups only in open habitats (Hirth, 1977). Similar phenomena have been observed in Roe deer, Capreolus capreolus (Maublanc et al., 1985), and Sika deer, Cervus nippon (Takatsuki, 1983).

Although the general tendency of tarucas to form social aggregations can be explained by the above model, a closer examination of the habitat is required to explain seasonal changes in social structure of the species. For example, it is unclear why adult sexes segregate and females form smaller groups during the fawning season, when food supplies are presumably most abundant and evenly distributed. Also, if predation favors the formation of large groups in open habitat, why do females not form even larger groups at a time when risk of predation of offspring is presumably greatest? In the next chapter, I seek to answer these questions by examining the habitat use and antipredator behavior of Hippocamelus antisensis .

CHAPTER 2. HABITAT USE BY MALES AND FEMALES

2.1 INTRODUCTION

In many species, males occupy different habitats than females (fish: Keast, 1977; reptiles: Schoener, 1967; birds: Peters and Grubb, 1983; Selander, 1966; and mammals: Bowers and Smith, 1979; Bowyer, 1984; Harrison, 1983; Nievergelt, 1981; Shank, 1982). Sexual differences in habitat use can influence the social dynamics of a species, since annual changes in the habitat requirements of each sex may determine their proximity. Consequently, one way to investigate the influence of the environment on social structure is to determine and compare habitat use by males and females.

Spatial segregation of males and females is widespread among social cervids, and typically takes place soon after the mating season (Bowyer, 1984; Brown, 1974; Chapman and Chapman, 1975; Clutton-Brock et al., 1982; Hirth, 1977; Takatsuki, 1983). The extreme sexual dimorphism of these species may facilitate habitat segregation of the sexes (Bowyer, 1984; McCullough, 1979). Some sex differences in habitat use have been documented (e.g. Staines et al. 1982). However, the role of niche separation of males and females is still poorly understood (McCullough, 1979; Shank, 1982).

A leading hypothesis to explain sexual differences in habitat use in social ungulates is that differential metabolic and nutritional requirements of males and females result in

differential food-habitat selection (Clutton-Brock et al., 1982; Geist, 1974a,b; McCullough, 1979; Nievergelt, 1981). This hypothesis assumes that the high costs of gestation and lactation, coupled with smaller body size, result in females having greater energetic and nutritional requirements per unit of body-weight than do males. These differences then lead females to select habitats with qualitatively better forage, and allow males to be less selective and subsist on poorer foods (Clutton-Brock and Harvey, 1983; Clutton-Brock et al., 1982; Geist, 1974a,b; McCullough, 1979). Furthermore, niche segregation may also lessen inter-sexual competition, especially during times critical for females (Geist, 1974a,b; Geist and Petocz, 1977). Some studies have shown that spatial segregation of the sexes is associated with differences in food habits (Charles et al., 1977; Staines et al., 1982; Takatsuki, 1980; Watson and Staines, 1978) or other metabolic requirements such as water needs (Bowyer, 1984). Other studies have produced ambiguous (Clutton-Brock et al., 1982; McCullough, 1979) and opposite (LaGory, 1985; Shank, 1982) results to those predicted by this hypothesis, indicating that other factors can cause sexual segregation.

An alternative hypothesis is that females segregate from males to reduce risks of predation to their young (LaGory, 1985; McCullough, 1979). Although this hypothesis has not been explicitly formulated to explain habitat segregation of the sexes in ungulates, it appears relevant for a number of important reasons: (1) sexual segregation is most pronounced during the season of births (Bunnell and Farr, 1983; De Vos et

al., 1967; Povilitis, 1983; Schaller, 1977); (2) with the exception of the sick and very old, young are the most vulnerable individuals to predation (Curio, 1976; Mech, 1970; Murie, 1944; Schaller, 1972; Sinclair, 1977; Wilson, 1984); and (3) unlike adults, young of many ungulates rely on hiding rather than on flight to escape predation during their first weeks or months of life (De Vos et al., 1967; Estes, 1974; Jacobsen, 1984; Lent, 1974; Leuthold, 1977). In many species, young go through a "hiding" phase that may last up to 4 months (Lent, 1974; Estes, 1974). Among cervids, hiding of young appears to be nearly universal (De Vos et al., 1967; Lent, 1974).

The effectiveness of hiding behavior as an antipredator strategy depends on the ability of young to find adequate concealment or cryptic background. Certain physical characteristics of open, mountainous habitats, such as rock outcrops and broken terrain, can offer considerable concealment. These features are used for protection against predation in some species (Murie, 1944; McFetridge, 1977; Schaller, 1977; Shannon et al., 1975; Smith, 1983). Thus, a major prediction of the predation hypothesis is that females should select habitats that provide good hiding places for their young during the birth season.

In the taruca, males and females separate most strikingly during the fawning season (Chapter 1). The species is markedly sexually dimorphic. Males are larger than females and only males grow antlers. Tarucas also live in a topographically diverse environment that offers a choice of

different habitats. However, it is not known if the sexes segregate by habitat or what factors cause their separation.

In this Chapter, I describe habitats in the study site at La Raya, Peru, and assess the extent and role of habitat separation of the sexes in Hippocamelus antisensis . I evaluate habitat use by female, male, and mixed-sex groups in relation to: (1) elevation; (2) slope of the terrain; (3) vegetation-type; (4) distance to water supplies; (5) concealment (provided by rock-cover and relief features); and (6) antipredator behavior and escape terrain. Although additional hypotheses are considered, I discuss ecological separation of the sexes mainly in light of the hypotheses that: (1) females select the best foraging habitats to meet higher metabolic demands of lactation; and (2) females select habitats that provide the greatest concealment for their fawns.

2.2 MATERIALS AND METHODS

2.2.1 Grid System and Environmental Factors Recorded

All of the analyses refer to the main study area (Fig. 1). I divided this area into 250x250-m quadrats and drew a grid system on a topographical map of La Raya (scale 1:25,000). A total of 1,264 quadrats were classified according to 8 ecological variables with the aid of the map, aerial and panoramic photographs, and terrestrial surveys of the area.

The following environmental factors were recorded at mid-point of each quadrat. (1) Elevation , to the nearest 25-m contour interval. (2) Vegetation-type , within a 50-m radius . Three broad classes were considered: "Long-Grass", dominated by perennial straw grasses (Calamagrostis , Stipa , Festuca) reaching heights of over 15 cm (but rarely measuring over 50 cm); "Short-Grass", lacking long grasses and dominated mainly by annual short grasses (Hordeum , Bromus) and forbs (Alchemilla , Gnaphalium , Hipchoeris) measuring 15 cm or less in height, and; "Marsh", dominated by perennial and annual forbs (Distichia , Hipchoeris , Luzula , Plantago) and grasses (Calamagrostis , Agrostis) growing in moist areas. Areas devoid of any vegetation were classed as "Bare". (3) Distance to nearest water supply , measured only if water location fell outside quadrat. Otherwise it was recorded as "present".

In addition, the following factors were recorded for the entire quadrat. (4) Average gradient of the slope , in

degrees. (5) Rockiness of terrain , in percent cover. (6) Amount of permanent snow/ice cover , in percent cover. (7) Number of troughs and/or ridges , only relief features large enough to conceal a deer-sized object were considered. (8) Presence/absence of terrace(s) . A list of these environmental factors and their relative frequencies are given in section 2.3.1 (Table 11).

2.2.2 Deer Observations and Data Recorded

Collection of data on deer distribution and habitat use was greatly influenced by the topographical features of the area. The rugged terrain made systematic transect sampling (e.g. Western , 1976) impossible. Also, because of its size (79 km²), I could not cover the entire area in one day. I, therefore divided the area into 8 subunits (Table 9) each of which could be covered in a day. This partitioning was based on geomorphology.

Tarucas were searched from fixed search routes and from natural vantage points. Once a deer group was found, I would stay at the location for as long as the group remained in sight. Time permitting, I continued to search for other groups in the same area, or moved on to another subunit. The biases inherent in this method and their possible influence on my results are discussed below (see sections 2.2.3 and 2.3.3).

Table 9. Size of the 8 subunits in the main study area.

SUBUNIT	No. of QUADRATS	km ²	% STUDY AREA
CHIMBOLLA	134	8.4	10.6
HUARIPINA	156	9.8	12.3
JATUNCUCHO	240	15.0	19.0
JUCHUYCUCHO	119	7.4	9.4
PULPERAPATA	58	3.6	4.6
TAMBO	190	11.9	15.0
VISCACHANE	124	7.8	9.8
YAHUARCOTA	243	15.2	19.2
TOTAL	1,264	79.1	100.0

Table 10 presents the total number of visits and the number of groups observed in each subunit during the entire study. Only group observations made while searching for deer in all representative habitats are included (ie. casual sightings have been omitted).

When a group of deer was located, the following additional environmental factors were recorded at the beginning, end, and every hour during the observation: (1) date ; (2) time ; (3) location : recorded on the map; (4) elevation : at the

Table 10. Number of visits to each subunit within the main study area and number of groups observed during the entire study.

SUBUNIT	No. VISITS	No. GROUPS
CHIMBOLLA	41	41
HUARIPINA	17	10
JATUNCUCHO	35	55
JUCHUYCUCHO	11	8
PULPERAPATA	32	5
TAMBO	6	0
VISACHANE	49	50
YAHUARCOTA	19	19
TOTAL	210	188

group's location to the nearest 25-m contour interval; and (5) vegetation-type : within 50-m radius around animals. The remainder factors (Table 11, section 2.3.1) were given the class of the quadrat in which the deer were observed. On occasions when I disturbed and flushed the deer, the topographic feature (e.g. trough, ridge, mountain-top, rock-outcrop) that caused me to lose sight of the animals was recorded as "escape cover".

Some records were not used in habitat analyses. These were: (1) observations after a group was disturbed by the observer; (2) the final record of observations less than 1/2 hr in duration; (3) the final record of observations more than 1/2

hr but less than 1 hr in duration if the record fell within the same hour-period as the first record (e.g. first record at 9:00 and final record at 9:45); and (4) casual observations (see above). A total of 310 observations were recorded during the entire study.

2.2.3 Data Analysis

In most analyses that follow I have used the MIDAS (Michigan Interactive Data Analysis System) statistical package. Habitat data included interval, ordinal and nominal variables. This precluded the use of some variables in a few analyses and required data transformation in others.

A description of the main study area was obtained from information gathered for all quadrats. Three types of analyses were used: 1) frequency distribution of the 8 environmental variables (interval data were divided into discrete categories); 2) partial correlations among interval and ordinal variables; and 3) frequency distribution of variables within five altitudinal levels.

My sampling techniques did not account for habitat availability for two reasons. First, repeated visits to a given subunit were not always comparable since I often searched an area only until a deer group was found. Thus on occasions I did search a whole subunit. Second, quadrats could not be searched equally, since visibility was influenced by distance and by differing topographic features (e.g. amount of rockiness,

direction of slope, and richness of relief features).

Although my analyses cannot accurately reveal habitat selection by tarucas, comparisons of habitat use between sexes or types of groups are possible. For these comparisons I only used data from quadrats where deer were observed. Observed frequencies were then compared to expected habitat frequencies. Since visibility could influence these comparisons, the results may still be biased. I evaluated this bias by checking for large deviations from expected habitat frequencies and determining the direction of the visibility bias for a particular variable. In general, however, deer were found more frequently in sites with reduced visibility. I therefore probably missed some groups, and thus may have underestimated actual use of the preferred habitats.

I assessed habitat use by groups rather than individuals for two reasons. First, preliminary tests of association showed the same trends when individuals or groups were compared. Second, it is very unlikely that all individuals in a group actively selected a given site. Individuals in a group moved cohesively, often in single file, between foraging or resting sites. An adult female usually led female or mixed-sex groups.

To compare the habitat use by female, male, and mixed-sex groups I divided the year into three periods. The first one, January through April, spanned the fawning season and had the highest monthly proportion of single-sex groups. The second period, May through August, included the mating season, which

coincided with the driest time of the year. During the last period, September through December, males shed their antlers and the rainy season sets in. In the last two periods the proportion of single-sex groups was very low. These three periods I refer to as "fawning", "mating", and "antler-shedding" seasons. Comparisons of habitat use were made as follows: 1) comparisons among female, male, and mixed-sex groups encountered during the fawning season; and 2) comparisons of each of the above group-types in the fawning season with mixed-sex groups found during the other two seasons.

2.3 RESULTS

2.3.1 Habitat and Relations between Environmental Factors

In a rugged, high mountainous terrain with open vegetation such as that found at La Raya, topography and other geomorphological features contribute greatly to the three-dimensional structure and heterogeneity of the habitat. The resulting spatial complexity is a mosaic of habitat conditions rather than well-delimited habitat-types. I first describe the features of the main study area: a) elevation, b) permanent snow-cover, c) slope, d) rock-cover, e) number of relief features, f) distance to water sources, and g) vegetation-types. Second, I assess relationships between pairs of environmental variables. Finally, I compare the habitats in five altitudinal levels.

General description of the area

Table 11 gives a summary of the habitat. The 1,400-m altitudinal drop from the highest peak to the lowest valley bottom in the area encompassed both a permanent ice/snow line (around 5,200 m) that changed little seasonally, and the uppermost limit of the vegetation (between 4,900 and 5,000 m). Approximately 90% of the area was free of permanent snow cover. During the wet, summer season, snow rarely accumulated below the permanent snow line, and it never stayed on the ground below the vegetation's upper limit for more than 3 days at a time. Thus

Table 11. Habitat description of the main study area according to the environmental variables recorded for each quadrat (N=1,264).

=====		
VARIABLE	CLASS	% of N

ELEVATION (m)	4,075-4,275	16.4
	4,300-4,575	31.4
	4,600-4,875	27.1
	4,900-5,175	19.8
	5,200-5,450	5.4
SLOPE (degrees)	<15	22.3
	>=15-<30	48.3
	>=30	29.4
RELIEF (sum of ridges and troughs)	<=2	70.1
	3-4	23.3
	>=5	6.6
ROCK COVER (%)	0	43.8
	<50	37.3
	>=50	18.8
PERMANENT SNOW COVER (%)	0	90.4
	<50	3.4
	>=50	6.2
TERRACE	absent	91.1
	present	8.9
VEGETATION TYPE	long grass	53.6
	marsh	11.2
	short grass	4.1
	bare ground	31.1
DISTANCE TO NEAREST OPEN WATER SOURCE (m)	present in quadrat	28.0/21.8 *
	absent; <=500	41.6/37.3
	absent; >500-<=1000	25.6/29.5
	absent; >1000	4.8/11.4

* Nov-May/Jun-Oct

snow cover was probably not a major factor affecting deer during the study. Most water supplies in the area (see below), however, originated from the permanent snow fields. The slope of the terrain varied from 0° to 50° (mean = 22°). Flat or gently sloping terrain was mostly associated with valley bottoms while steep terrain was characteristic of mid and upper mountain sides. About 70% of the area had slopes of 15° or steeper. Rock-outcrops, boulder fields, or rock escarpments (some massive) interspersed grass meadows and were present in 56% of all quadrats, mainly on mountain sides and tops. Rock-cover was one of the few features in this "open" environment that could provide good concealment for deer. Other factors that provided some concealment were troughs, ravines, shoulders, and ridges. About 30% of the quadrats had 3 or more of these relief features. Other relief features consisted of small terraces (few were larger than the 250x250-m quadrats) on mountain sides. These were uncommon (present in 9% of the quadrats) but seemed important for certain deer groups. Being flat, exposed areas, terraces offered little concealment except from below.

Open water sources were common. During the rainy season, 70% of the quadrats were located within 500 m of a water supply. During the dry season, this figure dropped to about 60%. Most water sources consisted of streams, but a few ponds and seasonal water-holes were also present. Finally, Long-grass type was present in 54% of all quadrats. Next were Marsh (11%), and Short-grass (4%). Appendix A lists and gives the mean number of plant species found in each of these vegetation-types. The remainder of the area (30%) lacked any vegetation.

Correlations between habitat variables

As expected, there were correlations between pairs of these variables (Table 12). The highest positive partial correlations occurred between amount of rock-cover and slope; distance to water and slope; and elevation and amount of rock-cover. There was no correlation between distance to water and amount of relief. A negative correlation existed during the rainy season between distance to water and amount of rock-cover but these variables were not correlated during the dry season. Since vegetation-types and terraces were recorded as present or absent, they were excluded from the correlation analyses.

Chi-square tests, however, revealed some important relationships. The proportion of quadrats lacking vegetation sharply increased with greater elevation, rockiness, slope, and relief ($p < 0.0001$ in all cases). The decrease of plant cover with elevation and the fact that the area contained the uppermost altitudinal limit of vegetation, suggest also a negative relationship between plant biomass per unit area and elevation within the study area. This was shown in a previous study in this area (Holgado et al., 1979). The proportion of areas with bare ground also increased with distance to water, during both the rainy and dry seasons ($p < 0.0001$ in both cases). The presence of vegetation was independent of the presence of terraces ($p > 0.05$).

There were also associations between particular vegetation-types and other variables. The proportion of

Table 12. Partial correlations between habitat variables. Only interval and ordinal variables were considered. The partial correlation coefficient for a given variable-pair was estimated with all other variables held constant. The correlation coefficient (R) and p values are shown. Since the distribution of free water sources varies with season, partial correlations for the rainy (November-May) and the dry (June-October) seasons are presented separately.

=====					
NOVEMBER-MAY			JUNE-OCTOBER		
-----			-----		
VARIABLE-PAIR	R	p	VARIABLE-PAIR	R	p

ROCK/SLOPE	.40	<.01	ROCK/SLOPE	.40	<.01
DISWATER/SLOPE	.32	<.01	ROCK/ELEV	.27	<.01
ROCK/ELEV	.28	<.01	DISWATER/SLOPE	.25	<.01
SLOPE/ELEV	.20	<.01	SLOPE/ELEV	.21	<.01
RELIEF/ROCK	.19	<.01	RELIEF/ROCK	.20	<.01
RELIEF/ELEV	.17	<.01	RELIEF/ELEV	.17	<.01
RELIEF/SLOPE	.14	<.01	RELIEF/SLOPE	.12	<.01
DISWATER/ELEV	.08	<.01	DISWATER/ELEV	.07	<.05
DISWATER/ROCK	-.10	<.01	DISWATER/RELIEF	.01	N.S.
DISWATER/RELIEF	-.05	N.S.	DISWATER/ROCK	.00	N.S.

N=1264; df=1259 for all cases.

quadrats with Long-grass or Marsh types decreased with increasing elevation ($p < 0.0001$ in both cases), rockiness ($p < 0.0001$ in both cases), and relief ($p < 0.05$, and $p < 0.01$ respectively). The proportion of quadrats with Short-grass type, in contrast, increased with elevation ($p < 0.0001$) and with greater rockiness of the terrain ($p < 0.01$). Short-grass habitat was also associated with terraces more than expected ($p < 0.05$). Long-grass and Marsh habitats occurred independently of presence of terraces ($p > 0.05$, in both cases). As expected, the proportion of marshy areas decreased with increasing distance to water year-round ($p < 0.0001$). During the rainy season, there was no association between the proportion of either Long-grass or Short-grass and distance to water ($p > 0.05$ in both cases). During the dry season, however, the proportion of both these two vegetation-types increased with increasing distance to water sources ($p < 0.01$, and $p < 0.001$ respectively).

Altitudinal levels

To illustrate the relationship between elevation and other habitat variables, I divided the main study area into 5 altitudinal levels (Table 13). Level 1 (4,075-4,275 m) consisted mainly of valley bottom and had good drainage, gently sloping terrain, and extensive cover by vegetation. This level had the highest proportion (30%) of quadrats with marshy vegetation. However, rock-cover and relief features were rare.

Level 2 (4,300-4,575 m) was characterized by high valley-bottoms and low mountain side, good drainage, terrain of

varying slopes, and good cover by vegetation. The proportion of Long-grass vegetation reached its highest value (83%) here. This level had little rock-cover and only a few relief features.

Level 3 (4,600-4,875 m) included mainly mid mountain sides. This level had a high percent of rock-cover (82% of quadrats had at least some rock-cover) and relief features were common (43% of quadrats had 3 or more troughs and/or ridges). It was also characterized by very steep terrain (slopes of 30° or steeper gradients were present in 44% of quadrats in this level). Water supplies were less common than they were in lower levels. About 64% of quadrats in this level lay within 500 m of water during the rainy season. This proportion dropped to 42% during the dry season, the lowest value among all levels. Some vegetation was present in 70% of the quadrats. The proportion of quadrats with Short-grass was highest (10%) in this level.

Level 4 (4,900-5,175 m) consisted of upper mountain sides and some mountain tops. As was the case for level 3, it had a high proportion of rock-cover, relatively high number of relief features, and very steep slopes. An important feature of this level is that it contained the uppermost limit of the vegetation. Only sparse vegetation, dominated by tall straw-grasses, and a few small patches of marshy vegetation were present. Here, a few scattered low shrubs, rarely measuring over 50 cm in height, were also found. Eighty-eight percent of the quadrats lacked vegetation.

Level 5 (5,200-5,450 m) included the highest mountain peaks in the area. Slopes were intermediate in steepness

between levels 2 and 3. Snow/ice fields covered most of the ground. This level had little rock-cover, few relief features, and lacked vegetation.

2.3.2 Habitat Use by the Deer

General

I observed groups of taruca most frequently (96%) on mountain sides and tops at a mean elevation of 4,661 m (± 10.7 SE). Deer were largely absent from two of the five altitudinal levels described above. I never observed tarucas in level 1 (main valley-bottom; 4,075-4,275 m), although they have occasionally been seen here after dusk or at dawn by La Raya personnel. This level was extensively used by alpacas and humans. Tarucas were seldom observed at level 5 (5,200-5,450 m) either. I did observe one group at 5,200 m on a snow-free rock-outcrop outside the main study area. Deer were seen at the permanent snow line once.

Habitat use comparisons

There were significant differences in habitat use among the different types of groups. I used two approaches to determine the extent and direction of these differences. First, I carried out Chi-square tests to compare use of each individual habitat factor by groups of different types. Tables B1 through B8 give percent use of each habitat variable and Tables B9

Table 13. Frequency distribution (in percent) of habitat variables within 5 altitudinal levels in the main study area. LEVEL 1= 4,075-4,275m; LEVEL 2= 4,300-4575m; LEVEL 3= 4,600-4875m; LEVEL 4= 4,900-5,175m; LEVEL 5= 5,200-5,450m. RELIEF= Sum of ridges and troughs; ROCK= Percent cover by rock; SNOW= Percent cover by permanent snow/ice; DISWAT= Distance to nearest open water source.

VARIABLE CLASS		LEVEL 1 N=207	LEVEL 2 N=397	LEVEL 3 N=342	LEVEL 4 N=250	LEVEL 5 N=68
		100.0%	100.0%	100.0%	100.0%	100.0%
SLOPE	<15	68.6	23.9	8.2	4.0	10.3
	>=15<30	25.6	49.4	58.2	48.8	60.3
	>=30	5.8	26.7	43.6	47.2	29.4
RELIEF	<2	92.8	74.8	57.0	59.6	77.9
	3-4	6.3	22.2	31.6	29.6	16.2
	>=5	1.0	3.0	11.4	10.8	5.9
ROCK	0 %	97.1	56.7	17.8	10.0	61.8
	<50 %	2.9	36.5	49.7	51.6	32.4
	>=50 %	0.0	6.8	32.5	38.4	5.9
SNOW	0 %	100.0	100.0	100.0	78.0	2.9
	<50 %	0.0	0.0	0.0	12.8	16.2
	>=50 %	0.0	0.0	0.0	9.2	80.9
TERRACE	absent	100.0	90.4	86.8	90.0	94.1
	present	0.0	9.6	13.2	10.0	5.9
VEGET	long grass	67.6	83.4	54.1	8.4	0.0
	marsh	30.4	11.8	7.0	3.2	0.0
	short grass	2.0	3.8	9.6	0.0	0.0
	bare ground	0.0	1.0	29.2	88.4	100.0
DISWAT	<=500m	84.5	70.5	64.0	67.2	55.9
NOV-MAY	>500m	15.5	29.5	36.0	32.8	44.1
DISWAT	<=500m	84.5	61.7	41.8	59.2	52.9
JUN-OCT	>500m	15.5	38.3	58.2	40.8	47.1

through B11 present statistical results of paired-wise group comparisons. I also used Chi-square analyses to test for associations between pairs of habitat variables in the areas where different types of groups were observed. I give these results in the text below (only p values of the Chi-square tests are shown). I compare these associations to correlations between the same pairs of variables in the study area in section 2.3.3.

The second approach uses multivariate discriminant analysis to determine which habitat factors best discriminate the different types of groups and to obtain an overall index of habitat use overlap. Since my data contained interval, ordinal, and nominal variables, all of these were transformed into dummy variables (Green, 1976; Nievergelt, 1981). There was good agreement between discriminant analyses and Chi-square tests; ie. the best variables for discriminating groups had in general the highest Chi-square values, and the direction of differences (given by the discriminant functions) was the same as that from contingency tables. Table C1 lists the dummy variables used, and Tables C2 and C3 presents the results of the discriminant analyses. I first examine habitat use differences during the fawning season (Jan-Apr) when sexual segregation took place. I then give results for inter-seasonal comparisons.

(a) Fawning-season comparisons

During the fawning season, female groups were found at significantly higher elevations (mean = 4,684 m \pm 28.2 SE) than were either male (mean = 4,573 m \pm 26.2 SE) or mixed-sex groups (mean = 4,550 m \pm 19.2 SE). These two latter groups did not differ in this respect (Tables B1, B9). These differences were partly explained by differences in daily vertical movement of the groups (Table B2). Mixed-sex groups showed a strong tendency to move vertically during the day, using lower elevations at dawn, then moving upwards as the day progressed ($p < 0.05$). Although male groups showed no significant differences ($X^2 = 6.6$, $p > 0.05$) in vertical distribution during the day, individual males showed the same vertical movement ($X^2 = 13.3$, $p < 0.01$) as did mixed-sex groups. Female groups, however, remained at relatively high elevations all day ($p > 0.05$).

Groups also differed with respect to the slope of the terrain (Tables B3, B9). Female groups used significantly steeper slopes than either male or mixed-sex groups. No differences in this regard were found between male and mixed-sex groups. Female groups always used steep terrain regardless of elevation ($p > 0.05$). In contrast, for male and mixed-sex groups the degree of slope used was dependent on elevation ($p < 0.0001$ in both cases). Male and mixed-sex groups occupied steeper terrain at higher elevations.

Groups were found in areas that differed significantly

in amount of rock-cover (Tables B4, B9). Female groups were always found in terrain with rock-cover, and used rockier areas than did either male or mixed-sex groups. Male groups also used areas with more rock-cover than did mixed-sex groups. The frequencies of use of rocky terrain were independent of elevation for all three group-types ($p > 0.05$ in all cases). For all three types of groups, there was a positive relationship between rockiness and slope of the terrain that they used ($p < 0.01$ for female and male groups, $p < 0.05$ for mixed-sex groups).

Male groups used areas with the least amount of relief (number of troughs and ridges in a quadrat) (Tables B5, B9). Female and mixed-sex groups did not differ in this respect. The use of areas with different amounts of relief was related to elevation for all three groups. The areas used by female groups had more relief features at lower elevations than they had at higher levels ($p < 0.05$), while the terrain used by male and mixed-sex groups increased in amount of relief as they moved to higher elevations ($p < 0.01$ and $p < 0.001$ respectively). A similar relationship existed for the use of terrain with varying degrees of relief and slope. Female groups occupied areas with greater amount of relief if the terrain was not steep and used areas with less relief on steeper terrain ($p < 0.001$). Male and mixed-sex groups, on the other hand, used areas with greater relief as they moved onto steeper terrain ($p < 0.05$ and $p < 0.0001$ respectively). There was also a dependency between rockiness and amount of relief in the terrain used by male and female groups. Female groups occupied terrain with greater rock-cover

in areas with little relief and vice versa ($p < 0.01$), while male groups used areas with increasing percent of rock-cover as they occupied terrain with greater amounts of relief ($p < 0.05$). Mixed groups used areas in which rockiness of the terrain was independent of amount of relief ($p > 0.05$). Finally, female groups were found on terraces significantly less frequently than other groups (Tables B6, B9). Male and mixed-sex groups did not differ in this regard (Table B9).

No differences existed in the use of vegetation-types between female and male or female and mixed-sex groups (Tables B7, B9). Female and mixed-sex groups were found farther away from free water sources than were male groups (Tables B8, B9). No differences in this regard were detected between female and mixed-sex groups.

(b) Inter-seasonal comparisons

To analyze seasonal shifts in habitat use I compared the three group-types observed during the fawning season with mixed-sex groups found during the mating and antler-shedding seasons. Outside of the fawning season female and male groups were uncommon. Thus, they are not included in the comparisons. Statistical results for the comparisons are given in Tables B10 and B11.

During the mating season (May-Aug), mixed-sex groups occupied higher elevations (mean = 4,802 m \pm 21.5 SE) than any other groups at any time during the year. Use of higher terrain

was associated with highest use (22.4%) of marshy vegetation, indicating a shift from drier to moister habitats during the dry season. This finding is important because a shift in relative use of types of vegetation took place when the sexes aggregated. Compared to female groups in the fawning season, these mixed-sex groups used significantly less steep and less rocky terrain. Mixed-sex groups in the mating season did, however, use steeper terrain than male or mixed-sex groups in the fawning season. The areas used by mixed-sex groups in the mating season and those occupied by female or mixed-sex groups in the fawning season did not differ with regard to amount of relief or distance to water. Mixed-sex groups used terrain with greater relief and were found farther from water sources during the mating season than were male groups during the fawning season. Finally, mating season mixed-sex groups, like fawning season female groups, made little use of terraces.

Mixed-sex groups during the antler-shedding season were found at high elevation (mean = 4,721 m \pm 20.8 SE), but not as high as that of mixed-sex groups in the mating season. They were, however, found at greater distances from water than any other group-type during the year. During this season, mixed-sex groups decreased their use of marshy habitats, indicating a return to using more xeric vegetation. During the antler-shedding season, mixed-sex groups used vegetation habitats with the same frequency as that of groups during the fawning season, indicating an absence of shifts in use of vegetation-types as the sexes segregated. Groups from the antler-shedding season did not differ from female groups in the fawning season in use

of steep terrain, but used significantly less rocky terrain than did the latter (Tables B4, B11). Compared to mixed-sex and male groups in the fawning season, antler-shedding groups used steeper slopes. Finally, antler-shedding groups used areas with little relief, as did male groups in the fawning season.

Results from stepwise multiple discriminant analyses (Tables C2-C3) agree broadly with the above results. In addition, they suggest that female and mixed-sex groups differed most during the fawning season, while male and mixed-sex groups were closest in overall habitat use. During the mating season, mixed-sex groups (which contained previously segregated females and their fawns) appeared closer in overall habitat use to female groups in the fawning season than to any other group. Mixed-sex groups in the antler-shedding season resembled mating season groups in habitat use, while they were most different from male groups in the fawning season.

To summarize, during the fawning season pregnant/lactating females occupied different habitats than groups containing adult males. In contrast, the habitats of male and mixed-sex groups were rather similar. Female groups were restricted to high elevations, while male and mixed-sex groups occupied lower elevations. Some mixed-sex and male groups, however, moved vertically each day. Thus, they used a wider range of habitats than did female groups. The most striking habitat difference lay in the use of very steep, rocky terrain by female groups. No other groups, inside or outside the fawning season, used rocky habitat to the same extent.

Female groups also used terrain with more troughs and ridges than did contemporary male groups, or mixed-sex groups outside the fawning season. Compared to other groups, female groups made little use of terraces. Groups containing females occurred farther away from water sources than did male groups. At the time of sexual segregation I detected no differences between female and other groups in the use of vegetation types, although there was a clear shift from xeric to moist vegetation when the sexes aggregated during the dry season. In contrast, no shifts in use of vegetation-types occurred as mixed-sex groups in the antler-shedding season broke apart into different group-types in the fawning season. Table 14 summarizes habitat comparisons for the fawning season.

2.3.3 Habitat Selection, Biases, and Correlations

I have shown that different group-types used the habitat differently. Three important questions remain: 1) were the different groups "selecting" or "avoiding" certain habitats?; 2) how did visibility affect my comparisons of habitat use?; and 3) were associations between habitat factors used by the deer in the direction predicted from habitat correlations for the whole study area? To answer these questions I relate habitat use to the actual frequency distribution of habitat variables and correlations among them. I restrict this analysis to female, male, and mixed-sex groups in the fawning season because during this period all group-types were observable.

Table 14. Summary of habitat comparisons among female, male, and mixed-sex groups during the fawning season (Jan-Apr). The symbols ">" and "=" mean significantly greater (at .05 level or less) and not significant respectively. Variables that were best discriminant between female/male, and female/mixed-sex group comparisons are also indicated.

=====		
HABITAT VARIABLE	GROUPS COMPARED	BEST DISCRIMINANT?

ELEVATION	FEMALE > MALE = MIXED	YES
SLOPE	FEMALE > MALE = MIXED	NO
ROCK-COVER	FEMALE > MALE > MIXED	YES
RELIEF	FEMALE = MIXED > MALE	YES*
TERRACE	MALE = MIXED > FEMALE	YES**
VEGETATION-TYPES	FEMALE = MALE; FEMALE = MIXED MALE (Short-Grass) > MIXED	NO
DISTANCE TO WATER	FEMALE = MIXED > MALE	NO

* Only in female/mixed comparison		
** Only in female/male comparison		

I earlier noted that my analyses could not fully account for habitat availability because of sampling techniques. Table 15 gives approximate expected habitat values for the areas monitored during the fawning season (Jan-Apr). I estimated expected values by correcting for the number of visits to each subunit and then tallying the corrected frequencies from all subunits. These values are only approximations since quadrats in a given subunit were not searched equally (see section 2.2.3), though I searched all representative habitats in an area during each visit.

Compared to expected values in Table 15, values for areas where deer were observed showed some large deviations. Female groups were found more frequently than expected on very steep and rocky terrain with high number of relief features between 4,600 and 4,875 m. These groups did not select or avoid terraces, and were indifferent to distance from water sources. Male groups occupied terraces more frequently than expected, and preferred areas with moderate rock-cover and near water supplies between 4,300 and 4,575 m. Males were indifferent to amount of relief and steepness of the terrain they used. Mixed-sex groups occupied more often than expected terraces, and terrain with moderate rock-cover, moderate slope, and many relief features at elevations between 4,300 and 4,575 m. Mixed-sex groups were unselective with regard to distance to water. Finally, all groups appeared to select short-grass habitat over the other two vegetation-types.

Were deviations from expected habitat values a

Table 15. Habitat variable frequencies during the fawning season (Jan-Apr). Actual values have been adjusted to number of visits to different subunits in the main study area (N=8,842). Permanent snow cover has not been included.

=====		
VARIABLE	CLASSES	% of N

ELEVATION (m)	4,075-4,275	4.6
	4,300-4,575	35.7
	4,600-4,875	28.1
	4,900-5,175	24.4
	5,200-5,450	7.2
SLOPE (degrees)	<15	18.3
	>=15-<30	47.7
	>=30	34.0
ROCK-COVER (percent)	0	32.3
	<50	40.8
	>=50	27.0
RELIEF (# of troughs and/or ridges)	<=2	59.3
	3-4	29.7
	>=5	10.9
TERRACE	absent	88.2
	present	11.8
VEGETATION-TYPE	Long grass	43.4
	Short grass	6.4
	Marsh	11.0
	Bare ground	39.3
DISTANCE TO NEAREST WATER SOURCE (m)	<=500	77.3
	>500	22.7

consequence of unequal visibility of deer in different areas? This is unlikely. Areas with good visibility (flat valley bottoms and low slopes lacking rock-cover and topographic relief) were searched at least as intensively as higher terrain. Though deer were easily spotted in the former areas, they were observed less frequently there. Thus, the deviations of female groups toward more broken, rockier terrain were probably real and the values obtained should be conservative. Group-type differences were probably also real. There is no reason to expect mixed-sex or male groups to be less visible than female groups in rugged terrain. The opposite was likely, since mixed-sex groups were larger in group size, and adult males, owing to their large body size and antlers, were generally more conspicuous than adult females.

Were associations in the use of different habitat factors in the direction expected from correlations between variables in the study area? This seemed to be the case only for male and mixed-sex groups. There were interesting exceptions in the case of female groups. Rockiness, relief, slope, and elevation were all positively correlated in the study area (Table 12). Despite this, the use of very steep terrain by female groups was independent of elevation (see page 82). In the tests of association of relief/elevation, relief/slope, and relief/rock-cover, female groups showed negative associations, not positive as expected and found for male and mixed-sex groups (see pages 83,84). This strongly suggests that female groups were not only highly selective in their habitat use, but were also able to compensate for the lack of some topographical

factor (ie. by choosing areas of greater relief if rock-cover was only moderate).

To summarize, during the fawning season, groups of tarucas used some habitats more frequently than expected. This was particularly true for female groups in their use of steep, rocky, and broken terrain. Deviations in habitat use from expected habitat values did not result from searching error or visibility bias, but reflected selectivity in the use of particular habitats by deer. When I tested for associations between pairs of variables in areas used by each group-type, the trends for male and mixed-sex groups were largely those expected from habitat correlations in the whole study area. In contrast, female groups responded to certain habitat features independently or in opposite direction to that expected from habitat correlations. In conclusion, in addition to differing from other groups in habitat use, female groups were highly selective in their use of habitats.

2.3.4 Antipredator behavior

Predators were present in the study area. In 1981, an alpaca herder found the half-buried body of a taruca fawn in a site above the vegetation line. Puma (Felis concolor) tracks were identified around the carcass. Pumas also killed some alpacas and captive vicunas during my stay at La Raya. I found puma tracks on two heavily used deer-feeding areas. Though I never observed pumas, they have occasionally been seen by herders during the day. One puma was killed by local people in

1981.

Other likely predators of deer were semi-feral dogs that belonged to alpaca herders, and were seen roaming in the study area up to several miles from their owners' shacks. Local people assured me that dogs chase and kill even adult deer. I witnessed one chase of a single male taruca by two dogs. The dogs gave up the pursuit and came back to the valley bottom after the deer disappeared over a high ridge. Tarucas responded to the sight or barks of a dog by stopping feeding or standing up if they were resting, and looking attentively in the direction of the dog. After a short time, the deer would rapidly climb up to steeper, rockier terrain or disappear over the nearest ridge or mountain top.

Andean foxes (Dusicyon culpaeus) were also abundant. I often heard their calls at dawn and saw them on four occasions during the day in areas frequented by tarucas. I saw no interactions between foxes and tarucas. Foxes probably represent no danger for grown deer, though they may have been capable of killing newborns (Whitehead, 1972). Andean foxes do prey on young vicunas (Koford, 1957; Franklin, 1983).

One way to study the response of deer to predators was to observe the reaction of tarucas to close encounters with the observer. Normally, as long as I kept more than 100 meters away and below the deer, tarucas would remain undisturbed and would resume their previous activity soon after spotting me. I approached deer at close range on 46 occasions. When I approached them slowly and in full view, the deer's reaction was

to walk away to a higher location and often out of sight. However, when startled at a distance of 50 m or less, they would immediately flee uphill, quickly disappearing from view. When a group was approached from above, they would sometimes go further down or run along the mountain side at first, but they always moved to higher terrain than the observer eventually. The topographic features that caused me to lose sight of the deer after a disturbance are shown in Table 16. For all groups, ridges or mountain tops were the most common (71%) escape cover, followed by rock-outcrops (27%).

Table 16. Escape cover used by deer groups. In instances when deer were disturbed or "flushed" by the observer, escape cover was defined as the topographical feature that caused the observer to lose sight of the animals.

ESCAPE COVER	GROUP-TYPE			ALL GROUPS
	FEMALE	MALE	MIXED-SEX	
	%(n)	%(n)	%(n)	%(n)
RIDGE/ MOUNTAIN TOP	58.3(7)	66.7(6)	81.0(17)	71.4(30)
TROUGH	8.0(1)	(0)	(0)	2.4(1)
ROCK OUTCROP	33.3(4)	33.3(3)	19.0(4)	26.8(11)

Tarucas exhibited a number of behaviors when alarmed. Occasionally, just prior to escaping, one animal (either male or

female) would give a "sneeze" sound that would immediately bring the attention of any individual not already alerted in the group. The sneezer could usually be identified since the behavior was accompanied by a rapid downward motion of the head. The animals' alertness, prior to fleeing, was often characterized by "stiff" walking, in which movements of the neck and legs were slow and exaggerated, and by tail-flicking. While fleeing, deer generally kept their tails up and rump hair erected. This made the rump-patch appear whiter and broader.

Although fleeing to higher and more rugged terrain was the most common response to disturbances among tarucas, there were some exceptions. On four occasions, all involving large solitary males, the animals did not escape but either walked a short distance away or simply did not move. In all cases the males eventually lay down in full view, staring calmly at me. I did not attempt to approach these males closer than 50 m.

On four occasions, females reacted in a very different manner. Unlike large solitary males, the females in question eventually fled but only after much stiff-walking, tail-flicking, and sneezing. Although two of these females were disturbed during the fawning season, I was unable to discover any fawns in the vicinity.

Very young fawns were never observed among groups that fled to higher terrain. The reaction of a small fawn and her mother was observed once. Both were found in an opening a few meters from a rock-outcrop. As soon as they spotted me they ran to the rocks. Shortly after entering the outcrop, the fawn hid

behind a large rock, while the female stopped and stared at me for several minutes. I did not attempt to follow closer. Soon the female also disappeared in the rock-outcrop. Although I never approached a fawn at very close range, it appears that threatened young fawns crouch down and "freeze" (D. Jara, pers. comm.).

2.3.5 Cryptic coloration and hiding behavior of fawns

Beside from being the smallest class, their unspotted dark-grey coats made fawns difficult to spot among rocks or rocky background. Moreover, Hippocamelus fawns appeared to have a "hiding out" period. During observations of female groups in the birth season, fawns remained hidden from view more often than did adults ($\chi^2=31.2$, $p<0.001$) or yearlings ($\chi^2=14.0$, $p<0.001$). If hiding behavior is pronounced during the first days or weeks after birth (Lent, 1974), then it is likely that I was unable to detect very small fawns. Females began to segregate on 11 January 1981. Before 25 February 1981, only two fawns were sighted in 2 out of 15 female groups observed during this period. Thereafter, fawns were observed in most (79%) female groups.

In conclusion, cougars, dogs, and foxes were present in the study area. The remains of a fawn suggested that it had been killed a cougar. The response of deer to dogs indicated that adult tarucas flee in the presence of predators. Generally, all types of groups climbed to higher terrain when I approached them closely (e.g. less than 50 m), but I never

observed very young fawns among escaping individuals. When fleeing, the animals darted toward ridges or rocky terrain where they usually disappeared from view. Behaviors such as sneezing, stiff-walking, tail-flicking, and white rump-patch exposure by tarucas were commonly associated with escape. These behaviors may have been used to alert others in the group. In a few occasions, large males did not escape when I approached them. It is possible that they did not regard me as a potential predator, or that they could have repelled my approach had I come any closer. My observations of small fawns were limited but suggest that young hide in response to impending danger. Fawns also appeared to go through a "hiding out" period that coincided with the segregation of their mothers from groups containing adult males.

2.4 DISCUSSION

Habitat segregation of the sexes in Hippocamelus antisensis took place during the fawning season, a period in which all pregnant and lactating females separated from groups that contained males. At this time, females moved away from large mixed-sex groups that occupied relatively open habitat. Once segregated, they formed smaller groups with other females and their young and occupied steeper, rockier, and more broken habitat than that of male or mixed-sex groups. Here, I first consider several hypotheses to explain why the sexes segregated. Second, I briefly compare the timing of sexual segregation of tarucas to that of other cervids and to mountain caprids.

Differential Food-selection

Most studies on differential resource exploitation by the sexes in ungulates have focused on food utilization (Bowyer, 1984; Charles et al., 1977; Clutton-Brock et al., 1982; Staines et al., 1982; Takatsuki, 1980; Watson and Staines, 1978). Some authors have concluded that sexual segregation is the result of differences in food habits, and that females occur in areas of better forage quality (Clutton-Brock and Harvey, 1983; Clutton-Brock et al., 1982; Geist, 1974 a,b). Despite some evidence against this hypothesis (Shank, 1982; McCullough, 1979), little attention has been paid to other factors.

My results suggest that the shift in habitat use by lactating tarucas was not determined by forage quality. First,

during sexual segregation, groups did not differ in frequency of use of different vegetation types. Second, shifts in use of vegetation habitats occurred as the sexes aggregated, not when they segregated. Third, plant biomass and productivity are negatively correlated with elevation (Holgado et al., 1979), and lactating females preferred higher elevations. Fourth, plant cover decreased with greater elevation, slope, rock-cover, number of relief features, and distance to water. If females were selecting more productive areas than those used by other groups, they should have used lower elevations and less steep, less rocky, and less broken areas that lay closer to water sources. This suggests that females actually used areas of poorer forage quality. Finally, it is unlikely that food shortage or a reduction in number and size of high quality patches were responsible for spatial segregation, since sexual separation took place during the growing season when food was most abundant and presumably more evenly distributed.

It could be argued that high quality vegetation, although less abundant, grew among rocks, but there are no data to support this. Female groups did select, as did other groups, short-grass habitat over other vegetation-types. Short-grass habitat increased with greater elevation and rock-cover, but it was also associated with terraces. Since male and mixed-sex groups, in contrast to female groups, selected terraces, one could also argue that this selection was the result of preference for areas with short-grass.

To suggest that females used habitats of inferior

forage relative to males is not far-fetched. Shank (1982), studying bighorn sheep (Ovis canadensis), and LaGory (1985), working on white-tailed deer (Odocoileus virginianus), found that females and young occupied habitats of poorer food quality than did adult males. In bighorns, poorer vegetation in female ranges was associated with broken, rocky cliffs. Higher quality forage in male ranges was associated with more open slopes. Shank (1982) concluded that differences in sheep diets simply reflected forage differences in the areas used by the sexes, and that sexual segregation was caused by some unknown factor. From a study of habitat structure and diets in mule deer (Odocoileus hemionus), Mahgoub (1984) concluded that other features, such as topography, were more critical than food resources in determining suitable deer habitat.

Social Antagonism

A second explanation is that social antagonism between the sexes causes them to segregate (LaGory, 1985; Takatsuki, 1983). My observations do not support this. I never observed adult males aggressively exclude or drive females away from areas used by males. Females also did not behave aggressively toward males. I believe that pregnant/lactating females chose to move away from the areas used by mixed-sex groups at the time of segregation.

There is disagreement in the literature regarding the role of male/female interactions in sexual segregation in ungulates. If males use habitats with poorer foods than

females, socially dominant males may move away from or avoid prime areas so that their mates and offspring can enjoy reduced competition for food resources (Geist and Petocz, 1977). Where males occupy better foraging habitats than females with young, dominant males may be excluding females (LaGory, 1985). Takatsuki (1983) proposed that lactating females exclude adult males from preferred areas, while Bowyer (1984) and McCullough (1979) concluded that male/female interactions did not influence spatial segregation of the sexes.

Clearly, we need detailed studies of food preferences, forage quality and availability, and social behavior of Hippocamelus to assess properly the food-selection and social-interaction hypotheses. My study, however, suggests that another factor was involved.

Predator avoidance

An alternative hypothesis is that lactating females selected areas that provided concealment to their young during the birth season. One assumption of this hypothesis is that habitats differ in the ease of detection of tarucas by predators. The tundra-like vegetation of La Raya provides little or no cover, but topographic features offer varying degrees of concealment. Among these, rock-cover seemed to be most critical. First, it provided hiding sites and cryptic background for the fawns. Second, it made undetected approach very difficult. Tarucas could scan their surroundings from rock-outcrops and thus spot approaching predators. In contrast,

ridges and troughs, though they concealed the deer from certain angles and long distances, actually made the deer vulnerable to close undetected approaches. My closest observations, without being detected by the animals, were of deer in small ravines or ridge-sides. Terraces also provided concealment for the deer from an observer located below. However, being exposed and flat areas, terraces made deer very conspicuous from above.

My results are consistent with the assumption that habitats differ in protection offered. Females with young preferred very rocky terrain, while they did not differ from mixed-sex groups in regard to relief of the terrain. In addition, female groups were found occupying terraces less frequently than other groups.

Another assumption of the predator avoidance hypothesis is that young fawns are more vulnerable to predation than are adults, once they have been detected. Though I have no direct evidence, this assumption seems reasonable. First, young fawns lack the stamina and agility of older individuals to flee from predators (Curio, 1976; Schaller, 1972) because neuromuscular development is incomplete (Jacobsen, 1984). Second, stamina in fleeing is probably critical at high elevations, where concentration of atmospheric oxygen is severely reduced and aerobic capacity for extreme muscular activity is limited (Hochachka et al., 1983). Finally, young lack experience of their surroundings, and accidents in mountainous terrain are common (Murie, 1944; Schaller, 1977). Knowledge of the area may be useful to traverse rugged terrain,

especially when an individual is being chased by a predator. Selective predation on young has been documented for many ungulates (review by Curio, 1976).

A third assumption is that differential vulnerability among age classes has selected for different antipredator behaviors. Taruca adults flee in the presence of predators, while I found that young fawns probably hide and freeze, like most other cervids (De Vos, 1967; Lent, 1974). The prone response of newborns to approaching predators is uncommon after one week in red deer, Cervus elaphus (Clutton-Brock, 1982), though it may still be used by 3-week old elk, Cervus canadensis (Altmann, 1963). Young cervids also go through a hiding phase characterized by long periods of separation from their mothers, during which the young remain highly immobile (Lent, 1974). This period lasts about 10 days in white-tailed deer, Odocoileus virginianus (Jacobsen, 1984), and 3 weeks in muntjac, Muntiacus reevesi, and roe deer, Capreolus capreolus (Lent, 1974). Predator avoidance may be the most important function of this hiding period (Clutton-Brock et al., 1982; Lent, 1974).

Although young may actively select hiding sites (Clutton-Brock et al., 1982; Lent, 1974; Schaller, 1977), the habitats chosen by females influence the availability of cover for their young (Riley and Dood, 1984). Among most mountain Caprinae, females select broken, rocky cliffs at the time of parturition and remain in this terrain when "nursery" groups of females and young are formed (Geist, 1971; McFetridge, 1977; Murie, 1944).

The only cervid species where young do not hide is caribou, Rangifer tarandus (De Vos, 1967; Lent, 1974), a highly mobile and gregarious species that lives in very open habitat (Whitehead, 1972). Young caribou are very precocial and follow their mothers from the first day. They cannot hide and do not freeze in response to predators (De Vos et al., 1967), but use large groups of conspecifics as protection (Lent, 1974). Interestingly, the caribou is also unique in that females, like males, grow antlers (Whitehead, 1972). Since caribou females do not segregate from males during the calving season, reduced sexual dimorphism may have developed to allow females to compete for food successfully with males (Clutton-Brock and Harvey, 1978). It is equally likely, however, that antlers have developed in female caribou to improve their ability to defend their young (Clutton-Brock et al., 1982). Some species where young do not hide from predators have developed group defence (e.g. muskox, Ovibos moschotus: Lent, 1974; buffalo, Syncerus caffer: Sinclair, 1977).

The last assumption is that predation has been a major risk factor for tarucas. I believe this to be the case, but have little direct evidence. Cougars were present in low numbers in my study area, and did kill one fawn. Andean foxes were common in the study area, and have been known to prey on young vicunas (Franklin, 1974; Koford, 1957). There were also some 15 to 20 stray dogs at La Raya, and these may be more important predators (Gavin et al., 1984; Roe and Rees, 1975).

Evidence linking the use of rugged, rocky terrain by

female tarucas to reduction in predation risk for fawns is circumstantial. Tarucas used this terrain to evade me when I approached or startled them from close distance, and also to escape from dogs. In mountain Caprinae, rugged, rock cliffs and outcrops are used by all age classes to escape from pursuing predators (Schaller, 1977; Smith, 1983). Geist (1971) states that this terrain is frequently used by sick and injured animals, presumably because these animals are more vulnerable to predation. Additional evidence comes from Murie's (1944) studies on Dall sheep, Ovis dalli, and wolves, Canis lupus. In the presence of heavy wolf predation, sheep were restricted to rugged cliff areas, and in the absence of wolves, sheep moved onto more open slopes.

A comparison between vicunas and tarucas can further illustrate the relationship between antipredator behavior and habitat structure. On occasions, both species can be found in adjacent areas (pers. obs.), but their behavior and habitat differ. Vicunas prefer very open and flat or undulating terrain (Franklin, 1983). Though I found them on mountain slopes at La Raya, vicunas did not occupy rugged and rocky terrain as much as tarucas did. This was particularly obvious when the animals escaped from disturbances. Vicunas rely on speed to avoid predators (Koford, 1957). Thus, vicunas fled along mountain-sides, avoiding rock-cliffs and outcrops, while tarucas climbed up to rugged terrain. The behavior of young and habitat during birth also differ in both species. Young vicunas can run as fast as their mothers within a few hours after birth, do not freeze in response to predators, and lack a hiding period

(Koford, 1957). If necessary, female vicunas mob and chase predators away from young during the birth season (Franklin, 1983). Finally, pregnant vicunas do not seek rugged, rocky terrain during parturition but give birth in the open (Koford, 1957; pers. obs.).

I conclude that during sexual segregation, lactating taruca females selected habitats offering adequate concealment. I suggest that selection of these habitats is a strategy to reduce predation risk for fawns. This hypothesis illustrates how a single factor, predation risk, may result in different patterns of habitat use if vulnerability to predation varies with age in different habitats (Werner et al., 1983). This hypothesis also explains the formation of smaller groups during periods of food abundance, when general theory (e.g. Estes, 1974) predicts formation of larger groups. During sexual segregation, lactating females might further decrease the chances of being detected by predators by forming smaller groups as well as selecting more concealing habitats.

Experiments involving manipulation of resources, tarucas, or predators are impractical or unadvisable since we are dealing with a large and endangered species. However, there are a number of ways in which different hypotheses could be tested under natural conditions. For instance, if food preferences differ in male and females, then the degree of spatial segregation of the sexes should be a function of the dispersion pattern of preferred plants. Thus, sexual segregation ought to be more pronounced in areas where preferred

items of each sex grow separately on different portions of the range. If on the other hand, the sexes have similar diets but segregate to reduce competition, then separation should be a function of food abundance. Therefore, sexual segregation should be more pronounced in years or areas where food is scarce or population density high. Since animals may not forage optimally in the presence of predators (Werner, et al., 1983), predator abundance in the study areas should also be monitored. If predation risk for young is a major factor responsible for segregation of the sexes, the degree of separation should be a function of dispersion of cover, variability in the concealment that each habitat can offer, and predator abundance. Segregation of males and females should be more pronounced in areas with greater heterogeneity of cover habitats and greater predator abundance. Results from different areas and years could be used to test for consistency among predictions. Finally, since these studies would be testing alternative consequences of individual-habitat interactions, quantitative information on yearly energetic and nutritional requirements of males and females, and on social, foraging, and antipredator behaviors of different age-sex classes are necessary to understand the mechanisms of sexual segregation.

Comparison with Mountain Caprinae

Tarucas are unique among cervids but resemble mountain Caprinae in social organization and habitat utilization. A major feature of taruca social dynamics is that sexual

segregation is confined to the birth season. Thus, adult males and females are found together nearly all year, as are some mountain caprids (e.g. bharal, Pseudois nayaur, Asiatic ibex, Capra ibex, wild goat, Capra nayaur, and chamois, Rupricapra rupricapra; Schaller, 1977). This pattern contrasts that of most seasonal breeding cervids, where males and females rarely intermix outside of the mating season (Bowyer, 1984; Clutton-Brock et al., 1982; De Vos, 1967; Hirth, 1977; Takatsuki, 1983). The fact that no other cervid resembles Hippocamelus in its caprid-like use of rugged and rocky mountainous terrain, suggests that the social organization of this species has been influenced by its unusual environment.

The use of restricted and localized areas by tarucas year-round may have facilitated the formation of mixed-sex groups outside the mating season. Although more detailed information is needed for comparisons across species of mountain Caprinae, some evidence suggest that Capra species are more restricted in their year-round movements and use a more specialized habitat than do Ovis species (Schaller, 1977). In contrast to goats, Ovis species show marked sexual segregation nearly all year (Geist, 1971; Schaller, 1977). Thus, tarucas resemble goats more than sheep in habitat and social structure.

APPENDIX A

During the study, 30 taruca feeding-sites were selected at random from a larger sample. Each site was classified as either LONG-GRASS, SHORT-GRASS, or MARSH vegetation-type (see section 2.2) On each site, vegetation was sampled along two 15-m transect lines which crossed at mid-point at right angles. The following tables (A1, A2, and A3) give the mean number of species and list identified species collected from 11 LONG-GRASS , 12 SHORT-GRASS, and 7 MARSH sites. Unless otherwise specified, plants for which only generic name is given represent single species. Although moss and lichen species were not collected, their presence in a site is noted.

Table A1. Plant species in LONG-GRASS vegetation-type.

SPECIES NAME	FAMILY	# SITES
<u>Luzula peruviana</u>	Juncaceae	8
<u>Calamagrostis antoniana</u>	Gramineae	6
<u>Geranium</u> sp	Geraniaceae	6
<u>Stipa</u> sp	Gramineae	6
<u>Gnaphalium</u> spp	Compositae	9*
<u>Gentiana</u> spp	Gentianaceae	6*
<u>Calamagrostis heterophylla</u>	Gramineae	4
<u>Alchemilla pinnata</u>	Rosaceae	3
<u>Luzula</u> sp	Juncaceae	3
<u>Poa gimnanta</u>	Gramineae	3
<u>Poa pearsonii</u>	Gramineae	3
<u>Arenaria lanuginosa</u>	Caryophyllaceae	2
<u>Baccharis</u> sp	Compositae	2
<u>Bromus lanatus</u>	Gramineae	2
<u>Calamagrostis vicunarum</u>	Gramineae	2
<u>Festuca dolichophylla</u>	Gramineae	2
<u>Scirpus rigidus</u>	Cyperaceae	2
<u>Stipa ichu</u>	Gramineae	2
<u>Aciachne pulvinata</u>	Gramineae	1
<u>Azorella</u> sp	Umbelliferae	1
<u>Baccharis</u> sp	Compositae	1
<u>Calamagrostis brevifolia</u>	Gramineae	1
<u>Calamagrostis chrysantha</u>	Gramineae	1
<u>Cerastium</u> sp	Caryophyllaceae	1
<u>Festuca rigescens</u>	Gramineae	1
<u>Hipochoeris sonchoides</u>	Compositae	1
<u>Hipochoeris taraxacoides</u>	Compositae	1
<u>Liabum</u> sp	Compositae	1
<u>Lobivia</u> sp	Cactaceae	1
<u>Lupinus microphyllus</u>	Leguminosae	1
<u>Muhlenbergia peruviana</u>	Gramineae	1
<u>Oryzopsis</u> sp	Gramineae	1
<u>Plantago</u> sp	Plantaginaceae	1
<u>Poa annua</u>	Gramineae	1
<u>Pycnophyllum</u> sp	Caryophyllaceae	1
<u>Sisyrinchium jamesonii</u>	Iridaceae	1
<u>Solanum</u> sp	Solanaceae	1
<u>Trifolium</u> sp	Leguminosae	1
<u>Valeriana</u> sp	Valerianaceae	1
LICHEN		3
MOSS		7

* Two species.

MEAN # SPECIES PER SITE = 15.6 + 1.41 SE

MEAN # UNIDENTIFIED SPP PER SITE = 5.3 + 1.09 SE

Table A2. Plant species in SHORT-GRASS vegetation-type.

SPECIES NAME	FAMILY	# SITES
<u>Alchemilla pinnata</u>	Rosaceae	8
<u>Luzula peruviana</u>	Juncaceae	6
<u>Scirpus rigidus</u>	Cyperaceae	6
<u>Calamagrostis vicunarum</u>	Gramineae	5
<u>Hordeum muticum</u>	Gramineae	5
<u>Bromus lanatus</u>	Gramineae	4
<u>Calamagrostis heterophylla</u>	Gramineae	3
<u>Gnaphalium sp</u>	Compositae	3
<u>Hipchoeris taraxicoides</u>	Compositae	3
<u>Stipa sp</u>	Gramineae	3
<u>Aciachne pulvinata</u>	Gramineae	2
<u>Calamagrostis antoniana</u>	Gramineae	2
<u>Geranium sessiliflorum</u>	Geraniaceae	2
<u>Avena sp</u>	Gramineae	1
<u>Azorella compacta</u>	Umbelliferae	1
<u>Bromus unioloides</u>	Gramineae	1
<u>Dissanthelium sp</u>	Gramineae	1
<u>Distichia muscoides</u>	Juncaceae	1
<u>Gentiana sp</u>	Gentianaceae	1
<u>Luzula sp</u>	Juncaceae	1
<u>Poa annua</u>	Gramineae	1
<u>Poa gymnantha</u>	Gramineae	1
<u>Pycnophyllum molle</u>	Caryophyllaceae	1
<u>Trifolium sp</u>	Papilionaceae	1
<u>Urtica sp</u>	Urticaceae	1
LICHEN		4
MOSS		5

MEAN # SPECIES PER SITE = 11.8 ± 1.28 SE

MEAN # UNIDENTIFIED SPP PER SITE = 5.6 ± 1.06 SE

Table A3. Plant species in MARSH vegetation-type.

SPECIES NAME	FAMILY	# SITES
<u>Distichia muscoides</u>	Juncaceae	7
<u>Hipchoeris</u> sp	Compositae	6
<u>Calamagrostis brevifolia</u>	Gramineae	5
<u>Agrostis</u> sp	Gramineae	4
<u>Festuca dolichophylla</u>	Gramineae	4
<u>Luzula peruviana</u>	Juncaceae	4
<u>Plantago</u> sp	Plantagianaceae	4
<u>Calamagrostis antoniana</u>	Gramineae	3
<u>Calamagrostis chrysantha</u>	Gramineae	3
<u>Poa</u> sp	Gramineae	3
<u>Dissanthelium</u> sp	Gramineae	2
<u>Azorella compacta</u>	Umbelliferae	1
<u>Calamagrostis rigescens</u>	Gramineae	1
<u>Carex</u> sp	Cyperaceae	1
<u>Gentiana</u> sp	Gentianaceae	1
<u>Poa gimnanta</u>	Gramineae	1
MOSS		7

MEAN # SPECIES PER SITE = 12.7 + 1.60 SE		
MEAN # UNIDENTIFIED SPP PER SITE = 5.4 + 1.07 SE		

APPENDIX B

Table B1. Percent vertical distribution of female, male, and mixed-sex groups (FEMALE, MALE, and MIXED-F) from January through April; mixed-sex groups from May through August (MIXED-M); and mixed-sex groups from September through December (MIXED-S) in the main study area. The three 4-month periods given above contain the fawning, mating, and antler-shedding seasons respectively. Out of the five altitudinal levels present, deer occurred only in three: :LEVEL 2= 4,300-4,575m; LEVEL 3= 4,600-4,875m; and LEVEL 4= 4,900-5,175m.

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LEVEL	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0%	100.0%	100.0%	100.0%	100.0%
	N= 47	N= 42	N= 72	N= 49	N= 51
LEVEL 2	31.9	69.0	76.4	10.2	19.6
LEVEL 3	51.1	21.4	15.3	59.2	68.6
LEVEL 4	17.0	9.5	8.3	30.6	11.8

Table B2. Percent vertical distribution of different deer group-types at 3 time periods during the day. Out of the 5 altitudinal levels present in the main study area, deer groups occurred in three: LEVEL 2= 4,300-4,575m; LEVEL 3= 4,600-4,875m; and LEVEL 4= 4,900-5,175m. The time periods considered are: PERIOD 1= 500-759hrs; PERIOD 2= 800-1059hrs; and PERIOD 3= 1100-1259hrs. Group-types are: FEMALE; MALE; MIXED-F (female, male, and mixed-sex groups from January through April); MIXED-M (mixed-sex groups from May through August); and MIXED-S (mixed-sex groups from September through December). The three 4-month seasons given above contain the fawning, mating, and antler-shedding seasons respectively.

LEVEL	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0%	100.0%	100.0%	100.0%	100.0%
PERIOD 1:	N=11	N=7	N=20	N=2	N=14
LEVEL 2	27.3	100.0	95.0	0.0	28.6
LEVEL 3	63.6	0.0	0.0	100.0	71.4
LEVEL 4	9.1	0.0	5.0	0.0	0.0
PERIOD 2:	N=18	N=14	N=29	N=21	N=15
LEVEL 2	22.2	78.6	79.3	4.8	13.3
LEVEL 3	50.0	14.3	10.3	61.9	66.7
LEVEL 4	27.8	7.1	10.3	33.3	20.0
PERIOD 3:	N=15	N=16	N=17	N=19	N=12
LEVEL 2	33.3	50.0	52.9	5.3	8.3
LEVEL 3	53.3	31.3	35.3	52.6	66.7
LEVEL 4	13.3	18.8	11.8	42.1	25.0

Table B3. Percent use of quadrats with different slopes by female, male and mixed-sex groups (FEMALE, MALE, and MIXED-F) from January through April; mixed-sex groups from September through August (MIXED-M); and mixed-sex groups from September through December (MIXED-S) in the main study area.

SLOPE	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0% N= 47	100.0% N= 42	100.0% N= 72	100.0% N= 49	100.0% N= 51
<15	6.4	21.4	6.9	0.0	3.9
15-30	48.9	57.1	75.0	69.4	41.2
30-45	44.7	21.4	18.1	30.6	54.9

Table B4. Percent use of quadrats with 0%, <50%, and ≥50% rock-cover by female, male, and mixed-sex groups (FEMALE, MALE, and MIXED-F) from January through April; mixed-sex groups from May through August (MIXED-M); and mixed-sex groups from September through December (MIXED-S) in the main study area.

ROCK-COVER	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0% N= 47	100.0% N= 42	100.0% N= 72	100.0% N=49	100.0.% N= 51
0	0.0	9.5	11.1	2.0	5.9
<50	34.0	59.5	81.9	63.3	70.6
≥50	66.0	31.0	6.9	34.7	23.5

Table B5. Percent use of quadrats with various amounts of topographical relief by female, male, and mixed-sex groups (FEMALE, MALE, and MIXED-F) from January through April; mixed-sex groups (MIXED-M) from May through August; and mixed-sex groups (MIXED-S) from September through December in the main study area. Topographical relief was measured by counting the number of ridges and troughs in each quadrat.

RELIEF	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0% N= 47	100.0% N= 42	100.0% N= 72	100.0% N= 49	100.0% N= 51
0-2	21.3	38.1	31.9	18.4	41.2
3-4	53.2	54.8	37.5	38.8	43.1
>4	25.5	7.1	30.6	42.9	15.7

Table B6. Percent use of terraces (YES) by female, male and mixed-sex groups (FEMALE, MALE, and MIXED-F) from January through April; mixed-sex groups from May through August (MIXED-M); and mixed-sex groups from September through December (MIXED-S) in the main study area.

TERRACE	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0% N= 47	100.0% N= 42	100.0% N= 72	100.0% N= 49	100.0% N= 51
NO	91.5	61.9	63.9	85.7	62.7
YES	8.5	38.1	36.1	14.3	37.3

Table B7. Percent use of different vegetation types (including areas with no vegetation) by female, male, and mixed-sex groups (FEMALE, MALE, and MIXED-F) from January through April; mixed-sex groups from May through August (MIXED-M); and mixed-sex groups from September through December (MIXED-S) in the main study area.

VEGETATION TYPE	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0% N= 47	100.0% N= 42	100.0% N= 72	100.0% N= 49	100.0% N= 51
LONG GRASS	68.1	50.0	76.4	51.0	76.5
MARSH	4.3	4.8	2.8	22.4	2.0
SHORT GRASS	25.5	35.7	18.1	4.1	17.6
BARE GROUND	2.1	9.5	2.8	22.4	3.9

Table B8. Percent use of quadrats with water sources $\leq 500\text{m}$ or $> 500\text{m}$ away by female, male, and mixed-sex groups (FEMALE, MALE, and MIXED-F) from January through April; mixed-sex groups from May through August (MIXED-M); and mixed-sex groups from September through December (MIXED-S) in the main study area.

DISTANCE TO WATER	GROUP-TYPE				
	FEMALE	MALE	MIXED-F	MIXED-M	MIXED-S
	100.0% N= 47	100.0% N= 42	100.0% N= 72	100.0% N= 49	100.0% N= 51
≤ 500	72.3	95.2	81.9	73.5	51.0
> 500	27.7	4.8	18.1	26.5	49.0

Table B9. Habitat comparisons between female, male and mixed-sex groups during the fawning season (Jan-April) in the main study area.

=====				
VARIABLE	COMPARISONS			
		FEMALE-MALE	FEMALE-MIXED	MALE-MIXED

ELEVATION	X2	12.36	23.77	0.81
df=2	p	<.01	<.0001	N.S.
SLOPE	X2	7.56	10.06	5.92
df=2	p	<.05	<.01	N.S.
ROCK-COVER	X2	13.10	48.31	11.56
df= 2	p	<.01	<.0001	<.01
RELIEF	X2	6.61	3.02	8.73
df= 2	p	<.05	N.S.	<.05
TERRACE	X2	11.14	11.49	0.04
df= 1	p	<.001	<.001	N.S.
VEGET-TYPE	X2	4.15	1.26	8.73
df= 3	p	N.S.	N.S.	<.05
DIST-WATER	X2	8.30	1.54	4.10
df= 1	p	<.01	N.S.	<.05

Table B10. Habitat comparisons between mixed-sex groups (MIXM) observed during the mating season (May-Aug) and groups (FEMALE, MALE, MIXF) observed during the fawning season (Jan-Apr) and mixed-sex groups (MIXS) during the antler-shedding season (Sep-Dec).

VARIABLE		COMPARISONS			
		MIXM-FEMALE	MIXM-MALE	MIXM-MIXF	MIXM-MIXS
ELEVATION	X2	7.56	33.50	51.10	6.05
df= 2	p	<.05	<.0001	<.0001	<.05
SLOPE	X2	6.08	11.76	5.52	8.97
df= 2	p	<.05	<.01	N.S.	<.05
ROCK-COVER	X2	9.83	2.45	16.54	2.19
df= 2	p	<.01	N.S.	<.001	N.S.
RELIEF	X2	3.29	15.39	3.29	10.81
df= 2	p	N.S.	<.001	N.S.	<.01
TERRACE	X2	0.79	6.79	7.00	6.85
df= 1	p	N.S.	<.01	<.01	<.01
VEGET-TYPE	X2	22.54	19.36	28.43	22.05
df= 3	p	<.001	<.001	<.0001	<.001
DIST-WATER	X2	0.02	7.78	1.24	5.36
df= 1	p	N.S.	<.01	N.S.	<.05

Table B11. Habitat comparisons between mixed-sex groups (MIXS) observed during the antler-shedding season (Sep-Dec) and groups (FEMALE, MALE, MIXF) observed during the fawning season (Jan-Apr).

VARIABLE		COMPARISONS		
		MIXS-FEMALE	MIXS-MALE	MIXS-MIXF
ELEVATION	X2	3.18	24.38	41.29
df= 2	p	N.S.	<.0001	<.0001
SLOPE	X2	1.13	13.67	18.24
df= 2	p	N.S.	<.01	<.001
ROCK-COVER	X2	18.96	1.31	7.35
df= 2	p	<.001	N.S.	<.05
RELIEF	X2	4.74	2.12	3.66
df= 2	p	N.S.	N.S.	N.S.
TERRACE	X2	11.25	0.01	0.02
df= 1	p	<.001	N.S.	N.S.
VEGET-TYPE	X2	1.62	7.10	0.20
df= 3	p	N.S.	N.S.	N.S.
DIST-WATER	X2	4.70	21.90	13.41
df= 1	p	<.05	<.0001	<.001

APPENDIX C

Table C1. List of environmental variables and the classes used as "dummy" variables for the stepwise multiple discriminant analysis. For each environmental variable one class does not appear as dummy variable and is listed without a variable number. Environmental variables correspond only to quadrats where deer were observed. Thus, two elevation classes (LEVEL 1= 4,075-4,275m; and LEVEL 5= 5,200-5,450m) do not appear in the list since no deer groups were observed in these altitudinal levels in the main study area.

=====		
ENVIRONMENTAL VARIABLE	No. OF DUMMY VARIABLE	CLASSES: DUMMY VARIABLES

ELEVATION	--	4,300-4,575
(m)	1	4,600-4,875
	2	4,900-5,175
SLOPE	--	<15
(degrees)	3	15-30
	4	30-45
RELIEF	--	0-2
(sum ridges/troughs)	5	3-4
	6	>4
ROCK-COVER	--	0
(%)	7	<50
	8	>=50
TERRACE	--	no
	9	yes
VEGETATION TYPE	--	bare ground
	10	long
	11	marsh
	12	short
DISTANCE TO NEAREST	--	<500
WATER SOURCE (m)	13	>=500

Table C2. Within-season results from two-group stepwise discriminant analyses carried out with "dummy" variables. Included are percent correct classification, Mahalanobis distance (D-SQUARE) between groups, and best discriminant variables for each two-group analysis. Groups are female (FEM), male (MAL), and mixed-sex (MIXF) observed during the fawning season (Jan-Apr). Best discriminant variables are those that were included in the discriminant functions on the final step of each analysis.

=====			
GROUPS USED IN ANALYSIS	% CORRECT CLASSIFICATION	D-SQUARE	BEST DISCRIMINANTS *

FEM/MAL	76.4	1.66	ROCK-COVER [8] (11.61) ELEVATION [1] (7.68) TERRACE [9] (5.69) ROCK-COVER [7] (5.50)

FEM/MIXF	84.9	3.98	ROCK-COVER [8] (78.03) ELEVATION [1] (19.42) RELIEF [6] (4.74)

MAL/MIXF	67.5	0.84	ROCK-COVER [8] (12.23) RELIEF [6] (8.72)

* For each environmental variable, the corresponding number, in [], and the F value, in (), for the dummy discriminant variables are also shown.

Table C3. Between-season results from two-group stepwise discriminant analyses carried out with "dummy" variables. Included are percent correct classification, Mahalanobis distance (D-SQUARE) between group means, and best discriminant variables for each two-group analysis. Each group-type (female= FEM, male= MAL, and mixed-sex= MIXF) from the fawning season (Jan-Apr) is discriminated against mixed-sex groups (MIXM) from the mating season (May-Aug), and mixed-sex groups (MIXS) from the antler-shedding season (Sep-Dec).

GROUPS USED IN ANALYSIS	% CORRECT CLASSIFICATION	D-SQUARE	BEST DISCRIMINANTS *
FEM/MIXM	71.9	1.42	VEGETATION [12] (18.68) VEGETATION [10] (13.19) ROCK-COVER [8] (4.15)
MAL/MIXM	86.8	4.30	ELEVATION [1] (57.03) ELEVATION [2] (29.13) VEGETATION [12] (24.65) ROCK-COVER [7] (5.29)
MIXF/MIXM	81.8	3.75	ELEVATION [1] (46.66) ELEVATION [2] (33.75) ROCK-COVER [8] (6.61) VEGETATION [11] (6.16)
FEM/MIXS	78.6	2.73	ROCK-COVER [8] (16.63) TERRACE [9] (13.57) RELIEF [6] (12.10) SLOPE [4] (7.40) DISTWATER [13] (5.85) RELIEF [5] (4.74)
MAL/MIXS	89.2	5.79	ELEVATION [1] (54.25) SLOPE [4] (28.78) DISTWATER [13] (25.24) SLOPE [3] (17.35) RELIEF [6] (14.81) ELEVATION [2] (13.26) VEGETATION [11] (11.19)
MIXF/MIXS	79.7	2.57	ELEVATION [1] (46.95) DISTWATER [13] (10.68) ROCK-COVER [8] (5.08)
MIXM/MIXS	75.0	1.89	RELIEF [6] (16.81) TERRACE [9] (15.71) SLOPE [3] (8.58) RELIEF [5] (5.53) ELEVATION [2] (4.81)

For each environmental variable, the corresponding number, in [], and the F value, in (), for the dummy variables are also shown.

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