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PATTERNS OF LIVESTOCK USE IN TIME AND SPACE IN THE SUMMER RANGES OF THE WESTERN PYRENEES: A CASE STUDY IN THE ARAGON VALLEY

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ABSTRACT Space-use patterns and rhythms of daily activity of cattle and sheep summering in the Western Pyrenees are described and the ecological factors that affect them are discussed. Differences among ruminants in relation to fiber tolerance and protein needs determine the preferred grazing areas. These and other morpho-physiological features (such as body size) lead to spatial stratification of animals along mountain slopes. Cattle need a high volume of forage intake so they graze on the lower ranges where availability is greatest and they avoid steep slopes and rocky outcrops. The pattern of space use by cattle throughout the summer season follows a concentration–expansion–concentration sequence determined by forage abundance and availability. The distribution of grazing cattle is affected by plant cover and the resting distribution by flatness and proximity to water. The grazing distribution of sheep is determined by shepherd strategy to allow the flock to benefit continually from optimum grass production.

Bimodal distribution of daily grazing behavior occurs in both cattle and sheep activity. Two peaks of maximum grazing occur, in early morning and at evening, but that trend may vary according to environmental conditions, especially temperature.

RÉSUMÉ *Diagrammes spacio-temporels relatifs au bétail dans les pâturages estivaux pyrénées: étude du cas de la vallée d'Aragon.* Cet article décrit les diagrammes d'utilisation de l'espace et les rythmes de l'actvité quotidienne des bovins et des moutons qui séjournent en été dans les Pyrénées occidentales, et examine les facteurs écologiques qui les affectent. Les différences parmi les ruminants en ce qui concerne la tolérance aux fibres et les besoins en protéines déterminent les zones de paissance favorites. Ces différences ainsi que d'autres caractéristiques morpho-physiologiques (telles que la taille du corps) entraînent une stratification spatiale des animaux sur les versants de montagnes. Les bovins nécessitent de grosses quantités de fourrage et ils paissent donc dans les pâturages à plus basse altitude, là où ils trouvent plus de fourrage et évitent les pentes raides et les affleurements roucheux. Le diagramme d'utilisation de l'espace par les bovins au cours de l'été suit la séquence concentration–expansion–concentration déterminée par l'abondance et la disponibilité du fourrage. La répartition spatiale des bovins en paissance est affectée par la couverture végétale et celle des bovins au repos par la planéité du terrain et la proximité de l'eau. La répartition des moutons est déterminée par la stratégie des bergers qui consiste à permettre au troupeau de bénéficier continuellement de la production optimale d'herbe.

La répartition bimodale du comportement journalier en matière de paissance se manifeste à la fois dans l'activité des bovins et des moutons. Deux pointes de paissance maximale se produisent, tôt le matin et le soir, mais cette tendance peut varier selon les conditions environnementales, en particulier la température.

ZUSAMMENFASSUNG *Verhaltensmuster der Viehbestände auf den Sommerweiden der Pyrenäen bezüglich Raum und Zeit.* In dieser Veröffentlichung werden Flächennutzung und tägliche Weideroutine beim Übersommern der Rinder- und Schafherden in den westlichen Pyrenäen beschrieben. Die ökologischen Faktoren, die beides beeinflussen, werden diskutiert. Die von Wiederkäuern bevorzugten Weideplätze ergeben sich aus artspezifischen Unterschieden in Fasertoleranz und Proteinbedürfniss. Diese und zusätzliche morpho-physiologische Eigenheiten (z.B. Körpergröße) führen zu räumlicher, hauptsächlich horizontaler Verteilung der Tiere entlang der Berghänge. Rinder brauchen große Futtermengen, daher weiden sie auf niedriger gelegenen Flächen, wo reichlich Futter zur Verfügung steht, während steile Hänge und Felsen gemieden werden. Die Flächennutzung während des Sommers folgt einem ausgeprägten Verhaltensmuster der Tiere, die sich versammeln, verteilen, und wieder zusammenkommen, je nach Futtermenge und -verfügbarkeit. Die Art and Weise, in der sich weidende Rinder verteilen, hängt vom Pflanzenbewuchs ab; währen Ebenheit des Geländes und Wassernähe die Ruheplätze bestimmen. Die Verteilung weidender Schafe wird durch die Führung der Schäfer bestimmt, die darauf achten, daß die Herde ständig optimalen Bewuchs vorfindet. Die äußeren Verhältnisse bestimmen bimodale Verteilungen im täglichen Weideverhalten der Rinder und Schafe. Es gibt zwei besonders intensive Weidezeiten: Am frühen Morgen und am Abend, jedoch kann sich dies je nach Umweltbedingungen, insbesondere der Temperatur, ändern.

RESUMEN *Pautas de uso del tiempo y el espacio en puertos estivales pirenaicos: un caso estudiado en el Valle del Aragón.* Se describen los usos del espacio y los ritmos de actividad del ganado vacuno y el ovino durante el verano en los Pirineos Occidentales, al mismo tiempo que se especula sobre los factores ecológicos que rigen tales utilizaciones. Las diferencias de tolerancia entre rumiantes, respecto a la fibra y por otro lado las necesidades de nitrógeno, inciden en las preferencias por las áreas pastorales. Los indicados y otros aspectos, morfo-fisiológicos, tales la talla, priman en la distribución altitudinal y topográfica del espacio utilizado en ladera. El vacuno requiere gran volumen forrajero y por ello pasta en depresiones, donde tales recursos alcanzan valores máximos de disponibilidad, evitando en cambio, pendientes acusadas y crestones rocosos. El vacuno durante su permanencia en estivas sigue una pauta estacional de: concentración—expansión—concentración, consecuencia de las disponibilidades forrajeras. Sobre la distribución del vacuno en pasto incide la densidad de la hierba; mientras reposa en cambio, elige superficies suaves y proximidad al agua. La distribución del ovino en pasto queda en manos del pastor. Una conducción correcta del rebaño, permite la utilización óptima de la producción herbácea.

En la actividad de ambas especies—vacuno y ovino—se observa comportamiento bimodal diario. Se manifiestan así dos picos de máxima actividad pastoral: por la mañana temprano y al anochecer; sin embargo, dicha tendencia varía de acuerdo con las condiciones ambientales; muy especialmente la temperatura.

INTRODUCTION

There is usually a herbaceous vegetation belt of alpine tundra in high mountains between the upper limit of forest and permanent snow cover. Timberline has often been artificially lowered so that the treeless belt is extended downward (Bliss, 1971). This belt is subject to strong seasonal fluctuations with a very active growing period and brief productivity peaks. Furthermore, environmental heterogeneity and biogeographic isolation, with the accompanying effects of vicariance, polyploidy, and endemism, have influenced the development of floristic complexity of the plant communities. The great diversity and high calorific content of the vegetation (Bliss, 1962) make alpine pastures excellent forage for herbivores (Klein, 1970).

This herbaceous biomass is available in large quantities only seasonally. It has been utilized by wild ungulates during seasonal migrations between plains and mountains since prehistoric time. Later, herders with domesticated animals practiced transhumance, often following the same trails (Bahn, 1983). There is evidence to support the notion that exploitation of Pyrenean pastures above treeline by domestic animals originated in the Neolithic period five thousand years ago. Although this ancient practice has conditioned the economy and culture of Pyrenean life, there are not many detailed studies describing summer range use from the perspective of animal ecology.

There is great contrast between resource utilization on the northern French slope and that on the southern Spanish side with regard to livestock breeds and kinds of animal production (Balcells, 1976). This paper describes research undertaken in a study area that is representative of current summer livestock practices in the Western Pyrenees of Spain.

This study in the summer pastures of Aisa Range aimed to elucidate three major aspects of the utilization patterns of large herbivores: feeding habits, space use, and daily activities. The objectives were to establish how these patterns are affected by ecological factors, and to infer from that information whether there is competition between ungulates or, contrarily, complementary resource partitioning.

Studies of animal feeding habits have been carried out earlier, and those of chamois have been well documented by Garcia-Gonzalez. During 1985 research was conducted to ascertain the diets and their mineral composition of all ungulates (Garcia-Gonzalez and Alvera, 1986; Garcia-Gonzalez and Montserrat, 1986). The methodology included identification of plant fragments in feces and chemical analysis of the main food plants. During 1986 more emphasis was given to spatial distribution and daily activity and the results on trophic ecology are used here to explain some trends in ungulate distribution and behavior.

VEGETATION CHARACTERISTICS OF THE STUDY AREA

Research was conducted in a belt of alpine pastures which has a planimetric surface of about 13 km^2. Its limits are those of the watershed that gives rise to the headwaters of the Estarrun River, a tributary of the Aragon River. The river basin, formed by two small converging valleys of glacial origin, is perpendicular to the axis of the Pyrenean range and faces south. The northern part of the basin is sheltered by the Bernera massif and the Aisa sierra, with maximum elevations of 2,450 and 2,643 m respectively. They are two calcareous mountain systems in the inner sierras of the Western Pyrenees (Soler and Puigdefabregas, 1970). In the south, the lowest altitudinal limit coincides with the upper timberline of *Pinus sylvestris* and *Pinus uncinata* forest which has been lowered to 1,600–1,800 m by pastoral activities. From a lithologic point of view, there are basically three kinds of materials. Flysch (i.e., marls alternating with sandstone in thin layers) extends up to approximately 2,000 m. The Bernera massif and the Aisa sierra, which are composed of massive limestone and limestone alternating with sandstone, jut out above it. Therefore, the substratum is mainly calcareous, although the soil is usually acidified on its surface; karst phenomena are frequent.

From an administrative point of view, the Estarrun watershed consists of three pastoral range units (locally named *puertos*), where 2,000 head of sheep and 300 head of cattle from Aisa district usually spend the summer. Goat husbandry is no longer important. In 1986, when the study was conducted, 218 cows, 52 heifers, 114 calves, and 3 bulls summered there on an open range. The sheep population of about 1,850 was herded by two shepherds. The study area also supports a stable population of 300 wild chamois (*Rupicapra rupicapra*), which usually divides into one or two large herds of 40–80 females with their kids, and several smaller groups. Controlled hunting of males takes place during June and September–November each year. Population structure, distribution, and feeding habits of the chamois have been described by Garcia-Gonzalez (1984) and Garcia-Gonzalez *et al.* (1985).

Alpine and subalpine pastures above 1,600–1,800 m in the Western Pyrenees consist of such a complex mixture of plant communities that their limits are sometimes difficult to establish. Neither is there any well-defined boundary between grasslands of the alpine and subalpine belts, so they are often referred to by the general name of "supra-forest grasslands", that is, pastures above timberline. In this study the term "alpine pastures" is used for this vegetation type.

Until recently the alpine vegetation in the Western Pyrenees was little known. The extensive floristic surveys carried out by botanists of the Instituto Pirenaico de Ecologia (Montserrat, 1971, 1974; Villar, 1980, 1982), and by other researchers, provide information on the main plant communities, although accurate studies on vegetation are lacking in certain areas. Figure 1, a schematic vegetation map, shows the main plant communities of the study area. Their principal species and ecological features can be summarized as follows (specific names according to Tutin *et al.*, 1964–1980):

1. Between 1,600 and 1,900 m, on valley bottoms opening to the south there are grasslands of *Cynosurion* and *Meso-Bromion* type (Montserrat, 1960) with *Bromus erectus, Cynosurus cristatus, Koeleria macrantha, Rhinanthus mediterraneus,* and *Sanguisorba minor.*
2. At the same elevation there are *Festuca paniculata* communities (*Scorzonero-Festucetum paniculatae,* described by Negre *et al.*, 1975) interspersed among the grassland types.
3. On steeper slopes, stony pastures in the form of semicircular steps (turf garlands) are formed on poor soils subject to intense cryoturbation phenomena. They correspond to the phytosociological alliance of *Saponarion caespitosae* (Montserrat and Villar, 1987) with dominant *Festuca gautieri. Galium pyrenaicum, Thymus* gr. *praecox,* and *Helictotrichon planifolium* are also common species in this environment.
4. In small basins and sites with long-lasting snow cover *Primulion intricatae* (Braun-Blanquet, 1948) occurs with *Horminum pyrenaicum, Primula elatior* ssp. *intricata, Alchemilla plicatula,* and *Carduus carlinoides.* This community has been described recently by Lazare and Mauric (1987) as a new phytosociological association.
5. Above 1,800 m, on poorly-aired and acidified soils, *Nardion* is found with *Nardus stricta* and *Trifolium alpinum.* It may appear under various conditions depending on floristic diversity.
6. Communities of *Crepidetum pigmaeae* are associated with scree slopes and block streams, with *Crepis pigmaea, Linaria alpina, Rumex scutatus, Nepeta nepetella,* and other of the *Iberidion spathulatae* phytosociological alliance (Braun-Blanquet, 1948).
7. On cliffs and crags there are rupicolous communities with *Petrocoptis pyrenaica, Saxifraga longifolia, Lonicera pyrenaica,* and *Rhamnus pumila;* they have been included in the *Saxifragion mediae* alliance.
8. Above 2,000 m, scree slopes in shady locations with a late-melting snow cover shelter communities of *Saxifragetum ajugifoliae* whose characteristic species are *Saxifraga praetermisa, Epilobium anagallidifolium, Ranunculus alpestris,* and *Hutchinsia alpina* (Arbella and Gomez, in press).
9. Communities of nitrophilous plants, such as *Rumex longifolius, R. alpinus, Urtica dioica, Chenopodium bonus-enricus, Corydalis solida,* and *Geranium pyrenaicum,* grow in livestock resting sites.
10. Hygrophilous communities, such as *Caricion fuscae* and *C. davallianae,* are found in wet lands, as well as spring vegetation with *Caltha palustris, Saxifraga aizoides,* and others.
11. Shrub patches of *Juniperus communis* with *Brachypodium pinnatum* and *Pinus sylvestris* are found between 1,600 and 1,800 m. They are the remains of the original forest.
12. Shrub communities of *Salicetum retusae-reticulatae* (Braun-Blanquet, 1948) are found on sites with long-lasting snow cover and on north-facing screes above 2,000 m. In the study area the endemic dwarf willow, *Salix pyrenaica,* is the typical species, whereas *S. retusa* and *S. reticulata* are very rare. *Festuca glacialis, Oxytropis pyrenaica,* and *Dryas octopetala* usually occur in association.

All these communities are usually closely overlapping. Moreover, there are certain plants, such as *Festuca rubra* and *Poa alpina* that are found everywhere and act as a kind of matrix for all the other communities.

On the basis of available biomass in the lower part of the study area (between 1,600 and 1,900 m) there is a production peak in July coinciding with the flowering of grasses at such altitudes. Another, though quantitavely smaller, production peak occurs in August at the 2,000–2,400 m level, when grasses below at 1,600 m are beginning to dry out.

Plant species growing in snowmelt sites (*Primulion intricatae* community) and those at a lower altitude and on south-facing slopes (*Meso-Bromion*) flower in June. The productive period of most grassy plants is over by October and only the presence of thistles and fungi attests to the summer passage of livestock.

METHODS

Field records were taken from July to September 1986. Cattle sojourn was shorter that year because of the lower than average August rainfall (Figure 2) that resulted in the lack of grass regrowth. The grazing for sheep, normally longer, was from 13 July to 30 September. Spatial distribution of cattle was appraised by mapping the total number of groups or individuals, seen from a fixed position, on plastic films superimposed on an air photograph of the Aisa range, at a scale of 1:12,500. Mapping was done at one-hour intervals two days a week. Sightings were plotted on a square grid with quarter-hectare units, and further superimposed on maps containing various types of information. Thematic maps, such as those representing slope, plant cover, plant nitrophilous sites, and watering points, were elaborated in order to correlate with distribution patterns. A topographic map, scale 1:10,000, was also employed, after corresponding scale adjustments.

Due to gregariousness and herding, sheep distribution was recorded only by mapping daily routes and main stops according to the former procedure. Sighting intervals were

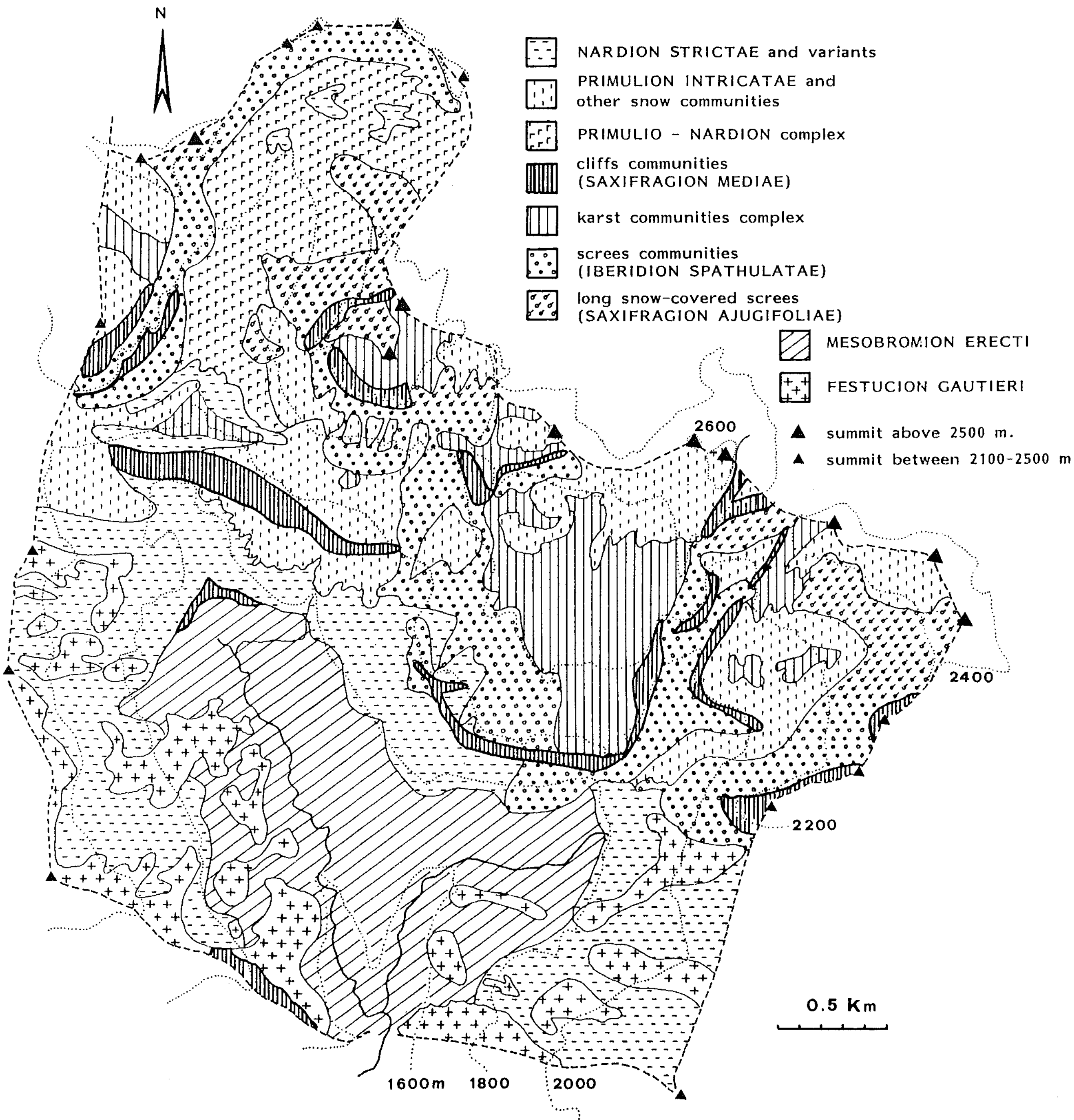


FIGURE 1. Topographic and vegetation map of the Aisa summer range (*puerto*) in the Spanish Western Pyrenees. Principal units according to the Braun-Blanquet (1948) phytosociological nomenclature. For simplicity some plant communities (e.g., nitrophilous, hygrophilous, *Festuca paniculata,* dwarf willows and *Juniperus communis,* numbered 2, 9, 10, 11 and 12 in the text) have been omitted. (Adapted from an unpublished map by D. Gómez and J. L. Remón).

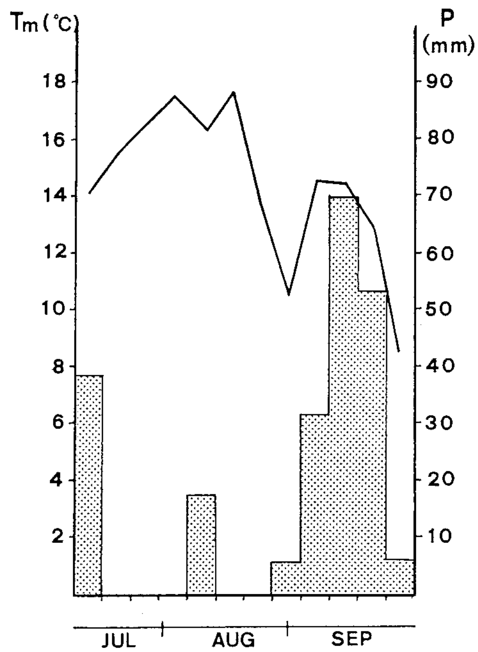


Figure 2. Weekly mean temperature (°C) and rainfall (mm) in the Aisa summer range at 1,600 m during the summer of 1986.

less frequent than for cattle. Specific factors in flock life, such as salt provision, watering, and resting places, were also noted.

Daily activity was studied by means of records on standardized cards at half-hour intervals during daylight. No night observations were made due to the resting behavior of both species. Daily records were taken three times a week for cattle and twice for sheep. Sequential observations involved the activity of 10–15 animals, detailed as feeding, resting (lying or standing), walking, and others (specified). Sex and age of each animal and some environmental factors, such as altitude, slope, orientation, phytogeomorphologic substratum, and subjective weather (wind and sunshine), were also noted. Climatic conditions were appraised from an automatic weather station located at the lower end of the valley which gives continuous temperature data (Figure 2). Microclimatic measurements of wind and temperature were also carried out at specific sites.

RESULTS AND DISCUSSION

General Patterns in the Use of Space

Distribution of the three species of ungulates during the summer period in the study area is shown in Figure 3. As noted earlier, sheep movements were largely determined by the decisions of the shepherd, except in September when the absence of cattle removed the need for human control, so that sheep were almost freely grazing. Cattle and chamois graze under unrestricted conditions, and their movements are determined by climatic factors, herbage availability, anatomical constraints, and interactions with the other species.

Spatial distribution of cattle, measured by the number of animals observed per quarter-hectare unit, gives an estimate of surface use intensity. The major topographic characteristics of cattle-grazing areas are low altitude, relative flatness, and abundant water. Prevailing plant communities are of *Meso-Bromion* and, to a lesser extent, *Nardion* types.

Several factors may explain the distribution pattern. The relatively big body size of cattle individuals demands a diet based on a high volume of forage intake, usually with high fiber content (Van Soest, 1982). The lower *puerto* has more lowland areas, deeper soil, and a greater water supply than the upper one, so that plant productivity is enhanced. Moreover, *Meso-Bromion* communities have a greater quantity of tall grasses such as *Bromus erectus, Koeleria macrantha, Cynosurus cristatus, Brachypodium pinnatum,* and *Festuca paniculata* which allow, therefore, a bigger bite intake. The proportion of grass in cattle diet is higher than in that of other ruminants and the proportion of fibrous parts (stems and sheaths) is also greater (Garcia-Gonzalez and Montserrat, 1986). On the other hand, the anatomical constitution of cattle prevents them from moving to the steep slopes and rocky areas on the northern boundary. Finally, western grasslands that are grazed by sheep acquire a short-stemmed herbage cover so that cattle cannot feed here although they may use these areas as resting places.

Figure 3 also shows sheep distribution during the summer of 1986. Surface utilization has not been quantified with the same accuracy as for cattle because of the particular sheep grazing system. Sheep graze in compact flocks, led by older individuals. Men and dogs intervene only when important changes in direction are necessary. The grazing intensity is fairly uniform. Night resting takes place near a shepherd's hut in an open sheepfold. In July, sheep ascend the moderate and steep slopes of the valley, grazing on *Nardion strictae* and *Festucion gautieri* communities. Their peculiar mouth morphology enables sheep to pick out preferred plants from among unacceptable ones such as bent (*Nardus stricta*) or broom fescue (*Festuca gautieri*) (Thomas and Fairbairn, 1956). Reduced body size allows sheep to traverse steep rough ground and to use stony pastures. In August, they ascend 200–600 m to the northwestern part of the summer range to pastures mainly of *Primulion* and *Nardion.* Grass here is still short and tender because of two interrelated phenomena: plant phenologic delay due to altitudinal increase, and the late melting of snow patches which gives access to new growing plants. Both factors are closely related to temperature decrease with altitude. Wild chamois, as do arctic ungulates (Skogland, 1984), follow plant phenologic progression

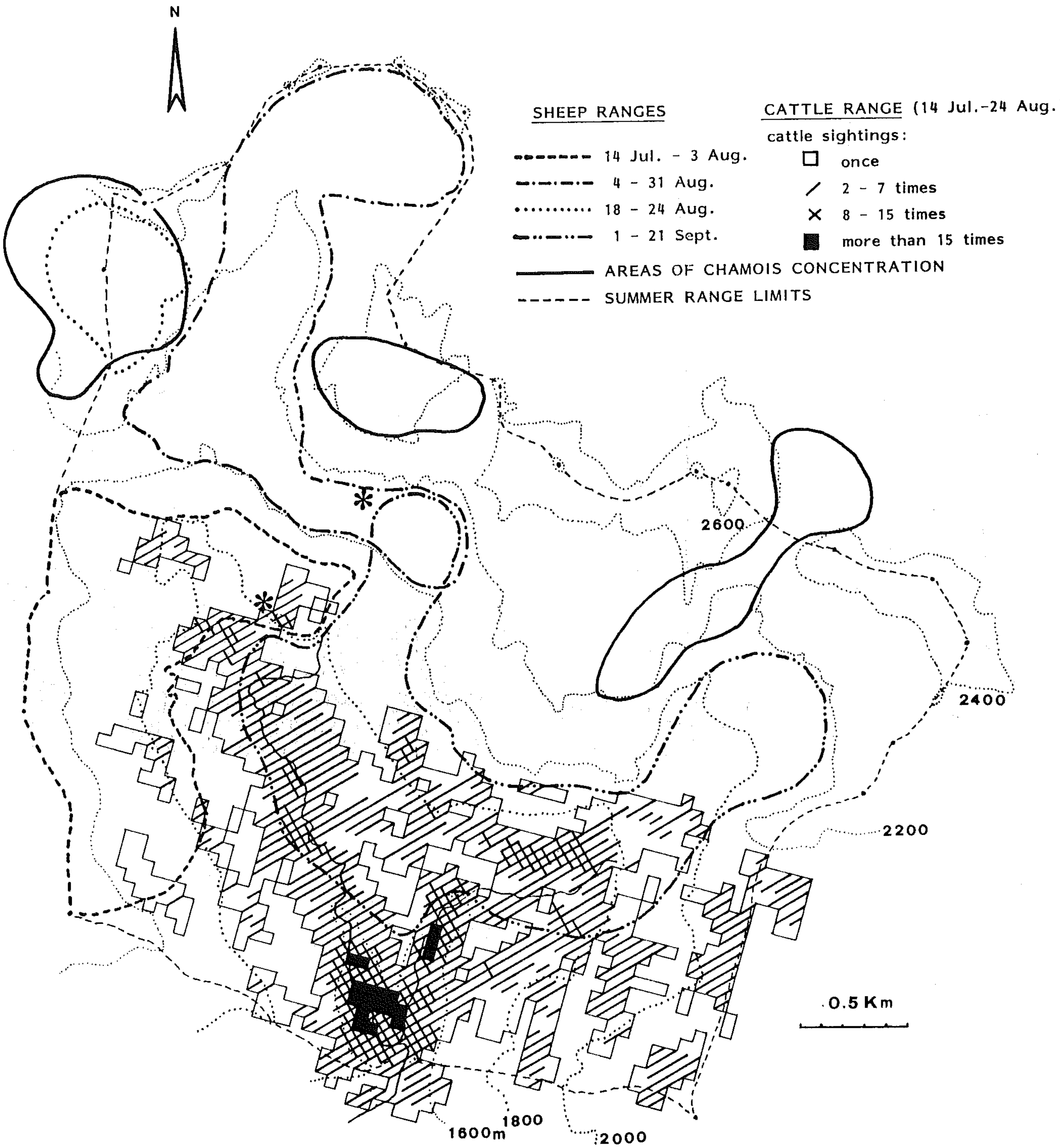


FIGURE 3. Spatial distribution of ruminants in the Aisa summer range during 1986. Sheep ranges indicate the customary courses used by herded flock for a determined period. Cattle presence is expressed as the number of sightings (involving one or more animals) per quarter-hectare unit. Cattle are free-ranging and chamois are wild. The night resting sites of sheep are shown by asterisks.

View of the study area with the Bernera massif (left) and Aisa Sierra (bottom right); the altitude ranges from 1,600 m in the valleys to 2,660 m on the summits; the geologic substrate is mainly calcareous. In summer cattle are found in the valley bottoms, sheep on mid-mountain slopes, and chamois near the summits.

from the beginning of spring, ascending progressively to reach upper summits (Garcia-Gonzalez, in press). Later, sheep follow a similar grazing pattern and shepherds imitate the behavior of wild herbivores, most frequently using the same trails (Fillat, 1984). Access to short and tender grass enables sheep to obtain a higher protein diet than cattle (Garcia-Gonzalez and Montserrat, 1986), in accordance with their nutritional demands (Van Soest, 1982).

During September, sheep descend to occupy the upper part of the cattle range (Figure 3). In some years when cattle remain longer, sheep alternate that area with the July range. In areas of the *Nardion-Bromion* complex, grass undergoes a new but smaller production peak at that time due to the combined effect of mid-summer rainfall and previous cattle grazing which promotes herbage regrowth (McNaughton, 1979). Shepherd strategy appears to move the flock to obtain benefits of optimum grass production on a constant basis (Figure 4); flocks are led upward during the first part of summer following the plant phenologic wave, and at the end of summer grazing is enhanced by rainfall and plant regrowth stimulated by previous graz-

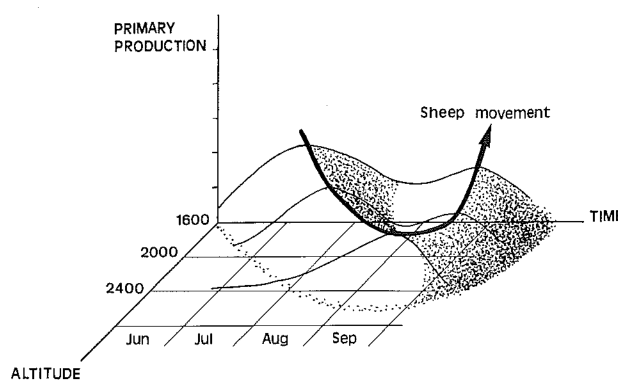
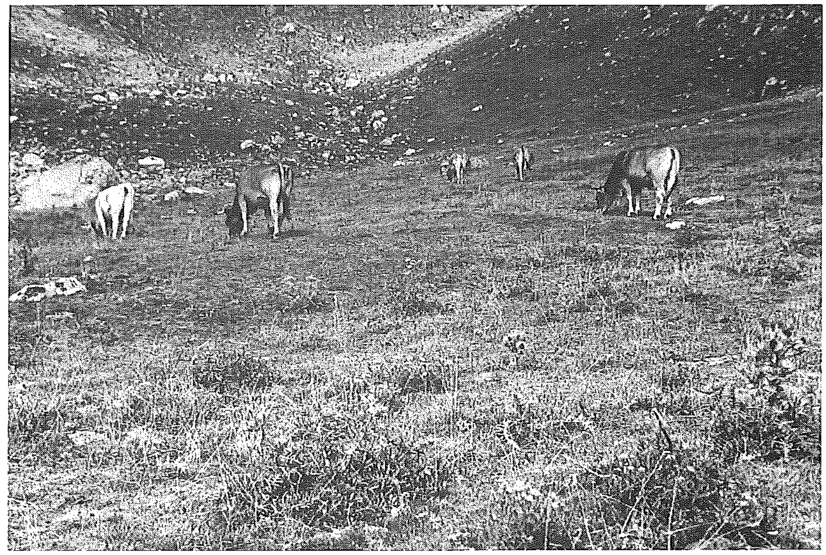
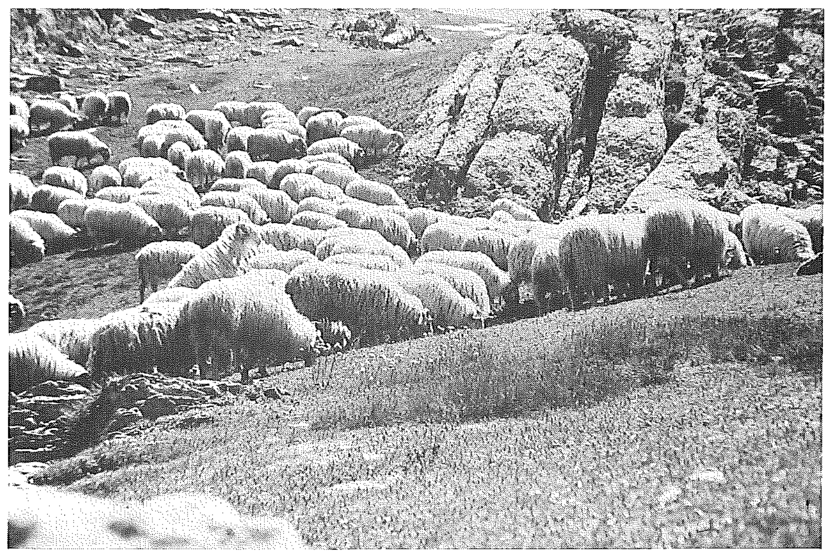


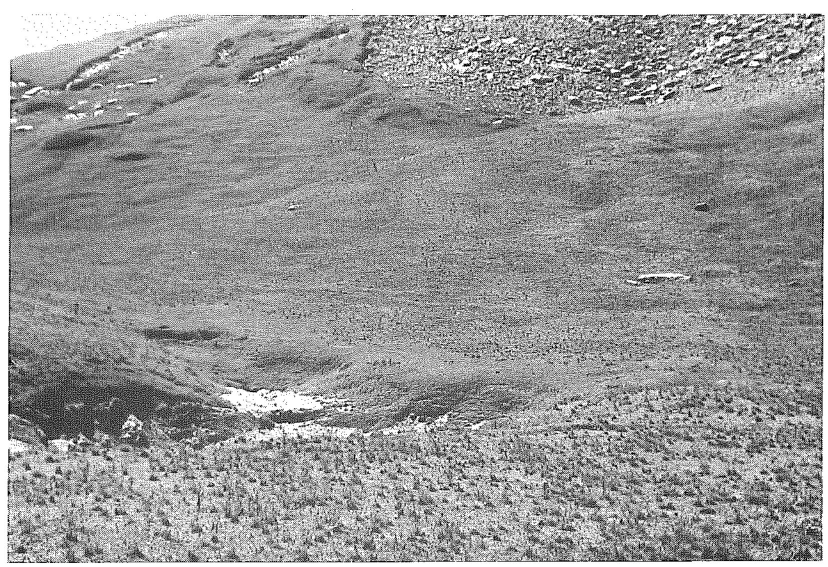
FIGURE 4. Idealized model of forage utilization by sheep in the Pyrenean summer ranges. Herding strategy consists of moving the flock so that it obtains optimal access to grass production throughout the season by considering both altitude (plant phenologic delay) and time (grass regrowth promoted by mid-summer rainfall and cattle grazing).



Typical cattle resting zones (*majadas*) are characterized by level ground or gentle slopes and availability of water; accumulation of cattle excrement gives rise to peculiar plant communities with many thistles (foreground) and nitrophilous species (*Polygonion aviculare*).



Sheep graze in close formation and reject certain unpalatable grasses such as *Nardus stricta* (foreground).



A broader view of pasture with rejected tufts of *Nardus stricta* after the sheep have moved on; selective grazing affects plant community dynamics.

ing. Specific differences in fiber tolerance and protein needs of ruminants are among the main causes determining preferred grazing areas (Jarman and Sinclair, 1979). The smaller ruminants graze the upper levels of mountain summer ranges and larger ruminants the lower ones. The outcome is a peculiar vertical stratification of animals in relation to body size (Figure 5). This pattern is very similar to that described by Bell (1971) in the Serengeti although underlying factors may differ. The general spatial distribution in the Pyrenean summer ranges shows how the use of resources is largely determined by interaction between the ecological features of the area and the biological characteristics of grazing animals.

FACTORS AFFECTING CATTLE DISTRIBUTION

The distribution of cattle has been analyzed in some detail in order to make evident other ecological factors that determine space use. Therefore, all cattle sightings have been divided into three consecutive periods of time so that the variations in space occupation over time are evident (Figure 6). Total time of observation was the same during the three periods. Surface units are squares of one quarter-hectare, as in Figure 3.

The pattern of space use seems to follow a concentration–expansion–concentration sequence throughout time. The differences in cattle distribution may be interpreted mainly in relation to forage abundance and availability. At the beginning of the season (situation A), cattle exploit areas at the low-to-middle altitudes, where food is most abundant at that time. The area occupied is relatively large, but many of the observations are occasional and the greater frequency of sightings corresponds to the sites with higher plant production and quality. In the middle of the season (situation B) cattle reach their maximum expansion. The distribution of cattle is then homogeneous throughout the area and single and high frequency observations are rare. As production begins to decline at the best forage sites the animals seek out new areas that were previously ignored. At the end of the season (situation C) cattle are concentrated near the entrance of the valley and the bottom of the eastern branch. Grass has dried up and pastures are almost exhausted, due to the scarcity of rainfall during August of that year (Figure 2). Animals stay close to the water; they barely move and do not search for new feeding sites.

Another way to assess ecological factors that influence cattle distribution is to group them according to behavioral

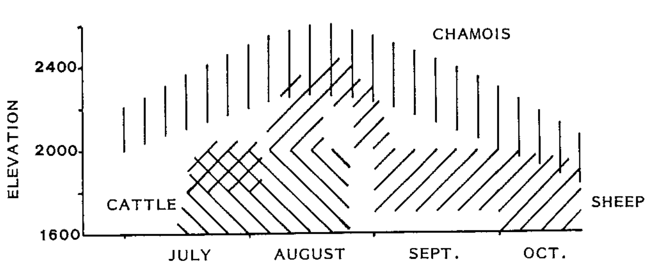


FIGURE 5. Vertical distribution of three species of ruminants in the study area during the 1986 summer period. (Sheep move in October to a neighboring pastoral unit at the same altitude.)

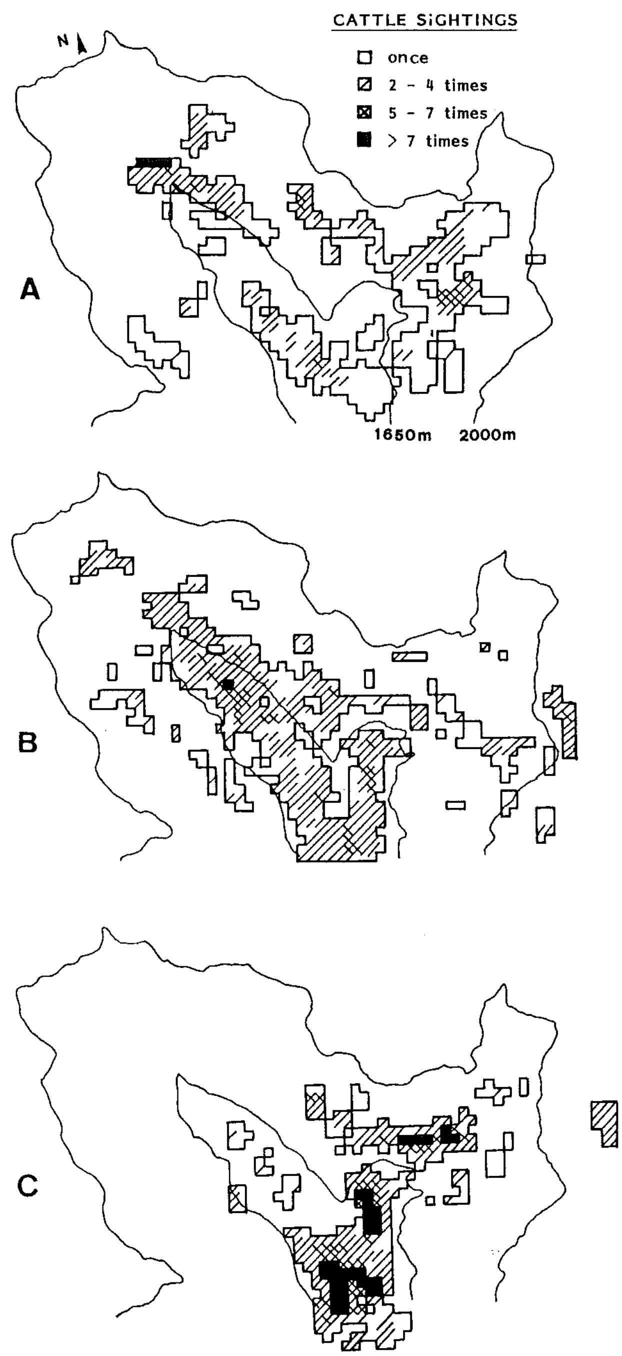


FIGURE 6. Temporal evolution of cattle distribution in the Aisa summer range: A, beginning of the season (mid-July); B, middle of the season (early August); C, end of the season (mid-August).

criteria. Two main cattle activities, in the sense of the amount of time spent, have been considered: grazing and daylight resting. In Figure 7A all the summer observations from 0500 to 0700 and from 1700 to 1900 (GMT), when grazing involves more than 70 percent of the animals, have been grouped. The resulting distribution, considering only presence/absence of animals, is superimposed on a map displaying those areas where vegetation cover is more than 70 percent of the surface. Both distributions are overlapped. Minor differences in overlapping patterns may be explained by the sampling character of the sighting records and by sheep grazing areas in the westernmost zone. This trend is interpreted because cattle distribution while grazing is largely determined by plant cover. This result is also in accordance with other studies of cattle distribution (Senft *et al.*, 1985a) and the trend is probably related to the selection of dense vegetation patches in order to minimize energy expenditure (Pyke, 1984).

To record daylight distribution of animals at rest, sightings between 1100 and 1300 (GMT) have been grouped. The presence or absence of cattle in the quarter-hectare grid was superimposed on a map of slope angles where only the flattest areas (that is, slopes less than 20%) are represented. A map showing stream flow during mid-August was also introduced (Figure 7B). Resting distribution does not always overlap with low-slope areas, but where it does not the resting places are near springs, as was observed by other authors (Senft *et al.*, 1985b). Therefore, it seems that resting distribution may be affected by a combination of two factors: gentle slopes and proximity to water. It may be further explained by taking into account that lying cattle always prefer smooth ground (all the nitrophilous plant communities are found on slopes of 0–10%), and also by the observed fact that before the evening grazing period cattle often ingest a considerable quantity of water (Low *et al.*, 1981).

It seems obvious that resting distribution is a result of a search for comfort by each individual animal (Senft *et al.*, 1985b). Site selection is, to some extent, related to the avoidance of biting insects. The Aisa range cattle try to escape insect harassment by seeking open and windy places, just as do other ungulates (Skogland, 1984; Duncan, 1985).

The Pattern of Daily Activity

A well-defined daily pattern consisting of two periods of grazing activity with an intermediate resting period has been reported in several studies of ungulates (Arnold, 1962; Favre, 1978; Gates and Hudson, 1983). The two peaks of maximum grazing normally occur close to sunrise and sunset. However, sometimes there are many grazing periods due to climatic and forage conditions. Day length also influences the rhythm of activity in temperate climates (Grubb and Jewell, 1974), but this factor was barely discernable during the three-month study period.

The three main activities of sheep and cattle (that is, grazing, resting, and walking) have been summarized on a daytime scale (Figure 8); others are of minor importance from a temporal perspective. Activities were recorded only in daylight because of predominant resting behavior in both species during the night. In Figure 8 arrows indicate the moment at which the sun reaches half the surface area of the Aisa range in early morning and in the afternoon. Sunrise and sunset occur, according to official time, two hours before and after this, respectively. The numbers of sheep correspond to the average of the July and August records in order to be compared with those of cattle. From our results some trends may be emphasized. First, the bimodal pattern of grazing behavior is evident in both cattle and sheep activity, although with a remarkable difference that is mostly related to the influence of the shepherds upon sheep behavior. Free-ranging cattle begin to graze as soon as the sun rises and continue until about 0900 (GMT) when many of the animals gradually become inactive and remain so until after the midday heat. The behavioral pattern of sheep is similar, but shepherds retain the flocks in an open sheepfold until mid-morning to prevent early grazing. Shepherds think that grass wet from dew is harmful to their animals, and therefore wait until the morning sun has almost completely dried the grass before allowing the flocks to graze. This habit may also deter the ingestion of parasites, which are enabled by the night moisture to reach the upper part of the grass leaves, and so prevent digestive disturbances in sheep (Spedding, 1968).

At approximately 0800 GMT the flocks are released and driven to the usual grazing areas, alternately grazing and walking throughout the morning until the midday heat restricts activity.

The delay in the morning feeding period is much shorter for sheep than for cattle; for sheep, the evening grazing period starts before that of cattle (Figure 8). The midday resting period, therefore, is much longer for cattle and their resting and grazing peaks are reached gradually, whereas sheep change activity more quickly. This is perhaps due to the gregariousness of sheep, a factor which is emphasized in that particular breed. In spite of the inequality in morning and evening grazing periods, induced by flock management, a similar study carried out on three breeds inhabiting a summer range in unherded conditions also recorded a significant difference, with the evening period being the more important (Bowns, 1971). The same study showed that sheep browsed on shrubs (oakbrush and snowberry) when grasses were wet and then grazed again when the herbage layer started to dry out. All three breeds walked for a greater period of time during the morning. In contrast, however, in other places and situations, the evening grazing period was longer than the morning period (Arnold, 1962; Favre, 1978). This behavior agrees with that shown by the Pyrenean herded sheep and it leads to the suggestion that these behavioral trends may be innate.

Another difference between cattle and sheep lies in the amount of time spent resting in a standing position. This is more prevalent in sheep because of their particular way of protecting their heads from the sun by placing them in the shadow of rocks or among the legs of other standing sheep.

The reduced importance of walking in cattle is also remarkable. It is probably due to both the lesser spatial separation between grazing and resting areas of cattle and

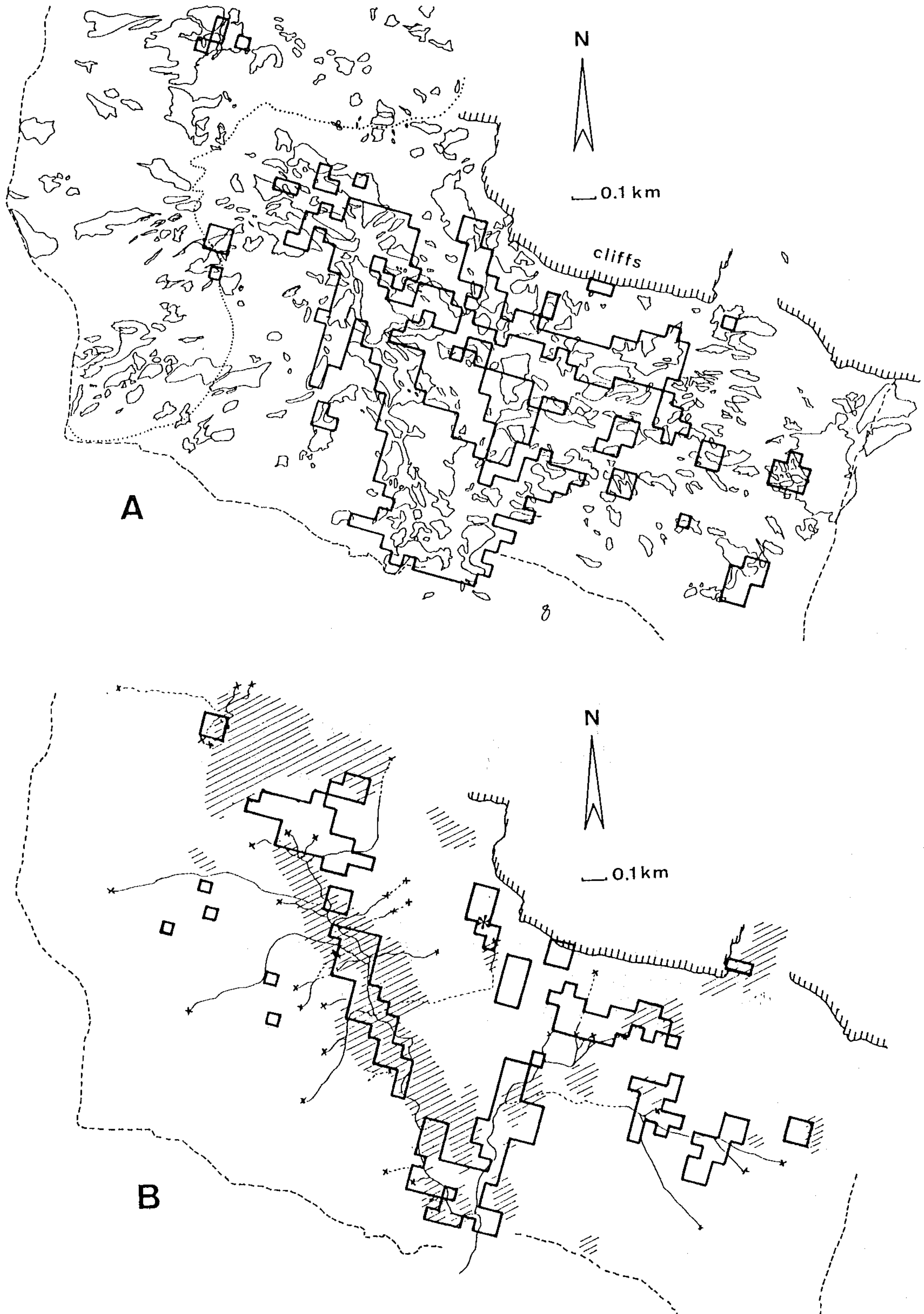


Figure 7. A. Grazing distribution of cattle in relation to plant cover. Irregular patches indicate more than 70% plant cover. Geometric surface displays presence of cattle per quarter-hectare square unit between 0500 and 0900 and between 1700 and 1900 GMT during the complete summer sojourn; the dotted line is the lower limit of the July and August sheep range; the discontinuous line is the summer range boundary.
B. Resting distribution of cattle in relation to slope angle and distance to water. Geometric surface indicates presence of cattle per quarter-hectare unit between 1100 and 1300 GMT during the complete summer sojourn. Crosses and thin lines show sources and water courses in mid-August. Discontinuous lines are intermittent running water. Hatched surface represents areas with slopes of less than 20%. The asterisk marks a watering place.

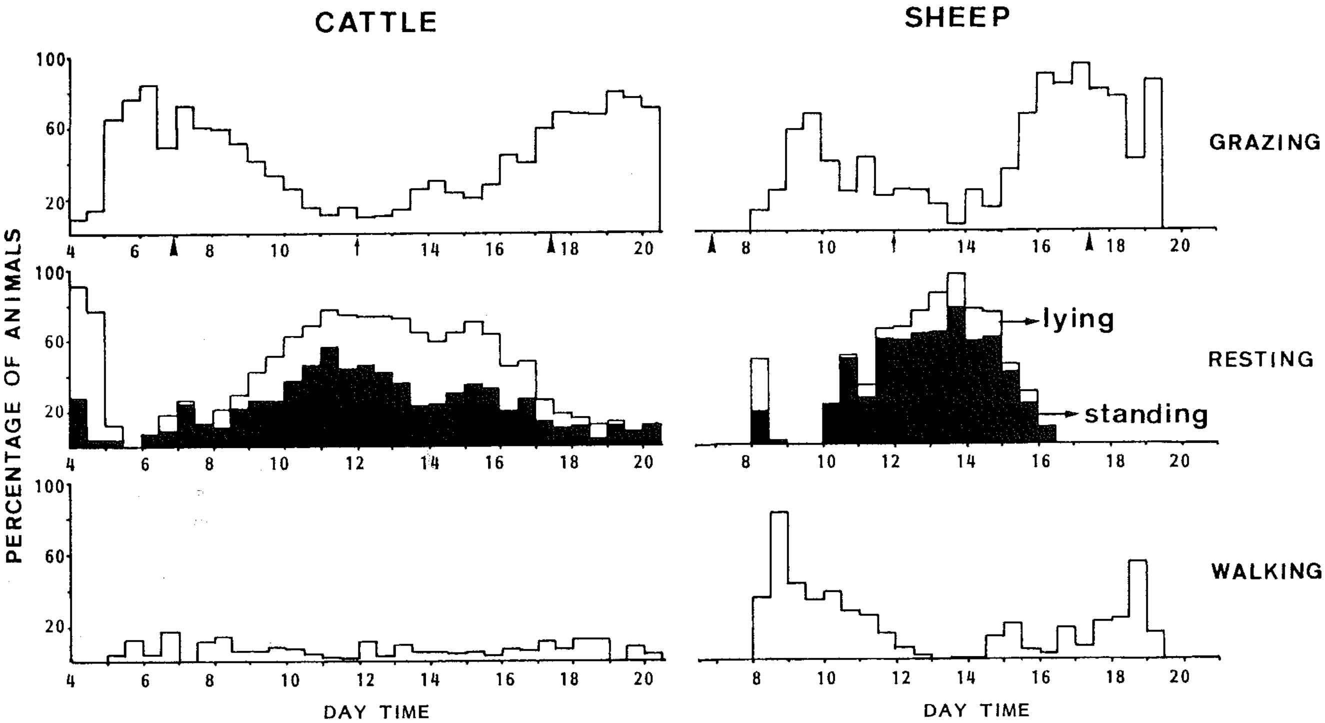


FIGURE 8. Proportional distribution of daylight activities of cattle and sheep during July and August 1986 in the Aisa summer range. Other activities, such as drinking and sucking, have not been represented.

to human influence. Cattle normally graze close to their resting and watering places (Roath and Krueger, 1982). Sheep have prearranged resting and grazing areas that are often remote from each other, and these change throughout the season according to the food availability which is dependent on the plant phenologic production wave (see Figure 4).

Variations in Daily Activity Patterns

As previously noted, daily activity patterns depend upon simultaneous interaction amongst several factors, chiefly day length, forage factors, weather, and herding strategy. It is generally accepted that grazing behavior is more affected by pasture conditions, whereas environmental features may have more influence upon non-grazing activities (Duncan, 1983; Senft *et al.*, 1985b). Nevertheless, the elucidation of a certain activity pattern in a particular situation usually requires a multifactorial approach (Arnold and Dudzinski, 1978). From the present study two examples have been selected that give insight into the particular effects of some of the above-mentioned factors.

Behavioral data recorded on cold days have been compared with data taken on hot days in order to detect possible effects of weather on cattle activity. The average daily mean temperature during cattle sojourn was 16.5°C, with 95% confidence limits of 15.6 and 17.4°C (n = 38). Sampled days with mean temperatures below and above the confidence limits were considered as cold and hot days respectively. The average of each activity at half-hour intervals for six cold and seven hot days was calculated, and it is represented in Figure 9. Some trends may be noted: daily temperature seems to have little effect on time devoted to grazing; the sum of grazing percentages between 0700 and 1900 GMT is very similar in both situations, although morning grazing appears to be somewhat more important on cold days. With regard to movement, animals walk more on hot days (difference significant by chi-square test: $\chi^2 = 29.1$; one degree of freedom). Walking activity seems to be homogeneously distributed throughout daylight time. It is estimated that the increase in walking on hot days is probably related to the search for fresh and windy places to diminish effects of the heat and to escape biting insects. High temperatures are likely to increase insect activity (Hughes *et al.*, 1981). However, the activity which seems to be the most affected by temperature is lying rest ($\chi^2 = 96.1$; one degree of freedom). Total resting is also enhanced in cold weather, but it is perhaps an indirect effect of minor movements on such days. Increase of lying time with temperature fall has also been reported by some authors (Arnold and Dudzinski, 1978; Norton, 1981) although others obtained contrary results (Duncan, 1985). We interpret our results in two ways: lying on the ground may be an adaptive behavior to decrease heat loss by reducing the temperature exchange surface or, more likely, the increase of time in a standing position on hot days may allow for greater ventilation to reduce insect harassment.

The daily behavior of sheep analyzed according to activities and months (Figure 10) indicates certain variations that can be interpreted as the influence of weather condi-

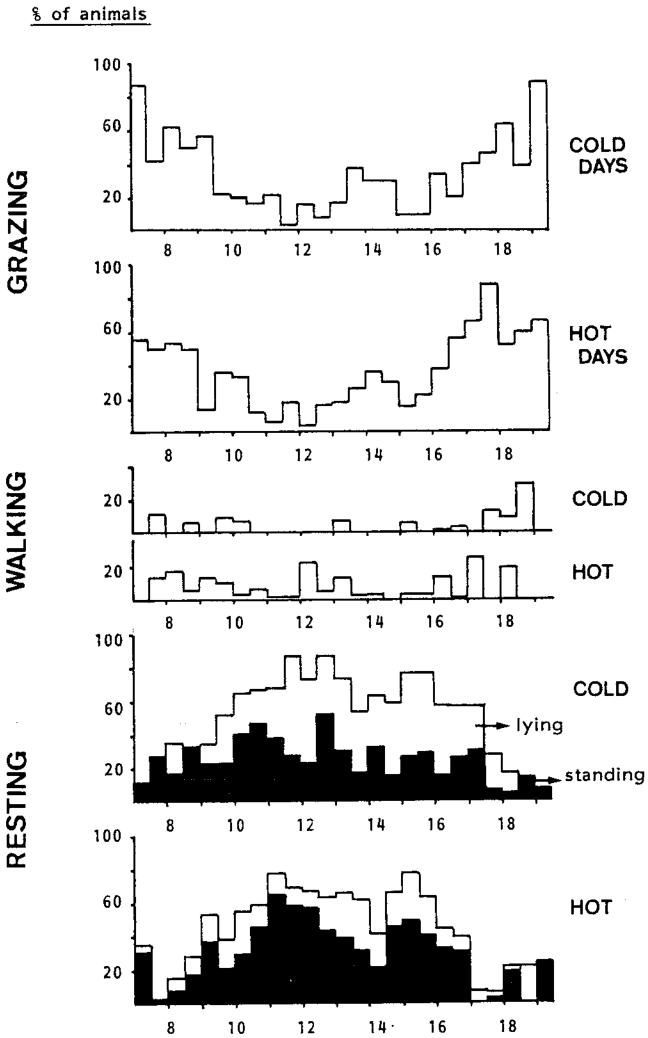


FIGURE 9. Influence of temperature upon the daily activity pattern of cattle.

tions and human control. The July daily behavior pattern is very similar to that displayed by the general model (Figure 8). Sheep start to move at 0830 GMT, walk quite a distance during the morning, and graze just a little (Bowns, 1971); as soon as the temperature increases significantly a long rest period in a prevailing standing position begins; at 1500 GMT the main grazing period begins and lasts until late at night; walking time is reduced. Cessation and beginning of grazing and resting are very pronounced and they usually occur without shepherd influence. By August sheep are removed to another pastoral unit at a higher altitude (see Figure 3). The temperature is cooler there (2°C less) and shepherd control decreases. This change in range conditions, especially less heat, is reflected by a decrease in the resting period and an increase in walking time. The grazing rhythm is then broken and grazing takes place throughout the day, although the evening grazing period still remains the most important one.

Cattle leave the summer range in September. Sheep then utilize the entire grazing area, especially the lower altitudes. The temperature is lower (see Figure 2) and the shepherds have less influence so that the behavioral trends of the previous months become less conspicuous: the decrease of resting and alternation between walking and grazing throughout the day. Activity periods become shorter and more numerous. Thus, the behavior patterns closely approach those described by some authors who have studied both free-ranging sheep (Favre, 1978) and domesticated wild ruminants (Ellis and Travis, 1975).

IMPLICATIONS FOR MANAGEMENT

1. Environmental adaptations take on different forms even in closely related species as a result of anatomical and physiological differences, often related to body size in ungulates (Leuthold, 1977). Such adaptations enable the grazing species to maximize access to available resources. From the present study it appears that it is possible to reduce interspecific competition by making use of the biological characteristics of each species to ensure efficient management; this can lead to an effective control of range carrying capacity. In addition, resource partitioning allows simultaneous grazing of several species and leads to a more complete exploitation of those grazing areas that are ecologically heterogeneous. This is evident especially in mountain areas with steep environmental gradients.

2. Knowledge of the variations in phenology and floristic diversity and the processes that cause them allows optimal exploitation of herbage. Some successful herding practices from ancient times appear to be based upon extensive accumulation of such indigenous knowledge.

3. Herding strategies in the highlands are based to a greater extent on the habits of wild ruminants in terms of behavioral patterns, spatial distribution, and even utilization of the same trails. Human manipulation of herd behavior is of relatively slight importance. An extensive knowledge of the local characteristics of each summer range, such as geomorphology, vegetation and its spatial and temporal distribution, watering places, and so on, is very important. Traditional herding apprenticeship has always been oral and the present reduction in the number of skilled traditional shepherds may result in a progressive decline in efficient summer range management.

4. Daily activity rhythms are species characteristic. Timing, duration, and intensity by which different activities arise are related to food availability, watering places,

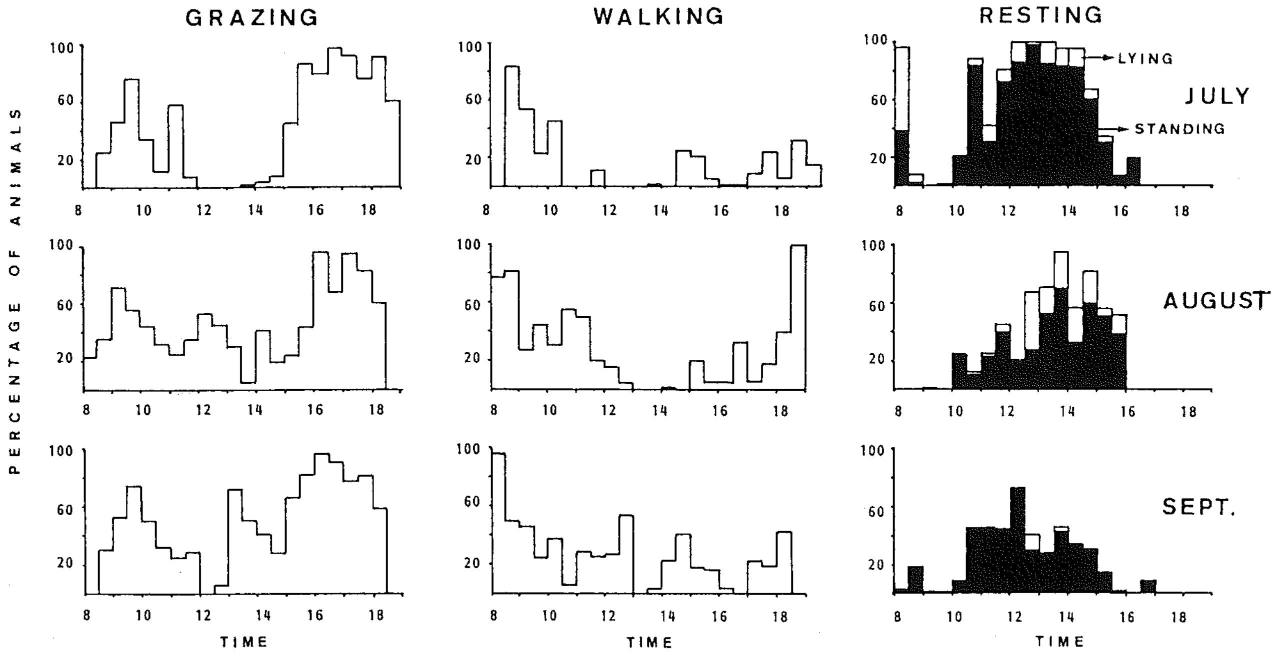


Figure 10. Daily pattern of the main activities of sheep and monthly variations.

climatic conditions, and human influence. Livestock management under such conditions must take into account the natural proclivities of the animals.

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