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Determination of animal behavior-environment relationships by Correspondence Analysis

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Abstract

The paper describes an analytical procedure to preliminarily investigate large scale animal-environment interactions. The method is based on Correspondence Analysis applied over a contingency table in which the columns are percentage categories of animal activities and the rows, states of environmental variables. Each cell entry in the table represents the number of times a row and a column have been recorded together. This means that investigation of animal-environment interactions does not require defining specific sampling stations, or subdividing the study area into environmental units; i.e. the method can be used in studies in which sampling consisted of following the animals and noting their activities and characteristics of the environment. The graphical display resulting from the analysis shows the main patterns of association between animal activities and environment, and its numerical output allows one to identify the variables that have played a major role in the display. Taking into account these variables and their associated animal activities, the method allows one to define archetypal habitat models for each animal activity. Correspondence Analysis of animal activities by environmental variable matrices may give insights about animal's perception of the environment. The use of the method is illustrated by analyzing habitat preferences of free-ranging cattle during 2 different seasons on an estate in Spain. Results indicate the validity of the method as a first global analysis of the relative importance of environmental variables for the distribution of the animal activities in the landscape.

Key Words: habitat preferences, multivariate analysis, dehesa, cattle, Mediterranean grasslands.

The analytical approach adopted when investigating animal habitat preferences largely depends on the degree of previous knowledge of such preferences. If animal-habitat relationships are well known and the objective is to test specific hypotheses, numerical procedures such as Generalized Linear Modeling can be used (McNaughton 1985). Whereas if the aim is to generate hypotheses, the variables measured can be too numerous to allow an effective use of these techniques. In this case, it can be difficult to gain an overall view of the relationships between habitat factors and animal activities and distribution from numerous separate analyses (Ter Braak 1986, Montaña and Greig-Smith 1990). Alternatively, this can be achieved by using multivariate techniques. For instance, data on the frequency of a number of animal activities at a series of sites can be analyzed by techniques of multidimensional scaling (e.g. Principal Components Analysis, Canonical Correspondence Analysis).

Ordination analyses have been widely used on data in which the sampling sites are considered as analytical entities (they are treated as variables). However, in studies aimed at determining what factors are conditioning the use the animals make of their territory, specific sampling sites may not have been considered (Coppock et al. 1986). For example, if the sampling consisted of following nomadic ungulates and noting characteristics of their feeding behavior (foraging velocity, biting rate, bite size) and of the vegetation they feed on (composition, height, plant density, phenological status). Is it possible to use multivariate analyses in cases like this? In this paper we show that relationships between environment and animal behavior can be easily highlighted by using Correspondence Analysis without considering sampling sites as part of the data. The basic idea is to apply this analysis to contingency tables in which animal activities and environmental factors are incorporated as multistate qualitative variables. This method produces a general descriptive overview of the environmental factors associated with each type of behavior, and provides information about the importance of each factor in conditioning animal activities. Moreover, by taking into account the more relevant environmental variables and the activities to which they are associated, it allows one to easily define archetypal habitat models for different sets of animal activities. The method works equally well with ordinal and cardinal qualitative variables, so it may be used as a complement to analyses with a more limited capacity of dealing with qualitative data such as regression (Ben-Shahar and Skinner 1988).

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Materials and Methods

Study Area

We illustrate the use of the method by analyzing data on cattle behavior and habitat factors gathered on a private estate, in the Madrid province, Spain. This estate is part of the "Parque Natural de la Cuenca Alta del Rio Manzanares", a protected area which preserves a large remnant of one of the most characteristic and ecologically valuable agroecosystems of central and southwest Spain: the *dehesa*, an open savanna-like holm oak (*Quercus rotundifolia* Lam.) woodland. This agroecosystem is characterized by the combination of most of the components of the natural Mediterranean forest, including tree and shrub species and wild fauna, with livestock raising, pastures, forestry practices and some rotating crops (Joffre et al. 1988). A considerable amount of ecological research has been conducted on the estate, including analyses of the spatial and temporal dynamics of pasture community succession (Pineda et al. 1981a, 1981b; Casado et al. 1985, Gómez-Sal et al. 1986, Espigares and Peco 1993), studies on the temporal behavioral patterns of cattle (De Miguel et al. 1991) and on their role in the transfer of matter throughout the ecosystem (Gómez-Sal et al. 1992).

The estate covers 3,000 ha, and its elevation ranges from 610 to 720 m. The climate is Continental-Mediterranean with most of the annual rainfall of 600 mm occurring in winter. The yearly mean temperature is 13°C, with extremes of –7°C and 37°C for January (coldest month) and August (warmest month) respectively. The area has undulating topography covered by granitic sediments (Fig. 1). Many parts of the estate are ploughed periodically to eliminate thickets and encourage pasture growth. This leads to a diversified landscape in which different successional stages (from pastures to cleared and dense woodlands) occur in close proximity. The wooded vegetation consists of woodlands and scattered trees, mainly holm oak in the intermediate and more elevated zones. Scattered ash trees (*Fraxinus angustifolia* Vahl.) occur in lowlands. Pastures are dominated by therophytes, and scrub vegetation consists mainly of holm oak in shrub form, together with *Cistus ladanifer* L., *Santolina rosmarinifolia* L., *Thymus zigys* L., *Daphne gnidium* L. and *Phillyrea agustifolia* L. High temperatures and drought in summer, and intense cold in winter lead to a sharp decrease in pasture production during these seasons. Consequently, cattle are supplied with additional fodder at these times.

Sampling

About 400 free-ranging cattle graze on the estate. Starting in early May, the behavior of cattle was surveyed in 35 sampling days distributed through 1 and a half years. The observation days were distributed weekly, although during some winter and early summer periods they occurred once a fortnight. The sampling was interrupted during 2 months in the first summer when the cattle were moved to a nearby estate. On sample days, both the behavior of cattle and environmental factors were recorded at 10 min. intervals from sunrise to sunset. To avoid influencing their behavior, the animals were followed on foot and observed from hidden positions, at least 100 m away. Before the first observation, an animal was chosen at random to serve as a guide during the rest of the day. Every 10 min., the size of the herd surrounding this animal was noted, and an area of observation of cattle activities and environmental factors was defined. This area was within a radius of ≈ 50 m around the guide animal. A maximum of 10 animals were taken into account in each observation. This consisted of recording the number of animals involved in 10 basic activities (Hafez and Schein 1969, Low et al. 1981a, 1981b), namely grazing, browsing, fodder ingestion, standing rumination, lying rumination, standing resting, lying resting, traveling, occasional displacement, and other occasional activities (e.g. defecating, urinating, cleaning). In addition, in each area of observation the aerial percentage cover of all tree and shrub species was visually estimated. Wind intensity (4 subjective categories), air temperature 1.5 m above the ground in a shaded position, and general geomorphological and vegetational characteristics were also noted. For analytical purposes, quantitative variables were subdivided into a number of states (Table 1), which were determined by arbitrary evaluation of the width of the ecological gradients existing on the study area (Ben-Shahar and Skinner 1988). Data analyzed in this paper are based on a total of 2,662 observations of cattle behavior and environmental factors.

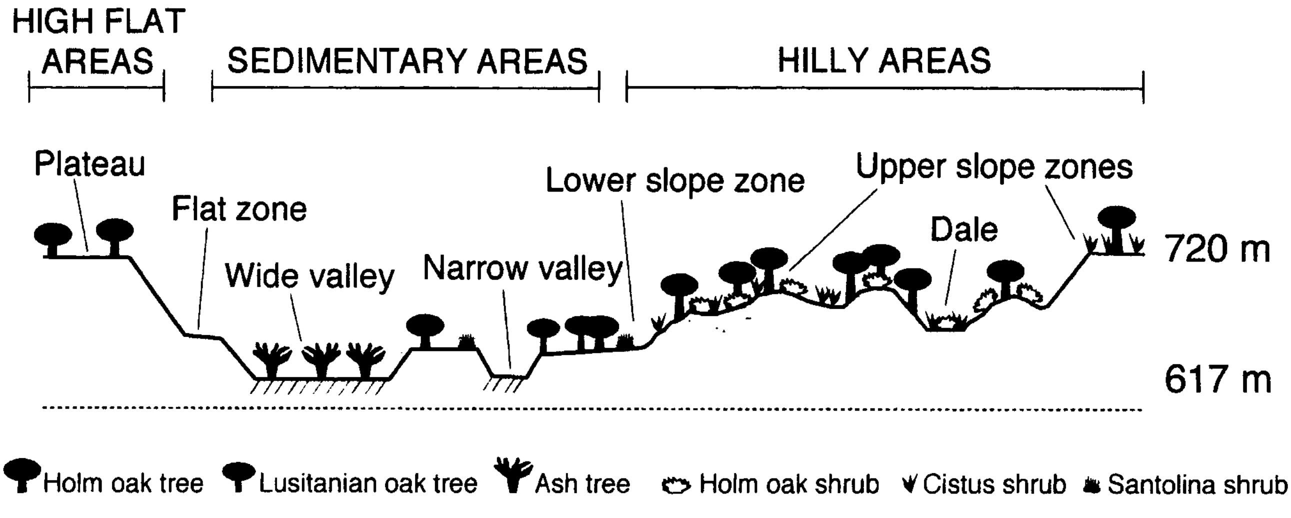

Fig. 1. Scheme of the range.

Data Analysis

Cattle behavior changed dramatically from season to season during the study (De Miguel et al. 1991). Accordingly, we analyzed the habitat preferences of cattle for groups of observation days which were typical for a season of the year. By using the taxonomic distance method (Engelman 1983), we classified the observation days according to the proportion of activity spent on the 10 basic types of behavior considered in the study. The dendrogram resulting from the analysis (not included) separated the days into 4 major groups (De Miguel 1989), namely spring, early summer, autumn-winter (hereafter called winter days), and an heterogeneous group including days with fodder supply. We illustrate the use of Correspondence Analysis for studying animal-habitat selection investigating the feeding behavior of the cattle in the winter and spring groups, each including 6 and 7 days, respectively. Within each day, the percentage of animals involved in each activity was calculated for each individual observation of cattle behavior. The calculation of percentage values involved all the activities sampled, although only 4 feeding activities, namely grazing, browsing, fodder ingestion and resting-ruminating, were considered for the ordination analyses.

Correspondence Analysis is a multivariate ordination technique commonly used in ecological studies, and several descriptions on its numerical properties are available in the literature (Greenacre 1984, Digby and Kempton 1987, Montaña and Greig-Smith 1990). This analysis displays rows and columns in a two-way contingency table as points in a multidimensional space. The contingency tables analyzed in the present study were created by expressing the states of the environmental variables (Table 1b) as the frequencies of occurrence of percentage classes of cattle feeding activities (Table 1a), with the rows being the states of the environmental variables and the columns, percentage classes of cattle activities. Specifically, each cell entry of each contingency table represented the number of times that a row and a column

Table 1. Variables used for Correspondence Analysis and their codes.

a) Behavioral variables

Parameter	% Categories	Codes	Parameter	% Categories	Codes
Grazing	0	G0	Fodder ingestion	0	F0
	1-10	G1		1-10	F1
	11-25	G2		11-25	F2
	26-50	G3		26-50	F3
	51-75	G4		51-75	F4
	76-100	G5		76-100	F5
Browsing	0	B0	Resting-ruminating	0	R0
	1-10	B1		1-10	R1
	11-25	B2		11-25	R2
	26-50	B3		26-50	R3
	51-75	B4		51-75	R4
	76-100	B5		76-100	R5

b) Environmental variables

Parameter	Categories	Codes	Parameter	Categories	Codes
Herd size	1-10	HD1	Temperature (°C)	-6-0	T1
(No. individuals)	11-25	HD2		1-5	T2
	26-75	HD3		6-10	T3
	76-200	HD4		11-15	T4
	>200	HD5		16-20	T5
Wind intensity	Negligible	WI0		21-25	T6
	Low	WI1		26-30	T7
	Medium	WI2		>30	T8
	Strong	WI3			
Holm oak tree (%)	1-20	TO1	Holm oak shrub (%)	1-20	SO1
	21-40	TO2		21-40	SO2
	41-60	TO3		41-60	SO3
Lusitanian oak (%)	1-20	TL1		61-80	SO4
	21-40	TL2	*Santolina* shrub (%)	1-20	SS1
Ash tree (%)	1-20	TA1		21-40	SS2
	21-40	TA2	*Cistus* shrub (%)	1-20	SC1
	41-60	TA3		21-40	SC2
				41-60	SC3
Geomorphology			Vegetation types		
Plateau		GM1	Grassland	VT1	
Upper zone with undulating relief		GM2	Open dehesa without scrub	VT2	
Upper zone of slope		GM3	Open dehesa with some scrub	VT3	
Middle zone of slope		GM4	Open dehesa with abundant scrub	VT4	
Flat zone in middle part of slope		GM5	Open woodland of Ash tree	VT5	
Flat zone in lower part of slope		GM6	Dense dehesa without scrub	VT6	
Lower zone of slope		GM7	Dense dehesa with scrub	VT7	
Dale without quaternary sediments		GM8	Dense woodland of Holm oak	VT8	
Narrow valley with sediments		GM9			
Wide valley with sediments		GM10			

were recorded together in a particular group of days. In the calculation process of the analysis, the points (i.e. rows and columns) are plotted in Euclidean space, and treated as vectors of relative frequencies or profiles. Thus, the positions of the points in the multivariate space do not depend on the total summation of their respective frequencies of occurrence, the so-called "masses" in the terminology of the Correspondence Analysis (Benzécri 1970). The points, however, are weighted differentially according to their respective masses for the definition of the ordination axes. Thus, although the directions of the principal multifactorial axes resulting from the analysis tend to reflect the directions of greatest dispersion of clouds of points, they are also conditioned by the masses assigned to the points (Greenacre and Vrba 1984). Two ordinations that can be jointly displayed result from the analysis, 1 for the columns (here percentage classes of animal activities) and 1 for the rows (states of environmental variables). The graphical output of the analysis reflects gradients of variation in the data. In general, the greater the distance between 2 behaviors along an axis, the greater the differences between the habitats on which they normally occur. The numerical output of the Correspondence Analysis provides information on the importance of the axes in explaining the total variability, as well as on the contribution of the axes to the inertia of the points in the multivariate space. The contribution values of the points to each axis are the basis for the interpretation of its ecological significance (Ben-Shahar and Skinner 1988). In our case, we considered relevant all the variables' states that exhibited absolute contribution greater than 2 at least for 1 axis (Greenacre 1984). In the case of cattle activities, we considered all their percentage classes in order to show trends in cattle habitat use.

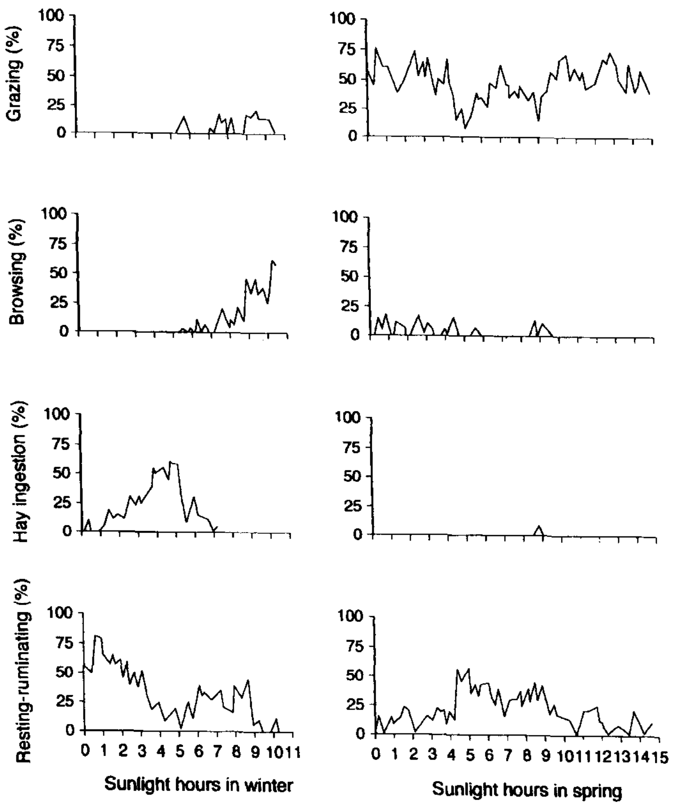

Fig. 2. Daily patterns of 4 cattle feeding activities in winter and spring seasons. For each group of days, curves were obtained by calculating the average percentage value of an activity at a particular time of the day. Calculations were performed using 10 min. intervals. Sunrise time is indicated by 0.

Results and Discussion

Interpreting the ordination results considered the daily patterns of variation in feeding activities of the cattle in winter and spring (Fig. 2). The ordination results were used to define archetypal habitats (Fig. 3b and 4b) for each feeding activity in each season. These archetypal habitats were built taking into account the variables' states adjacent to each behavioral category in each ordination plane.

Winter

The first 2 principal axes of the winter data ordination accounted for 38.4% + 18.3% = 56.7% of the total inertia. Axis 1 showed the main characteristics of cattle behavior in this season. It reflected a transition in terms of behavior and habitats occurred throughout the winter days, with the mornings being dominated by fodder ingestion and resting-ruminating, and the evenings by foraging activities. Thus, the negative end of axis 1 was characterized by various intensities of fodder ingestion and resting-ruminating, as well as by low intensity grazing (Fig. 3). Fodder ingestion and resting-ruminating were the most important activities in winter, as reflected by their percentages of daily occurrence (19% and 46%, respectively). The coincidence of various percentage classes of the fodder ingestion and resting-ruminating activities in the same part of the multivariate space (Fig. 3) indicates that they often occurred in the same sites though alternating in their intensities (see also Fig. 2). The manner in which fodder was distributed in the estate may account for these results. The fodder was delivered to the same place each morning for several days. Early in the morning, when the temperature was still very low (–6 to 5°C), the cattle began waiting for the fodder in this place, forming a large herd (ranging from 76 to >200 animals) as indicated by the negative end of axis 1. While waiting, the cattle remained resting and ruminating (Fig. 2), and eventually eating fodder from previous days, or grazing if there was pasture available. Once the fodder had been delivered, its ingestion became the most important activity for a period of 2 hours (Fig. 2). After this period, the animals remained in the same place resting and ruminating for 2–3 hours, and then began searching for additional food for the rest of the day (Fig. 2). The characteristics of the places in which fodder was supplied were reflected by negative end of axis 1 (Fig. 3). These were mainly open dehesa habitats without scrub, and open woodlands of ash tree, located on low plains and wide valleys, respectively.

The positive end of axis 1 was dominated by browsing and grazing activities (Fig. 3), which occupied only a small portion of the activity of the animals during day-time (9%). These activities occurred mainly in the evening (Fig. 2) and in small herds (1 to 25 individuals), though in different types of habitat as indicated by axis 2 of the ordination (Fig. 3). Further inspection of data showed that each winter evening was dominated by 1 of these 2 activities (i.e. they tended to be mutually exclusive in temporal terms). Browsing increased towards the positive end of axis 2. The lowest intensities of this activity were associated with habitats of open dehesa with abundant shrubs of the species *Cistus ladanifer* which is rarely consumed by cattle (personal observa-

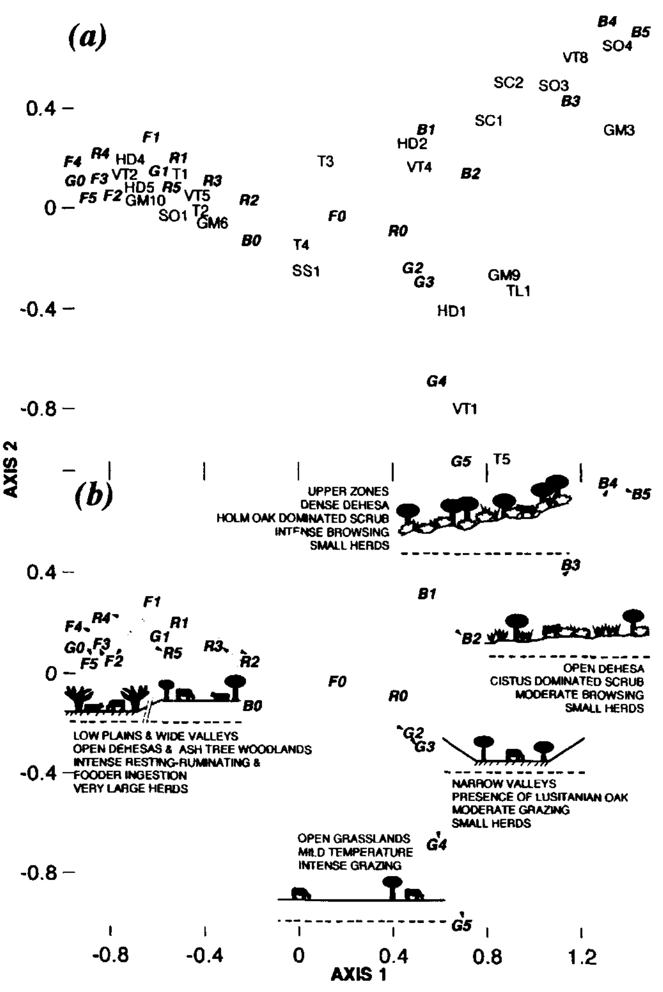

Fig. 3. Correspondence Analysis of the winter data (with scarce grass). Only environmental variables' states with relatively high absolute contribution to at least 1 axis (Table 2) are presented and were considered for interpretation. Codes are explained in Table 1. Geomorphological and vegetational representations are explained in Fig. 1. Figs. a and b are given separately to facilitate interpretation, but may be directly superimposed. a. Crude ordination result. Percentage classes of cattle feeding activities are in bold. b. The percentage classes corresponding to each cattle activity are connected by arrows, showing directional gradients (increase in values). Diagrams were drawn according to the positions of the states of the variables in the ordination result, and illustrate archetypal habitats for different types of cattle behavior.

tion). Intense browsing was related to more appropriate habitats for this activity. It took place on upper slope woodlands with abundant holm oak in shrub form, which is a highly suitable species for browsing. These results reflect the behavior displayed by cattle on winter evenings when traveling from the site in which fodder was supplied to brush areas (Gómez-Sal et al. 1992). During the course of these displacements the animals eventually spent some time browsing in open dehesa areas because it was necessary to pass through them to reach the upper slope woodlands. The low temperatures associated with the positive end of axis 2 of the ordination (Table 2) suggested that the concentration of animals in brush areas was linked to a searching for shelter against adverse weather.

In contrast to browsing, grazing increased towards the negative end of axis 2 (Fig. 3). Moderate grazing was associated with moderate temperatures and narrow valleys with presence of Lusitanian oak (*Quercus faginea* Lam.) trees which is indicative of deep fertile soils (De Miguel 1989). The pasture communities of such areas are typically dominated by perennial grass species (*Agrostis catellana* Boiss. & Reuter, and *Festuca ampla* Hackel) capable of maintaining relatively high productivity during winter. Intense grazing occurred in open grasslands and notably was associated with the mildest winter temperatures (T5: 16–20°C). In this way, the high absolute contribution of the variable T5 to axis 2 of the ordination (Table 2) indicates that temperature was an important factor in determining the kind of feeding activity exhibited by the cattle during winter.

Spring

Similar to the case of the winter data, the first 2 principal axes of the spring data ordination accounted for 38.7% + 18.4% = 57.1% of the total variance. Intense resting-ruminating activity, nonexistent to light grazing and herds of 26–200 animals occurred in the positive end of axis 1, where they were associated with relatively high temperatures, and open plateau grasslands on which wind speed is normally high. The cattle often rested and ruminated in these windy spots during the afternoon hours of the hottest spring days (Fig. 2) presumably to avoid being disturbed by biting flies (Senft et al. 1987) which are particularly active in this period of the day (Fig. 4). Another kind of habitat preferred by cattle to rest and ruminate is illustrated by the negative end of the axis 2. This part of the multivariate space was dominated by dense dehesa with some scrub, high percentage cover of holm and Lusitanian oak trees, and herds with more than 200 animals. These variables showed high absolute contribution to axis 2 (Table 3), and define a kind of habitat characterized by tree shadows in which the cattle can find shelter from the sun (Fig. 4). The high percentage cover of Lusitanian oak trees suggest that these were cool areas, suitable to rest and ruminate when temperature is high. The overall percentage of daily time devoted to resting and ruminating in spring was 25%.

Grazing and browsing increased towards the negative end of axis 2 (Fig. 4), indicating that these activities tend to occur in similar habitats in spring. Contrasting with what happened in winter, when the cattle spent only one tenth of the day foraging, the percentages of daily occurrence of grazing and browsing in spring were 50% and 1%, respectively. The fodder given to the cattle in winter may account for these differences. On the other hand, the large proportion of time devoted to grazing in spring suggests that browsing consisted of occasional events during grazing bouts (Fig. 3). The high availability of pasture in spring may explain these results, since it is likely that grazing alone could fulfill the food requirements of the animals in this season. According to the graphic display of the ordination (Fig. 4), intense grazing and occasional intense browsing events, were associated with dales and lower zones of slopes occupied by open dehesa woodlands with some scrub. In addition, the ordination also shows that moderate grazing and light browsing and resting-ruminating took place in open dehesa habitats at the upper zone of slopes. The concentration of grazing activity in lowlands may be explained by the potentially large herbage production of these areas, which is a consequence of the high water and nutrient availability of soils (Casado et al. 1985). In contrast with resting-ruminating, intense grazing activity occurred mainly in dispersed small herds, as indicated by the proximity of the variable HD1 (herd of 1–10 animals) to the percentage class of the grazing activity G5 in the multivariate space (Fig. 4).

Factors Influencing Cattle Feeding Behavior

The data indicate that food availability was of prime importance in determining activity patterns and habitat preferences of the cattle. For instance, this was reflected by the daily distribution of animal activities in winter which seemed to be strongly determined by the manner in which the fodder was supplied in the estate. Thus, whereas the occurrence of resting and ruminating was markedly associated with the places and time in which fodder was provided, grazing and browsing were virtually relegated to the evening time (Pratt et al. 1986, Putman et al. 1987). Moreover, when browsing dominated winter evenings, it occurred in areas exhibiting an abundance of the most favored shrub species of the cattle in the estate (holm oak in shrub form). Similarly, in spring, when herbage was available all over the estate, intense grazing was clearly associated with fertile lowlands having high production. At this time browsing visiting browsing areas was negligible. Accordingly, the feeding behavior of the cattle seems to conform with the behavior of optimal predators which tend to specialize on the most profitable prey (in this case vegetation type), even when food is abundant in the home range (Duncan 1983, Crawley 1983, Senft et al. 1987).

Pratt et al. (1986) also found that food was of prime importance in determining the habitat preferences and activity patterns of both cattle and ponies in the New Forest, England. However, they found that shelter was an important consideration at all times during winter, since in this season the animals restricted their foraging to communities providing cover. Similarly, Duncan (1983) reported that the behavior of a herd of horses in a Mediterranean wetland in France was primarily determined by food abundance, whereas weather and biting insects had some effects on horses' distribution, particularly for non-feeding activities. Environmental factors other than food also strongly condition the behavior of the study cattle. In spring, increased temperatures and/or activity of biting insects during midday were associated with an intensification of resting and ruminating activities, either in dense woodlands of holm and Lusitanian oaks or in windy places. Similarly, during winter evenings, weather conditions seemed to be particularly important in determining whether cattle grazed in exposed open areas or in grasslands of narrow valleys, or browsed in sheltered woodlands. These areas were associated with relatively low, moderate and high temperatures, respectively.

Our results suggest a consistent relationship between herd size and animal activity in the 2 seasons. Moderate and intense grazing and browsing activities were associated with herds of small size (from 1 to 25 individuals), while moderate and intense resting-ruminating activity was associated with large groups. This was the case even in spring when cattle behavior was not conditioned by fodder supply. These variations in the herd behavior could be associated with the distribution of the areas most appropriate for feeding or resting-ruminating. For example, if preferred feeding areas were numerous and too small to be exploited by large groups of animals, or only a few areas were suitable for resting-ruminating. The first possibility seems to be quite likely, bearing in mind that the spatial variation of vegetation types in the estate is large, and that the animals were apparently highly selective in terms of the areas they preferred for feeding. Under

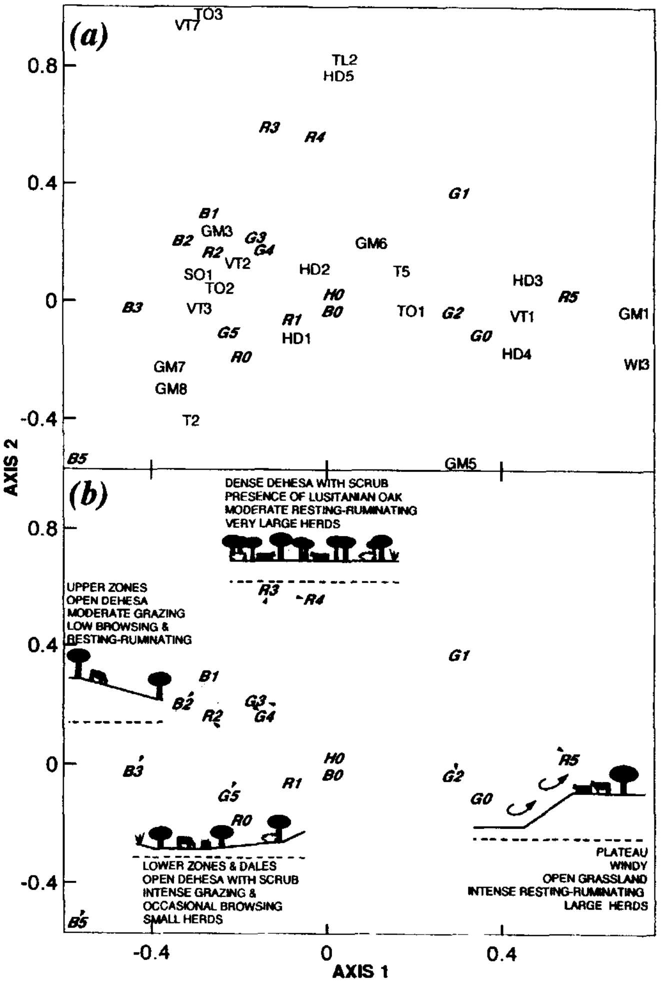

Fig. 4. Correspondence Analysis of the spring data (with pasture widely available). Conventions as in Fig. 3.

such circumstances, the distribution of the animals in small foraging herds may increase their efficiency in using available food resources, particularly when those resources are scarce. For example, foraging in small groups may reduce competition for food, and the likelihood of over-exploiting the best food-providing places or "wasting" the food available in other smaller areas (Crawley 1983, Pullian and Caraco 1984). Due to the high heterogeneity of the estate in terms of geomorphology and vegetation structure the second possibility seems to be less likely. A third alternative would be that cattle are highly social animals, with strong social cohesiveness and herding behavior (Pratt et al. 1986, Begon et al. 1990).

Correspondence Analysis of Animal Activities by Environmental Variable Matrices

Community ecology provides some examples in which Correspondence Analysis has been applied on contingency tables of species (either plants or animals) by states of environmental variables (Greenacre and Vrba 1984, Ben-Shahar and Skinner 1988, Rodríguez et al. 1995). Montaña and Greig-Smith (1990) compared this approach with the more classical one of considering sites as analytical entities for the analysis. This comparison was based on an artificial data set in which relationships among several hypothetical response and explanatory variables (which could represent hypothetical animal activities and environmental factors, respectively) at a series of sites were established by the authors. Correspondence Analysis of the matrix of response variables by states of explanatory variables only needed 2 axes to adequately reflect all the original relationships between the variables. Conversely, Correspondence Analysis applied to the matrix of response variables by sites needed 6 axes for the same purpose. (Note that in this latter case the relationships between response and explanatory variables were not derived from calculations of the analysis, but they were established a posteriori, taking into account the correlations of the sites' scores with the explanatory variables). This result is not surprising, since conceptually the 2 analyses had different goals: the first 1 looked for relationships between response and explanatory variables, whereas the second 1 searched primarily for trends of variation of the response variables at the sites. Nevertheless, the result is useful since it demonstrates the greater validity of the first approach when the objective is to identify relationships between animal activities and environmental factors.

In this paper, Correspondence Analysis has been applied over true contingency matrices created by expressing the states of environmental variables as frequencies of occurrence of different categories of animal activity. This means that the variable states and categories of cattle behavior with potentially greater weight in the analysis have been those exhibiting higher total frequencies of occurrence (i.e. those with greater mass value). In theory, the approximation followed here would attempt to detect those habitat characteristics which are most associated with the principal animal activities in the area under study. If, on the contrary, one wished to by-pass the particular characteristics of the study area and to obtain more general results, the weight of the rare variables could be increased in the analysis by some form of data standardization, for example assigning equal masses to all the variable states (Greenacre and Vrba 1984). In practice, such transformations are usually unnecessary (Digby and Kempton 1987), particularly when the analysis is applied over true contingency tables (Greenacre 1984). This is because Correspondence Analysis provides an intrinsic scaling of the data by row and columns averages (Digby and Kempton 1987), which results in rarer variables actually having greater weight in the analysis than if only their total frequencies of occurrence were taken into account (Hill 1973, Digby and Kempton 1987). An example of this is provided by the categories of cattle activity high grazing and no browsing (i.e. G5 and B0) in the winter ordination. Compared with the other behavioral categories, no browsing exhibited the highest mass in winter, whereas high grazing had only an intermediate value (masses = 0.212 and 0.024, respectively) (Table 2). In spite of this, both no browsing and high grazing had similar absolute contribution to the axis 1 of the ordination (absolute contribution = 6.02 and 6.51). Furthermore, whereas no browsing had only an intermediate absolute contribution to axis 2, high grazing exhibited the highest absolute contribution to this axis (absolute contribution = 5.13 and 46.42).

According to Greenacre and Vrba (1984), there are no generally accepted rules to enable an appropriate choice to be made in relation to the reweighting of the variables. However, these authors recommend that, whatever the decision, the worker should always calculate and carefully examine the unweighted masses of the variables, especially when interpretation proceeds

Table 2. Composition of the 2 principal axes of the Correspondence Analysis performed over the winter data. Name, name of the variable; Mass, mass of the variable (see Methods); Acon, absolute contribution of the axis to the inertia of the elements. Only environmental variable states with absolute contribution > 2 to at least 1 axis are presented. Variable codes defined in Table 1.

In terms of states of environmental variables				In terms of percentage classes of cattle activities			
Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶	Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶
VT1	14	331	1535	G0	206	150	744
VT2	22	395	46	G1	5	4	5
VT4	14	206	73	G2	5	74	38
VT5	22	204	1	G3	5	94	64
VT8	12	943	829	G4	4	78	349
TL1	8	361	111	G5	24	651	4642
SO1	39	320	3	B0	212	602	513
SO3	13	811	589	B1	1	14	14
SO4	3	215	212	B2	2	69	8
SS1	17	0	204	B3	6	371	223
SC1	8	281	210	B5	10	860	1054
SC2	16	677	740	B6	19	2180	1890
GM3	305	428	76	F0	191	480	20
GM6	50	201	92	F1	1	8	8
GM9	2	65	510	F2	2	46	3
GM10	17	200	9	F3	11	252	11
T1	13	201	14	F4	11	420	54
T2	24	203	10	F5	34	838	13
T3	77	3	228	R0	124	1378	186
T4	23	0	200	R1	16	174	125
T5	8	278	1596	R2	9	7	0
HD1	40	779	1213	R3	11	50	24
HD2	225	367	342	R4	3	76	12
HD4	11	251	29	R5	88	1124	80
HD5	58	1006	89				

† Multiplied by 1,000.
¶ Multiplied by 100.

Table 3. Composition of the 2 principal axes of the Correspondence Analysis performed over the spring data. Conventions as in Table 2. Variable codes defined in Table 1.

In terms of states of environmental variables				In terms of percentage classes of cattle activities			
Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶	Name	Mass†	Axis 1 Acon¶	Axis 2 Acon¶
VT1	53	1784	69	G0	70	2015	411
VT2	31	381	197	G1	5	100	389
VT3	26	424	2	G2	12	213	1
VT7	1	20	1164	G3	42	244	942
TO1	77	639	24	G4	38	162	615
TO2	47	634	46	G5	83	873	610
TO3	1	20	1164	B0	235	28	0
TL2	3	0	989	B1	2	30	93
SO1	28	449	109	B2	6	94	137
GM1	12	1438	5	B3	4	162	0
GM3	11	152	302	B5	3	200	439
GM5	2	29	218	F0	249	0	0
GM6	36	68	638	R0	136	1256	1384
GM7	9	223	212	R1	5	6	10
GM8	10	244	438	R2	18	226	274
WI3	6	690	123	R3	22	78	3955
T2	5	99	428	R4	5	1	735
T5	59	417	383	R5	64	4318	6
HD1	77	75	557				
HD2	54	12	311				
HD3	15	699	54				
HD4	5	232	82				
HD5	3	0	989				

† Multiplied by 1,000.
¶ Multiplied by 100.

to the less stable features of the data. By doing this, the author can always avoid giving too much attention to weak trends.

Applications of the Technique

Correspondence Analysis of animal activities by environmental variable matrices is a versatile method in numerical terms. It provides a non parametric description of the relationships between the variables under study, which can be either quantitative and qualitative (Table 1). Thus, the method can be used as a complement to analyses with a limited capacity of dealing with qualitative data such as regression (Ben-Shahar and Skinner 1988). In addition, whereas regression analyses are used to explain 1 response variable using several explanatory variables, Correspondence Analysis may analyze large numbers of both kinds of variables simultaneously. Hence, it can be useful for preliminary investigations of behavioral problems that can be conceptualized as multivariate. For example, it could be used to analyze plant species preferences of ungulates using chemical and morphological properties of the forage. (Note that whereas qualitative variables like plant species identity do not require any modification, quantitative variables such us forage fibber content or biting rate must be subdivided into categories before analysis).

The method may also provide clues about animals' perception of the environment. Most studies on animal behavior-environment relationships consist of identifying subunits within a study area (plant communities, habitat types, landscapes) and searching for differences between them in terms of animal behavior. The ideal way of defining such subunits is to use criteria that match animals' perception of the characteristics under study (Senft et al. 1987). However, since this is unknown, the environmental subunits are usually defined arbitrarily. Correspondence Analysis of animal activities by environmental variable matrices allows a different approach. With this technique there is still subjectivity in the selection of the variables to be considered in the study. However, due to the way that Correspondence Analysis operates, the importance that each environmental variable has in the result largely depends on its degree of association with animal behavior. Therefore, the definition of habitat types can be made taking into account relevant environmental variables (i.e. those with high loadings in the analysis) and the animal activities to which they appear associated in the graphical display. These habitat types would be archetypal models, since they were constructed using characteristics of the preferred places to perform each animal activity. From an applied stand point, these model habitats could be used as reference to both subdividing the study territory onto environmental units, and/or modifying existing habitats to meet the animals' requirements. For example, shrub removal practices are common in the dehesa grazing systems (Joffre et al. 1988) and are probably necessary in order to maintain economically viable levels of pasture production (Huntsinger and Bartolome 1992). However, our results suggest that it can be damaging for cattle to excessively diminish the shrub areas (Gómez-Sal 1992). In particular, since they were preferred over the open grasslands during the coldest winter evenings, probably because they offer both plants for browsing and shelter against low temperatures.

To conclude, Correspondence Analysis allows the determination of characteristics of the habitats in which each type of animal activity is usually performed. This method is appropriate for searching for broad relations between animal behavior and a number of aspects of the environment. Thus, it can be a useful tool for hypothesis generation about the habitat characteristics which may be important for a causal explanation of spatial variation of the animals' behavior.

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