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Social segregation and the maintenance of social stability in a feral cattle population

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Abstract. The social structure of a feral cattle, *Bos taurus*, population in Doñana (southwest Spain) was studied. Social affinity among individuals was related to their age–sex classes. Cows and young animals formed stable social groups or cow-herds based on long-term social links among their members. The members of a given herd shared a common home range and maintained an active spatial and social segregation with members of other social groups. Both for its stable composition and for its fidelity to a home range, a herd constitutes a stable social environment. The stability of social structure and the mechanisms involved in its maintenance in Doñana cattle are discussed in the context of a controversy raised by apparently contradictory findings on bovine social behaviour.

A general theory concerning the relationship between the ecology and social behaviour of ungulates (Geist 1974; Jarman 1974) predicts a social structure for large ruminants based on the strongly gregarious behaviour of individuals. This is in accordance with the results of several studies on social and grouping behaviour of bovine species such as feral cattle, *Bos taurus* (Daycard 1990; Lazo 1992a), American buffalo, *Bison bison* (Lott 1991a) and African buffalo, *Syncerus caffer* (Sinclair 1977). The theory predicts, and many studies have confirmed, the existence of fluctuations in gregariousness in response to habitat structure, food availability, reproductive behaviour and risk of predation (see Lott 1989, 1991b), and among bovines this variability in grouping behaviour is widespread (Hall & Moore 1986). The theory does not affirm, however, whether the rules governing the association among individuals are shared by related species under similar ecological circumstances.

Data on the social organization of bovine species such as the gaur, *Bos gaurus* (apparently small unstable groups: Schaller 1967), American buffalo (random association among females in large groups: Lott & Minta 1983), the European bison, *Bison bonasus* (some persistent associations among adult cows forming the nucleus of social groups: Krasinska et al. 1987) and the African buffalo (stable herds as the basis of the social structure: Sinclair 1977; Prins 1989) seem to be contradictory in the framework of the aforementioned general theory. It would be surprising that populations of related species, living under similar ecological conditions, showed common patterns of gregariousness but differed in the nature of the associations formed. Thus, other bovids share general models of social organization: the instability of associations is well known in medium-sized species such as the wildebeest, *Connochaetes taurinus* (Prins 1989), the kob, *Kobus kob* (Wanzie 1988) and the common eland, *Tragelaphus oryx* (Hillman 1987), and in sheep species stable associations among females seems to be a rule (*Ovis aries*: Arnold et al. 1981; Lawrence 1990; *O. canadensis*: Festa-Bianchet 1991).

Contradictory results are even found among studies on a single species such as cattle. Kimura & Ihobe (1985) described the social organization of the feral cattle on Kushinoshima Island in terms of a random association of animals with overlapping home ranges. Quite discrepant with their results are those of Reinhardt et al. (1978), Reinhardt & Reinhardt (1981) and Veissier et al. (1990), whose works are centred on social interactions and kinship as the basis of strong social bonds among mature animals. Hall (1986) indicated that there is little evidence of personal affinities among Chillingham cows, and it is known that Swona feral cattle forage as a single herd (Hall & Moore 1986). Among highly social and polygynous species such as cattle, however, females should be disposed to maintaining stable social bonds because these can improve feeding

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efficiency and offspring defence (Greenwood 1980); males, in contrast, are less sociable. Thus feral bulls maintain a grouping behaviour independent of that of cows and are usually seen as solitary animals out of the reproductive season, whereas mature cows tend to aggregate in accordance with the influence of habitat structure on both the predation risk to neonates and food abundance (Lazo 1992a).

Several aspects of the socioecology of feral cattle have recently been studied on populations as the Chillingham Park herd (Hall, 1986, 1989), the Amsterdam Island cattle (Daycard 1990) and the Doñana feral cattle (Lazo 1992b), but there are few published results on the nature of the association among the cows of these populations. In this paper I describe the results of a 3-year study on the feral cattle of Doñana (southwest Spain), a population in which all animals are individually identifiable. Initial evidence suggested that cattle do not group at random and that their social organization is based on closed groups. My aim in this study was to characterize the patterns of association among Doñana cattle, the resultant social structure of the population and the mechanisms involved in its maintenance. I discuss the nature of the association among individuals and the significance of the stability of the social organization in the context of the apparently contradictory findings on bovine social behaviour.

METHODS

Study Area and Animals

Doñana's feral cattle live in the Biological Reserve of Doñana (37°N, 6°W, southwest Spain), a 67 km^2 area enclosed by a barbed wire fence. The climate is typically Mediterranean with hot, dry summers and mild, wet winters. Four main habitats (pine forest, sand dunes, scrubland and marshland) including a great variety of herbaceous plant communities are present (Rogers & Myers 1980; Lazo 1992b). The plant communities more heavily used by feral cattle for feeding are the marshland when it is dry, grasslands at the ecotone zone between the scrubland and the marshland, and lagoon meadows located around permanent ponds at the ecotone between sand dunes and the scrubland (Lazo & Soriguer 1993). Biomass dynamics at these pastures follow marked seasonal patterns that vary between plant communities.

Cattle range freely over the Reserve. They are not managed except that 30–50% of calves born each year are culled; no supplementary food is provided. All animals can be recognized individually by morphological features such as coat coloration, presence of white spots and size and shape of horns. No more than 140 individuals older than 1 year were simultaneously present on the Reserve from January 1987 to December 1989, but 247 different animals were present over the whole study period. The age–sex structure was biased towards mature females (3 years or older), which represented 56% of the population in October 1989. The contribution of other age–sex classes on the same date was: 15% young females (up to 2 years old), 20% young males (up to 4 years old) and 9% mature males (Lazo 1992c).

Animal Locations

Between January 1987 and December 1989 I located cattle in the field on 309 days from a car or on horseback, following routes that maximized the number of sightings of animals. Special care was taken to obtain a uniform survey of all zones of the Reserve. I recorded the number and identity of all animals I located. I estimated their position using a coordinate system that divided the Reserve into 2742 quadrats each of 150 × 150 m. A total of 17 603 individual locations were obtained but only 13 691 (corresponding to 145 animals) were used in the analysis after calves (animals in their first calendar year) and individuals located fewer than 20 times for the whole study period were excluded.

Social Affinity

An index of social affinity between individuals (S) was estimated for each of the 10 440 possible dyads:

$$S = N_{A,B}/\min\,(N_A,\ N_B)$$

where $N_{A,B}$ is the number of combined locations of individuals A and B, N_A is the number of locations of individual A, and N_B is the number of locations of individual B. A combined location was considered when both members of a dyad were observed as part of a group (at least two animals that showed cohesive behaviour and spatial distribution and were more than 150 m away from other individuals or groups; Lazo 1992a). The index takes values between 0 (no combined location for a dyad) and 1 (when the animal with the lower number of locations was always observed in the same group with the other member of the dyad). This index seems to be more appropriate than others usually employed in related studies (e.g. Grassia 1978; Lott & Minta 1983; Kimura & Ihobe 1985) because it is not sensitive to differences in location probability between the members of the dyad. A possible bias in the value of the index arising from a small number of locations can be corrected by considering only individuals with at least 20 locations.

I subjected the symmetric matrix of social affinity indexes to a cluster analysis using UPGMA (Unweighed Pair–Group Method Using Average Linkage; Sneath & Sokal 1973). Cluster trees allowed differentiation of groups of individuals with homogeneous index values. Because the index value reveals the intensity of the social affinity between two animals, I have considered clusters as accurate estimates of the composition of current social units.

Because the social affinity analysis includes data from 3 consecutive years, I have considered a male as young if born in 1984 or later (i.e. younger than 5 years during most of the study period), otherwise adult; for females I fixed the limit in 1986.

Home Range Behaviour

I estimated the size and location of the home range of each individual using the minimum convex polygon method (Jennrich 1969). The position of the activity centre (the mean of the coordinates of all locations: Hayne 1949) was also estimated. An index of home range overlap (V) was calculated for all possible dyads of individuals in a cluster:

$$V = 2P_I/(P_A+P_B)$$

where P_I is the area of the polygon delimited by the intersection of the home ranges, P_A is the area of the home range of individual A and P_B is the area of the home range of individual B. Using a subset of 40 animals, 10 randomly chosen from each cluster, I also calculated the value of the index between each animal of the subset and all the others belonging to a different cluster.

I estimated a global composite home range and 12 seasonal composite home ranges for each cluster using the locations of all animals in the group. I employed the harmonic mean method excluding the 25% outermost points (Dixon & Chapman 1980) to delimit heavily used areas within the home ranges. The seasonal periods considered in this study were winter (November to January), spring (February to April), summer (May to July) and autumn (August to October); this approach to seasonality reflects most accurately the fluctuations in abundance and distribution of cattle food in Doñana (Lazo 1992b).

RESULTS

Social Affinity among Individuals

The cluster analysis of the values of the social affinity index (S) shows at least four clusters (labelled LGN, MTZ, PLC and QMD; Fig. 1) composed of animals showing high values of social affinity among themselves but lower affinity with members of other clusters. The four main clusters separate very early in the tree (Fig. 1): the average values of the index among members of two different clusters is in most cases very near to zero. Within a cluster, the values of S are high but the absolute value of the index for a dyad is related to the age–sex class of its members. Males considered as adult for the entire study period tended to associate in a cluster mainly with other adult males, but the S value for the association of a bull with either a bull or any other animal is in general among the lowest. The highest values of S are for dyads composed of adult females and a young male or female, probably most of these last corresponding to mother–offspring bonds (see Fig. 1). Despite this relation, adult cows mainly associated with other adult cows, young cows with adult and young cows, and young bulls with young animals of both sexes and adult bulls.

Spatial Behaviour of Cows

Cows in the same cluster had home ranges whose centres of activity were very close to one another. The complete set of these points shows a clustered spatial distribution which delimits four areas of the Reserve (Fig. 2); for that reason I have given the four clusters and the four areas of the Reserve the same identification labels. The average value of the index of home range overlap (V) among members of the same cluster is in all cases very high, but differs between clusters

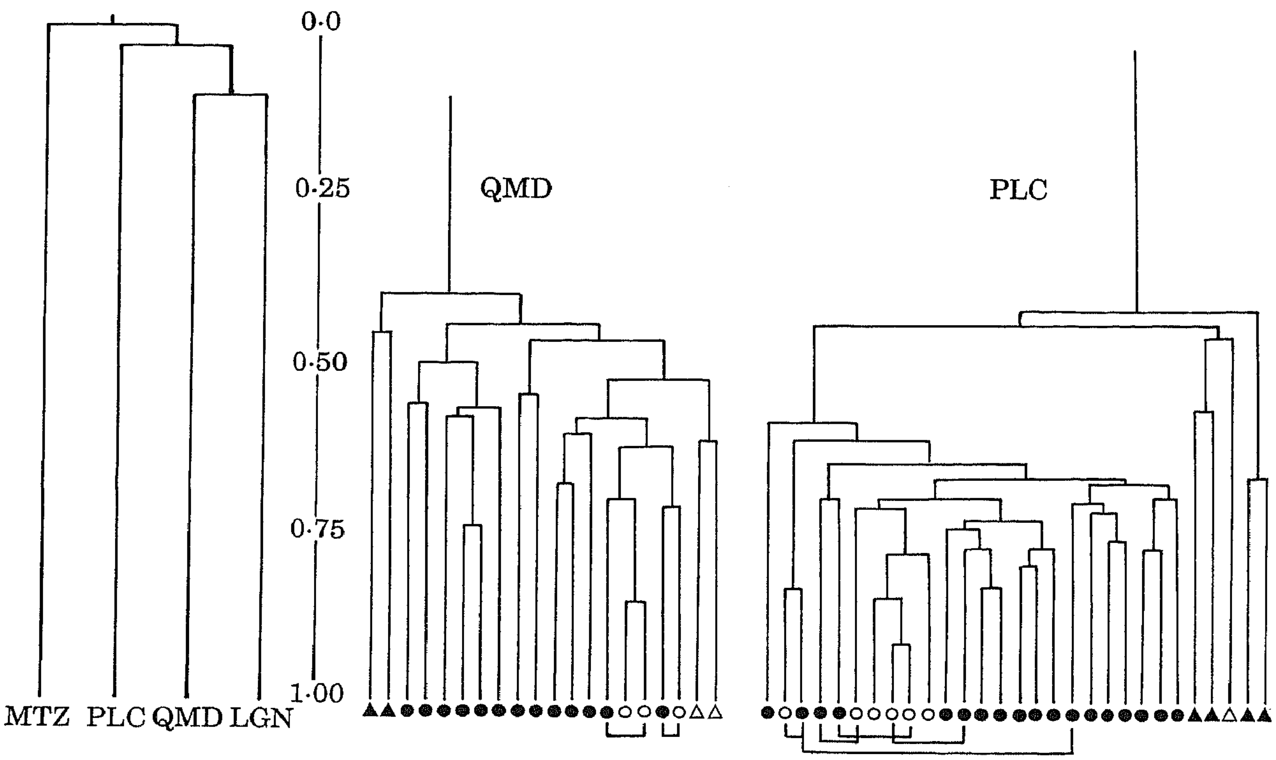

Figure 1. Cluster analysis (UPGMA method) of individuals with respect to the value of the social affinity index (*S*). The first tree is a simplification of the global tree in which only the four main branches appear; the second and third trees represent in detail two of these branches or clusters labelled QMD and PLC. The vertical scale represents the value of the social affinity index. ▲: Adult males; △: young males; ●: mature females; ○: young females. Mother–offspring bonds, when known, are represented by lines connecting two individuals.

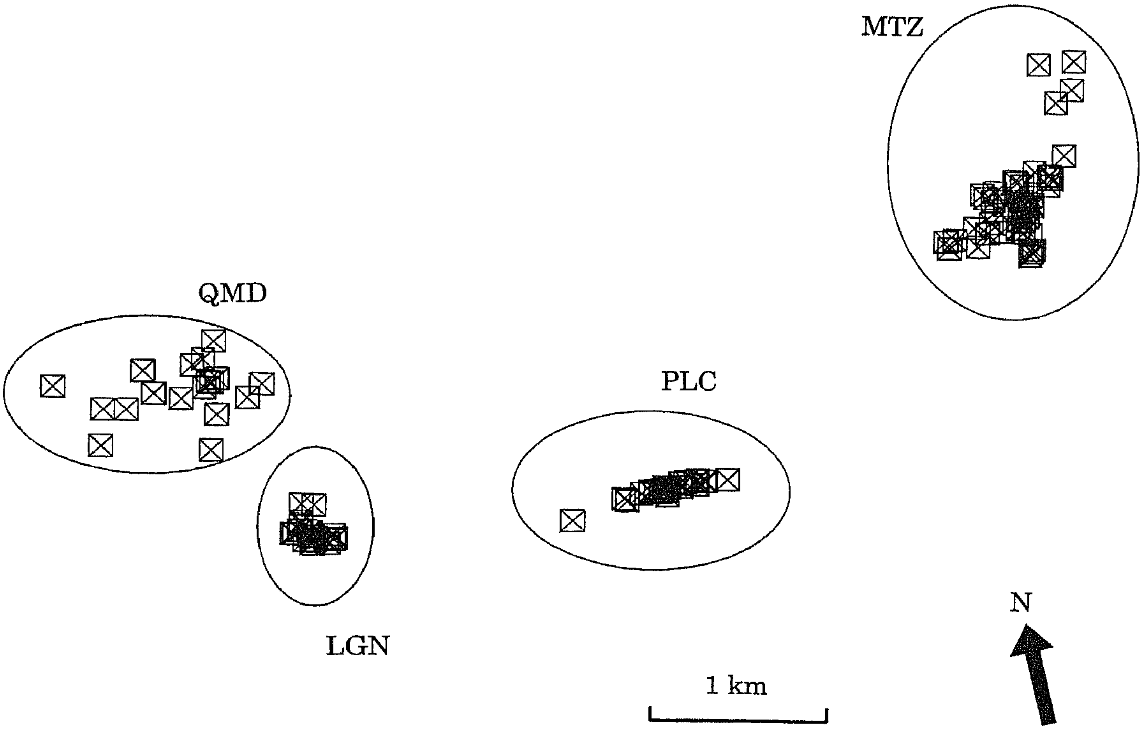

Figure 2. Spatial distribution of the activity centres corresponding to the global home ranges of the females. Four zones in the Reserve are delimited.

Table I. Average values of the index of home range overlap (S)

	Within-herd			Inter-herd		
Herd	S	SE	N	S	SE	N
LGN	0·679	0·013	169	0·126	0·006	300
MTZ	0·643	0·006	817	0·079	0·006	300
PLC	0·817	0·005	231	0·119	0·006	300
QMD	0·808	0·008	136	0·102	0·006	300

Within-herd values are for dyads of members of a herd; the inter-herd values estimate the average overlap of the home ranges of 10 randomly chosen members of a given herd with 30 randomly chosen members of the other herds, 10 from each herd. N=Number of dyads.

(Kruskal–Wallis test: $H=259·5$, $df=3$, $P<0·001$); these values of V estimated within a cluster are greater than the average overlap among home ranges of cows of different clusters (Table I). Considering both the high values of the social affinity index among females and their overlapping home range behaviour I have used the term 'cow-herd' to refer to these clusters.

Cow-herd Composition

Although cow-herds are defined both by female home range behaviour and social affinity, all the age–sex classes are represented in these social groups (Table II). However, adult male participation in the cow-herds was low, both because it had a marked seasonal character and because of the low number of bulls (Lazo 1992a). Cow-herd composition was constant from year to year, changes arising from mortality and natality excluded. No consistent movement of females from one herd to another was detected, and all cows ($N=16$) whose mothers were known and that calved during the study period reared their offspring in the same cow-herd in which they were reared. Cows rarely joined herds other than their own: only 2·9% ($N=1849$) of all groups observed in the field were 'mixed parties'; that is, groups composed of cows belonging to two different herds. When these mixed parties were formed, agonistic behaviour arose between cows of different herds in close proximity. These interactions were mainly butts and only females were involved. They usually resulted in one of the animals moving away, as is common in cattle agonistic behaviour (Kabuga et al. 1991); I observed these interactions more frequently in mixed parties than in intra-herd parties.

Table II. Number of animals of each age–sex class in the four herds in autumn 1989

	LGN	MTZ	PLC	QMD
Young females	4	8	5	4
Mature females	14	32	20	13
Young males	6	17	1	2
Mature males	3	5	2	3
Calves*	13	19	15	5

*Born 1989.

There was no seasonal trend in the frequency of formation of these groups ($\chi^2=6·77$, $df=3$, $P>0·05$), but the participation of the four cow-herds in them was quite different ($\chi^2=64·56$, $df=3$, $P<0·001$); 55·6% ($N=52$) of all mixed parties were formed simultaneously by LGN and QMD cows. I observed no mixed groups with participation of cows of three different herds.

Herd Home Range Behaviour

Global composite home ranges (i.e. the area that includes all the individual home ranges of members of a single cluster) varied between 1243 ha (PLC herd) and 2635 ha (MTZ herd) when estimated by the minimum convex polygon method; home ranges of LGN and QMD herds were, respectively, 1299 and 2034 ha. The average value of the index of home range overlap was 0·31 (range: 0·15 for the PLC–QMD overlap, 0·55 for the LGN–QMD overlap). When considering seasonal composite home ranges, average overlap was considerably smaller: 0·05 in winter, 0·08 in spring, 0·10 in summer and 0·05 in autumn, which

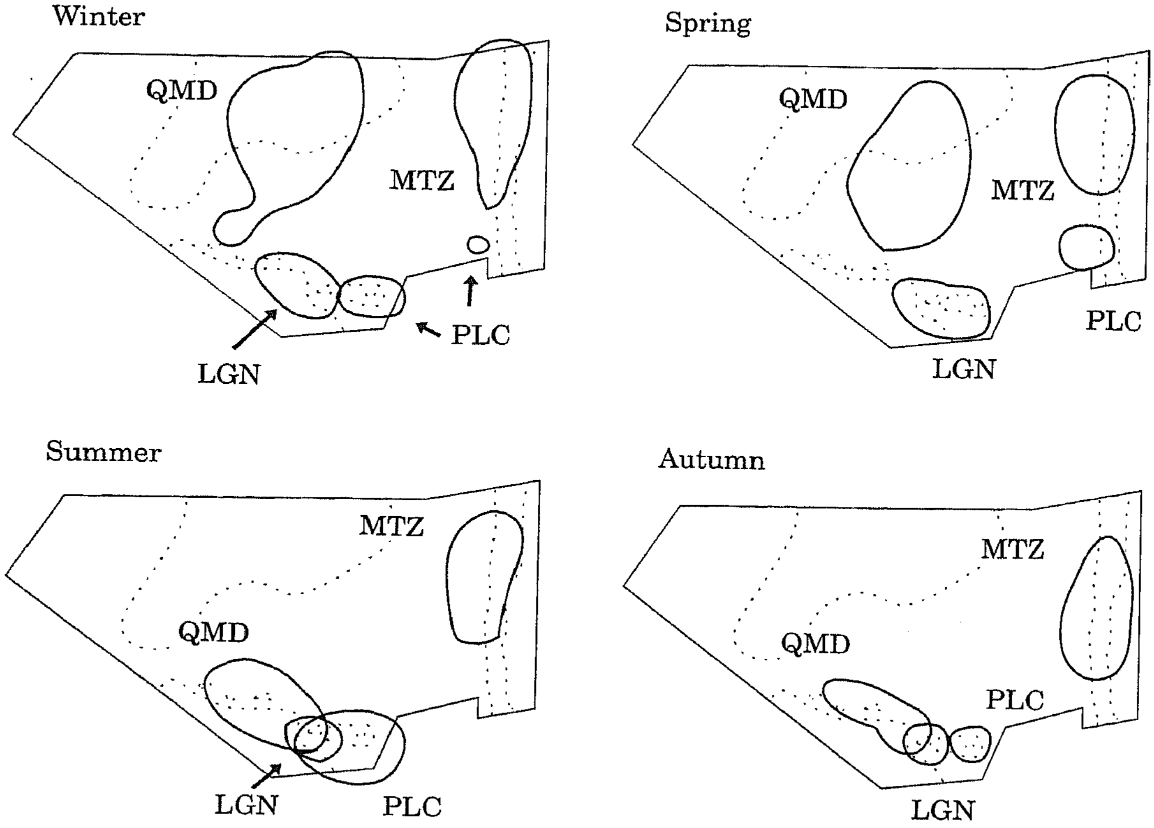

Figure 3. Position and relative size of the seasonal composite home ranges of the four cow-herds. Home ranges were estimated using the Harmonic Mean method (Dixon & Chapman 1980) excluding the 25% outermost points.

suggests that the overlap zones tended not to be used simultaneously by the herds in the same season. Most of the highest values of this index corresponded to the overlap between the areas of LGN and QMD. Because minimum convex polygons usually include large proportions of unused areas within a home range, however, the zones really being shared by different cow-herds must be considerably smaller and of low intensity of use (see below).

In all seasons the overlap between the areas of most intensive use within the composite home ranges was very low, or even zero in winter and spring (Fig. 3). Shifts in the location of these areas were responsible for the variation in the average overlap between composite home ranges. The QMD herd shifted its area of intensive use from spring to summer and maintained it unchanged during autumn; in winter the QMD herd moved again towards the area it occupied during spring. The PLC herd showed a very similar pattern shifting its location between seasons, but the LGN herd changed the size of its area from one season to another rather than shifting its location. As a result of these changes, the average distance between the activity centres of herds PLC, LGN and QMD varied significantly between seasons ($F_{3,24}=10{\cdot}7$, $P<0{\cdot}001$), being smaller in summer and autumn than in winter and spring (Fig. 3). The area of most intensive use of the MTZ herd overlapped in neither season with the areas of the other herds.

DISCUSSION

My results disagree with other studies on the grouping behaviour of feral cattle (Kimura & Ihobe 1985) and on the social structure of related species such as the North American bison (Lott & Minta 1983) and the gaur (Schaller 1967) which describe unstable and random patterns of association among cows. Highly stable social groups have been described for other bovine species, however, such as the African buffalo (Sinclair 1977; Prins 1989); these probably benefit individuals by increasing feeding efficiency (Sinclair 1977; Festa-Bianchet 1986; Albon et al. 1992) and by synchronizing behaviour (such as feeding, watering and ruminating) and biological processes (such as reproduction). In Doñana cattle, taking the population as a whole, 75% of all births took place over 4 months in 1987 and in 1988, and 6 months in 1989 (Lazo 1992b), but if cows are grouped by herds these periods averaged 3·25 months in 1987, 2·75 in 1988 and 4·25 in 1989. Parturition time is thus more synchronized within a herd, which may be beneficial in several ways (for a recent discussion on this topic see Berger 1992). Furthermore, the simultaneous presence of a high proportion of cows with calves synchronizes gregarious tendencies within the herd (Lazo 1992a) and is probably an important feedback mechanism counteracting group instability.

Reinhardt (1980), Reinhardt & Reinhardt (1981) and Veissier et al. (1990) described long-term associations between cows of domestic cattle and their offspring in a herd. Family groups have been described for water buffalo, *Bubalis bubalis* (Tulloch 1978), and in Doñana cattle such long-term associations within a herd between cows and their descendants probably enhance the cohesion and stability of the social groups. Owing to the lack of female dispersal, the probability of two cows being related must be very high within a herd and much lower for cows from different herds. Cooperation among female kin in a group allows the defence of resources and of offspring (Festa-Bianchet 1991) and the existence of a strong philopatry in females towards their natal group enhances kinship in the social unit and can even facilitate the evolution of altruistic traits among relatives (Greenwood 1984), all having repercussions on the social cohesion of the groups.

Levels of Social Organization

Fusion–fission societies have been described for different orders of mammals including ungulates (Sinclair 1977; Ménard et al. 1990; Packer et al. 1990; Whitehead & Khan 1992). The groups of feral cattle at Doñana show a typical fusion–fission behaviour that reflects a social structure with two levels of organization. At a low level the animals form unstable groups (parties) that change in size and composition depending on ecological factors (Lazo 1992a), as a result of large groups splitting and the fusion of two or more small groups. These parties are subgroups of the cow-herds, which are stable social groups that reflect a higher level of social organization. The benefits of a fusion–fission society with two levels of organization are evident because changes in the ecological conditions are reflected in the size and composition of the parties but not in the basic social unit. The two levels of social organization are regulated by different mechanisms: the social cohesion of parties depends on fluctuations in food abundance and distribution, reproductive status, predation risk and other ecological factors (Prins 1989; Lazo 1992a); in contrast, herds are maintained by long-term, social bonds. Much of the disagreement about the stability of the social structure of bovine species could be due to studies focusing on only one level of organization. Thus, Krasinska et al. (1987) reported unstable grouping in the European bison, but suggested a higher level of organization among adult cows. If studies on social behaviour are carried out only in the short term, it is not surprising that they find only unstable social groups.

Social Segregation

Doñana feral cattle within a social group hardly ever mix with components of other herds. Sinclair (1977) reported temporal mixing of herds of African buffalo but aggression occurred only when, rarely, a cow tried to integrate into a herd other than her own. In Doñana cattle, agonistic behaviour observed among members of different herds in mixed parties may undoubtedly play an important role in maintaining social segregation. The main mechanism preventing social contact between herds, however, is the maintenance of exclusive home ranges which minimizes encounters between individuals compared with a free-ranging system with random mobility patterns. Spatial aggregation of cows within the home range of a herd could also diminish encounter probabilities with cows of other herds, but although gregariousness fluctuates seasonally (Lazo 1992a) I have found no seasonal trend in the detection of mixed parties (see Results). This suggests that mixed parties do not form at random and that the animals are avoiding this kind of aggregation when two herds are close together. The occasional encounter between members of two herds may be the result of both groups of animals responding to the same factors, such as food distribution, resulting in a similar habitat and space use within the overlap zone (Wrona & Dixon 1991).

The maintenance of exclusive home ranges cannot be interpreted as resource-defence behaviour by feral cattle herds. Non-overlap of home ranges is not sufficient evidence of defence if intruders are not removed (Grant et al. 1992). The agonistic interactions observed in mixed parties cannot be considered as active site-defending behaviour since the two herds exploit the same resources in the overlap zone. In winter and spring the herds maintain large home ranges (see Fig. 3) and individuals form small parties; however, in summer and autumn individuals form large parties and restrict their movements to small areas in which food and water concentrate (Lazo 1992a). Under such conditions proximity among herds is greater and the maintenance of exclusive home ranges seems more difficult; however, as the frequency of mixed parties does not increase it seems that spatial segregation among herds is promoting social isolation more than the exclusive exploitation of a territory or home range.

Inter-herd Relationships

Hall (1988) reported the maintenance of stable home ranges for life by adult bulls of free-ranging Chillingham cattle. In Doñana cattle, the stability of herd home ranges parallels the stability in the composition of the social groups. Social segregation among cow-herds therefore determines the spatial distribution of cattle in Doñana. As shown by the seasonal variation in the spacing behaviour of the LGN herd, the close spatial proximity among herds limits the size and location of the seasonal home ranges. In summer and autumn this herd occupies only a small portion of its annual range, coinciding with the closeness of QMD and PLC. LGN is the cow-herd that shares a major portion of its home range with others and is involved more frequently in the formation of mixed parties and thus in inter-herd agonistic interactions. This means an intensive pressure of other herds on the LGN herd as the result of similar patterns of habitat and space use during the seasons in which food is not scarce but highly concentrated in LGN's annual home range (Lazo 1992b). If the maintenance of social stability by means of social isolation is important, a herd such as LGN could restrict its seasonal home ranges rather than share its area with other cow-herds. Because the energetic economics of territoriality make it unlikely in large ruminants, the maintenance of the population social structure by dominance relationships rather than by territorial behaviour is expected (Lott 1991a). In this sense, the LGN herd is acting like a subordinate herd with respect to PLC and QMD, moving and reducing its home range as the proximity with other herds in summer and autumn increases. Similar cases of expanding–contracting home range areas of neighbouring social groups have been described for primates, the inter-group competition often being mediated by the relative dominance ranks of the groups involved (Cheney 1986). Within ungulates, dominance relationships among social groups have been described previously for feral horses, *Equus caballus* (Miller & Denniston 1979), and cattle established an inter-breed hierarchy when animals from different single-breed groups were put together (Kabuga et al. 1991). Dominance cannot therefore be ignored as a mechanism involved in inter-herd relationships and consequently in the regulation of the stability of the social structure of non-territorial highly social ungulates that forms stable groups.

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