*Etología*, 2: 9-20 (1992)

# Comparison of social patterns during the rut within three European populations of Corsican mouflons (*Ovis gmelini*)

R. Bon[1,2], G. González[1], I. Estévez[2]. & J.M. Recarte[2]

1. I.R.G.M.–I.N.R.A., CRA Toulouse BP 27, 31326 Castanet-Tolosan Cédex, France.
2. Dpto. de Biología Animal (Etología), Fac. de Ciencias, Avda. San Alberto Magno s/n., Univ. de Córdoba, 14004 Córdoba, España.

ABSTRACT. *Comparison of social patterns during the rut within three European populations of Corsican Mouflons (*Ovis gmelini*).*– A comparative analysis of three wild populations of mouflons revealed major differences in their social organization during the breeding season. In the most typical Mediterranean biotope (Cazorla), males whatever their age, showed a strong tendency to be alone isolation, which can be interpreted as a precocious involvement in breeding activities. Furthermore, mouflons in this area live in small groups owing to the existence of heavily forested area and the scarcity of the resources. Conversely, in Carlit and Caroux, mouflons showed a marked trend to gather during this season. In Caroux, there was lower proportion of lonely males and a higher simultaneous presence of all male classes in mixed groups the in than Carlit. In this area, oldest males could be less behaviourally exclusive compared to the younger ones. Ecological factors and social processes may induce obvious different social tendencies both between age/sex classes in a given population and between different populations, and thus a different social organization during the rut.

KEY WORDS. Rut, Grouping pattern, Populational structure, Socioecology, Intraspecific variability, *Ovis gmelini*

## Introduction

So far, many ecologists studying mammals have established correlations between species-specific patterns of social organization and their environment (Crook, 1970; Eisenberg et al., 1972; Alexander, 1974; Estes, 1974; Geist, 1974; Jarman, 1974; Clutton-Brock & Harvey, 1977; Schaller, 1977; Poole, 1985).

However, various researchers have considered the intraspecific variability of social systems as a fundamental biological aspect rather than as an aberrant behaviour (Crook, 1970; Lott, 1984). Variability in social organization has been shown for various ungulates (Leuthold, 1970; Walther, 1972; Franklin et al., 1975; Schaller, 1977; Georgii, 1980; Schaal, 1982, 1987; Bon et al., 1986; Jarman & Southwell 1986; Teillaud, 1986; Maublanc et al., 1987), including mating systems (Nievergelt, 1974; Emlen & Oring, 1977; Rubenstein, 1986; Schaal, 1987).

Except for few exceptions (Schaller, 1977; Berger, 1979; Shackleton & Shank, 1984; Berducou & Bousses, 1985; Bon et al., 1986), researche on flexibility on the social organization of mountain ungulates is rather scarce. Among the species inhabiting European massifs, the populations of mouflons (*Ovis gmelini*) resulting from numerous introductions performed in continental Europe from 1950 to 1960, certainly cover the largest diversity of habitats. Thus, because of its particular status, this species appears as a good model for studying the variability of social

parameters with respect to various types of environment.

Ecological variables are thought to influence or constrain the range of types of social organization and lability in mating system between different populations in different environmental or density situations are expected (Emlen & Oring, 1977).

The aim of this work is to compare Mouflon social grouping patterns during the full rut between three populations living in different habitats. The social parameters analysed were group size, group types and social tendencies.

## Material and Methods

### Study areas

The study was carried out both in France, in the Parc National du Carlit (eastern Pyrénées) in 1981-82 and the Massif du Caroux-Espinouse (Hérault) from 1984 to 1986, and in Spain, in the Parque Natural de la Sierra de Cazorla, Segura y las Villas (Andalucía) in 1987 (fig. 1).

Cazorla is a forested mountain region (1000 to 2000 m) with a strong Mediterranean climate (see Fandós, 1986). Upon this typical Mediterranean climate are superimposed mountain conditions. Five sympatric species of wild ungulates inhabit the area, namely wild boar (*Sus scrofa* L.), red deer *(Cervus elaphus),* mouflon *(Ovis gmelini),* fallow deer *(Dama dama),* and Spanish ibex *(Capra hispanica),* the last two of which in high densities.

Caroux is a low mountain area which lies from 300 m to 1100 m. The climate is characterized by a transition from a Mediterranean to an oceanic influence (Baudière, 1970; Auvray, 1983). Three species of ungulates live there: mouflon, wild boar and roe deer *(Capreolus capreolus),* the latter being at the limit of its distribution area.

Carlit area ranges from 1400 to 2900 m in altitude. The climate is characterized by continental and oceanic influences combined with a Mediterranean one in the southern parts (Gonzalez, 1984). Mouflons share the biotope with isards *(Rupicapra pyrenaica).*

Cazorla is a very wooded area, while forest and open areas are balanced in Caroux and, in Carlit forest account for only 20% of the area. There is a clear gradient of decreasing Mediterranean conditions from Cazorla to Carlit.

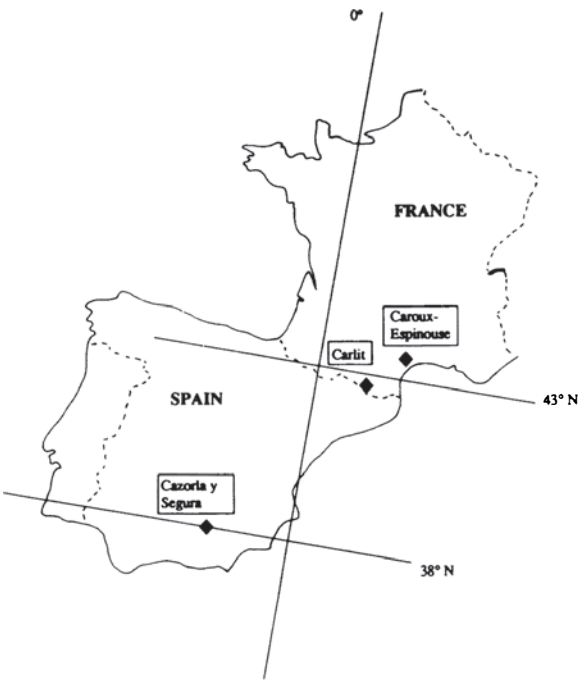


FIGURE 1. Location of the three study areas.
Localización de las tres áreas de estudio.

### Data collection

Along systematic itineraries (20 in Carlit, 17 in Cazorla, and 32 in Caroux), the age and sex of the observed animals and the composition of the group to which they belonged to, were recorded. All data were collected during one mon around the peak of matings which were estimated as follows: if it is

assumed that the gestation period varies slightly (150 to 155 days: Rougeot, 1969), the maximum period of matings can be estimated by subtracting the gestation time from the maximum lambing period in spring for each area (Carlit: Gonzalez, 1984; Caroux: Cugnasse, 1982; Bon et al. (in prep.); Cazorla: Dardaillon, pers. comm. The peak took place at the end of October-beginning of November in Carlit, and at mid-November in Caroux and Cazorla.

Five age/sex classes were defined: $\geqslant$ 4 years old (M4), 2-3 years old (M3), $\geqslant$ 1 year old males (M2), 1 year old ewes (F) and lambs (L).

Like other authors (Krämer, 1969; Jarman, 1974; Wittenberger, 1980) a group was defined, regardless its permanence, as a gathering of individuals within 25 m with one another, exhibiting spatial and social cohesion.

Four classes of group size with 1, 2 to 5, 6 to 10, 11 and more individuals, were considered.

Of the 36 group types resulting from the observed association of the various age/sex classes, 19 were selected accounting for the greatest proportion. These latter were labelled with the symbols of the age/sex classes belonging to the observed groups (e.g. adult males alone: M4, groups of oldest males: M4M4, females with lambs: FL, etc...). For better understanding, we called matriarchal groups those containing at least one ewe, one lamb and/or one young male. Mixed groups resulted from the association of at least one adult male (M3 and/or M4) with one ewe, or with a matriarchal group.

Social tendencies (Bon & Campan, 1989) were defined as the relative proportion of individuals of a given age/sex class involved in the different group types. These groups may already contain one or more animals of the age/sex class considered.

## Statistical analysis

G test and $X^2$ test were used in order to compare group size and group type distributions respectively. A Z test was used to compare two proportions.

In order to test the effect of the study area (i=1, 2, 3) on the distribution of the age/sex classes (j=1, 2,..., 5) in the group types (k=1, 2,..., 10) (i.e. the social tendencies), a log linear model (McCullagh & Nelder, 1983) was employed. Because of their low frequency, different group types were grouped in larger categories:

- M4M2FL: M4FL + M4M2FL + M4M2F
- M3M2FL: M3FL + M3M2FL
- M2FL: M2FL + M2F + FL
- M4M3M2FL: M4M3FL + M4M3M2FL

The modality "alone" refers to solitary animals of each age/sex class.

Let xijk be the number of mouflons in the site i, belonging to the age/sex class j and observed in the group type k. This value is an observed frequency in the (i, j, k) cell of a contingency table and represents a realization of a random variable Xijk whith a mean theoritical frequency mijk. This contingency table is incomplete because cells corresponding to the intersection of age/sex class j and group types k not including this age/sex class are structurally empty. As daily observation of groups were independent, was assumed Xijk as an independent variable even if some mouflons were observed more than one time. The model with interactions between the three factors is:

$$\log mijk = \mu + \alpha i + \beta j + k + (\alpha\beta)\, ij + (\alpha)\, ik + (\beta)\, jk + (\alpha\beta)\, ijk \qquad (1)$$

for all i, j, k belonging to the non-empty cells. Three factors are expectee to affect the observed frequencies:

1) site with 3 levels;
2) age/sex (AS) with 5 levels;
3) group type (GT) with 10 levels.

$\alpha i$, $\beta j$ and k are the parameters of the model corresponding to the classifying factors S, AS and GT; $(\alpha\beta)ij$, $(\alpha)ik$, $(\beta)jk$ and $(\alpha\beta)ijk$ the four interaction factors S.AS, S.GT, AS.GT and S.AS.GT, $\mu$ is the intercept corresponding to the general mean (noted 1 in the generalized linear model results).

In order to test the effects of the three factors on the age/sex classes distribution in the group types, we considered different submodels derived from the complete model (1). The difference of deviance

between a model and a submodel was used to test each hypothesis. Such tests were likelihood ratio tests. The difference of deviance roughly follows a $X^2$ distribution with degrees of freedom (df) equal to the difference of df related to the deviance of each model.

## Results

### Structure of the sampled populations

One sequence of models yielded the goodness-of-fit statistics (table I). Assuming that first differences of the deviance have, in the appropriate hypothesis, an approximate scaled chi-squared distribution, it is clear that the model containing S.GT and AS.GT interactions only provides a reasonable fit. The addition of the S.AS interaction yields no further explanatory power. The model best fitting the count data is: log mijk = $\mu + \alpha i + \beta j + k + (\alpha\beta)$ ij + $(\alpha)$ ik + + $(\beta)$ jk.

Therefore, there was no significant differences of the structure of populations between the areas. On the other hand, the participation of the age/classes in the different group types differed between the sites. Consequently, different group type distributions were found.

In order to look for the social characteristics of each areas, social tendencies, group size and group type distributions have been analyzed in detail.

TABLE I. Goodness-of-fit statistics for a sequence of models fitted to the mouflon data.

[Resultados de las distintas hipótesis contrastadas con el fin de analizar el efecto de los diferentes factores sobre las tendencias sociales.]

| Model | Deviance | First difference | df | Mean deviance |
|---|---|---|---|---|
| 1 | 2231.9 | | | |
| | | 595.8 | 2 | 297.9 |
| S | 1636.1 | | | |
| | | 498.8 | 4 | 124.7 |
| S + AS | 1137.3 | | | |
| | | 706.8 | 9 | 78.5 |
| S + AS + GT | 430.6 | | | |
| | | 259.2 | 18 | 14.4 |
| + S. GT | 171.4 | | | |
| | | 127.2 | 16 | 8.0 |
| + AS. GT | 44.2 | | | |
| | | 12.6 | 8 | 1.6 |
| + S. AS | 31.6 | | | |
| complete | 0.0 | | | |

### Social tendencies of the age/sex classes

#### 1. Males

A comparison between the three zones (fig. 2) revealed a clear significant gradient (table II): whatever their age, males in Cazorla tended to be isolated very often while in Carlit they exhibited the weakest tendency. Conversely, they were mostly included in mixed groups in Carlit, whereas their proportion in Cazorla was the lowest one. Males in Caroux lay in an intermediate position in relation to their associative tendencies, but as far as mixed groups are concerned they exhibited trends more similar to those of the rams in Carlit than to those of the Cazorla ones.

In Carlit, M4 and M3 were more often associated together, whereas in Caroux and, especially in Cazorla, they seemed to avoid one another (table II). The M4 in Caroux and Cazorla tended to gather relatively more often with peers of the same class than in Carlit, whereas the frequency of M3 associated with ewes without M4, increased from Carlit to Cazorla.

#### 2. Females and lambs

Females and lambs showed very similar tendencies. They were mostly included in mixed groups in Carlit and Caroux (fig. 2) whereas they took part in few of them in Cazorla (table II), particularly lambs. In this last zone, females were more balanced between matriarchal groups (about 42%) and mixed ones (about 33%). Single females were never observed in Carlit and Caroux, whereas they amounted to 10% in Cazorla.

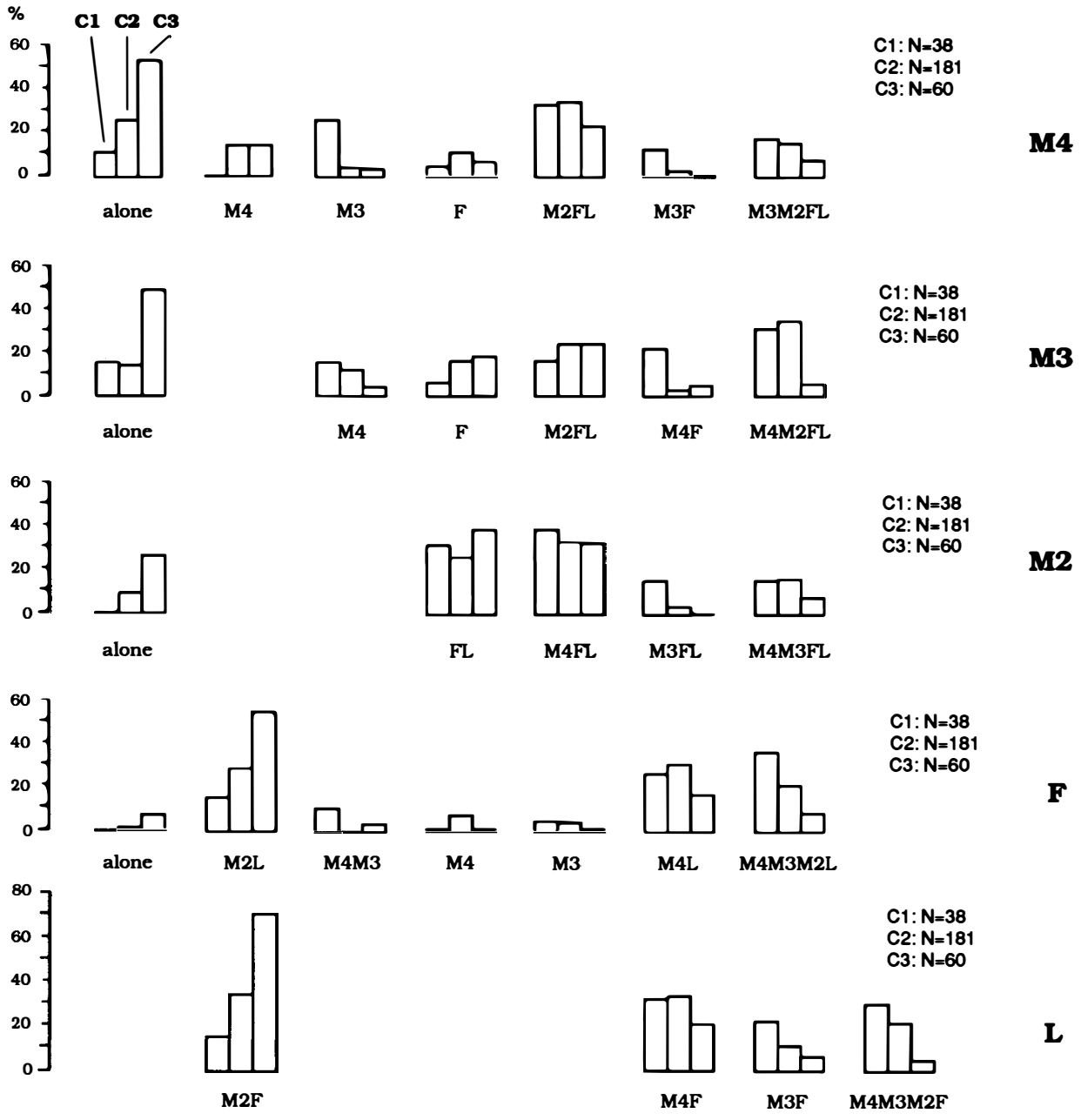


FIGURE 2. Social tendencies of the age/sex classes: C1) Carlit; C2) Caroux; C3) Cazorla.
[Tendencias sociales de cada clase de edad y sexo: C1) Carlit; C2) Caroux; C3) Cazorla.]

TABLE II. Comparison of the social tendencies of the age/sex classes between the three areas.
[Comparación de las tendencias sociales de las clases de edad y sexo entre las tres áreas.]

| | Carlit vs Cazorla | | Caroux vs Cazorla | | Carlit vs Cazorla | |
|---|---|---|---|---|---|---|
| M4 alone | z = – 4.28 | p < 0.001 | z = - 4.48 | p < 0.001 | z = - 1.68 | p < 0.05 |
| M3 alone | z = - 3.04 | p < 0.005 | z = - 3.41 | p < 0.001 | z = 0.15 | NS |
| M2 alone | | | z = - 1.9 | p < 0.05 | | |
| M4 in mixed groups | z = 2.4 | p < 0.01 | z = 3.54 | p < 0.001 | z = 0.4 | NS |
| M3 in mixed groups | z = 1.89 | p < 0.05 | z = 2.06 | p < 0.05 | z = - 0.08 | NS |
| M2 in mixed groups | z = 1.94 | p < 0.05 | z = 0.24 | NS | | z = 1.88 |
| p < 0.05 | | | | | | |
| M4 with M3 | z = 5.1 | p < 0.001 | z = 4.6 | p < 0.001 | z = 1.98 | p < 0.05 |
| F in mixed groups | z = 7.02 | p < 0.001 | z = 6.4 | p < 0.001 | z = 3.4 | p < 0.001 |
| L in mixed groups | z = -5.56 | p < 0.001 | z = -5.04 | p < 0.001 | z = - 2.63 | p < 0.005 |

## Comparison of group size and grouping patterns

### 1. Group sizes

There was a difference between the three areas ($G=33.4$, $df=6$, $p<0.001$) in the frequency of classes of group size (fig. 3). Caroux and Carlit were similar ($G=1.5$, $df=3$, NS). The heterogeneity arose from Cazorla since the paired comparisons Carlit-Cazorla ($G=14.6$, $df=3$, $p<0.001$) or Cazorla-Caroux ($G=30.1$, $df=3$, $p<0.001$) were significant. In Cazorla, the proportion of lonely individuals or small groups was very high, whereas groups of more than six animals were scarce. Conversely, in Caroux and Carlit, large herds were frequently observed and gatherings exceeding six mouflons accounted for 25% of the groups.

### 2. Group types

Again the three areas differed ($X^2 = 65.9$, $df = 14$, $p<0.001$) in their social groupings (fig. 4a). Comparison in pairs also revealed differences (Carlit-Caroux: $X^2 = 24.3$, $df = 7$, $p<0.001$; Carlit-Cazorla: $X^2 = 37.8$, $df=7$, $p<0.001$; Caroux-Cazorla: $X^2 = 36$, $df=7$, $p<0.001$).

There were two clear differences from Carlit to Cazorla: first, an increasing proportion of M4, F, FF and matriarchal groups; in Cazorla, the latter were the most abundant (among them, mother-lamb associations account for 30%). Conversely, mixed associations were the most frequent gathering pattern in Carlit (about 60%) and decrease markedly in Cazorla where they were less frequent (25%). Male herds, with similar proportions in Caroux and Carlit, were more often seen than in Cazorla. Furthermore, in this last zone, and particularly in Caroux, the occurence of M3 was scantier than that of M4 while, in Carlit, their proportion was similar to that of M4.

Examining more closely the mixed herds, a similar percentage of M3 associated with females and youngs without M4 was observed, whatever the area. But, there was a slight decreasing tendency from Carlit to Cazorla (fig. 4b). On the other hand, in Caroux and Carlit, the proportion of M4 included in matriarchals groups without M3 was high and similar for both ($X^2=1.3$, $df=1$, NS), in contrast with what was actually observed in Cazorla (Carlit-Cazorla: $X^2=3.1$, $df=1$, $p<0.05$). The simultaneous presence of M3 and M4 associated with ewes and youngs did not

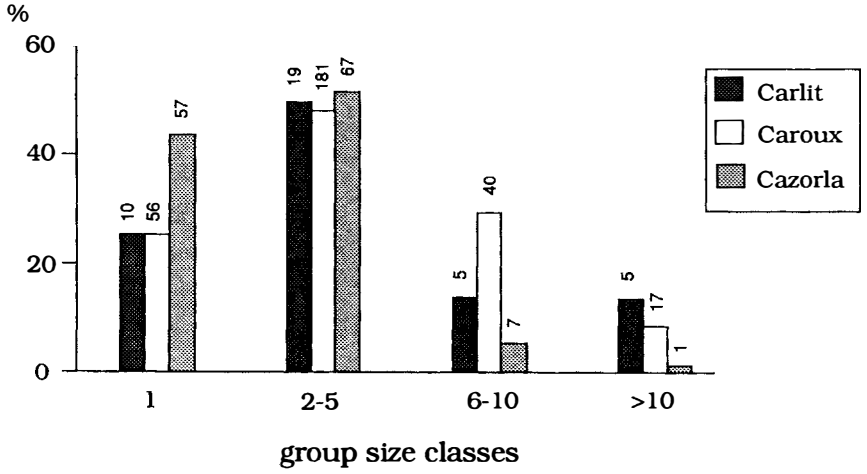


FIGURE 3. Proportion of the group size classes (numbers above columns show sample size).
[Proporción de las clases de tamaño de grupo (los números sobre las columnas indican los tamaños de muestra).]

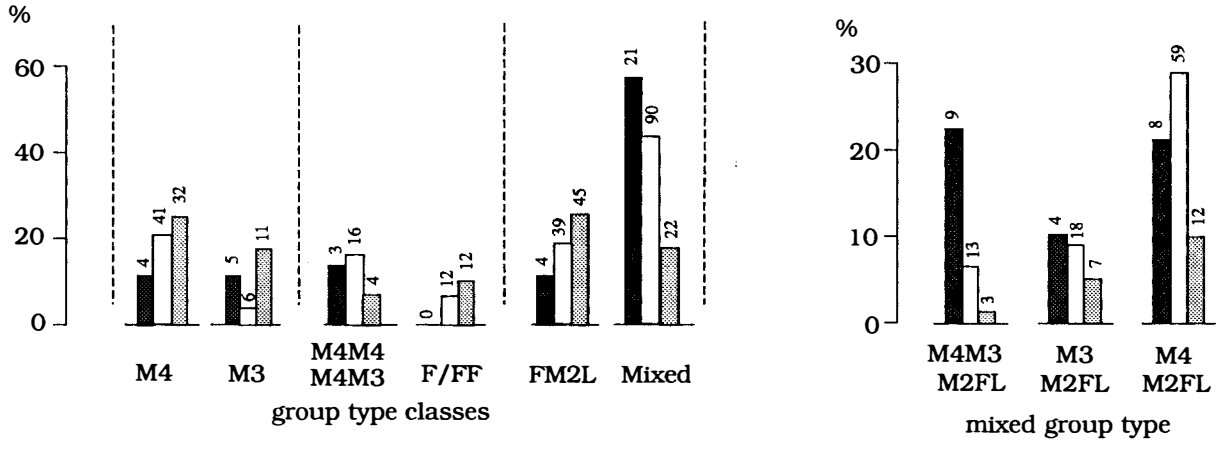


FIGURE 4. Group type proportion (numbers above columns show sample size).
[Proporción de los tipos de grupo (los números sobre las columnas indican el tamaño de muestra).]

differ between Caroux and Cazorla ($X^2 = 2.8$, df = 1, NS) and was very low compared with its occurence in Carlit (Carlit-Caroux: $X^2 = 10.8$, df = 1, $p<0.01$). Overall, the presence of M3 and M4 with ewes was scant and similar for Cazorla and Caroux. The pattern was different in Carlit, where the simultaneous presence of M4 and M3 in mixed herds was characteristic.

## Discussion

The coincidence of births with the growing season in northern latitudes is an evolutive ecological adaptation in order to improve the survival chances of the newborns (Geist, 1974; Bunnell, 1982; Thompson & Turner, 1982). In temperate regions or in mountain biotopes where seasons are very clear-cut, mating season is short and predictable. But even in some temperate climates, the lambing period may greatly vary between massifs (Pfeffer, 1967; Schaller, 1977). The more precocious mating period in Carlit is related to the Alpine climate and good summer availability which allow the ewes to enter in estrus early in autumn (Festa-Bianchet, 1988; Edge & Odum-Edge, 1990). The strong summer mediterranean influence in Caroux and above all in Cazorla delayed the maximum lambing period (Stewart, 1982) and then delayed rutting period in more arid biotope (Nievergelt, 1974; Lenarz, 1979; Leslie & Douglas, 1979; Alados, 1985).

Ecological conditions are known to affect the social behaviour of ewes. Current evolutive theories argue that the main problem for females is to survive and rear their offspring(s) (Emlen & Oring, 1977; Wittenberger, 1980; Clutton-Brock et al., 1982). As female and lamb survival strongly depends upon ecological factors, female social behaviour is very sensitive to feeding conditions. It is well established that group size depend on various factors such as habitat structure (Estes, 1974; Geist, 1974; Jarman, 1974), food availability and anti-predator behaviour (Bradbury & Vehrencamp, 1976; Berger, 1979; Krebs & Davies, 1981; Pulliam & Caraco, 1984; Clark & Mangel, 1986; Festa-Bianchet, 1988), as well as on other ecological factors such as the climatic conditions (Underwood, 1982; Grubb, 1988). High dispersion of females and hence the large proportion of small groups in Cazorla probably result from more wooded covertry (Hillman, 1987; Jarman, 1974; Schaal, 1982; Maublanc et al., 1987) and lower food availability arising from the Mediterranean biotope and interspecific competition compared with Carlit and Caroux. Between these last two areas, the results show no significant differences in the group size distribution pattern. This may be a result of an ecological equivalence of biotopes during this season.

On the other hand, theories of mating systems argue that the best strategy for males which do not invest in rearing youngs is to maximize their mates (Bradbury & Vehrencamp, 1976; Emlen & Oring, 1977; Wittenberger, 1980; Clutton-Brock et al., 1982; Risenhoover & Bailey, 1985). Mouflon and bighorn populations are characterized first by a high segregation between males and females outside the mating period, and second by an obvious promiscuous mating system (Geist, 1974; Lenarz, 1979; Auvray, 1983; González, 1984; Bon & Campan, 1989). Thus, if these hypotheses are supported, reproductive males would adapt their behaviour to female social behaviour.

The high proportion of single males is typical in the rutting season in all populations of wild sheep (Grubb & Jewell, 1966; Pfeffer, 1967; Geist, 1971; Auvray, 1983; González, 1984, 1985). Female dispersion amplifies this phenomenon and accounts for the greater tendency of rams to be alone in Cazorla. Conversely, the highest proportion of mixed groups and the scarcity of single males in Carlit reflect a more synchronous mating activity. Thus, an increasing grouping tendency of receptive females would induce the gathering of competitive males, and an increase of group size.

Males in Cazorla exhibited a marked tendency to be isolated even when yearling, a tendency increasing with age. This could result of a particular socialization process (Berger, 1979). In a comparative study, Berger showed that desert lambs which live in a poorer social context were more often without peers than Chilcontin (Alpine population) lambs. This social process is bound to account for their future social tendencies leading desert lambs to

be lonelier when adult. Furthermore desert lambs exhibited sexual behaviour earlier than Alpine lambs. In the rutting season, both social processes and precocious sexual behaviour may have a positive convergent effects on the earlier sexual activities of the yearling males which explain the divergence between Cazorla and the more northern populations.

Concerning male social tendencies, the large proportion of mixed herds with males M3 and M4 in Carlit seems to reveal a less exclusive, competitive behaviour between male classes than in Caroux and Cazorla, which can be ascribed to the higher sociability developed during the socialization process in the Alpine biotope. Alternatively, this finding could also be explained by the high proportion of M3 in Carlit, so that the M4 in Carlit cannot prevent younger rams from courting the females.

## Acknowledgements

We are grateful to Dr. L. Arias de Reyna, Pr. R. Campan and Dr. P. Recuerda for their helpful comments on the manuscript. Drs. S. Im and J. Badia provided valuable support in statistical analyses. This work has been supported by a French-Spanish "Action Intégrée/Acción Integrada" during the study period. Two of us further beneficiate of a Spanish grant.

## Resumen

*Comparación de los patrones sociales durante el celo en tres poblaciones de muflón (*Ovis gmelini*).*

Las variables ecológicas determinan la organización social y los sistemas de apareamiento de muchas especies, encontrándose una gran variabilidad entre poblaciones de una misma especie. Se pretende comparar las tendencias sociales de cinco clases de edad y sexo en tres poblaciones europeas de muflón (*Ovis gmelini*) durante el pico de reproducción, calculado por la diferencia entre el periodo máximo de nacimientos y el periodo de gestación. Un gradiente de medio alpino a mediterráneo distingue respectivamente las zonas de Carlit, Caroux y Cazorla.

La comparación poblacional no revela diferencias entre las zonas. El análisis log-linear muestra una diferencia importante en las tendencias sociales de las distintas clases de edad y sexo, y según el área (tabla I). En el biotopo más mediterráneo (Cazorla) los machos, independientemente de la edad, muestran una fuerte tendencia a estar aislados (fig. 2), lo que para los jóvenes se podría interpretar como una participación precoz en las actividades reproductoras (Berger, 1979). Además, en esta zona, los muflones viven en grupos de tamaño reducido (fig. 3), debido seguramente tanto a que el área es más boscosa como a que los recursos son más escasos. Cazorla se caracteriza también por una fuerte proporción de grupos matriarcales, mientras que la de los grupos mixtos es menor. Por el contrario, en Carlit y Caroux, los muflones forman grupos de gran tamaño en esta estación. La mayor diferencia entre ambas es la proporción menor de machos aislados y la mayor presencia simultánea de todas las clases de machos en grupos mixtos en Carlit. Parece que en esta zona, los machos más viejos podrían presentar una menor exclusión comportamental frente a los más jóvenes, y/o que estos últimos sean demasiado numerosos para que los machos viejos les impidan acercarse a las hembras. Los factores ecológicos y los procesos sociales pueden inducir tendencias sociales claramente distintas entre las clases de edad y sexo, dentro del mismo área y entre las distintas áreas, y por tanto organizaciones sociales diferentes durante el celo.

## References

Alexander, R.D., 1974. The evolution of social behaviour. *Ann. Rev. Ecol. Syst.,* 5:325-383.

Alados, C. 1985. Group size and composition of the Spanish ibex (*Capra pyrenaica* L.) in the Sierra of Cazorla and Segura. In: *The Biology and Management of Mountain Ungulates:* 134-146 (S. Lovari, Ed.). London: Croom Helm.

Auvray, F., 1983. Recherche sur l'éco-éthologie du Mouflon (*Ovis ammon musimon* Schreber, 1782) dans le massif du Caroux-Espinouse (Hérault) en

vue de définir de nouveaux sites d'accueil. Thèse 3ème cycle, Université Sciences et Techniques du Languedoc.

Baudière, A., 1970. Recherches phytogéographiques sur la bordure méridionale du Massif Central français (les Monts de l'Espinouse). Thèse Doctoral Etat, Universite Sciences et Techniques du Languedoc.

Berducou, C. & Bousses, P. 1985. Social grouping patterns of a dense population of chamois in the Western Pyrénées National Park, France. In: *The Biology and Management of Mountain Ungulates:* 166-175 (S. Lovari, Ed.). London: Croom Helm.

Berger, J., 1979. Weaning, social environment and the ontogeny of spatial association in Bighorn Sheep. *Biol. Behav.,* 4:363-372.

Bon, R., Campan, R., Dardaillon, M., Deméautis, G., González, G. & Teillaud, P., 1986. Comparative study of the seasonal variations of the social structure in three french wild ungulates. *Wiss. Z. Humbolt-Univ. Berlin, Math. Nat.,* 35:254- 258.

Bon, R. & Campan, R., 1989. Social tendencies of the Corsican moufflon, *Ovis ammon musimon,* in the Caroux- Espinouse massif (South of France). *Behav. Proc.,* 19:57- 78.

Bradbury, J.W. & Vehrencamp, S.L., 1976. Social organization and foraging in Emballonurid bats. II. A model for the determination of group size. *Behav. Ecol. Sociobiol.,* 1:383-404.

Bunnell, F.L., 1982. The lambing period of mountain sheep: synthesis, hypotheses, and tests. *Can. J. Zool.,* 60:1-14.

Clark, C.W. & Mangel, M., 1986. The evolutionary advantages of group foraging. *Theor. Pop. Biology,* 30:45-75.

Clutton-Brock, T.H. & Harvey, P.H., 1977. Primate ecology and social organization. *J. Zool.* (London), 183:1-39.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D., 1982. *Red Deer. Behavior and Ecology of Two Sexes.* Chicago: Chicago University Press.

Crook, J.H., 1970. Social organization and the environment: aspects of contemporary social ethology. *Anim. Behav.,* 18:197-209.

Cugnasse, J.M., 1982. Evolution démographique des mouflons dans le Massif du Caroux. *Bull. mens. ONC,* 59:24-32.

Edge, W.D. & Odun-Edge, S.L., 1990. Population characteristics and group composition of *Capra aegagrus* in Kirthar National Park, Pakistan. *J. Mammal.,* 71: 156-160.

Eisenberg, J.F., Muckenhirn, N.A. & Rudran R., 1972. The relation between ecology and social structure in primates. *Science,* 176:863-874.

Ernlen, S.T. & Oring, L.W., 1977. Ecology, sexual selection, and the evolution of the mating system. *Science,* 197:215- 223.

Estes, R.D., 1974. Social organization of the African Bovidae. In: *The behaviour of ungulates and its relation to management:* 166-205 (V. Geist & F. Walther, Eds.). Morges: IUCN.

Fandós, P., 1986. Aspectos ecológicos de la población de cabra montés (*Capra pyrenaica* Schinz, 1938) en las Sierras de Cazorla y Segura (Jaén). Tesis Doctoral, Universidad Complutense de Madrid.

Festa-Bianchet, M., 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia,* 75:580-586.

Franklin, W.L., Mossman, A.S. & Dole M., 1975. Social organization and home range of roosevelt elk. *J. Mammal.,* 56(1):102-118.

Geist, V., 1971. *Mountain Sheep.* Chicago: Chicago University Press.

Geist, V., 1974. On the relationship of social evolution and ecology in ungulates. *Amer. Zool.,* 14:205-220.

Georgii, B., 1980. Home range patterns of female Red Deer (*Cervus elaphus* L.) in the Alps. *Oecologia,* 47:278-285.

González, G., 1984. Ecoéthologie du mouflon et de l'isard dans le massif du Carlit (Pyrénées Orientales). Thèse 3ème cycle, Université Paul Sabatier.

González, G., 1985. Les groupes sociaux d'isards et de mouflons, au massif du Carlit (Pyrénées Orientales). *Gibier Faune Sauvage,* 4:85-102.

Grubb, P. & Jewell, P.A., 1966. Social grouping and home range in feral Soay sheep. *Symp. Zool. Soc. Lond.,* 18:179-210.

Grubb, T.C., 1988. Changes in the flocking behav-

iour of wintering English titmice with time, weather and supplementary food. *Anim. Behav.*, 35:794-806.

Hillman, J.C., 1987. Group size and association patterns of the common eland *(Tragelaphus oryx). J. Zool.* (Lond.), 213:641-663.

Jarman, P.J., 1974. The social organization of antelope in relation to their ecology. *Behaviour*, 48:215-266.

Jarman, P.J. & Southwell, C.J., 1986. Grouping, associations, and reproductive strategies in Eastern grey kangaroos. In: *Ecological Aspects of Social Evolution. Birds and Mammals:* 399-428 (D.I. Rubenstein & R.W. Wrangham, Eds.). Princeton: Princeton University Press.

Krämer, A., 1969. Soziale organisation und sozialverhalten einer gemspopulation (*Rupicapra rupicapra* L.) der Alpen. *Z. Tierpsychol.*, 26:889-964.

Krebs, J.R. & Davies, N.B., 1981. Living in groups and defending resources. In: *An Introduction to Behavioural Ecology:* 69-91 (J.R. Krebs & N.B. Davies, Eds.). Oxford: Blackwell Scientific Publications.

Lenarz, M.S., 1979. Social structure and reproductive strategy in desert bighorn sheep *(Ovis canadensis mexicana). J. Mammal.*, 60(4):671-678.

Leslie, D.M. & Douglas, C.L., 1979. Desert Bighorn sheep of the River Mountains, Nevada. *Wildl. Monogr.*, 66:1-56.

Leuthold, W., 1970. Observations on the social organization of Impala. *Z. Tierpsychol.*, 27:693-721.

Lott, D.F., 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour*, 88:266-325.

Maublanc, M.L., Bideau, E. & Vincent, J.P., 1987. Flexibilité de l'organisation sociale du chevreuil en fonction des caractéristiques de l'environnement. *Rev. Ecol. (Terre Vie)*, 42:109-133.

McCullagh, P. & Nelder, J.A., 1983. *Generalized linear models.* London: Chapman and Hall.

Nievergelt, B., 1974. A comparison of rutting behaviour and grouping in the Ethiopian and Alpine ibex. In: *The behaviour of ungulates and its relation to management:* 324-340 (V. Geist & F. Walther, Eds.). Morges: IUCN.

Pfeffer, P., 1967. Le mouflon de Corse (*Ovis ammon musimon* Schreber, 1782); Position systématique, écologie et éthologie comparées. *Mammalia*, 31:1-262.

Poole, T., 1985. *Social behaviour in Mammals.* Glascow: Blackie.

Pulliam, H.R. & Caraco, T., 1984. Living in Groups: Is There an Optimal Group Size?. In: *Behavioural Ecology: An Evolutionary Approach:* 122-147 (J.R. Krebs & N.B. Davies, Eds.). Oxford: Blackwell Scientific Press.

Rubenstein, D.I., 1986. Ecology and Sociality in horses and zebras. In: *Ecological Aspects of Social Evolution. Birds and Mammals:* 282-302 (D.I. Rubenstein & R.W. Wrangham, Eds.). Princeton: Princeton University Press.

Risenhoover, K.L. & Bailey, J.A., 1985. Relationships between group size, feeding time, and agonistic behaviour behaviour of mountain goats. *Can. J. Zool.*, 63:2501-2506.

Rougeot, J., 1969. Accélération du rythme de la reproduction chez le mouflon de Corse *(Ovis ammon musimon)* au moyen de cycles photopériodiques semestriels. *Ann. Biol. Anim. Bioch. Biophys.*, 9:441-443.

Schaal, A., 1982. Influence de l'environnement sur les composantes du groupe social chez le daim *Cervus (Dama) dama* L. *Rev. Ecol. (Terre et Vie)*, 36:161-174.

Schaal, A., 1987. Le polymorphisme du comportement reproducteur chez le Daim d'Europe *(Dama d. dama).* Contribution à la socio-écologie des Cervidae. Thèse 3ème cycle, Université Louis Pasteur.

Schaller, G.B., 1977. *Mountain Monarchs. Wild Sheep and Goats of the Himalaya.* Chicago: Chicago University Press.

Shackleton, D.M. & Shank, C.C., 1984. A review of the social behavior of feral and wild sheep and goats. *J. Anim. Sci.*, 58(2):500-509.

Stewart, S.S, 1982. Late parturition in bighorn sheep. *J. Mammal.* 63: 154-155.

Teillaud, P., 1986. Strategies alimentaires et statut social chez le sanglier en captivité. *Behav. Proc-*

*ess.*, 12:327-347.

Thompson, R.W. & Turner, J.C. 1982. Temporal geographic variation in the lambing season of bighorn sheep. *Can. J. Zool.*, 60:1781-1793.

Underwood, R., 1982. Seasonal changes in african ungulate groups. *J. Zool.* (London), 196:191-205.

Walther, F.R., 1972. Social grouping in Grant's gazelle (Gazella granti Brooke 1827) in the Serengeti National Park. *Z. Tierpsychol.*, 31:348-403.

Wittenberger, J.F., 1980. Group size and polygamy in social mammals. *Am. Nat.*, 115:197-222.

(Recibido: 23 mayo 1990)