Habitat selection and social behaviour in a Pyrenean chamois population (*Rupicapra pyrenaica pyrenaica*)

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ABSTRACT

The aim of this work was to study habitat selection and sexual segregation in Pyrenean chamois in relation to the reproductive strategy–predation risk hypothesis. This study was conducted in the Cadí-Moixeró Nature Reserve from 2001 to 2003. During foot surveys, groups of Pyrenean chamois were observed and individual animals were identified by age and sex. For each group, altitude, predominant vegetation cover, slope orientation, and distance from escape terrain were studied. A clear sexual segregation was observed, with males selecting mid-elevations (mid-range altitudes) and pine or bush areas, and females selecting grassland areas. Females showed seasonal altitudinal migration to a larger extent than males, with a high presence of females with offspring in the highest altitudes in summer. Males used bush areas with low presence of forage throughout the year, using them as mating areas in winter. Females with offspring were observed in areas with better forage quality. Female groups were larger than male groups. Although it is necessary to study the diet quality in males and females further, the reproductive strategy–predation risk hypothesis could explain the high level of sexual segregation observed in the Pyrenean chamois population of the present study.

Keywords: chamois, *Rupicapra pyrenaica pyrenaica*, sexual segregation

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INTRODUCTION

The Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*) is an endemic chamois subspecies of the Pyrenean mountain range (Nascetti *et al.*, 1985) and, at least in Spain, it is a very important source of income in some areas (Marco *et al.*, 1995).

Pyrenean chamois live in an ecosystem with pronounced seasonal and spatial variations in climate and food availability. Several factors can influence habitat selection in chamois, including environmental factors such as topography, geology, and climate; environmental variables such as weather, snow, food, predators, competitors, and disturbance; and internal factors such as intraspecific competition, sex, age, and physiological state (Elsner-Shack, 1985).

There is some evidence that the Cantabrian chamois (*Rupicapra pyrenaica parva*) uses mainly south-facing slopes during cold months and north-facing slopes in summer (Pérez-Barbería and Nores, 1994). Hamr (1985) described a seasonal altitudinal pattern in habitat use in Alpine chamois (*Rupicapra rupicapra*), which moved to the highest altitudes in summer and autumn, and showed differences between sexes in habitat use. In Pyrenean chamois, Pepin *et al.* (1992) described a greater use of forested areas from October/November to the beginning of spring compared with the rest of the year. According to Stewart *et al.* (2002), the presence of livestock could cause a different use of habitat in ungulates in general and this could be applied to Pyrenean chamois in particular (Herrero *et al.* 1996). According to Hamr (1988), in a zone characterized by a long absence of terrestrial predators and the presence of the golden eagle (*Aquila chrysaetos*) as the main predator, Alpine chamois preferred a downslope escape terrain with tree cover compared to the high-altitude cliffs preferred by Apennine chamois (*R. pyrenaica ornata*), where wolves (*Canis lupus*) were present. In addition, Schröder (1985) claimed that trophy hunting could influence the distribution and migration of mountain ungulates. Bleich (1999) concluded that the hunting strategies of different predators could cause a range of different responses in ungulates to the threat of predation. According to this author, these antipredatory strategies can include the selection of specific areas.

Some authors have described sexual segregation in Pyrenean chamois (Gerard and Richard-Hansen, 1992) as well as in other subspecies: Alpine chamois (Shank, 1985), Cantabrian chamois (Pérez-Barbería and Notes, 1994), and Apennine chamois (Lovari and Cosentino, 1986). Sexual segregation has recently received much attention (Bowyer and Kie, 2004; Mooring *et al.*, 2003; Ruckstuhl and Neuhaus, 2000), and a large number of hypotheses to explain its occurrence in ungulates have been proposed (Bleich *et al.*, 1997; Main *et al.*, 1996). According to the sexual dimorphism body size hypothesis, sexual segregation occurs because sexual differences in body size lead to different energy requirements and hence food selection, with males exploiting more abundant and lower quality forage than smaller-bodied females, which must be more selective and look for less common high-quality forage (Clutton-Brock *et al.*, 1984; Illius and Gordon, 1987; Main *et al.*, 1996). In contrast, the reproductive strategy–predation risk hypothesis suggests that males and females pursue different strategies to maximize reproductive

success, with males maximizing body condition for the mating season and females maximizing offspring survival. Sexual segregation is higher when offspring are more vulnerable to predation, with females selecting safer zones than males, which select zones with higher pasture quality (Bleich *et al.*, 1997; Festa-Bianchet, 1988; Mooring *et al.*, 2003).

Our objectives were to study (1) habitat selection in Pyrenean chamois in relation to population parameters such as composition and group size, and seasonal changes, and (2) the possible occurrence of sexual segregation in relation to the reproductive strategy predation–risk hypothesis. It was predicted that if sexual segregation occurs in the studied population, females with kids will select safer areas than males.

MATERIALS AND METHODS

Study area

This study was conducted in the Cadí-Moixeró Nature Reserve, in the north-east of Spain (42°15'N, 1°41'E). The Nature Reserve, a mountain region adjacent to the Pyrenees, lies between an altitude of 800 and 2,648 m. It comprises the pre-Pyrenaic orographic area, constituted by the Cadí and Moixeró mountain ranges, which are mainly calcareous in nature, forming a mountain barrier stretching from west to east for some 30 km. The annual rainfall ranges from 1,500 mm on the eastern side of the mountains to 700 mm in the western lower areas, which are the most protected from maritime winds. Snow is present for approximately 6 months of the year in the highest areas, above 2,300 m (from November to May). The average annual temperature fluctuates between 0°C and 11°C.

Alpine meadows occur from an altitude of about 2,200 m and are covered with a great variety of graminous plants, *Festuca airoides* being the predominant one, and other plants such as *Gentiana acaulis* spp. *alpina* or *Androsarce carnea* also being present. Below 2,200 m, there are *Pinus uncinata* forests and areas with bushes such as *Juniperus nana, Rhododendron ferrugineum* and *Arctostaphylos uva-ursi* (Gurri, 1997). *Festucetum scopariae*, a plant community typical of the subalpine calcalreous slopes of the Cadí range, is also present at this altitude. The main species are *Festuca scoparia, Festuca indigesta* var. *durissima, Avena montana, Poa alpina*, and *Sesleria coerulea*. The forage quality of these species is very low (Folch, 1981). In the middle and lower zones, *Pinus sylvestris* forests are the main vegetation, with an underbush predominantly comprised of *Buxus sempervirens* (Gurri, 1997).

In the whole Nature Reserve, the chamois population was estimated at 2,300 individuals when this study was conducted. In the study zone, an area of 12 km² situated in the central part of the Nature Reserve between 1,600 and 2,500 m, a population of 250–300 chamois was present according to data from 2001–2003 (140–168 adults: 35–42 males and 105–126 females, and 110–132 yearlings and kids). This zone was selected due to the high density of chamois previously observed (20–25 chamois/km²). Other ungulates present are red deer (*Cervus*

elaphus), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). A large part of the Nature Reserve is a hunting reserve, chamois being the main hunted species. In the study period, more than 40 animals were hunted each year, between September and December.

Sampling procedure

From January 2001 to December 2003, observations of Pyrenean chamois groups were made during foot surveys over the whole study area using different linear transects that were randomly combined so that they did not start each day from the same point at the same hour. Every two weeks a minimum of 2 transects and a maximum of 6 were carried out. A total of 300 transects (95 in 2001, 113 in 2002, and 85 in 2003) were carried out during the whole study, 16% in winter, 23% in spring, 31% in summer, and 30% in autumn. Two animals were considered as being part of the same group if they were less than 50 m apart (Berducou and Bousses, 1985; Ferrari and Rossi, 1985, Frid, 1997). Solitary animals were recorded as groups of one. Each animal was classified according to sex (male or female) and age (adult, kid or yearling). Usually, kids were born between late May and late June. In accordance with Gerard and Richard-Hansen (1992), one-year-old kids arbitrarily became yearlings when the first newborn kid of the following generation was observed. Animals were observed from distances of between 20 and 300 metres and sex and age were always determined using binoculars. In case of doubts about age or gender, the observer tried to approach the group without disturbing them. Only those groups for which all individuals could be classified were included in the study. Groups were divided into five main categories: male, female, female with offspring (FKS), mixed (groups with at least 1 adult male and 1 adult female), and yearling groups (formed mainly of yearlings with up to 2 young males).

Fertility rates were calculated every year in July by counting females with newborn kids in relation to the total females observed.

Altitude, distance from escape terrain, slope orientation, and predominant vegetation types were recorded in a total of 2,402 locations where chamois groups were observed (Bleich *et al.*, 1997). To study the zone, after finishing all the observations, a table of random north and east coordinates was made, selecting only combinations of the two that fell inside the study area. Thereafter, points selected were registered in a global positional system navigator (GPS Garmin 12) by means of the north and east coordinates selected and the oziexplorer software (RTM SL, Spain). The same quantity of points as groups of Pyrenean chamois observed (2,402) were studied. The study area was covered on foot for three weeks to find and record the exact location in the field of each point and the variables altitude, distance from escape terrain, slope orientation and predominant vegetation types were recorded.

Altitude ranged between 1,600 and 2,500 m. Escape terrain was defined as forest or as a slope of more than 45°, considering three distances to these terrains: less than 20 m; between 20 and 100 m; and more than 100 m (Lovari and

Consentino, 1986; Pérez-Barbería and Nores, 1994). The distances were calculated with a distantiometer and the use of reference points. Since the study area was in a mountain range stretching from east to west, only two possibilities were considered for orientation: north-facing slope and south-facing slope. Four possibilities were considered for the predominant vegetation cover: Pine forest (*Pinus uncinata* and *Pinus sylvestris*), grassland (alpine or subalpine meadows), bush area (*Juniperus nana, Rhododendron ferrugineum*, and *Buxus sempervirens*), and rocky ground area.

The four calendar seasons were used for this study. Winter was defined as January to March, during the coldest months of the year. Spring was defined as April to June, including the birth period. Summer, from July to September, after the birth period, included the driest and hottest months of the year. Lastly, autumn, from October to December, included the pre-rut and rut seasons.

Statistical analyses

In order to study group size, mean, SE and typical group size (TGS) were calculated according to Jarman (1974).

Habitat selection was studied for the different classes of individuals (male, female, kid, and yearling) and group type (male, female, FKS and mixed groups) applying logistic regression to use-availability data as described by Thomas and Taylor (2006) and Johnson *et al.* (2006). The use of the different habitats by animals was corrected for their availability in the study area and the Proc Logistic of the Statistical Analysis System (SAS; software SAS Institute Inc. 1999–2001) was used. Three models were considered: (1) type of vegetation, in which bush was considered as the reference category; (2) distance from the escape terrain, in which >100 m was considered as the reference category; and (3) altitude, which was considered as continuous and studied for each season.

A general model process, considering group size as a count variable, was applied for each season separately using the Proc Genmod of SAS to study the relationship between this variable and the following independent variables: group composition, predominant vegetation cover, altitude, slope orientation, and distance from escape terrain. A negative binomial regression was applied to all models (Cameron and Trivedi, 1988). In all cases, the residual maximum likelihood was used as a method of estimation. The least square means of fixed effects (LSMEANS) was used when analysis of variance indicated differences at $P < 0.05$. In all cases, the accepted significance level was $P < 0.05$.

RESULTS

Description of the population

A total of 2,402 Pyrenean chamois groups with a total of 22,078 animals were observed (42.5% females, 27.0% kids, 16.2% yearlings, and 14.3% males). Differences in the percentage of each age–sex class were found between seasons

(X^2 = 89.44; *d.f.* = 9; *P* < 0.0001). Females represented the lowest percentage in spring (39%) and the highest in winter (46%), in contrast to the yearling class, with 19% in spring and 13% in winter. Males had the lowest percentage in summer (13%) and the highest in autumn (15%). The kid class was very stable throughout the year, representing 26.5%, 26.9%, 27.0%, and 27.3% of the total population for winter, spring, summer, and autumn, respectively. A different seasonal altitudinal distribution was observed in males and females (Figure 1). The male/female ratio was 0.33. Fertility rates were 66%, 55%, and 58% for 2001, 2002, and 2003, respectively.

The groups most commonly observed were male groups, followed by FKS and mixed groups. However, differences by seasons were observed. Percentage and size of each group type for each season and for the whole year are shown in Table 1.

Habitat selection

The distribution of the area, groups of animals and males and females for vegetation cover, altitude, distances from escape terrain and slope orientation is shown in Figure 2. Animals were found mainly on south-facing slopes (Figure 1). Male groups selected negatively for rocky, pine, and grassland areas (Table 2). In contrast, female, FKS, and mixed groups were found in similar percentages to the availability of these habitats (Table 2). When the animals were considered individually, females, yearlings and kids, but not males, selected positively for the grassland areas (Table 3). Male groups, but not female, FKS, and mixed groups, selected positively for distance to escape terrains of between 20 and 100 m (Table 2). When the animals were considered individually, the preferences of males for distances from 20 to 100 m to escape terrain in relation to more than 100 meters was higher than in the case of females, yearlings, and kids (Table 3). When altitude was analysed by season, no evidence of selection was found for any of the groups (Tables 4 and 5). Seasonal changes in habitat selection for the three main group classes: male, FKS, and mixed groups are shown in Figure 3 for altitude and vegetation cover, and in Figure 4 for distance from escape terrain.

Group size

In winter, only group composition had a significant effect on group size (X^2 = 233.28; *d.f.* = 4; *P* < 0.0001), with a tendency being found for distance from escape terrain and habitat (X^2 = 5.77; *d.f.* = 2; *P* = 0.0558; X^2 = 7.28; *d.f.* = 3; *P* = 0.0636, respectively). In spring, group composition and distance from escape terrain were statistically significant (X^2 = 353.31; *d.f.* = 4; *P* < 0.0001; X^2 = 19.11; *d.f.* = 2; *P* < 0.0001, respectively). In summer, group size was dependent on group composition, habitat, altitude, and distance from escape terrain (X^2 = 309.35; *d.f.* = 4; *P* < 0.0001; X^2 = 31.38; *d.f.* = 3; *P* < 0.0001; X^2 = 35.29; *d.f.* = 4; *P* < 0.0001; X^2 = 9.23; *d.f.* = 2; *P* = 0.0099, respectively). Autumn was similar to summer, with an effect of group composition, habitat, altitude, and distance from escape terrain (X^2 = 592.02; *d.f.* = 4; *P* < 0.0001; X^2 = 21.62; *d.f.* = 3; *P* < 0.0001; X^2 = 46.77; *d.f.* = 4; *P* < 0.0001; X^2 = 9.63; *d.f.* = 2; *P* = 0.0081, respectively).
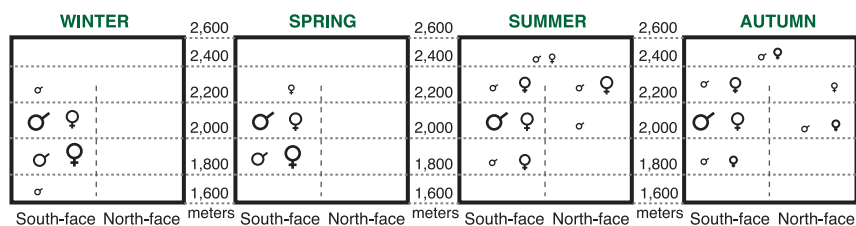
Figure 1   Male and female presence for altitudes and seasons in the study area. The size of each symbol is proportional to its percentage of the total in each class. Only percentages higher than 3% appear in this figure. An increase of 5% represents an increase of two points in symbol size. The central vertical line represents the mountain, and divides it in south-facing and north-facing slopes.

Mixed groups were the largest group type throughout the whole year ($P < 0.0001$ in all comparisons). FKS groups were bigger than male, female, and yearling groups ($P < 0.0005$) in all seasons. Yearling groups were bigger than male and female groups ($P < 0.05$) throughout the whole year, and male groups were bigger than female groups only in summer ($P < 0.0001$).

Group size was smaller in pine forest than grassland, bush, and rocky ground area in summer and autumn ($P < 0.0001$ in all comparisons). In winter, only the grassland and bush areas had a bigger group size than pine forest ($P < 0.05$). No differences were observed in spring.

In winter, spring and summer, groups were bigger at distances of more than 100 m from escape terrain than at distances of less than 20 m ($P < 0.05$). In spring and autumn, it was also observed that groups from between 20 and 100 m from escape terrain were bigger than groups located at less than 20 m ($P < 0.01$).

In summer, group size in areas from 1,800 to 2,000 m was smaller than in areas at 2,000 to 2,200 m, and at 2,200 to 2,400 m ($P < 0.0001$). In autumn, group size in areas at 2,200 to 2,400 m was higher than below 2,200 m ($P < 0.05$) and, at the same time, group size from 1,800 to 2,000 m was smaller than above 2,000 m ($P < 0.0001$). Mean size for male, FKS, and mixed groups in relation to distances from escape terrain is shown in Figure 4.

DISCUSSION

Description of the population

Demographic parameters observed in this study were similar (although in the lower range) to those found in other Pyrenean chamois populations. The mean fertility rate of 60% observed in our population was in accordance with the mean values collected by Garin and Herrero (1997), but lower than the 70% reported by Pérez-Barbería and García-González (2004) as the mean value for different Pyrenean chamois populations. The sex ratio of 0.33 was similar to the sex ratio of 0.38 observed in Berducou *et al.* (1982), but lower than the 0.61 reported as the mean

Table 1 Percentage, mean group size with the standard error (SE) and typical group size (TGS) of the different group types (male, female, female with offspring – FKS, mixed, and yearling groups) of Pyrenean chamois for the whole year, and percentages and means with the SE for each season

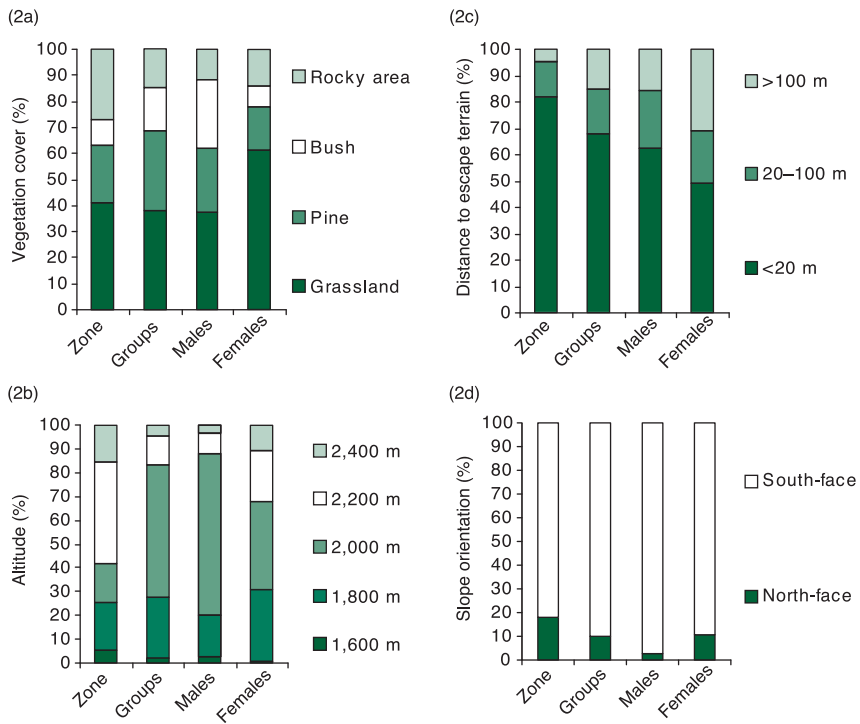| Groups	Total			Winter		Spring		Summer		Autumn	
	%	Mean ± SE	TGS	%	Mean ± SE	%	Mean ± SE	%	Mean ± SE	%	Mean ± SE
Male	35	2.2 ± 0.08	4.4	35	2.4 ± 0.20	25	2.2 ± 0.17	36	2.8 ± 0.17	42	1.7 ± 0.09
Female	6	1.9 ± 0.12	3.0	6	2.2 ± 0.30	10	1.8 ± 0.21	6	1.8 ± 0.20	3	2.0 ± 0.32
FKS	31	11.0 ± 0.48	26.7	34	9.4 ± 0.69	31	8.7 ± 0.49	36	12.8 ± 0.98	25	11.9 ± 1.18
Mixed	21	21.6 ± 1.00	45.1	22	18.4 ± 1.68	21	25.0 ± 2.46	16	26.3 ± 2.38	26	17.9 ± 1.33
Yearling	7	4.7 ± 0.28	7.4	3	4.3 ± 1.33	13	4.7 ± 0.43	6	4.7 ± 0.53	4	4.7 ± 0.55

Figure 2 Habitat parameters (predominant vegetation cover: 2a; altitude: 2b; distance from escape terrain: 2c; and slope orientation: 2d) in the study zone compared to the selection made by the total groups of Pyrenean chamois, and for all males and females separately.

Table 2 Coefficients of probability functions for vegetation cover and distance from escape terrain according to group type of Pyrenean chamois (male, female, FKS, and mixed)

		β	SE	X^2	P-value
Male groups					
Vegetation	Intercept	−0.8546	0.1399	37.3177	<0.0001
	Rocky	−1.9575	0.3102	39.8253	<0.0001
	Pine	−1.2693	0.3248	15.2747	<0.0001
	Grassland	−2.0041	0.2699	55.1514	<0.0001
Escape terrain	Intercept	−2.1540	0.1300	274.4773	<0.0001
	<20m	−0.4492	0.1594	7.9374	0.0048
	20–100 m	0.7113	0.1510	22.1956	<0.0001
Female groups					
Vegetation	Intercept	−1.9597	0.5542	12.5033	0.0004
	Rocky	−0.1259	0.8034	0.0246	0.8755
	Pine	0.2286	0.9096	0.0632	0.8016
	Grassland	−0.0686	0.7231	0.0090	0.9244
Escape terrain	Intercept	−1.9362	0.3038	40.6173	<0.0001
	<20m	−0.5743	0.3951	2.1125	0.1461
	20–100 m	0.2067	0.3874	0.2849	0.5935
FKS groups					
Vegetation	Intercept	−2.2743	0.3328	46.7156	<0.0001
	Rocky	0.2560	0.4485	0.3257	0.5682
	Pine	−0.0107	0.5780	0.0003	0.9852
	Grassland	0.6321	0.3958	2.5506	0.1103
Escape terrain	Intercept	−1.7598	0.1563	126.8026	<0.0001
	<20m	−1.0038	0.2289	19.2262	<0.0001
	20–100 m	0.0176	0.2021	0.0076	0.9305
Mixed groups					
Vegetation	Intercept	−2.0677	0.2888	51.2712	<0.0001
	Rocky	−0.3031	0.4356	0.4841	0.4866
	Pine	−0.1630	0.5226	0.0973	0.7551
	Grassland	0.4763	0.3504	1.8474	0.1741
Escape terrain	Intercept	−1.7132	0.1451	139.4076	<0.0001
	<20m	−0.8857	0.2063	18.4339	<0.0001
	20–100 m	−0.3190	0.1977	2.6035	0.1066

Table 3 Coefficients of probability functions for vegetation cover and distance from escape terrain according to animal category of Pyrenean chamois (male, female, yearling, and kid)

		β	SE	X^2	P-value
Males					
Vegetation	Intercept	−0.9343	0.0666	196.6144	<0.0001
	Rocky	−1.8153	0.1427	161.8902	<0.0001
	Pine	−1.7573	0.1863	89.0136	<0.0001
	Grassland	−1.4732	0.1111	175.7261	<0.0001
Escape terrain	Intercept	−2.0235	0.0532	1448.0855	<0.0001
	<20m	−1.0204	0.0748	186.3102	<0.0001
	20–100 m	0.6663	0.0637	109.4879	<0.0001
Females					
Vegetation	Intercept	−2.4896	0.0793	985.9238	<0.0001
	Rocky	−0.1260	0.1153	1.1948	0.2744
	Pine	−0.2160	0.1464	2.1763	<0.1402
	Grassland	1.1985	0.0897	178.6764	<0.0001
Escape terrain	Intercept	−1.7907	0.0351	2600.4490	<0.0001
	<20m	−1.3355	0.0520	659.3310	<0.0001
	20–100 m	−0.3351	0.0476	49.4535	<0.0001
Yearlings					
Vegetation	Intercept	−2.1810	0.1077	410.3053	<0.0001
	Rocky	−0.6556	0.1783	13.5158	0.0002
	Pine	−0.7060	0.2321	9.2531	0.0024
	Grassland	0.8610	0.1258	46.8348	<0.0001
Escape terrain	Intercept	−1.8146	0.0555	1067.4391	<0.0001
	<20m	−1.5011	0.0852	310.6577	<0.0001
	20–100 m	−0.1973	0.0731	7.2873	0.0069
Kids					
Vegetation	Intercept	−2.4175	0.0937	665.4911	<0.0001
	Rocky	−0.2872	0.1415	4.1206	0.0424
	Pine	−0.9293	0.1699	29.9096	<0.0001
	Grassland	1.1183	0.1067	109.7474	<0.0001
Escape terrain	Intercept	−1.8299	0.0434	1781.4570	<0.0001
	<20m	−1.1695	0.0657	317.1288	<0.0001
	20–100 m	−0.5697	0.0576	97.7234	<0.0001

Table 4 Coefficients of probability functions for altitude in different seasons (spring, summer, autumn, and winter) according to group type of Pyrenean chamois (male, female, FKS, and mixed)

		β	SE	X^2	P-value
Male groups					
Spring	Intercept	0.0449	0.1269	0.1249	0.7238
		−0.3769	0.0610	38.1428	<0.0001
Summer	Intercept	3.6860	0.2093	310.1815	<0.0001
		−1.5451	0.0754	419.5137	<0.0001
Autumn	Intercept	−0.3676	0.0805	20.8657	<0.0001
		−0.3039	0.0314	93.4408	<0.0001
Winter	Intercept	1.1070	0.1344	67.8050	<0.0001
		−0.9497	0.0689	190.1862	<0.0001
Female groups					
Spring	Intercept	−0.9544	0.2325	16.8474	<0.0001
		0.1297	0.1063	1.4877	0.2226
Summer	Intercept	−0.6444	0.4002	2.5928	0.1074
		−0.0113	0.1289	0.0159	0.8996
Autumn	Intercept	2.6845	0.9828	7.4614	0.0063
		−1.0738	0.3855	7.7599	0.0053
Winter	Intercept	−0.3622	0.3572	1.0286	0.3105
		−0.1670	0.1681	0.9875	0.3204
FKS groups					
Spring	Intercept	7.8042	0.5035	240.2523	<0.0001
		−3.1217	0.1975	249.8624	<0.0001
Summer	Intercept	−2.1055	0.1414	221.7857	<0.0001
		0.3844	0.0480	64.1275	<0.0001
Autumn	Intercept	−1.5162	0.1506	101.3749	<0.0001
		0.1637	0.0532	9.4618	0.0021
Winter	Intercept	−0.3666	0.2056	3.1783	0.0746
		−01648	0.0967	2.9029	0.0884
Mixed groups					
Spring	Intercept	6.9713	0.3820	333.0461	<0.0001
		−2.8062	0.1461	368.7449	<0.0001
Summer	Intercept	−0.8502	0.2615	10.5736	0.0011
		0.0523	0.0838	0.3888	0.5329
Autumn	Intercept	−1.3236	0.1151	132.2507	<0.0001
		0.0890	0.0413	4.6507	0.0310
Winter	Intercept	−0.6253	0.1951	10.2725	0.0014
		−0.0339	0.0906	0.1401	0.7082

Table 5 Coefficients of probability functions for altitude in different seasons (spring, summer, autumm, and winter) according to animal category of Pyrenean chamois (male, female, yearling, and kid)

|		β	SE	X^2	P-value
Males					
Spring	Intercept	10.2387	0.2129	2312.7607	<0.0001
		−4.0996	0.0830	2439.0944	<0.0001
Summer	Intercept	4.5131	0.1529	871.2148	<0.0001
		−1.8561	0.0562	1090.5452	<0.0001
Autumn	Intercept	−0.8412	0.0506	276.8443	<0.0001
		−0.1043	0.0189	30.5460	<0.0001
Winter	Intercept	0.4674	0.0724	41.6441	<0.0001
		−0.6002	0.0357	283.2388	<0.0001
Females					
Spring	Intercept	−0.1667	0.0316	27.9137	<0.0001
		−0.3918	0.0126	969.6841	<0.0001
Summer	Intercept	−4.1643	0.0561	5530.4161	<0.0001
		1.0894	0.0173	3944.8816	<0.0001
Autumn	Intercept	−2.3956	0.0614	1521.6397	<0.0001
		0.4893	0.0205	569.6744	<0.0001
Winter	Intercept	−0.8431	0.0469	322.5741	<0.0001
		0.0747	0.0216	11.9804	0.0005
Yearlings					
Spring	Intercept	−0.0113	0.0430	0.0694	0.7923
		−0.4612	0.0174	700.9054	<0.0001
Summer	Intercept	−5.3332	0.1065	2507.5019	<0.0001
		1.4572	0.0320	2077.3971	<0.0001
Autumn	Intercept	−2.3956	0.0614	1526.6397	<0.0001
		0.4893	0.0205	569.6744	<0.0001
Winter	Intercept	−0.8077	0.1008	64.1735	<0.0001
		0.0571	0.0464	1.5122	0.2188
Kids					
Spring	Intercept	−0.1024	0.0368	7.7338	0.0054
		−0.4204	0.0148	808.8177	<0.0001
Summer	Intercept	−4.000	0.0714	3136.4468	<0.0001
		1.0346	0.0222	2168.0578	<0.0001
Autumn	Intercept	−2.3844	0.0443	2902.7267	<0.0001
		0.4853	0.0148	1077.7105	<0.0001
Winter	Intercept	−0.8416	0.0632	177.3053	<0.0001
		0.0739	0.0291	6.4732	0.0110
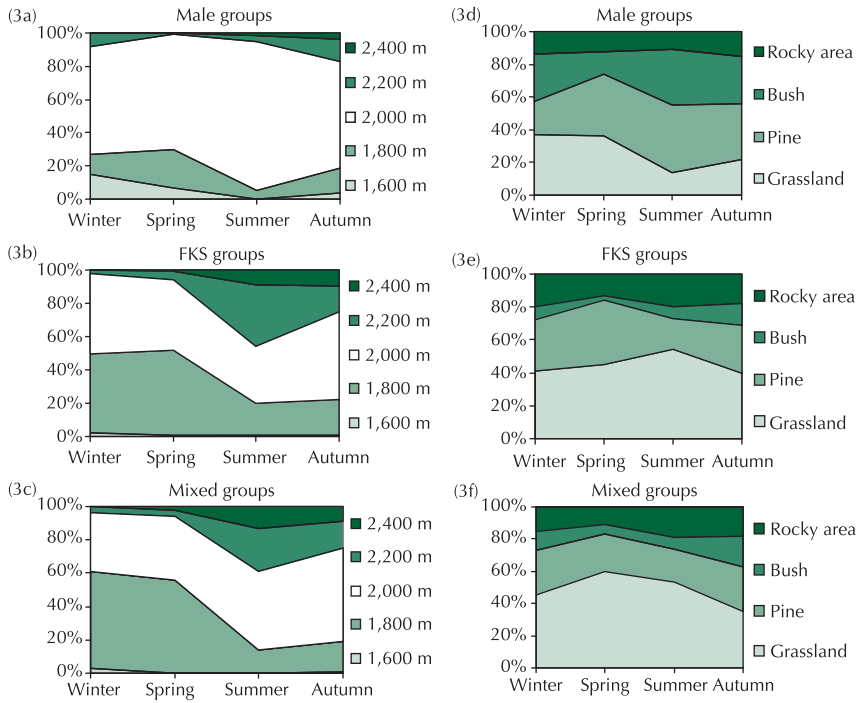
Figure 3 Habitat parameters (altitude: 3a, 3b and 3c; and predominant vegetation cover: 3d, 3e, 3f) throughout the year for male, female with offspring (FKS), and mixed groups.
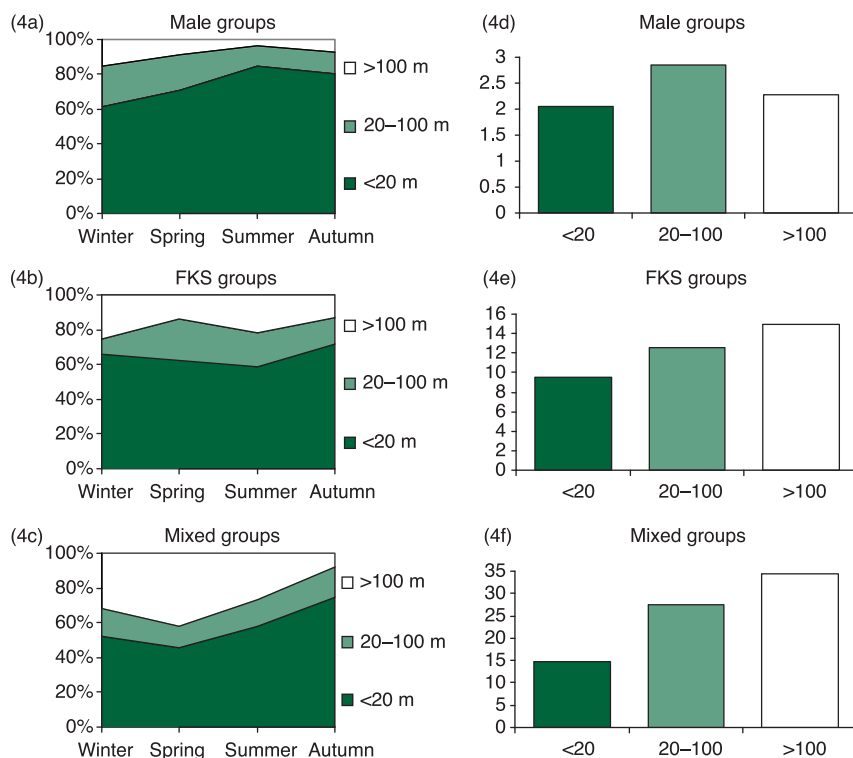
Figure 4 Distances from escape terrain for male, female with offspring (FKS), and mixed groups throughout the year (Figures 4a, 4b, and 4c), and their mean group size in relation to the three categories of distances from escape terrain: <20m; 20–100m; >100m (Figures 4d, 4e, and 4f).

value for different Pyrenean chamois (Pérez-Barbería and García-González, 2004). However, García-González and Hidalgo (1989) observed a sex-ratio of 0.30 in a hunting reserve, concluding that trophy hunting could account for the marked deviation of sex ratio from 1. In fact, trophy hunters usually prefer to harvest males, as these individuals tend to have the largest body and horn size (Hutchins and Geist, 1987). Historically, hunting reserve managers have considered normal an unbalanced ratio caused by the preference for males in trophy hunting. Data collected in the hunting reserve in which this study was conducted show an increase in the sex-ratio from 0.33 in 1989 to 0.48 in 2004. However, in our study area a sex-ratio of 0.33 was observed, revealing a higher pressure on males through hunting.

Only 21% of the total observations were mixed groups, meaning that 79% of the groups were segregated by sex. This sexual segregation was in accordance with Hamr (1985) and Shank (1985). The highest percentage of mixed groups was observed in autumn, the rut season, and was lowest in summer, when it accounted for only 16% of all groups. These results were in accordance with Gerard and Richard-Hansen (1992).

Habitat selection

Chamois has been associated with rocky and open vegetation areas (Lovari and Cosentino, 1986; Elsner-Shack, 1985), but García-González and Cuartas (1996) observed a Pyrenean chamois population living predominantly in montane/subalpine forest. In our study, grassland was the predominant vegetation cover where Pyrenean chamois groups were observed. However, male groups selected negatively for this vegetation cover and female, FKS, and mixed groups used these areas as frequently as expected. When animals were considered individually, it was found that males preferred the bush areas and females, yearlings, and kids the grasslands areas.

A clear relationship existed between habitat selection, sexual segregation, and altitudinal migration. This altitudinal migration has been described by several authors in chamois (Lovari and Cosentino, 1986; Pepin *et al.*, 1992). However, Hamr (1985) described a different pattern of altitudinal migration between sexes, with males staying mostly below the tree line and females congregating both above and below it. In our study, a clear altitudinal pattern could be defined for FKS and mixed groups. For instance, only 6% of FKS groups were above 2,200 m in spring compared to 46% in summer, and only 18% of mixed groups were below 2,000 m in autumn compared to 61% in winter. In contrast, for male groups, this altitudinal migration was not so evident. In fact, male groups were found mainly at an altitude from 2,000 to 2,200 m throughout the year, with 64–90% of the total male groups observed at this altitude. The smaller altitudinal migration observed in male groups in comparison with FKS and mixed groups had clear consequences for habitat selection. Pine and bush areas were the predominant vegetation cover for male groups, with the highest value in summer, when practically all of them were between 2,000 and 2,200 m. In fact, pine and bush areas represented 67% of the predominant vegetation cover at this altitude. In contrast, for FKS and mixed groups the predominant vegetation cover was grassland. The migration to high altitudes of FKS groups in summer led to their high use of grassland areas, as these accounted for 45% of the area above 2,200 m.

Some authors have described the importance of livestock in this altitudinal migration. Stewart *et al.* (2002) observed elk (*Cervus elaphus*) to use lower altitudes when cattle (*Bos taurus*) were not in the study area. According to Herrero *et al.* (1996), Pyrenean chamois (unlike other chamois populations) do not migrate to high altitudes in summer due to the presence of livestock in such areas. In our study, after cattle were taken to areas of between 1,600 and 2,200 m in late June, a large number of chamois females went to higher altitudes, where cattle were not present. In fact, although small groups of Pyrenean chamois were found at around 50 metres from grazing or lying cattle, no evidence of actual intermingling was observed. However, when cattle left the study area in autumn, female chamois did not return to lower altitudes. Therefore, the effect of livestock may be more complex than previously thought.

Another possible explanation for the altitudinal migration in summer could be

the changes in pasture quality with altitude. However, Gonzalez (1985) suggested that the altitudinal migration observed in mouflon (*Ovis ammon*) was caused mainly by temperature rather than by food requirements, because new grass shoots were growing in the lower areas that the animals were abandoning. Also, Elsner-Shack (1985) concluded that reasons other than food requirements determined the summer grouping of Alpine chamois.

Group size

The highest group sizes were found in grassland areas, in the higher altitudes, more than 100 m from escape terrain, and they were formed mainly by mixed and FKS groups. The lowest group sizes were found in pine and bush areas, in the lowest and mid-altitudes, less than 20 m from escape terrain, and they were formed mainly by male and female groups. This is in accordance with Pérez-Barbería and Nores (1994), who concluded that the presence of offspring was an important factor in determining the tendency to aggregate in Cantabrian chamois. At the same time, Gerard and Richard-Hansen (1992), studying a Pyrenean chamois population, concluded that the highest group size in summer was due to a closer bond between females and kids in this season. Berducou and Bousses (1985) described for a Pyrenean chamois population the highest aggregation of individuals after the birth period, mean group size being two times higher in June than in November.

High altitude sites are often steep and have good visibility. In general, areas with good visibility should decrease the risk of predation (Ouellet *et al.*, 1996). According to Schaller (1977), mountain ungulates could be very dependent on steep and rugged terrain to avoid predation. However, an increase in group size in more open areas could also be considered a good antipredator strategy (Jarman, 1974). Dorrance and Lawrence (1976) reported that predation rate on domestic sheep (*Ovis aries*) was higher in forested habitats compared with grassland and foothills. The presence of females with offspring in the higher altitudes and the higher distances from escape terrain, mainly in summer, when the risk of predation for offspring is supposed to be higher, suggests that females with offspring are safer in big groups in open grassland areas than in small groups close to escape terrain. In fact, although only 5% of the study area was located more than 100 m from escape terrain, the presence of mixed, FKS, and male groups at this distance was 24, 18, and 8% respectively. Therefore, it could be concluded that at least in our study area, two different strategies exist for predator avoidance in Pyrenean chamois, with males using zones close to escape terrain and females with offspring selecting open areas and forming larger groups.

Although sexual segregation has been explained by factors such as different body size between sexes or social factors (Main *et al.*, 1996), the reproductive strategy–predation risk hypothesis has received massive support in ungulates (Bleich *et al.*, 1997; Festa-Bianchet, 1988; Miquelle *et al.*, 1992). According to this hypothesis, males and females pursue different strategies to maximize reproductive success, with males maximizing their body condition and females maximizing

survival of offspring. Thus, females prefer safe habitats, even though containing less sources of food for offspring, whereas males prefer areas with better food availability to increase their body size and be more competitive during the rut period (Mooring *et al.*, 2003). One of the predictions of this hypothesis is that sexual segregation will be higher after the birth period, when offspring are more vulnerable, and this is in accordance with the results of our study. However, further studies looking at diet quality in males and females are needed to confirm the reproductive strategy–predation risk hypothesis.

Males were observed in the same areas (bush areas from 2,000 to 2,200 m) throughout the year. According to Hardenberg *et al.* (2000), the early occupation of mating territories gives male Alpine chamois a reproductive advantage, as the mean number of females per hour in each male territory during the rut is higher in territories that were occupied by males early in the year. In the study zone of Hardenberg *et al.*, (2000), the territories defended by males during the rut were clustered on a south-facing slope that was relatively free of snow in the rut period. These areas have been considered by some authors to be a winter refuge (Brustet and Catusse, 1995). The bush areas with pines that males selected in the present study could also be considered winter refuges, as males used them the whole year, including the rut season.

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