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SOCIALITY AND RELATIONSHIPS IN ALPINE IBEX (*CAPRA IBEX*)

Jean-Charles VILLARET* & Richard BON**

INTRODUCTION

There are conflicting results as to whether ungulate group composition is shaped by ecological factors or whether intrinsic factors play a role. Except in elk (*Cervus canadensis*) (Franklin & Lieb, 1979; Jenkins & Starkey, 1982) and African elephants (*Loxodonta africana*) (Moss & Poole, 1983), no permanent associations are known among non relatives adults (Leslie & Douglas, 1979; Boyd, 1981; Singer & Doherty, 1985; Hillman, 1987; Lawrence, 1990; Festa-Bianchet, 1991; Richard-Hansen, 1992). Associations among individuals would result from co-occurrence and successive encounters at attractive ecological points within overlapping home ranges (Lott & Minta, 1983; Lawrence & Wood-Gush, 1988). According to Lawrence (1990), sociality in sheep is based on a general gregariousness rather than on specific social bonds. Festa-Bianchet (1991) proposed that the bighorn sheep (*Ovis canadensis*) social system has been "shaped by antipredator and foraging strategies that rely on learned traditions".

Le Pendu *et al.* (1995) found that mother and daughter can maintain a strong link in mouflon (*Ovis orientalis*). Although cows in bison (*Bison bison*) and chillingham cattle (*Bos taurus*) do not form permanent associations, females close in rank were more likely to interact, and to be nearest neighbours and groupmates (Lott & Minta, 1983; Hall, 1986). Bouissou & Hövels (1976) also showed that familiarity between heifers resulted in less agonistic interactions, more time feeding, in spatial associations and formation of subgroups of familiar animals. Predator detection and time spent foraging is reduced as group size increases (Berger, 1978; Alados, 1985; Risenhoover & Bailey, 1985). Therefore, female fitness would be enhanced by stable associations and familiarity.

Males were reported to live in loose groups in elk (*Alces alces*) and red deer (*Cervus elaphus*) (Franklin & Lieb, 1979; Clutton-Brock *et al.*, 1982; Jenkins & Starkey, 1982). But they were more sociable in white tailed-deer (*Odocoileus virginianus*) (Hirth, 1977) and lived in more stable groups than did females in Soay

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and domestic sheep (*Ovis aries*) (Grubb, 1974; Arnold *et al.*, 1981). Yearling males were shown to associate with other age and sex classes as expected by chance in European mouflon (*Ovis gmelini*) (Bon *et al.*, 1993). Adult males interact primarily with similar-rank congeners (Clutton-Brock *et al.*, 1982; Appleby, 1983; Lott & Minta, 1983; Rutberg, 1986; Freeman *et al.*, 1992) or associate with similar-aged peers (see Bon *et al.*, 1993; Le Pendu *et al.*, 1995; Villaret & Bon, 1995). Grubb & Jewell (1966) suggested the existence of stable seasonal bonds between Soay rams (*Ovis aries*) outside the rut. Moss & Poole (1983) found that pairs of male elephants were observed relatively frequently, although the time period on which this association rate was based was not provided. Recently Rowell & Rowell (1993) found that rams formed long-term relationships.

Alpine ibex is a gregarious species living in open-membership groups, with a common social and spatial segregation between the sexes (Francisci *et al.*, 1985; Villaret & Bon, 1995). Gregariousness, general and specific social preferences (i.e. association with other age and sex classes, and social bonds with individual animals) of yearling and adult ibexes are analysed in a small population, outside the rut. Rut was excluded because of its confounding effect. Our objective is to find grouping rules that may explain social organisation. Because of advantages provided by grouping and familiarity, high gregariousness and stable bonds between females were expected. We addressed the question as to whether males are less gregarious than females and whether male grouping may be based on age and social bonds. Yearling males were expected to show less clear-cut social patterns than adults and inter-annual variations because of their gradual social transition from female to male groups. We argue that social segregation that occurs among the sexes will also occur among males of different age. Because changes in association among individual males may reflect changes either in gregariousness or in sexual social segregation, we measured the proportion of time males were alone, within female and male groups.

MATERIAL AND METHODS

STUDY AREA

This study was conducted in the Sous-Dine massif (46° N, 60° E) which is part of the Bornes-Aravis massif in the Northern French Alps. It is a karstic plateau between 1 700 and 2 000 m surrounded by cliffs and prolonged by slopes with foothills at 600 m. Precipitation ranges from 1 200 to 2 000 mm during 120 to 150 days per year, with snow fall lasting from November to the beginning of May above elevations of 1400 m. Spruce (*Picea excelsa*) forests cover the northern slopes, are mixed with beeches (*Fagus sylvestris*) on the southwestern slopes, whereas in the southeastern part, the tree line gives way to alpine meadow.

Ibexes were re-introduced in 1976 (10 males and 5 females) and numbered 27 individuals in 1989 (16 males, 11 females; Table I). Ibex populations are totally protected like all in France. Alpine ibexes lived here with 200 chamois (*Rupicapra rupicapra*). From June to September, about 800 cows summer in the area. Foxes (*Vulpes vulpes*) and Golden eagles (*Aquila chrysaetos*) are potential predators of kids, while adults have no natural predators.

DATA COLLECTION

The study area was censused monthly in 1988 and 1989 in order to locate groups and determine their composition. Rut occurs from mid-October to

mid-January and kidding in June, when ibex age was incremented by one year. On the whole, 36 tracks in 13 census periods of 2 to 4 consecutive days (minimal and maximal intervals of 10 and 33 days between census periods) and 29 tracks in 11 units of 2 to 4 consecutive days (minimal and maximal intervals of 5 and 42 days) were done respectively in 1988 and 1989. An individual was included in a group when his distance to the nearest neighbor was ≤ 50 m. Ibexes could be recognized using an "identity card" based upon photographs, natural marks and horn characteristics. Male age was estimated by counting horn annuli at short distance; female age was more problematic to estimate and probably less accurate. In 1988, 13 males older than 19 months at mid-January were considered in the analysis. From January 1989, 3 new males 19 months old were recruited, elevating the male population to 16 individuals. They were considered in the analyses only in 1989 because they had not been recognized in 1988.

DATA ANALYSIS

The probability of locating each animal was estimated as the number of times it was seen at least once per census divided by the total number of censuses. The average number of animals (typical group size g), of females (gf) and of males (gm) experienced by each ibex were calculated according to Jarman's method (1982) by considering all their observations in different group compositions.

Knowing the number N of adults (≥ 1 years old) in the population, the expected numbers of females and males $N_{i(\text{exp})}$ with each ibex if it associates unselectively may be assessed as follows: $N_{i(\text{exp})} = P_i \cdot N_a$ where P_i is the proportion of females and males seen in the population and N_a the total number of animals seen with each ibex. Jarman & Southwell (1986) suggested the following index to reflect to what extent the number of animals seen with one subject differs from expected: $N_{i(\text{exp})} - N_{i(\text{obs})}/N_a$.

The probability of each individual being with another adult of the same sex was estimated following Festa-Bianchet (1991) as: $T = (n_i - 1)/(N - 1)$ where n_i is the number of individuals of the same sex and N the number of adults in the group. The expected association frequency between two adults is:

$$E = \sum_{i=1}^t (n_i - 1)/(N - 1)$$

where t is the total number of sightings of each individual. All the observations of an ibex in different group compositions were considered. The probability of being with an adult of the opposite sex was calculated with n_i and N , where n_i represents the number of adults of opposite sex together with the target animal in the group, and N is the number of adults in the population.

Several indices have been used to measure association frequency between individuals. Cairns & Schwager (1987) criticized 4 of them because of biases implicit in each method. Ginsberg & Young (1992) proposed using the Simple Ratio, which was considered to be the least biased method. However, selecting one index above another prevents comparisons with other studies. Furthermore, ibexes differed in their tendencies to be alone, to be with same-sex or with opposite-sex partners, to such an extent that the data contains a certain amount of bias. Because

of these biases, we systematically calculated the Half-Weight, Twice-Weight, Simple Ratio and Square Root indices for each subject. To reduce bias due to multiple occurrences of one individual during a census, the Square Root index was calculated for each pair-wise association by scoring the first sighting of a given pair as suggested by Cairns & Schwager (1987). The indices were calculated as follows and vary from 0 (never seen together) to 1 (always seen together):

$$\begin{aligned} \text{Half-Weight:} & \quad x / x + y_{ab} + 1/2 (y_a + y_b) \\ \text{Twice-Weight:} & \quad x / x + 2 y_{ab} + y_a + y_b \\ \text{Simple Ratio:} & \quad x / x + y_{ab} + y_a + y_b \\ \text{Square Root:} & \quad x / \sqrt{(x + y_a + y_{ab})(x + y_b + y_{ab})} \end{aligned}$$

where

x is the number of times individuals A and B are found together
 y_a is the number of times only individual A is found
 y_b is the number of times only individual B is found
 y_{ab} is the number of times individuals A and B are found in separate groups

The association indices calculated by the 4 methods were highly correlated (all pair-wise comparisons $r_s \geq 0.99$, $P < 0.001$). The Twice-Weight index gave the lowest values and differed least from the Simple Ratio (mean difference \pm SD, $X = 0.042 \pm 0.029$) while the Square Root gave the highest values and differed least from the Half-Weight method ($X = 0.004 \pm 0.004$). Mean difference between Twice-Weight and Square Root indices was $X = 0.092 \pm 0.049$.

Dendrograms generated by a hierarchical agglomerative cluster analysis produced by the unweighted pair-group method using average linkage were represented to appreciate association frequencies between dyads with the Twice-Weight and the Square Root methods (see Lott & Minta, 1983).

Only males were considered to assess annual stability in inter-individual association patterns because of insufficient accuracy in female recognition by the observer in 1988. A rowwise matrix correlation Kendall tests have been applied to compare 1988 and 1989 associations and correlations between pairs of rows were tested by a simple Kendall's tau test using MATMAN Program (De Vries *et al.*, 1993). To test whether males associated together with other males as often in the two consecutive years, we applied a Wilcoxon's matched-pairs signed ranks test.

RESULTS

GREGARIOUSNESS

Males were seen more often during censuses (Table I; two-tailed Mann-Whitney test: $U = -2.5$, $p = 0.01$) and tended to be more often alone ($U = -1.7$, $p = 0.09$) than females. Males were more often alone as they aged ($r_s = 0.75$, $p < 0.01$).

Females experienced larger typical group size (g) ($U = -2.62$, $p < 0.001$) but lived in groups containing fewer adults of the same sex than males (Table I;

TABLE I

Composition of the ibex population, gregariousness and typical number of animals (g), males (gm) and females (gf) experienced by ibexes in Sous-Dine (French Alps) from mid-January to mid-October 1989.

	age (N) ¹	% alone	% seen	g	gm	gf	Females O (E)	Males O (E)	P ²
Males									
Satanas	≥ 13 (12)	29	41	5.3	5	0	0 (14.7)	36 (21.3)	***
Barrabas	12-13 (9)	10	31	6.1	5.3	1	3 (13.5)	29 (18.5)	**
Diabolo	11-12 (16)	12	55	8.7	5.5	2.7	14 (49.9)	104 (68.1)	***
Belzebuth	8-9 (19)	22	66	8.9	6	2.7	15 (56.7)	119 (77.3)	***
Vichnou	6-7 (20)	14	69	8.6	6	3.6	13 (49.5)	104 (67.5)	***
Lucifer	6-7 (25)	9	86	8.7	5.7	3.4	16 (60.1)	126 (81.9)	***
Taranis	5-6 (22)	9	76	9.1	5.5	3.2	18 (71.9)	152 (98.1)	***
Toutatis	4-5 (20)	12	69	8	6.1	2	6 (51.2)	115 (69.8)	***
Belenos	4-5 (19)	14	66	6.3	5.2	1.7	8 (33.8)	72 (46.2)	***
Atos	3-4 (22)	0	76	9.5	5.6	3.1	25 (73.6)	149 (100.4)	***
Portos	3-4 (17)	4	59	8.7	5.9	2.6	14 (49.1)	102 (66.9)	***
Aramis	3-4 (19)	4	66	9.2	5.6	2.5	20 (57.5)	116 (78.5)	***
Pan	2-3 (13)	0	45	8.1	4.8	2.7	15 (28.3)	52 (38.7)	*
Kevin	1-2 (19)	5	66	8.8	2.4	2.8	32 (24.1)	25 (32.9)	NS
Merlin	1-2 (19)	8	66	10.8	5	3.5	44 (51.6)	78 (70.4)	NS
Lancelot	1-2 (19)	5	62	9.8	4.2	3.1	31 (33)	47 (45)	NS
Females									
Melusine	≥ 15 (12)	53	41	7.4	1	2.7	13 (6.1)	1 (7.9)	*
Morgane	11-12 (18)	4	62	9.5	2.9	3.1	23 (19.6)	22 (25.4)	NS
Raven	7-8 (18)	0	62	12.5	5.6	3.5	49 (37.4)	37 (48.6)	NS
Carabose	6-7 (18)	9	62	9.8	3.5	3.5	44 (24.3)	12 (31.7)	***
Beltane	5-6 (17)	5	59	12.3	5.6	3.5	45 (35.7)	37 (46.3)	NS
Ninianne	5-6 (9)	0	31	8	0	3.7	17 (7.4)	0 (9.6)	***
Viviane	4-5 (10)	0	34	9.5	4	2.8	27 (16.1)	10 (20.9)	*
Marianne	4-5 (13)	20	45	10	3.5	3.3	28 (14.8)	6 (19.2)	**
Falbala	3-4 (16)	0	55	10.7	3.9	3.5	45 (26.1)	15 (33.9)	***
La Mariotte	3-4 (12)	0	41	11.3	3.2	2.7	22 (13.9)	10 (18.1)	NS
Julie	2-3 (19)	4	66	10.1	3.4	3.5	45 (27)	17 (35)	**

¹ (N) refers to the number of times each animal was seen at least once during the censuses.

% alone is the proportion of time an animal was seen alone and % seen is the ratio an animal was seen at least once during a census: the total number of censuses. O (E) are the observed and expected numbers of males and females. In the case of females, males 1-2 years were not taken into account.

² Difference between observed and expected distributions, χ^2 tests. * P < 0.05, ** P < 0.01, *** P < 0.001.

U = -3.8, p < 0.001). Typical group size (g) decreased with male age ($r_s = -0.6$, p = 0.02) while average numbers of males (gm) or females (gf) experienced were not correlated with male age (respectively $r_s = 0.405$ and $r_s = -0.36$, both p > 0.05).

GENERAL PATTERNS OF ASSOCIATIONS

There was a strong inter-individual variation between females in their tendency to be seen with at least one male (range 0-83%) and this seemed

independent of age. All females were seen with more females and fewer males than expected, but this was significant in only 7 of 11 cases. When only males $\geq 2-3$ years old were considered, the association frequency with at least one male decreased (range 0-47 %) and in all these cases, females were seen with more females and fewer males $\geq 2-3$ years old than expected, although the number of significant differences between observed and expected distributions did not vary (Table I). 96 % of male-female groups involving males $\geq 2-3$ years old ($N = 27$) were observed prior to June.

Males $\leq 2-3$ years old were seen in female groups in more than 50 % of observations. Sexual segregation increased with male age, although after age 5 male occurrence in female groups remained stable in about 20 % of observations (Fig. 1).

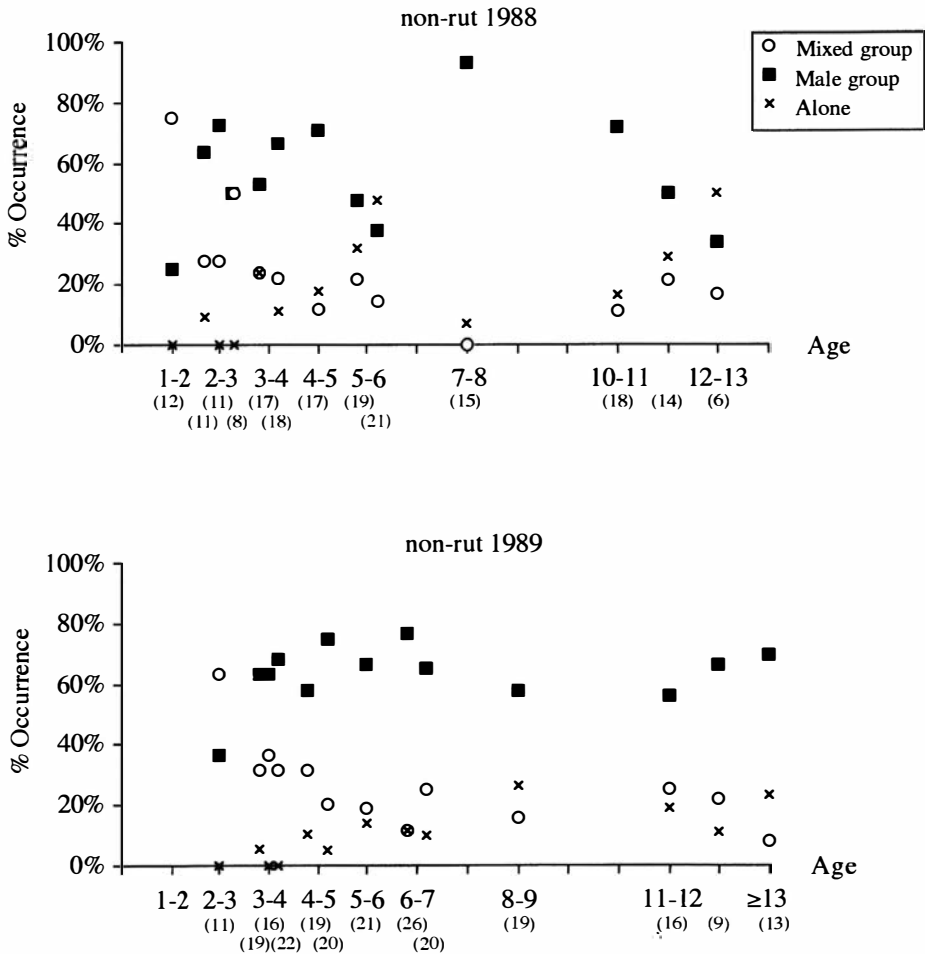


Figure 1. — Percentage of male ibex seen alone, in female and male groups according to their age in 1988 and 1989 outside the rut in Sous-Dine (French Alps). Numbers into brackets represent sample size.

The number of males and females seen with males 1-2 years old did not differ significantly from expected by chance, while older males were seen with males more and with females less than expected (Table I). Half of the males were seen with males of each age class as often as expected, including 3 males \leq 2-3 years old, as well as the 2 oldest (Table II). Males of \leq 2-3 years of age were in company with some immediately older males more than expected, and less often with much older males (Table II). Almost all males \geq 3-4 and \leq 12-13 years old were seen with younger and older males less than expected, and associated among themselves more than expected. Significant differences were found between males of the same age class.

TABLE II

Preference of male ibex for age cohort associates expressed as the difference between observed and expected numbers of males seen with each male ibex outside the rut (see methods).

	1-2	2-3	3-4	4-5	5-6	6-7	8-9	11-12	12-13	\geq 13	P^1
Satanas (\geq 13)	-20	-4	+2	-5	+2	+6	+13	+2	+4		NS
Barrabas (12-13)	-10	+7	-13	+7	-3	0	+4	0		=7	NS
Diabolo (11-12)	-14	-6	+3	0	+12	+7	+7		-5	-4	***
Belzebuth (8-9)	-13	-5	+9	0	+5	+3		+5	-4	-1	*
² (6-7)	-12	-1	+4	+5	+5	+4	+2	+	-5	-3	NS
Taranis (5-6)	-10	-3	+12	0		+4	+3	+6	-6	-5	***
Toutatis (4-5)	-15	-4	+10	0	+4	+7	+5	+2	-4	-4	***
Belenos (4-5)	-6	+3	-3	-4	+3	+13	-2.5	-1	-2.5	-7	NS
² (3-4)	-8	-4	+12	0	+6	+2	+3	0	-5	-4	*
Pan (2-3)	0		-5	+6	+3	+8	-3	-5	+3	-5	NS
Kevin (1-2)	-1	+2.5	+16	+11	-3	-1	-7	-7	+5	-7	NS
Merlin (1-2)	+2	-4	+16	-4	+4	+1	0	0	-7	-7	NS
Lancelot (1-2)	+18.5	-7	+14	-7	+6	-7	0	-4	-7	-7	*

¹ Comparison between the distributions of observed and expected numbers of males associated with each male ibex, χ^2 test. Bold characters indicate cells for which post-hoc contribution \geq 1.8. ² Males of this age had very similar distributions ($P > 0.95$; χ^2 test) so that the mean observed and expected values were considered. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

INTER-INDIVIDUAL ASSOCIATIONS

Of all the possible co-occurrences of ibexes in a group ($N = 351$), only 70 % were observed. Most of the pair-wise associations not observed involved one male and one female (81 %). Associations between individuals of the same sex were very fluid and similar, i.e. only 9 % and 12.5 % of the possible pairs of females and males were not observed. However sexual differences were found in the tendency to form bonds.

Both dendrograms performed with Twice-Weight and Square Root indices proved to be very similar. For the sake of clarity, we show the cluster of Square Root association indices (Fig. 2). The matrix shows that intra-sex linkage values were much higher among males than females ($U = -4.56$, $p < 0.001$). Female-

female indices were significantly higher than female-male ones for only 6 females. The differences became significant for 2 other females when 1-2 year-old males were omitted. Except in 2 cases, females showed weak linkages, with a percentage of association averaging 20 ± 17 %. The mean Square Root index among females ($N = 55$) was 0.20 ± 0.17 . Only a few females exhibited close bond with one another, with 12.7 % having a Square Root index > 0.4 . Thus few female sub-groups may be distinguished. However, the observed/expected (O/E) frequency of pairwise association averaged 2.41 ± 1.79 ($N = 110$), suggesting that females did not group together at random. Here, the number of scores N was twice the number of possible dyads because the probability of pairing combination varied for each female of a dyad.

All males except the 1-2 year old had higher male-male than male-female association indices (all $p < 0.01$; U-tests). The mean percentage of male-male associations averaged 27 ± 20 %. The mean Square Root association index among males was 0.27 ± 0.19 with a mean O/E = 1.54 ± 1.10 ($N = 240$). Males ≤ 2 -3 years old were loosely associated with the other males, except Merlin and Lancelot who were often together. Kevin and Merlin, two 1-2 year-old males, were frequently seen with a different female (Morgane and Ravel). Association indices between the females and both other young males were low, especially for Pan (2-3 year old). As reported before, the oldest males were almost never seen with females. They were often observed more frequently with immediately younger males than with much younger males. Close linkages were however observed among ≥ 3 -4 and ≤ 11 -12 year-old males, often involving several peers, forming small nuclei of individuals. In 69 % of cases ($N = 45$), Square Root indexes were ≥ 0.4 . The younger of these males tended to form stronger associations with females than with older males.

STABILITY OF INTER-MALE ASSOCIATIONS

Males were located more often in 1989 than in 1988 (Wilcoxon signed-ranks test, $T = -3.01$, $p < 0.01$). This may be due because the observer was more fully trained after the 1988 season. Although this possibility cannot be discarded, data revealed that the level of sociality of males differed between both periods. The seven males < 4 -5 years in 1988 showed similar general social patterns in both years (Fig. 1). In contrast, older males showed different patterns, although statistical significant differences were found only for one male 5-6 years old, possibly due to small sample size. In particular, both 5-6 year-old males and both oldest males were more often alone and less often in male groups in 1988 than in 1989. Except for the youngest, the occurrence of males within female groups was very similar during both years ($G = 6.76$, 10 df, $p = 0.70$ and $G = 9.58$, 11 df, $p = 0.61$; in 1988 the 7-8 year-old male was not taken into account as it was not observed with females). When considering the occurrence of males in male groups, there was a higher inter-individual variability in 1988 ($G = 20.27$, 11 df, $p = 0.07$) than in 1989 ($G = 4.22$, 11 df, $p = 0.97$) (Fig. 1).

Unexpectedly, the 1-2 year-old male that associated preferentially with immediately older males in 1988 seemed to associate with other males regardless of their age in 1989. Males ≥ 2 and ≤ 11 years old clearly tended to associate with similar or immediately older males although it was less marked in 1988 than in 1989. Males were observed to form pair bonds and small subgroups in both years

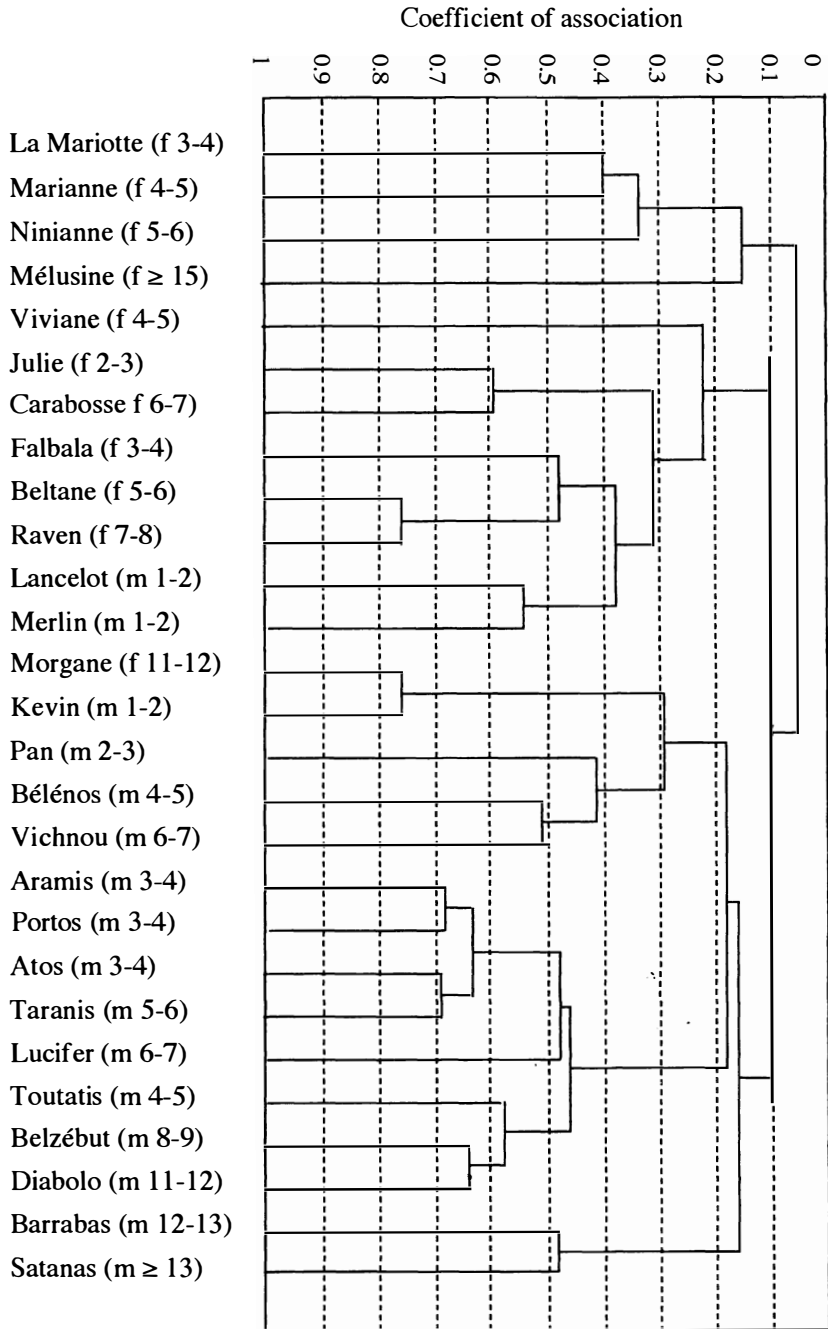


Figure 2. — Unweighted pair group average-link cluster analysis of association indices (Square Root index) among ibexes outside the rut in 1988 in Sous-Dine (French Alps).

(Fig. 3). Both association matrices were positively correlated ($K_r = 174$, p -right = 0.016, one tail test). However males showed stronger bonds in 1989 than in 1988, although significantly only for 5 males. Pairwise comparisons with Kendall test revealed that association patterns were correlated for only 3 males (respectively 10-11, 7-8 and 5-6 years old in 1988), indicating inter-individual variation in the stability of associations. It appears that from 1988 to 1989, changes resulted from an increase of association frequency between individuals, changes of peers without increase in association frequency, and an increase of association frequency with the same peers.

The youngest (Pan, 1-2 years in 1988) and the two oldest males (Satanas and Barrabas) had low association indices in both years. Pan also changed its association pattern by being less observed with the three immediately older males and more frequently observed with two much older males. Barrabas, contrary to Satan, tended to conserve the same patterns of association. In the second year, they associated more frequently, being somewhat apart from the youngest male. The intermediate aged males showed much higher values of association indices, but not necessarily with the same partners. Atos (2-3 years old in 1988) showed the strongest frequency of association with Pan in 1988 and was loosely associated with the other males. In 1989, he was rarely observed with Pan and showed more consistent pattern, strongly linked with males of similar age. The other males \leq 4-5 years old in 1988 rather than showing stronger bonds modified their patterns by associating more frequently with older males, except the two oldest ones. Only three males (Diabolo, Belzebuth, Lucifer) revealed a similar distribution of bonds (Kendall Tau, $p < 0.05$), with two of them strengthening the bonds.

Despite the re-arrangements of social links that occurred from one year to the next, it is noteworthy that pairs and sub-groups were maintained from 1988 to 1989, such as those including Aramis, Portos, Toutatis and Taranis or Belzebuth, Diabolo and Vichnou (Fig. 2).

DISCUSSION

COMPARISONS WITH OTHER UNGULATE SPECIES

The mean association index among female ibexes was much lower than in North American elk (Franklin & Lieb, 1979; Jenkins & Starkey, 1982) but higher than in bison (Square root index: 0.2 vs 0.103), in non-related reindeer (*Rangifer tarandus*) (Twice-weight index: 0.13 vs nonrutting AI < 0.1 ; Fig. 2, p. 745) and between ewes and their adult daughters in Bighorn sheep (O/E = 2.41 vs 1.53) (Lott & Minta, 1983; Hirovani, 1990; Festa-Bianchet, 1991). Mean association frequency was slightly higher than those found between relative hinds, with the exception of mother and daughter (Clutton-Brock *et al.*, 1982; Fig. 9.7, p. 187).

Such interspecific differences are not easy to account for. Franklin & Lieb (1979) argued that stable bonds among females in their population may be linked with habitat stability, as has been suggested by others (Hirth, 1977; Leuthold, 1978; Jenkins & Starkey, 1982; Green *et al.*, 1989). Mountain ungulates live in unpredictable habitats, in which available areas and feeding resources vary with the seasons. This may prevent the formation of stable social bonds. However, differences in bond strength among females were also reported, as in giraffe

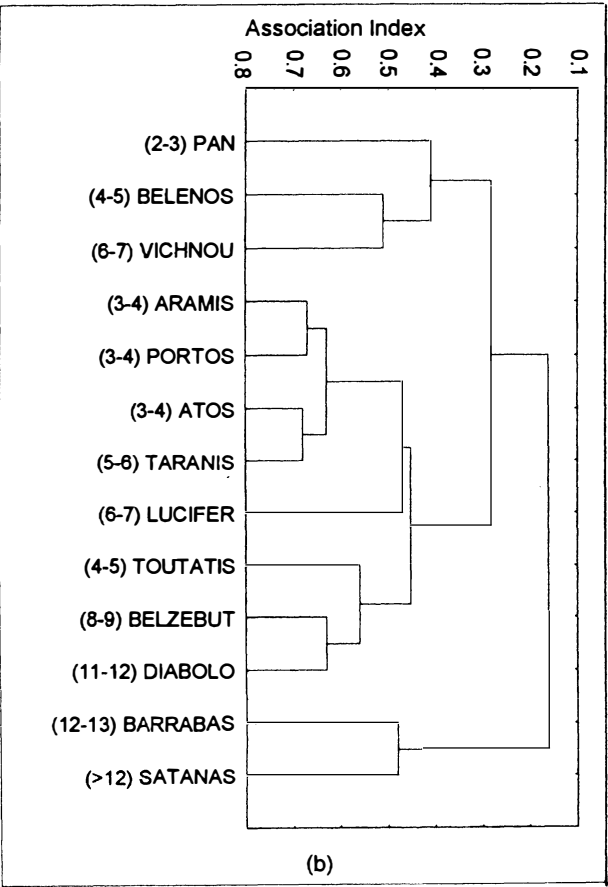
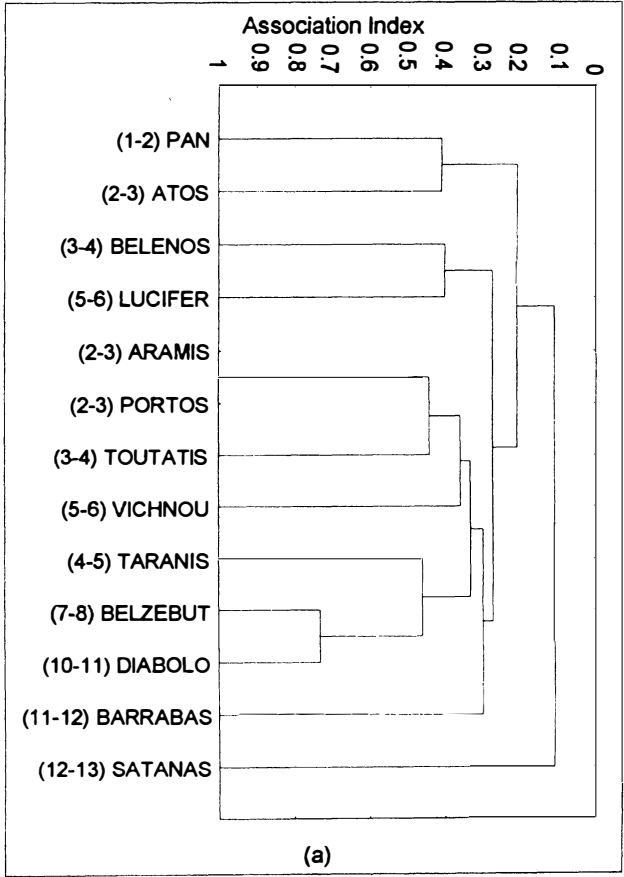


Figure 3. — Unweighted pair group average-link cluster analysis of association indices (Square Root index) among male ibexes outside the rui in 1988 and 1989 in Sous-Dine (French Alps).

(*Giraffa camelopardalis*) (Pratt & Anderson, 1979), elk (Franklin & Lieb, 1979), bison (Green *et al.*, 1989) and Pyrenean chamois (*Rupicapra pyrenaica*) (Richard-Hansen, 1992). Whether the few dyads that were observed consisted of mother-adult daughters was unknown. Generally, mother-young bonds in ungulates are not long lasting (Green *et al.*, 1989; Hirotsu, 1990; Festa-Bianchet, 1991; Lawrence, 1991; Richard-Hansen, 1992). The relatively high coefficient of association may be due to the small size of the population, so that stable bonds were more probable than in large populations.

Unlike elk and red deer (Franklin & Lieb, 1979; Clutton-Brock *et al.*, 1982), male ibexes displayed stable bonds with some peers, as do domestic rams (Grubb, 1974; Arnold *et al.*, 1981; Rowell & Rowell, 1993). The results indicate that association was not due to chance, because some pairs were frequently observed. Furthermore, males showed affinity with only some males, including those of the same age, which suggests that they may develop specific preferences. Although this ibex population was small and forced us to be cautious regarding interpretations, gregariousness alone was an unlikely explanation for our results, because male grouping changed with age, is dependent on age, and because bonds among males tended to be stable during 2 years.

SEXUAL DIFFERENCES IN SOCIAL TENDENCIES

In wild caprins, females ibex are reported to live in larger groups and to be less often alone than males (Grubb & Jewell, 1966; Geist, 1971; Leslie & Douglas, 1979; Singer & Doherty, 1985; Bon & Campan, 1989; Richard-Hansen *et al.*, 1993). In this study, females were less often alone but lived with fewer same-sex adults than males which formed closer bonds and were involved in a more structured social network. Restriction into rocky habitat is considered as a female strategy to reduce predation risks in mountain ungulates (see Bon *et al.*, 1995). This type of habitat may simply prevent females to form large and stable groups (Francisci *et al.*, 1985) and so to develop high level of sociality. However, because females lived in larger groups than males, it is difficult to confer this sexual difference to habitat type. Indeed, our results suggest that females could be less motivated than males to form inter-adult social bonds in Sous-Dine.

Several authors have suggested that affinities among males were based on sharing home ranges (Grubb & Jewell, 1966; Moss & Poole, 1983; Hall, 1986). General gregariousness and co-occurrence in preferred ecological areas is an unlikely explanation for the male ibex grouping observed in this study. First, they were more numerous than females so that strong bonds were statistically less probable for males than for females. Second, because of the small size of the population, males probably used common areas, so that loose associations suggest indifference or avoidance while close associations and relatively stable sub-groups probably result from mutual attraction.

Specific sexual motivation and experience may be involved in the stability of social bonds in ungulates. Early in life, males interact with pseudo-sexual and agonistic behaviours and play more than females, which engage in more locomotor play (see Bon, 1991; Rothstein & Griswold, 1991; Hass & Jenni, 1993; Bon & Campan, 1996). Such differentiation of social behaviour may reflect a sexual difference in the level of motivation. Affiliative interactions among adult females are rarely reported. In this study, the few existing bonds were restricted to two

females, suggesting a lack of affinity as shown in caprins (Leslie & Douglas, 1979; Boyd, 1981; Singer & Doherty, 1985). In contrast, frequent play fights among similar-aged male ibexes were observed in summer (Nievergelt, 1967), and among European mouflon in spring (Bon unpublished data). Spring and pre-rut concentrations of bighorn sheep rams (Geist, 1971) would allow them to practice social skills (Festa-Bianchet, 1986). Male maturation up to adulthood in sexually dimorphic ungulates lasts longer than females; males are considered neotenic or progenic (Geist, 1971; Gould, 1977) in the sense that they are sexually mature when still in a morphologically juvenile form. Delayed maturation in males is associated with a series of distinguishable body and behaviour phenotypes (Geist, 1968). This would allow a complex network of interactions and high opportunities for stable bonds among males.

Male social tendencies (see Mason 1978 for a presentation of social dispositions or social tendencies) changed during ontogeny. Sexual social segregation increased as males grew old, as in other caprins (Nievergelt, 1967; Geist, 1971; Bon & Campan, 1989; Festa-Bianchet, 1991). In addition, we also found that social segregation among males increased with age difference, as previously shown in ibex (Nievergelt, 1967; Villaret & Bon, 1995).

Young males exhibited unclear social patterns, ranging from close bonds with one female, affinity for same-aged males to loose associations with older males as in sheep species (Grubb & Jewell, 1966; Geist, 1971; Bon & Campan, 1989; Bon *et al.*, 1993; Le Pendu *et al.*, 1995). Rothstein & Griswold (1991) showed how yearling bison males directed more olfactory investigations towards yearling females and more aggressive interactions towards other yearling males. The social instability of young males is probably linked to their maturation and to a switch of social preference from females to same-sex peers.

Adult males from 2 to 12 years old showed more stable social choices. However, the patterns of association were less clear than expected, perhaps because the presence of a small number of individuals and the general gregariousness of ibex may lead males of different ages to coexist (Nievergelt, 1967).

Old animals appeared less sociable than younger ones, as in European mouflon, bighorn sheep and chamois species (Pfeffer, 1967; Geist, 1971; Shank, 1985; Richard-Hansen, 1992; Hass & Jenni, 1993). Shank (1985: 122) considered social and spatial segregations of old male chamois as a trade-off between dependence for feeding resources and a "need for solitude" reflecting social intolerance. Richard-Hansen (1992) suggested that lower sociability may be inherent in old animals. However, old non-reproductive buffaloes were reported to group together, apart from the younger males (Sinclair, 1977). The oldest ibexes may seem less sociable than younger ones because peers of the same condition (physical and social) are rare and their association is thus less probable. This trend may be reinforced if social affinities are set up during juvenile life (Hunter & Davies, 1963; Bouissou & Hövels, 1976; Broom & Leaver, 1978; Winfield *et al.*, 1981). Adults which lost familiar peers may be less prone to link with non-familials.

STABILITY OF INTER-MALE BONDS

Richard-Hansen (1992) reported some frequent associations of short duration between male Pyrenean chamois (*Rupicapra pyrenaica*) but few males were

followed more than one year. Long-term associations between males have been found in African elephants and domestic sheep (Moss & Poole, 1983; Rowell & Rowell, 1993). Our results suggest that male ibex form and maintain close social bonds during two consecutive non-rut periods.

Changes in bond network over a two year period are not easy to account for. Demographic factors have been invoked as a major cause of limitation in protracted relationships (Richard-Hansen, 1992; Rowell & Rowell, 1993). But, in Sous-Dine, no cases of mortality among adult males were noted and only three 1-2 year-old males were recruited in 1989. It appears that social tendencies and strength of bonds change with male age. Young males and old males sociality have been discussed earlier when comparing the sexes. Males ≥ 2 and ≤ 11 years did not modify their general social patterns (alone, within female and male groups) but changes occurred with respect to inter-individual associations. In 1989, the tendency of males ≥ 2 and ≤ 11 years to associate with similar or immediately older males was less clear than in 1988 but bonds were stronger in 1989 than in 1988. As young adult males join older ones more consistently in 1989, it follows a more stable social system and higher opportunity for association among adult males. With two exception (Vichnou and Satanas), ≥ 6 year-old males in 1988 showed the highest level of stability in bond network, which probably reflects a stable period in the maturation of male social behaviour.

These results need to be confirmed with other studies on larger populations where recognizable or marked animals also represent a large proportion of animals. General inter-attractiveness or gregariousness as proposed by Gerard & Richard-Hansen (1993), and more subtle rules should probably be taken into account when explaining ungulate social organization (Rowell & Rowell, 1993; Bon & Campan, 1996).

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SUMMARY

Gregariousness, inter-individual and general patterns of association of adult ibex (*Capra ibex*) were studied outside the rut in 1988, and comparatively in 1988 and 1989 for males in a small population (Sous-Dine massif, French Alps). Females were less often alone, lived in larger groups albeit with fewer same-sex adults than males. As they aged, males were more often alone and lived in smaller

groups, while typical numbers (see « typical group size » of Jarman, 1982) of males and of females were independent of their age. Females tended to be more with females than with males and most of them formed loose bonds. 1-2 year-old males associated with individuals of both sexes as expected by chance, whereas > 2 year-old males lived in groups where they clearly outnumbered females. The oldest males showed loose bonds with other males. Those 3-4 to 11-12 years old were seen less often than expected with either younger or older males, associated preferentially with individuals in the same age interval and formed close bonds among themselves resulting in relatively stable sub-groups. Males < 5 years old did not change their general patterns of association but did show weaker social bonds in 1988 than 1989. In contrast, > 4 year-old males tended to be alone more often and less in all-male groups in 1988, while their occurrence in female groups did not vary. Males > 4 years old also displayed more stable networks of association than younger males. Some pairs and sub-groups of males aged 2 to 11 years were consistent during the two consecutive years.

RÉSUMÉ

La grégarité et les types généraux et particuliers d'association ont été étudiés en dehors du rut, entre bouquetins des Alpes adultes (*Capra ibex*) en 1988, puis comparativement entre mâles en 1988 et 1989, dans une petite population (massif de Sous-Dine, Alpes françaises). Les femelles étaient moins souvent isolées, vivaient dans des groupes plus grands mais avec moins d'adultes de même sexe que les mâles. En vieillissant, les mâles ont été plus souvent vus seuls et dans de plus petits groupes, alors que le nombre typique (« typical group size », Jarman, 1982) de mâles et de femelles étaient indépendants de l'âge. Les femelles tendaient à être avec davantage de femelles que de mâles et la plupart d'entre elles formaient des liens lâches. Les mâles de 1-2 ans s'associaient avec des individus des deux sexes de façon aléatoire alors que les mâles > 2 ans vivaient en groupes où le nombre de mâles dépassait largement celui des femelles. Les mâles les plus âgés formaient des liens lâches avec les autres mâles. Ceux de 3-4 à 11-12 ans furent vus moins souvent qu'espéré tant avec des plus jeunes qu'avec les plus vieux, s'associaient préférentiellement et formaient des liens étroits entre individus du même intervalle d'âge, ceci aboutissant à la formation de sous-groupes relativement stables. Les mâles < 5 ans n'ont pas modifié leurs patrons généraux d'association mais ils ont formé des liens sociaux plus lâches en 1988 qu'en 1989. Au contraire, les mâles > 4 ans tendaient à être plus souvent seuls et moins souvent dans des groupes de mâles en 1988 alors que leur présence dans des groupes de femelles n'a pas varié entre 1988 et 1989. Les mâles > 4 ans avaient également un réseau d'association plus stable que les plus jeunes. Quelques paires et sous-groupes de mâles âgés de 2 à 11 ans ont été régulièrement vus durant les deux années.

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