



Social cohesion in groups of sheep: Effect of activity level, sex composition and group size

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Abstract

We investigated the effects of activity, group size and sex composition on the cohesion of merino sheep (*Ovis aries*) groups. Mixed-sex (50% of each sex) and single-sex groups of 2, 4, 6 and 8 sheep were placed within 491-m² arenas located in natural pastures and were video recorded during 6 daily hours. The behaviour, orientation and location of each sheep were then extracted from the films at 1-s intervals. We analysed the polarisation of individual orientations, mean inter-individual and nearest neighbours' distances, as well as the frequency of pairs of nearest neighbours according to their sex within mixed-sex groups. Sheep were more aggregated than predicted under the null hypothesis of random spatial distribution for all group compositions and sizes. Sheep were more spread out and less aligned in half-active than in all-active groups, showing that social cohesion was reduced by a lack of activity synchronisation. The highest proximity between individuals was found in resting groups, yet alignment was low. The polarisation peaked in all-active groups. Mean inter-individual distance did not vary and the nearest neighbour distance decreased as group size increased. When sheep were all-active or all-resting, mixed-sex groups were more spread out than single-sex ones, with a greater distance between opposite than between same-sex individuals. Nearest neighbours of the same sex were also more frequent than

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random. Our results show that social cohesion can be modulated by activity synchrony but also by social affinity.

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1. Introduction

Shoals, herds or flocks of vertebrates remain cohesive for varied periods of time, ranging from only a few minutes to several weeks or even several months (Wilson, 1975; Southwell, 1984; Marchal et al., 1998; Croft et al., 2003). Although considerable attention has been dedicated to the costs and benefits of group living (Hamilton, 1971; Krause and Ruxton, 2002; Estevez et al., 2007), relatively little attention has been paid to the mechanisms underlying and the factors affecting group cohesion (Boinski and Garber, 2000; Schülke and Kappeler, 2003).

Cohesion implies that group members remain at a short distance from one another, within the range of communication. This should be true when group members are all active or all at rest. When groups include individuals engaged in different activities, they are likely to be less cohesive and to split more often than groups of animals engaged in the same activity. Indeed, greater distance being created between active and inactive individuals than between individuals engaged in the same activity, could ultimately make the group split (Rook and Penning, 1991; Conradt and Roper, 2000). When all group members are in motion, cohesion further implies polarisation of body orientations, otherwise the animals would exhibit diverging trajectories leading to group fragmentation (Huth and Wissel, 1992; Gueron et al., 1996; Conradt and Roper, 2005; Focardi and Pecchioli, 2005).

Group cohesion also relies on the motivation of individuals to stay together and maintain inter-individual distance (Hediger, 1955; McBride et al., 1963). In a number of vertebrates, males and females tend to segregate socially outside the mating season (Ruckstuhl and Neuhaus, 2005) even when both sexes inhabit the same habitats (Cransac et al., 1998; Conradt, 1999; Kie and Bowyer, 1999; Bon et al., 2001; Bonenfant et al., 2004). The ‘social affinities’ hypothesis suggests that social segregation stems from sex-related differences in the motivation to interact with conspecifics: males would seek partners to interact with, whereas females interact little, being indifferent or avoiding the interactions performed by males (Bon and Campan, 1996; Le Pendu et al., 2000; Guilhem et al., 2006). Greater attraction between individuals of the same sex would make single-sex groups more cohesive and less prone to split than mixed-sex groups whatever the level of activity within the groups.

In the wild, a number of external factors may affect the decision of animals to choose habitat types, and/or join groups of preferred composition and size and it is rather difficult to disentangle their respective effects. In order to study the specific effects of activity and sex on group cohesion, we performed experiments by introducing groups of merino sheep (*Ovis aries*) of controlled sizes in the same pastures. Because sheep were monitored over a relatively long period during the day, we were able to compare the level of social cohesion when all group memberships were active or resting (synchronous) and when only half of them were active (asynchronous).

We tested the effects of activity, group size and group composition on group cohesion by measuring and comparing the degree of polarisation, the inter-individual distance and the nearest neighbour distance within male, female and mixed-sex groups. On the basis of what has been argued above, we expected (1) the inter-individual distance to be larger in asynchronous groups

than in synchronous ones, (2) body orientations to be strongly polarised when all group members were active, and (3) lower polarisation of orientations and greater inter-individual distance in mixed-sex than in single-sex groups whatever the activity.

2. Materials and methods

2.1. Study area and subjects

Fieldwork was carried out at the experimental farm of Domaine du Merle (5.74° E and 48.50° N) in the South of France, from November 2003 to February 2004. We used 34 Arles merino horned males (median age = 3 years, range = 1–7) and 32 females (median age = 9 years, range = 5–11) randomly chosen from a group of males ($N = 66$) and a flock of females ($N = 900$). The subjects were familiarised with one another by being kept together in a 1-ha pasture for 5 weeks before starting the experiments. All animals were identified with a number on both flanks and on the rump. Each ewe received a vaginal sponge containing 30–40 mg of progesterone every 14 days to block oestrus and to prevent sexual interactions.

2.2. Experimental set-up and procedure

Three 25 m-diameter arenas, each placed at a distance of 22.5 m from a 7 m-high tower, were delimited by sheep fences in a field of native wet Crau meadows, predominantly composed of graminoids, clover *Trifolium* sp. and plantain *Plantago lanceolata* (Bosc et al., 1999). Visual contact with both the immediate surroundings and adjacent arenas was prevented by a 1.2 m-high green polypropylene net. The space between the arena fences and the polypropylene net delimited a “waiting area” around each arena (Fig. 1).

The experimental design consisted of randomly allocating a male group, a female group and a mixed-sex group (sex ratio 1:1) of the same size to each of the three arenas, then observing them simultaneously. Four group sizes were considered, namely 2, 4, 6, and 8 individuals (space allowance: 245, 123, 82, and 61 m² per head). The order in which group sizes were tested was chosen randomly, and this was replicated five times.

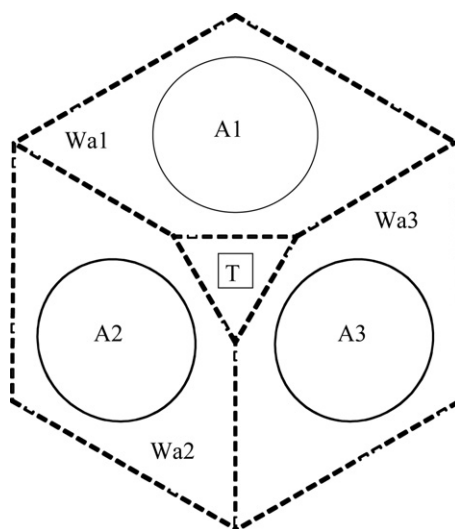


Fig. 1. Experimental set-up consisting of three 25 m-diameter circular arenas (A) delimited by electric fences (unbroken lines) and visually isolated by the 1.2 m-high green polypropylene netting (dotted line) delimiting three adjacent waiting areas (Wa). A 7.5-m observation tower (T) was located at the centre of the set-up.

Each individual was randomly allocated to one group size and composition in each replicate. Familiarisation of individuals with the experimental set-up and their social group began at 10:00 h the day before experiments, by introducing the three groups to be tested into the appropriate waiting areas. At 17:00 h, the groups were introduced into the experimental arenas, in preparation for testing the next day.

The tower and arenas were moved three times within the field, in order to prevent excessive food depletion. Sward heights were measured (± 0.5 cm) within the arenas, using an HFRO sward stick (Barthram, 1986) the evening before the groups were introduced. Sward height and estimated herbage biomass did not vary significantly between the different group sizes and compositions (average sward height and biomass, respectively, 7.5 cm and 1042.3 kg DM/ha; see also Micheleni et al., 2006).

2.3. Data collection

The behaviour of sheep in each arena was recorded on video from 10:00 h to 16:00 h with three digital camcorders (Sony DCR-TRV950 E) mounted on the top of the tower and connected to a PowerBook laptop. The laptop was programmed to take a snapshot from each camera every second ($N = 21,600$). Video recordings made in the same conditions before the start of the experiment showed that the behaviours of interest (grazing, standing, moving, interacting, or resting) could be reliably identified from snapshots taken at such a time interval. One set of observations involving groups of eight animals was discarded from the analyses because of disturbance from external visitors.

On each digital snapshot, each individual was tracked visually on a monitor screen, using a software that we developed in the laboratory (JG). For each individual, two points on the ground were identified which were estimated to be the midpoints between the two forelegs and between the two hindlegs. Then the location of the sheep was calculated using a true perspective projection (Horn, 1999). The accuracy of the sheep locations was assessed by comparing the coordinates extracted from digital snapshots (X_c, Y_c) with those obtained in the field by using a laser rangefinder (X_l, Y_l) (Impulse model 200LR, Laser Technology Society Inc.). The coordinates obtained by each method were highly correlated, the estimated error of locations extracted from snapshots being < 0.5 m (respectively: $X_c = 1.005X_l - 0.123$, $r = 0.99$, and $Y_c = 0.987Y_l - 0.196$, $r = 0.99$, both $P < 0.001$, $N = 226$) relative to the laser measurements. Each animal's orientation was determined from a line drawn by joining the points between the hindlegs and forelegs. The inter-individual distance was calculated using the co-ordinates of the points midway between the forelegs of each sheep.

2.4. Statistical analyses

For spatial analyses, one snapshot every 360 were selected ($\Delta t = 6$ min; total: 60 snapshots per group), and among them the snapshots for which all the group members were active ('all-active group'), only half were active ('half-active group'), and all were resting ('all-resting group'). When all sheep were active, neither angular deviation between animals' orientation nor inter-individual distance were found to be auto-correlated between successive snapshots, so all snapshots belonging to the active bouts were included in the analyses. In resting- and half-active groups, because the resting sheep had stayed almost in the same positions, we only kept included the first snapshot of each bout.

Group polarisation was estimated by calculating the mean angular deviation S of individual orientations for each snapshot, using the formula (Zar, 1999):

$$S = \frac{180^\circ}{\pi} \sqrt{2(1-r)} \quad \text{with} \quad r = \sqrt{X^2 + Y^2}, \quad X = \frac{1}{n} \sum_{i=1}^n \cos a_i, \quad Y = \frac{1}{n} \sum_{i=1}^n \sin a_i$$

and a_i the body orientation of each of the n group members. S values 0° for perfect alignment of the n individuals. Under the hypothesis that the body orientations follow a random uniform distribution between 0° and 360° , S is a random variable whose median varied with group size. S for groups of 2, 4, 6, and 8 individuals under the hypothesis of random distribution of orientations (over 360°) was computed by running 30,000, 15,000, 10,000, and 7500 simulations, respectively. The medians of experimental S and S_0 were compared using sign tests. If the null hypothesis of random uniform distribution was rejected, we then

fitted the values of S with those obtained by simulation assuming that the group members' orientations followed a von Mises distribution (Batschelet, 1981), i.e., a normal-like angular distribution that is symmetrical around a modal value. The best fit between experimental and simulated values was obtained by tuning the parameter of concentration κ of the von Mises distribution. For each tested value of κ , the numbers of simulations performed per group size were identical to those run for the random uniform distribution.

Data from groups monitored the same day, which experienced the same random environmental conditions, and snapshots of the same groups were considered not independent. Accordingly, analyses were performed using mixed effect linear models including day and group as random factors (Laird and Ware, 1982).

First, we tested for the effect of group activity level (all-active, all-resting or half-active) on each spatial variable (mean angular deviation, mean inter-individual distance and mean nearest neighbour distance). Thereafter, for each group activity level, we tested the effect of group composition (male, female or mixed-sex), of group size (considered as a continuous variable) and of the interaction between these two variables. Since the expected value S_0 depended on group size (see above), the analysis was performed using the dependent variable $S' = S - S_0$, where S_0 is the mean of the values obtained by simulation with the angular distribution that best fits the data.

Within the half-active groups, we compared mean inter-individual distance between pairs of sheep engaged in the same activity and pairs with one active and one resting individual. For that purpose, we used models including the fixed-effect variables pair activity, group composition, group size, and their interactions.

Social segregation within mixed-sex groups of >2 individuals ($N = 14$) was estimated by computing the proportion of same-sex nearest neighbours on each snapshot, irrespective of activity, over the 6 h per group. Under the null hypothesis of a random distribution of males and females within groups, the expected proportion of same-sex pairs is $P_e = (N/2 - 1)/(N - 1)$ where N is group size. The difference (D) between the observed and expected proportions of same-sex pairs was compared to 0, using a one-sample Student's t -test. We then investigated the effect of group activity on D , using a mixed-effect linear model in which group was included as a random factor. Finally, for each activity level, we examined the effect of group size and composition on D , using a model in which group and snapshot as random factors.

Data normality was checked with the Kolmogorov–Smirnov test and homoscedasticity with the Levene test. The angular deviation S was transformed by $S_1 = \ln(S/(81.03 - S))$ and the inter-individual and nearest neighbour distances were log transformed to fulfil the normal distribution hypothesis. When ANOVA showed significant differences, post hoc Tukey tests were used to detect which factor levels differed. Statistical tests were performed with SPSS (version 11.0) and the nlme package of R software.

3. Results

Sheep were noticeably aggregated, as shown by the values for inter-individual distance and nearest neighbour distances, which were much smaller than those predicted by a random uniform distribution of sheep in the arenas (Fig. 2, Table 1). This was true whatever the group size and composition, or the level of activity within the groups.

3.1. Effect of activity level

Mean angular deviation differed according to activity level ($F_{2,2501} = 37.7$, $P < 0.0001$). The distribution of sheep orientations did not differ significantly from a random uniform distribution in half-active groups (sign test: $n_+ = 99$; $n_- = 119$; $P = 0.176$). By contrast, the departure was significant in active ($n_+ = 374$; $n_- = 1785$; $P < 0.0001$) and resting groups ($n_+ = 63$; $n_- = 120$; $P < 0.0001$). For active groups, the best fit between experimental and simulated data was

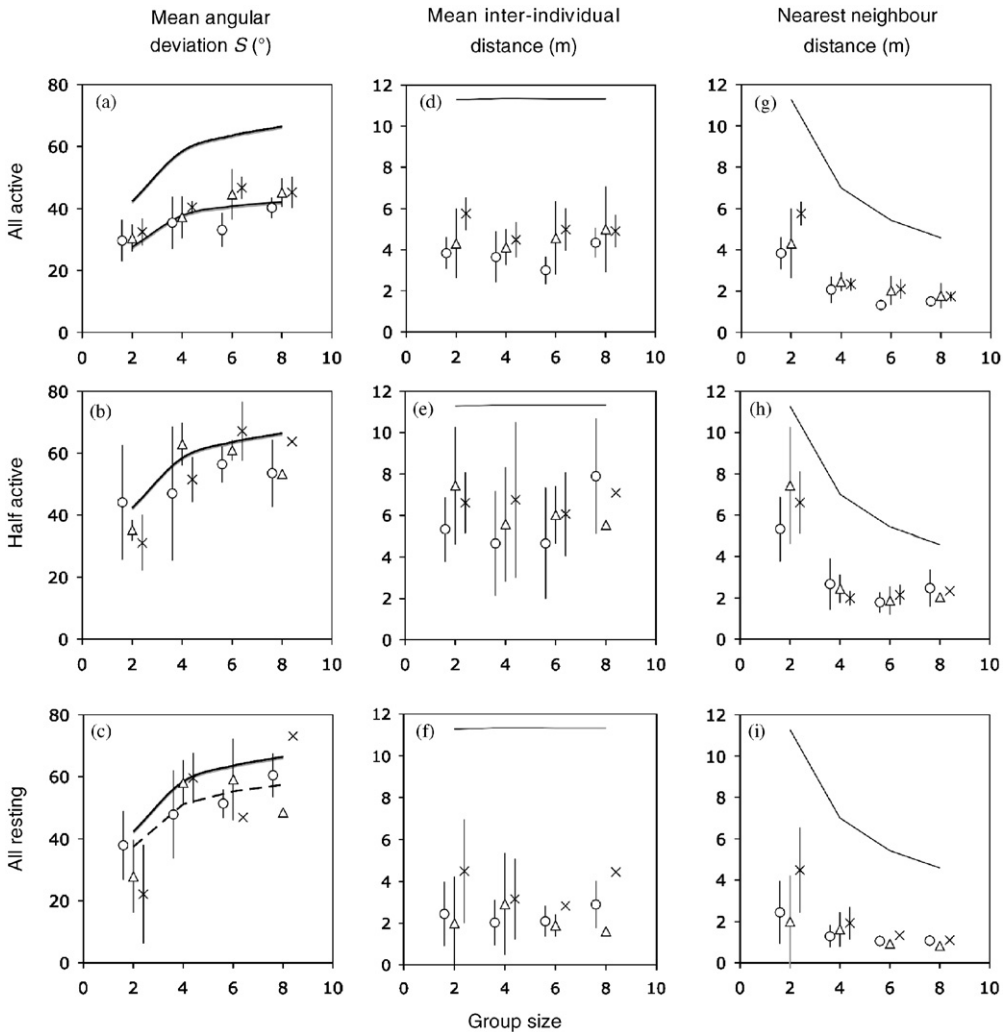


Fig. 2. Mean (\pm CI) angular deviation of animal orientation, inter-individual and nearest neighbour distances within male (open circle), female (open triangle) and mixed-sex groups (cross) according to group size and the level of activity of groups. Black lines indicate the values for random orientation and distances between sheep located randomly within the arena. Grey line and dashed line indicate mean angular deviations for simulated groups, from which individual orientations were extracted using a von Mises distribution with, respectively, $\kappa = 1.85$ and $\kappa = 0.89$ (see Section 2).

obtained with a von Mises distribution ($\kappa = 1.85$), i.e., an unimodal and symmetric distribution for which 91% of orientations are within 180° . For resting groups, the best fit was obtained with a von Mises distribution ($\kappa = 0.89$), for which only 75% of orientations are within 180° .

Activity level also influenced the mean inter-individual distance ($F_{2,2502} = 63.4$, $P < 0.0001$). Sheep were further apart in half-active groups than in active or resting groups (both $P < 0.001$), and closer together when resting than active ($P < 0.0001$). The same effect of activity level was found on the nearest neighbour distance ($F_{2,2502} = 39.3$, $P < 0.0001$, Tukey tests: all $P < 0.0001$).

Table 1

Results of linear models analysing the effects of group composition (male, female or mixed-sex), group size (2, 4, 6 or 8) and their interaction on mean angular deviation, mean inter-individual and nearest neighbour distances in active, half-active and resting groups

Factor	<i>d.f.</i>		Mean angular distance ^a (°)		Inter-individual distance (m)		Nearest neighbour distance (m)	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
All active								
Size	1	17	0.04	0.84	2.16	0.16	19.34	0.001
Composition	2	34	0.4	0.64	2.94	0.066	3.64	0.037
Size × composition	2	34	1.64	0.2	0.56	0.57	0.96	0.39
Half active								
Size	1	16	0.1	0.8	0.18	0.67	12.56	0.003
Composition	2	25	1.37	0.27	0.89	0.42	0.77	0.47
Size × composition	2	25	1.2	0.32	0.23	0.8	0.54	0.59
All resting								
Size	1	17	1.31	0.27	0.69	0.42	2.83	0.11
Composition	2	20	1.38	0.27	3.57	0.047	6.23	0.008
Size × composition	2	20	1.65	0.22	0.33	0.72	2.17	0.14

^a Analysis was performed by using $S' = S(\text{observed}) - S(\text{simulated})$ where $S(\text{simulated})$ was computed from von Mises distribution of orientations with $\kappa = 1.85$ and $\kappa = 0.89$ in active and resting groups, respectively, and from uniform circular distribution of orientations in half-active groups.

3.2. Effect of group size and composition

Whatever the activity level and group composition, group size did not affect significantly the degree of group polarisation (Fig. 2a–c), and mean inter-individual distance (Fig. 2d–f) whereas nearest neighbour distance declined as group size increased (Fig. 2g–i, and Table 1).

No significant effects of group composition were found on the degree of polarisation (Table 1). In half-active groups, inter-individual distance was the same whatever the group composition (Fig. 2e and h, Table 1). By contrast when all sheep were active or when all were resting, mixed-sex groups tended to be more spread out than single-sex groups (Fig. 2d, f, g, and i and Table 1). When all sheep were active, we also found that male groups were more closely packed together, with nearest neighbours closer than in female groups (both $P < 0.001$, Fig. 2d and g).

3.3. Mean inter-individual distance in half-active groups

In accordance with the results previously obtained, we found no significant effect of group size ($F_{1,11} = 2.2$, $P = 0.16$) on mean inter-individual distance in half-active groups, when simultaneously analysing the effects of group size, group composition and pair activity (all-active, half-active, and all-resting pairs). However, a significant interaction between group composition and pair activity was detected ($F_{4,215} = 3.3$, $P = 0.01$). Thus we considered male, female and mixed-sex groups separately (Table 2). We found that mean inter-individual distance varied significantly with pair activity whatever group composition (male groups: $F_{2,47} = 3.19$, $P = 0.05$; female groups: $F_{2,110} = 55.4$, $P < 0.001$; mixed-sex groups: $F_{2,58} = 29.9$, $P < 0.001$) and that it was significantly greater in half active than in active or resting pairs in female and mixed-sex groups (Tukey tests, female groups: $P < 0.03$; mixed-sex groups: $P < 0.01$; Table 2).

Table 2

Median (percentiles 25–75) inter-individual distances between pairs of active, half-active and resting sheep within half-active male, female and mixed-sex groups

Activity pairs	Male groups	Female groups	Mixed-sex groups
Active–active	4 (2–8)	4 (3–8)	3 (2–5)
Active–resting	5 (3–8)	7 (4–9)	6 (5–9)
Resting–resting	3 (2–5)	2 (2–4)	1 (1–4)

3.4. Segregation between male and female within mixed-sex groups

Within mixed-sex groups of 4, 6, and 8 individuals, nearest neighbours of the same sex were found more frequently than would be expected from a random distribution ($t_{13} = -7.1$, $P < 0.0001$, Table 3). This within-group social segregation did not vary significantly with the group activity level ($F_{2,15} = 3.01$, $P = 0.08$). By contrast, it became less marked as group size increased for active or half-active groups (active: $F_{1,12} = 6$, $P < 0.03$; half-active: $F_{1,8} = 26$, $P = 0.001$). Males were also more likely to be nearest neighbours of same-sex peers than were females in these groups (active: $F_{1,479} = 42.7$, $P < 0.0001$; half-active: $F_{1,30} = 7$, $P = 0.01$; Table 3). Furthermore, the nearest neighbour distance between same-sex sheep was smaller than those between opposite-sex sheep within active and resting groups (respectively, $F_{5,7956} = 3.36$, $P = 0.005$ and $F_{5,453} = 4.7$, $P < 0.001$), though not within half-active groups (Fig. 3).

4. Discussion

The present study shows that activity level is a major component affecting group cohesion in sheep. Merino sheep were closest together when in resting groups, as reported for Thomson's gazelles (*Gazella thomsonii*; Walther, 1977), cows (*Bos taurus*; Shiyomi and Tsuiki, 1999) and both domestic and wild sheep (Arnold and Pahl, 1974; Le Pendu et al., 1996; Blanc et al., 1999). Moreover resting groups remained slightly but significantly polarised.

When active, merino sheep also maintained short inter-individual distances although slightly more distant than when resting, likely because of imperfect synchrony of movement, together

Table 3

Mean (\pm S.E.) differences between observed and expected frequencies of same-sex pairs of nearest neighbours, within mixed-sex groups of 4, 6, and 8 sheep, according to the level of activity

Nearest neighbours	Group size		
	4	6	8
All active			
Male–male	0.18 \pm 0.01	0.18 \pm 0.01	0.07 \pm 0.01
Female–female	0.11 \pm 0.01	0.12 \pm 0.01	0.03 \pm 0.01
Half active			
Male–male	0.31 \pm 0.02	0.24 \pm 0.03	0.04 \pm 0.07
Female–female	0.25 \pm 0.03	0.07 \pm 0.05	-0.01 \pm 0.08
All resting			
Male–male	0.13 \pm 0.05	0.05 \pm 0.08	0.16 \pm 0
Female–female	0.13 \pm 0.09	-0.03 \pm 0.17	0.16 \pm 0

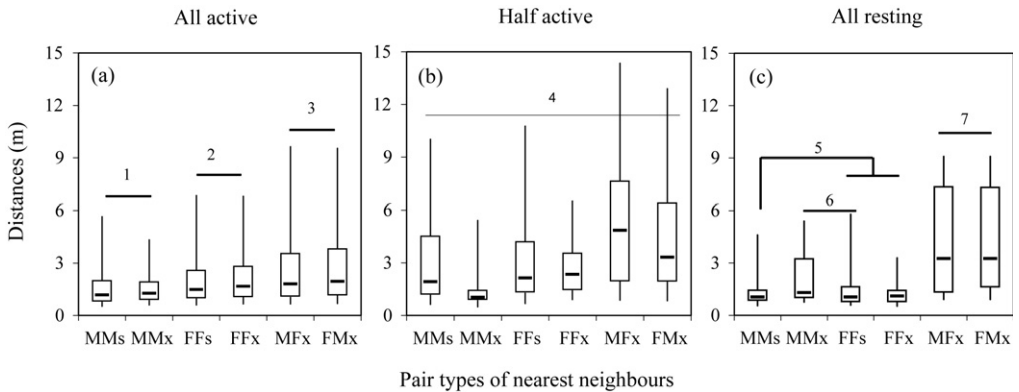


Fig. 3. Distances to nearest neighbours (M: males, F: females) within single-sex (s) and mixed-sex (x) groups where sheep were (a) all-active, (b) half-active, and (c) all-resting. Horizontal lines indicate homogeneous subsets, following Tukey's test: (1) $P = 1.00$; (2) $P = 1.00$; (3) $P = 1.00$; (4) $P = 0.29$; (5) $P = 0.97$; (6) $P = 0.19$; (7) $P = 1.00$.

with stochastic changes in direction, for instance related to the search for food items. When compared to resting groups, active groups were more polarised, suggesting that movement contributes strongly to alignment and social cohesion. Group polarisation may have resulted from (1) a tendency for individuals to align with neighbours, i.e., to adopt a parallel position, or (2) a tendency to approach neighbours as a result of social attraction, requiring individuals to move in the direction of the target sheep, or to keep the target sheep within their visual field. Under assumption (2), alignment will simply be a by-product of combined attraction and movement and may easily explain the differences between resting and active groups. Mathematical models allowed exploring both scenarios and their implications at larger scales (see Parrish et al., 2002 for review) and yet experimental quantifications are still needed to characterise relationships between individual-level behaviours and group-level patterns.

Half-active groups of merino sheep were more spread out than either all-active or all-inactive groups, and showed a degree of polarisation equivalent to that expected from a random uniform distribution. Grazing sheep need to move to find forage, which will inevitably increase the distance and reduce the degree of alignment between them and their resting peers.

In ungulates, both grazing and resting activities last over rather long periods, and half active level corresponds to short transient phases between collective grazing and resting periods (see Gautrais et al., in press). Nonetheless the half-active phase remains a critical time during which group cohesion is weakened. Conrard (1998) suggested that a lack of activity synchrony should enhance the probability of group splitting. Our spatial measurements on the internal structure of sheep groups confirmed that a low degree of activity synchrony makes the groups less cohesive, even if group splitting was not observed in our experiment. The high gregariousness of merino sheep (Arnold, 1985), the homogeneity of the pastures and the limits imposed by fences may explain why half-active groups did not split. It is also likely that if active sheep were able to go further away from resting peers, increasing distances between them would have stimulated the resting sheep to become active, in order to maintain group cohesion. In the wild additional factors such as the potential attraction of neighbouring groups and habitat heterogeneity (e.g., patchiness of resources or disruption of visual contact) may counteract the attraction of other group members and lead to group splitting. However, Turner et al. (2005) showed that female buffalo (*Syncerus caffer*) might stay associated even when part of them was feeding while the other part

was resting. Similarly, Villerette et al. (2006) did not find any effect of activity asynchrony on group splitting probability in fallow deer (*Dama dama*), suggesting that motivation is important in determining whether animals stay together (Le Pendu et al., 1996; Pérez-Barbería et al., 2005; Michelena et al., 2005). The present study confirms that social attraction is one major component of group cohesion.

In the particular case of dimorphic ungulates, Conradt (1998) and Ruckstuhl (1998, 1999) predict that individuals would incur higher costs to synchronize their activity in mixed-sex than in single-sex groups because the duration of foraging and ruminating bouts differs between males and females. As a consequence, single-sex groups are expected to be more stable and frequent than mixed-sex groups. However, the predictions that activity budgets of males and females would differ and that mixed-sex groups would therefore be less synchronized were not verified in the experimental conditions described here (Michelena et al., 2006). The present study demonstrates that even when all individuals are engaged in the same activity, mixed-sex groups were slightly more spread out, likely due to smaller intra- than inter-sex nearest neighbour distances. This agrees with previous results showing higher intra-sex attraction in both merino and Soay sheep (Michelena et al., 2004, 2005; Pérez-Barbería et al., 2005). The fact that the level of activity synchrony did not affect the degree of social segregation within the mixed-sex groups, suggests that the high inter-individual attraction in merinos makes group splitting unlikely in absence of habitat heterogeneity in resource distribution or disruption of visual contact (see also Arnold, 1985).

In our experiment, the spread of the group was not affected by group size, leading to greater closeness among group members as group size increased, in both active and resting groups, as already observed in grazing mountain goats (*Oreamnos americanus*, Risenhoover and Bailey, 1985), African buffalos (Prins, 1989), isards (*Rupicapra pyrenaica*, Richard and Pépin, 1990) and feral goats (*Capra hircus*, Calhim et al., 2006). Warburton and Lazarus (1991) obtained such an effect when simulating the movement of individuals inside groups. One basic hypothesis in their model is that individuals approach their nearest neighbours when too far, and avoid them when under a threshold of proximity. In small groups all individuals hold a peripheral position and can freely move away from a neighbour located at a too small distance. By contrast, in large groups, individuals located at the centre are entirely surrounded and cannot avoid neighbours without simultaneously approaching another one. These physical constraints in largest groups can explain the shortening of mean nearest neighbour distance.

Further experiments are needed in order to examine whether the rules of group cohesion we evidenced at a small scale are involved at a larger scale in the pattern structuring of large groups. Arnold and Maller (1985) suggested that beyond a critical size, the cohesion of the group as a whole likely decreases. These authors assumed that sheep only take a few neighbours into account, which would promote local polarisation and aggregation but also the formation of subgroups when groups become large. If confirmed, such a critical size probably can be expected to vary across sheep breeds. Sibbald et al. (2000) have shown that in groups of 10 Scottish Blackface ewes maintained at similar space allowances than in the present study, the mean inter-individual distance were only a little smaller than those corresponding to a random distribution whereas the merinos were always more aggregated. Whether such differences across breeds or species depend on the interaction range of individuals remain to be explored.

5. Conclusion

Our results indicate that activity synchrony enhances group cohesion in group-living animals. In accordance with the 'social affinities' hypothesis, they show, in merino sheep, that mixed-sex

groups are less cohesive than single-sex ones even when all the group members exhibit the same global activity. However, further experiments are needed to fully understand the mechanisms underlying social cohesion and their sensitivity to factors such as group size, space allowance and animal density, and to determine the extent to which social cohesion depends upon differences in the social behaviour of various biological models.

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Animal care and experimental manipulations were applied in conformity with the rules of the French committee for animal experimentation ethic.

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