



Allelomimetic synchronization in Merino sheep

JACQUES GAUTRAIS*, PABLO MICHELENA*, ANGELA SIBBALD†, RICHARD BON* & JEAN-LOUIS DENEUBOURG‡

*Centre de Recherche sur la Cognition Animale, Université Paul Sabatier

†Macaulay Institute, Craigiebuckler, Aberdeen

‡Ecologie Sociale et Systèmes Complexes, Université Libre de Bruxelles

(Received 19 June 2006; initial acceptance 7 February 2007;
final acceptance 9 February 2007; published online ■ ■ ■; MS. number: 9002R3)

Changes between the inactive (resting/ruminating) and active (grazing, walking) states in groups of Merino sheep were studied in the field for different group sizes (two, four, six or eight) of either male or female animals over 6-h periods. The amount of synchrony within groups was high (60–80%) and is attributed to the mutual adjustment of behaviour by group members. To quantify this process, changes in the number of active individuals were fitted by a time homogeneous continuous time Markov chain model. We found that the probability of an individual becoming active increased with the number of active conspecifics in the group and decreased with the number of inactive conspecifics. The reverse effect was found for the probability of becoming inactive. A model of this individual decision-making process is fitted to the data and predictions of the model are shown to account for the synchrony observed within the group. Group synchronization is thus presented as a self-organized dynamic system, where collective oscillations between activity and inactivity arise stochastically from the coupling between individual Markov processes.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: activity synchronization; allelomimetism; continuous time Markov chain; decision-making; Merino sheep; positive feedback; sheep; stochastic process; ungulate

Many studies of group-living animals focus on the functional benefits of finding food and sexual partners, or escaping predators (Krause & Ruxton 2002). However, there have been fewer experimental studies of how individual decision making influences group dynamics (Fernández-Juricic et al. 2006). In gregarious species, activity synchrony between group members is generally considered to be necessary for social cohesion, because the more discrepancy there is between the activities of individuals, the more likely are the groups to split up (Engel & Lamprecht 1997; Conratt & Roper 2005; Focardi & Pechiol 2005). In the case of ruminants, individuals typically alternative between periods of activity (foraging) and inactivity (resting/rumination) and synchrony within groups has been reported (Rook & Penning 1991a; Coté et al.

1997; Michelena et al. 2006), although the degree of synchrony can vary with group composition (Conratt 1998; Ruckstuhl & Neuhaus 2002).

How individual decisions to switch between activity and inactivity influence synchrony at the group level is a central issue in understanding group dynamics. Synchrony can be achieved by two main mechanisms. First, concurrent behaviours can result from individuals responding to environmental cues (van Oort et al. 2005), for example the foraging synchrony that is commonly seen at dusk and dawn (Dudzinsky & Arnold 1979; Mayes & Duncan 1986; Rook & Penning 1991a; but see Maier & White 1998). This mechanism can operate whether the animals are able to see one other, although the synchrony is liable to be short lived (Bon et al. 2005), especially if individuals have different physiological needs (Conratt 1998). Second, synchrony can be produced by social facilitation (Clayton 1978), when individuals match their behaviour to that of other animals in the group. According to Clayton (1978), '... where environmental stimuli only provide gross synchrony, socially facilitated behaviour will provide finer-scale synchrony, and, what is functionally important, greater cohesion of the social group'. In

Correspondence: J. Gautrais, CRCA, UMR 5169, Université Paul Sabatier, 118 route de Narbonne, F-31062 Toulouse cedex 04, France (email: gautrais@cict.fr). A. Sibbald is at the Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, U.K. J.-L. Deneubourg is at the Service d'Ecologie Sociale, CP 231, ULB, Boulevard du Triomphe, 1050 Brussels, Belgium 21.

some species one or two individuals in a group can act as leaders, for example chicks (Roden & Wechsler 1998), heifers (Dumont et al. 2005) and gorillas (Watts 2000; Conradt & Roper 2005). However, in many vertebrates which live in open-membership groups, synchrony is more likely to result from imitation (Wechsler & Brodman 1996; Rajaratnam & Redman 1999) through a process called allelomimeticism (Scott 1956; Deneubourg & Goss 1989), which embodies the case of equally shared, mutual social facilitation (Clayton 1978). Quantifying this process requires detailed information about the behaviour of each member of the group over a significant period of time, during which the environmental conditions remain constant. Unfortunately, such data are still unattainable for wild ungulates, because of the intense monitoring required, and the difficulty of controlling environmental factors, such as the patchiness of food resources or disturbance from biting insects (Maier & White 1998; Palestis & Burger 1998).

In a previous paper (Michelena et al. 2006), we analysed data from an experiment with male, female and mixed-sex groups of Merino sheep grazing freely in small, homogeneous grass plots. We tested a basic assumption of the activity budget hypothesis (Conradt 1998), that sexual segregation can result from a lack of synchrony between the sexes. We showed that pairwise synchrony was indeed higher between animals of the same sex than the opposite sex. Since synchrony between visually isolated groups was no greater than would be expected by chance, there was no evidence that environmental cues were involved. We concluded, therefore, that the activity synchrony observed within the various groups arose from allelomimeticism.

The data set used by Michelena et al. (2006) comprises sequences of activity and inactivity bouts, and their durations, for all individuals in each of the groups. In this paper we have focused on the data for single-sex groups and quantified group dynamics for each sex and group size. Assuming all group members to be the same, we then derived mean behaviour at the individual level. Finally, we present an individual-based model of the system which accounts for the group becoming synchronized.

METHODS

Study Area, Animals and Experimental Set-up

The study took place at the experimental farm of Domaine du Merle (5.74°E and 48.50°N) in the south of France. Data were collected from November 2003 to February 2004. Thirty four Arles Merino horned males and 32 adult oestrous-blocked females, randomly selected from a herd of 66 male and 200 female sheep, were used. All subjects were familiarized with each other in a 1-ha pasture for 5 weeks before the beginning of the experiments.

Groups were composed of two, four, six and eight individuals, all males, all females or with a sex ratio of 1:1. On each day of the experiment, one male, one female and one mixed group, all of the same group size, were allocated to three adjacent, visually isolated arenas (Fig. 1). All combinations of group size and sex ratio were replicated five times, with group sizes observed in random

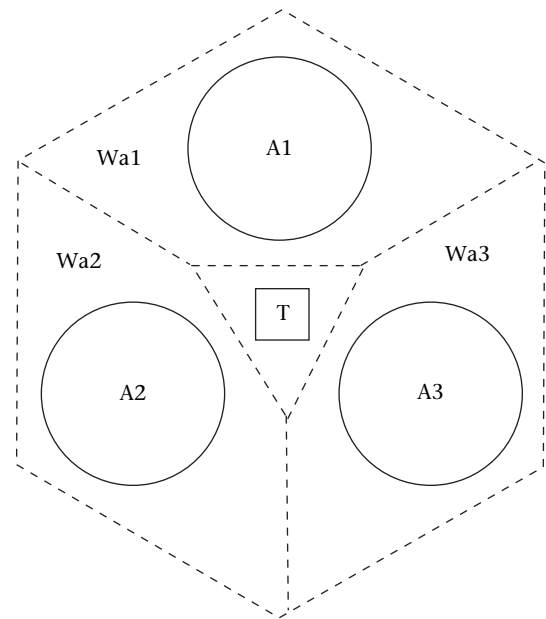


Figure 1. Experimental set-up showing the three arenas (A) delimited by electric fences (plain line), located within waiting areas (Wa) which were enclosed by green polypropylene netting (dotted line), with the observation tower (T) at the centre.

order within each replicate. Individuals were used once in each replicate, and allocated randomly to groups.

Each arena was a fenced circle of 25 m diameter (space allowances 245, 123, 82 and 61 m² per head for group sizes two, four, six and eight, respectively) in a field of native wet Crau meadow, mainly covered by graminoids, clover *Trifolium* sp. and plantain *Plantago lanceolata*. The animals were able to familiarize themselves with their groups from 1000 to 1700 hours in a waiting area of the same pasture, after which they were introduced into the arenas (Fig. 1). Simultaneous video recording of the three arenas took place the following day from 1000 to 1600 hours, using three digital camcorders (Sony DCR-TRV950 E) anchored at the top of a 7-m-high central tower and connected to a PowerBook laptop. The laptop was programmed to take a snapshot from each camcorder every second for 6 h ($n = 3 \times 21\,600$ snapshots/day). This high sampling frequency ensured that every behavioural event was recorded in continuous time. Further details of the experimental procedures can be found in Michelena et al. (2006).

Data Collection

From each of the digital snapshots ($n = 1\,296\,000$), the behaviours of individual animals were visually classified as grazing, standing, walking and lying (resting/ruminating). Unfortunately, one observation day with groups of eight animals was disturbed by hunters, and the corresponding data were consequently discarded. In addition, the behaviour of some sheep was occasionally impossible to identify for short periods ($n = 560$ periods, min duration = 1 s, max duration = 869 s, median = 95 s, 90% < 5 min, 6% of the snapshots), hereafter referred to as

censored time. Only the data for the single-sex groups were used in the analysis.

Variables of the Dynamics

Focusing on behaviour at the individual level, activities were described for each animal using a binary state (active versus inactive), as in previous studies (Coté et al. 1997; Ruckstuhl 1999; Sibbald et al. 2000). The active state comprised grazing, standing and walking. The inactive state comprised only lying (resting/ruminating). At any time, the individual can switch states with a given probability. This probability is expressed as a probability per unit time, that is a switch rate (in /s) that can vary with time. The individual activation rate (the rate at which the individual switches from the inactive to the active state, denoted by λ) is distinguished from the individual inactivation rate (the rate at which the individual switches from the active to the inactive state, denoted by μ). The evolution of individual state is a stochastic process.

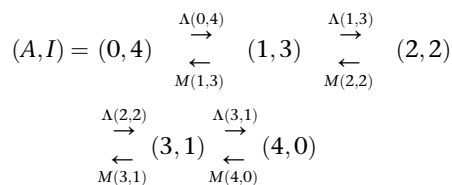
At the group level, the collective state $S(t)$ can be described at time t by the number A of individuals which are active at that time (for a given group size N , the number I of inactive individuals is always $N - A$). Hence, the collective state $S(t)$ can have $N + 1$ values ($0 \leq A \leq N$). Group members were said to be in concurrent states when all individuals were in the same state (either all active, $A = N$, or all inactive, $I = N$, i.e. $A = 0$). We have quantified synchrony using a simple concurrence index (CI), equal to the proportion of observed time for which the group members were in concurrent states.

Since each observation period started at an arbitrary time (1000 hours), the initial condition $S(0)$ could have taken any value of A . $S(t)$ then evolved by ± 1 unit each time an individual switched states, as a result of stochastic individual processes. $S(t)$ can change at any time with a given probability, expressed as a probability per unit time, that is a collective change rate (in /s). The collective activation rate (the rate at which one member becomes active, denoted by Λ) is distinguished from the collective inactivation rate (the rate at which one member becomes inactive, denoted by M).

Hypothesis on the Dynamics

To investigate the effect of mutual facilitation, we quantified how the collective change rates Λ and M were modulated by the current numbers of conspecifics active (A) and inactive (I). We first checked that these rates depended only on A and I , namely that (1) they were not time dependent as long as A and I remained unchanged (a Markov property) and (2) their dependence on A and I was the same throughout the whole observation time (a time homogeneity property). In such a case, the evolution of $S(t)$ forms a time homogeneous continuous time Markov chain (CTMC) and the collective change rates fully describe the dynamics (see Appendix). Accordingly, they are hereafter denoted by $\Lambda(A, I)$ and $M(A, I)$.

For a given group size (e.g. $N = 4$), the process can be depicted as follows:



Note that each group size (N) yields N collective activation rates and N inactivation rates ($2N$ collective change rates).

Quantification of the Dynamics

We quantified the dynamics, at the collective level, separately for each sex. For each group size N , the $2N$ collective change rates $\Lambda(A, I)$ and $M(A, I)$ were estimated from the observed evolution of $S(t)$ over the full observation time T (6 h). Overall, we thus obtained $(2 + 4 + 6 + 8) = 20$ collective activation rates for each sex, corresponding to 20 distinct couples (A, I) , and therefore 20 inactivation rates.

Assuming interchangeable individuals, we then derived the mean behaviour at the individual level. The 40 mean individual switch rates $\lambda(A, I)$ and $\mu(A, I)$ were derived from $\Lambda(A, I)$ and $M(A, I)$, after correction for the number of individuals available to make the switch. The activation rate $\lambda(A, I)$ is corrected for the number of inactive individuals $I = N - A$:

$$\lambda(A, I) = \frac{\Lambda(A, I)}{I}$$

Correspondingly, the inactivation rate is corrected for the number of active individuals A :

$$\mu(A, I) = \frac{M(A, I)}{A}$$

Since $\lambda(0, N)$ is the rate for an individual becoming active when no other animal is already active, it will be termed the spontaneous activation rate and, similarly, $\mu(0, N)$ will be termed the spontaneous inactivation rate.

Finally, we fitted for each sex the 40 mean individual switch rates (combining group sizes) to an analytical expression which accounts for spontaneous switch rates and both the inhibitory and the stimulating effects of conspecifics, for any group size N :

$$\lambda(A, I) = \lambda_0 \beta^{I-1} (1 + \alpha_\lambda A)$$

$$\mu(A, I) = \mu_1 \beta^{A-1} (1 + \alpha_\mu I)$$

The rationale for this expression is developed in the Results section. Since this expression specifies the switch rates for an individual in a group as a function of the states of the other members of the group, it embodies an individual-based model of the synchronization process.

Statistical Procedures

Collective change rates

Collective change rates $\Lambda(A, I)$ and $M(A, I)$ were estimated from $S(t)$, using the package msm (Jackson et al.

2003) and the statistical software R (R Development Core Team 2005). This package fits any CTMC by maximum-likelihood estimates of the change rates (details in Jackson 2005). The procedure handles the presence of censored times, that is when the behaviour of animals was unknown. The five replications were treated as different subjects. Note that this estimation procedure requires the Markov property and the time homogeneity property.

Markov property

To check the Markov property, we considered each collective state (A, I) separately. For a given collective state (A, I) , a sojourn time is the duration between the time at which the group entered the state and the time the group left it, whether this change was due to an activation $(A + 1, I - 1)$ or an inactivation $(A - 1, I + 1)$. Under the Markov property, the sample of all the sojourn times in (A, I) would fit an exponential distribution, indicating a constant probability per unit time to leave (A, I) . We used a Kolmogorov–Smirnov test (Haccou & Meelis 1992) on 24 sets of sojourn times for each sex, since there are $(N + 1)$ possible (A, I) couples per group size N (two, four, six and eight). To test globally for the Markov property from this multiple test, a Holm correction was used to adjust the 24 P values (Holm 1979). The Holm correction is the Bonferroni correction modified to be valid under arbitrary assumptions. Bonferroni corrections yielded the same results.

Time homogeneity

To check for time homogeneity, we tested the effect of time elapsed since the beginning of the observation period (max time 6 h) on the sojourn times. We used an F test on the slope of the regression of the log-transformed sojourn times plotted against their starting times (Haccou & Meelis 1992). The Holm correction was applied separately for males and females, and also with all cases combined, to test for global time homogeneity.

Testing group synchrony

The proportion of time for which the group members were in concurrent states (CI) could have included periods of chance synchrony. Chance synchrony depends on the mean proportion of time that individuals spend active (P_a). Under the null hypothesis of independent behaviours, the probability density function of $S(t)$ would follow a binomial distribution of the parameter P_a , with the number of degrees of freedom equal to the group size (N). Hence, the probability of finding all individuals in concurrent states would be

$$CI_{\text{null}} = \Pr\{N \text{ active}\} + \Pr\{0 \text{ active}\} = P_a^N + (1 - P_a)^N.$$

Experimental values of CI were accordingly compared with the value of CI_{null} computed for a similar P_a .

Model Validation

We first validated the use of a CTMC model for the quantification of collective change rates. We then validated

the individual-based model by comparing the synchrony it predicted against the synchrony observed in the field.

The collective change rates describe the instantaneous probability per unit time that $S(t)$ changes at time t . The actual evolution of $S(t)$ over the observation period T can be summarized as the proportions of time $\Pi_T(A)$, $0 \leq A \leq N$, that the group spent in each of the possible collective states A . Note that $CI = \Pi_T(0) + \Pi_T(N)$ and is a convenient way to approximate $\Pi_T(A)$, $0 \leq A \leq N$. For an infinite observed time T , the collective change rates $\Lambda(A, I)$ and $M(A, I)$ fully determine $\Pi_T(A)$, i.e. $\Pi_T(A) \xrightarrow{T \rightarrow \infty} \Pi^*(A)$, where $\Pi^*(A)$ is the stationary distribution (see Appendix). For a finite observed time T , $\Pi_T(A)$ can also be predicted from the collective change rates, but taking into account the initial state. To test the relevance of using a CTMC model, we thus compared the distributions of time spent in each collective state computed from the experimental data $\bar{\Pi}_T(A)$ with $\Pi_T(A)$ and $\Pi^*(A)$. $\Pi_T(A)$ was computed by numerical integration, with the procedure totlos provided by the package msm, using the estimated collective change rates, the observed finite time T and the initial state $(A = 0, N)$. $\Pi^*(A)$ was derived analytically (see Appendix).

To compare the amount of synchrony predicted by the individual-based model with the amount of synchrony observed experimentally, we built a statistical test to test the hypothesis that the experimental values of the CI could be accounted for by the model. The mean and 95% confidence interval of CI under the model hypothesis were estimated using 10 000 Monte-Carlo simulations for each combination of group size and sex, starting with a random number of active individuals. We concluded to a good agreement of the model with the data when the experimental values of CI fell within the 95% confidence interval. Simulations were performed in continuous time (not using time steps) using a dedicated R program.

RESULTS

Activity Synchrony

The mean proportion of time that sheep spent active (P_a) ranged from 60% to 80% over all groups. The animals were in concurrent states most of the time and the time needed by the whole group to shift from concurrent activity to concurrent inactivity (or back) tended to be short (Fig. 2). CIs were higher than those predicted by the null hypothesis of independent behaviours, although they decreased slightly as group size increased (Fig. 3). CIs tended to decrease less with group size in males than in females, which is consistent with the higher pairwise index of synchrony for males reported by Michelena et al. (2006).

Time Homogeneity and Markovian Property

The hypothesis of time homogeneity of sojourn times was rejected in eight cases out of 48 (four in males and four in females). After the Holm correction, only one case appeared to be time sensitive, namely when females in groups of eight were all active (adjusted- $P = 0.016$) (see Fig. 2). The hypothesis that sojourn times had

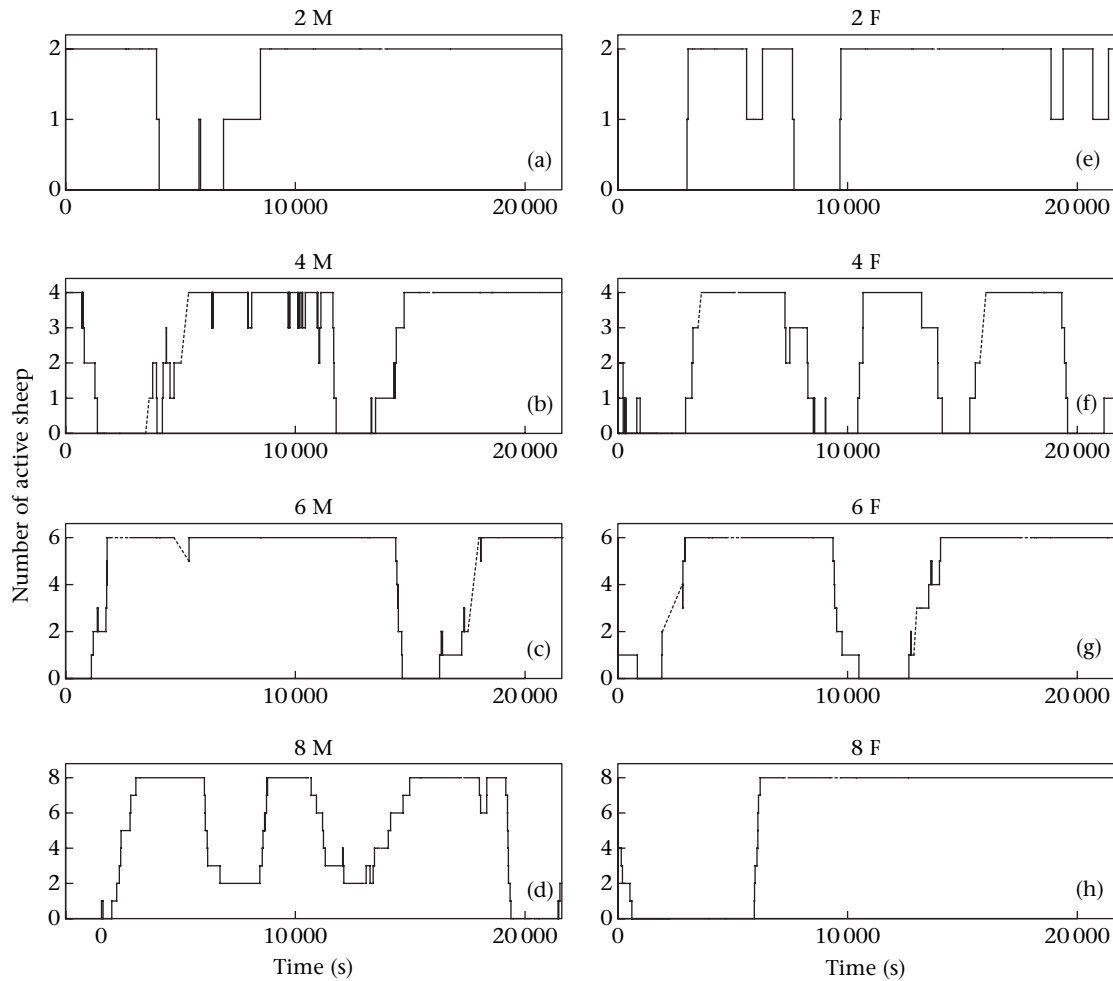


Figure 2. Examples of the number of active individuals (y -axis) in groups of two, four, six or eight male (M; a–d) or female (F; e–h) sheep, plotted at 1-s intervals (x -axis). Dotted lines indicate periods during which behaviour could not be identified.

Markovian properties was rejected in 12 cases in male and eight in female groups. After the Holm correction, however, only four cases in males ($N = 4$, $A = 1$, $\chi_{51}^2 = 0.42$; $N = 4$, $A = 3$, $\chi_{43}^2 = 0.32$; $N = 6$, $A = 0$, $\chi_{27}^2 = 0.44$; $N = 6$, $A = 5$, $\chi_{50}^2 = 0.33$, $\text{adj-}P < 0.01$ in all cases) and one case in females ($N = 6$, $A = 5$, $\chi_{31}^2 = 0.35$, $\text{adj-}P = 0.02$) appeared skewed towards shorter sojourn times, as evident from the negative values returned by the Barlow test applied to each (Haccou & Meelis 1992).

Collective Change Rates

The collective change rates $\Lambda(A, I)$ and $M(A, I)$ were estimated by CTMC analysis for each combination of group size and sex. To test for the robustness of these estimates, the distributions $\bar{\Pi}_T(A)$ of the relative time spent by the groups in each collective state A (0, 1, 2, ..., N active sheep) were then compared with the distributions $\Pi_T(A)$ and $\Pi^*(A)$ predicted by the collective change rates (Fig. 4). A good agreement was found between the experimental values and the stationary distribution, especially in males. The fitted model tends, however, to predict slightly too much time with the animals all active

($A = N$) and correspondingly too little time with the animals all inactive ($A = 0$), especially in female and larger groups. Taking into account the finite time of observation, however, the two predicted distributions $\bar{\Pi}_T(A)$ starting with all sheep active or inactive can be regarded as the limits of a confidence interval around the stationary distribution $\Pi^*(A)$. Figure 4 shows that the observed values for all combinations of group size and sex fall within the confidence limits, confirming the good agreement between predicted and experimental data. Consequently, estimates of mean individual switch rates $\lambda(A, I)$ and $\mu(A, I)$ could be confidently derived from corresponding estimates of $\Lambda(A, I)$ and $M(A, I)$.

Individual Switch Rates

The individual activation rate $\lambda(A, I)$ increased sharply as the number of sheep already active increased (Fig. 5), a clear indication of imitation. For example, in groups of eight males, the activation rate for the last individual becoming active was about 20 times higher than that of the first one. Inactivation rates $\mu(A, I)$ increased by the same order of magnitude in relation to the number of

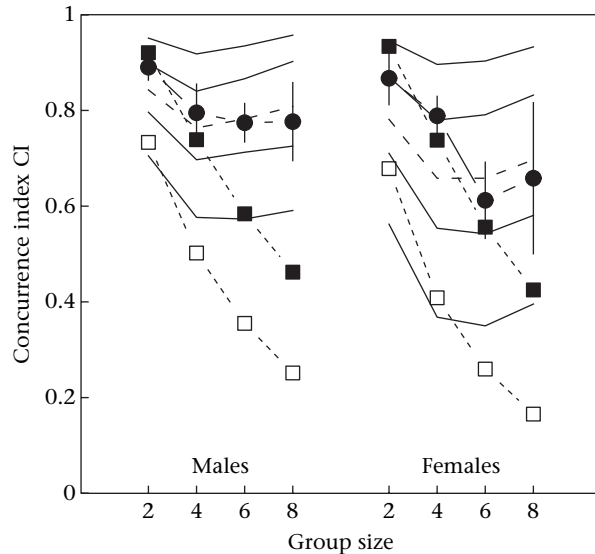


Figure 3. Expected CI for groups of two, four, six or eight male or female sheep (●: mean \pm SE), under the hypothesis of independent behaviours using estimated values for spontaneous switch rates (□: mean) or with all individuals initially active (■: upper limit of the 95% confidence interval), and expected CI over a 6-h period under the individual-based model hypothesis (bold dotted lines: mean values, plain lines: first and third quartiles, bold lines: 95% confidence interval).

conspecifics already inactive (Fig. 5). These effects appeared weaker in females than in males. In addition, we found that for a given number of individuals to imitate (i.e. already in the opposite state), switch rates decreased as group size increased. For example, the second individual becoming active has a lower probability of doing so in groups of two than in groups of eight. This was true in particular for spontaneous switch rates $\lambda(0, N)$ and $\mu(0, N)$ (Fig. 6), where there were no conspecifics to imitate. Overall, this means that activation rates were enhanced by the number of individuals already active and inhibited by the number of individuals still inactive, with the reverse true for inactivation rates.

Individual-based Model

This experimental quantification yielded for each sex a set of 40 mean individual switch rates $\lambda(A, I)$ and $\mu(A, I)$, each of which depends on the group size and combines both the enhancing and inhibiting effects mentioned above. To disentangle these two effects, we fitted an analytical expression which accounts separately for each of them, and is valid whatever the group size. As it involves only the number of active and inactive conspecifics which modulate a basic spontaneous switch rate, this expression constitutes an individual-based rationale for the decision-making process.

First, the inhibitory effect was fitted from the spontaneous rates (for which the stimulating effect does not operate). Assuming that spontaneous switches are inhibited to the same extent by all visible conspecifics in

the same state ($N - 1$), we considered a simple inhibitory proportional hazard model:

$$\begin{aligned} \lambda(0, N) &= \lambda_0 \beta^{N-1} \\ \mu(N, 0) &= \mu_1 \beta^{N-1} \end{aligned} \quad \text{where } \beta < 1.$$

$\lambda_0 = \lambda(0, 1)$ and $\mu_1 = \mu(1, 0)$ extrapolate spontaneous switch rates to the case of an animal in a group but behaving independently.

To estimate β , we regressed each of the four data sets of log-transformed spontaneous rates $\lambda(0, N)$ and $\mu(N, 0)$, for activation and inactivation in males and females, against group size N . The slopes were all close to 0.8, with largely overlapping confidence intervals (males, activation: 0.75–0.93, inactivation: 0.67–0.89; females, activation: 0.60–0.92, inactivation: 0.78–0.85). The closeness of the four values, obtained independently, shows the relevance of this simple model. Consequently, for the sake of simplicity, we set $\beta = 0.8$ in all cases (fit shown in Fig. 6). The intercepts of the four regressions were

$$\begin{array}{ll} \text{Males} & \lambda_0 = 9.43 \times 10^{-4}/s \quad \mu_1 = 1.77 \times 10^{-4}/s \\ \text{Females} & \lambda_0 = 4.88 \times 10^{-4}/s \quad \mu_1 = 1.23 \times 10^{-4}/s. \end{array}$$

Once the spontaneous switch rates and the inhibitory effect of conspecifics in the same state had been established, the stimulating effect of conspecifics in the other state could be fitted, assuming a simple linear function of their number:

$$\begin{aligned} \lambda(A, I) &= \lambda_0 \beta^{I-1} (1 + \alpha_\lambda A) \\ \mu(A, I) &= \mu_1 \beta^{A-1} (1 + \alpha_\mu I) \end{aligned} \quad \text{where } \alpha_* > 0.$$

The two values α_λ and α_μ were estimated for each sex by linearly regressing $\lambda(A, I)/\lambda_0 \beta^{I-1} - 1$ against A (and correspondingly $\mu(A, I)$ against I), with the intercept forced to 0, and heteroscedasticity corrected by weighting by the inverse of the confidence interval for $\lambda(A, I)$ (and correspondingly $\mu(A, I)$). We obtained

$$\begin{array}{ll} \text{Males} & \alpha_\lambda = 0.49 \quad \alpha_\mu = 3.42 \\ \text{Females} & \alpha_\lambda = 0.33 \quad \alpha_\mu = 1.83 \end{array}$$

The normality of the residuals was verified by Shapiro tests, testing the four data sets (α_λ and α_μ for males and females) both separately and together (all $P > 0.4$).

Finally, to evaluate the overall error introduced by this two-step regression, we compared the rates computed from the fitted analytical expression with the experimental ones, combining all group sizes and sexes. The model fitted the experimental switch rates fairly well (Fig. 5, linear regression of analytical values against observed values with zero intercept: slope = 1.02 ± 0.01 , $R^2 = 0.99$, log-transformed values).

Model Validation

This individual-based model was validated by a quantitative comparison between the predicted values of the CI and the experimental values.

The predicted values of CI were computed from Monte-Carlo simulations reproducing the experimental conditions (group size, sex, and observed time). A typical

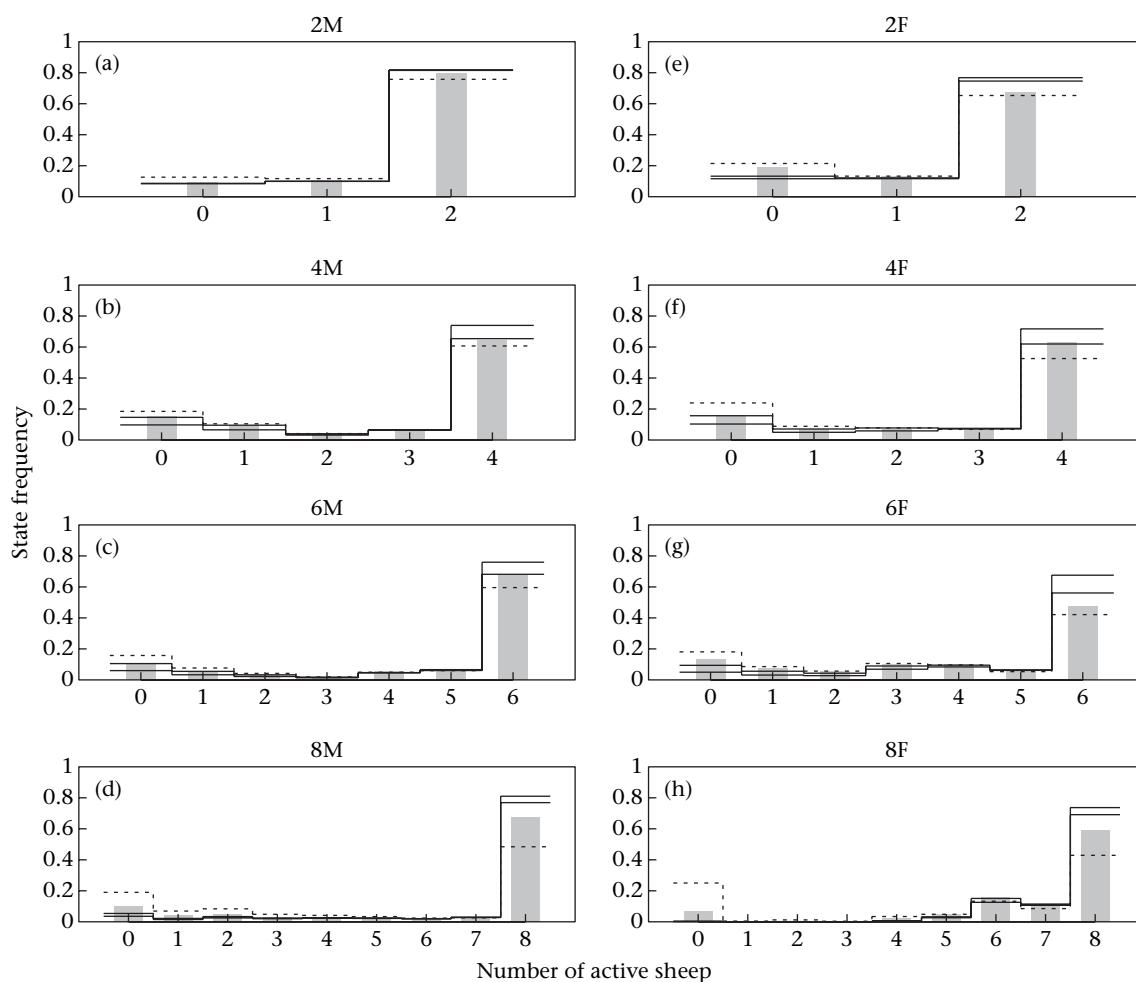


Figure 4. Distributions of the relative time (y -axis) that the experimental groups spent with A individuals active (x -axis), for group sizes of two, four, six or eight males (M; a–d) or females (F; e–h) (grey bars), with corresponding distributions computed from the estimated transition rates, predictions for infinite time (plain lines), over 6 h starting with all individuals active (bold line) and over 6 h starting with all individuals inactive (dotted line).

example of the simulated evolution of the number of active sheep $S(t)$ is illustrated in Fig. 7, contrasted with the evolution that would be obtained with independent sheep (setting $\alpha_* = 0$, $\beta_* = 1$, so that individuals switch at spontaneous rates λ_0 and μ_1). The individual-based model is clearly sufficient to produce the collective oscillations between activity and inactivity concurrence that were observed experimentally.

To test the statistical significance of the model, the mean value, quartiles and 95% confidence intervals of the expected values of CI under the model hypothesis are given in Fig. 3. In all cases, the experimental values fell within the interquartile range, so that the model hypothesis was not rejected ($P > 0.5$). This was true also for the corresponding Pa values (not shown).

Because group synchronization can also be caused by circadian cycles of activity, under the control of nonsocial factors (e.g. simultaneous activation at dawn), we estimated the expected distribution of CI when all sheep started in the same state, either active or inactive, but behaved independently thereafter. The predicted CI reached higher values when starting with all sheep active,

yet only the experimental values for groups of two fell below the upper limit of the predicted confidence interval ($P < 0.05$ for $N > 2$; Fig. 3). This means that an initial synchronization, triggered by a nonsocial signal, could not account for the high levels of synchrony that were observed. This also means that the 6-h observation period was long enough for any influence of initial synchrony to disappear.

DISCUSSION

In this study we quantified the synchrony that emerged in groups of sheep, as a result of individual decisions to switch between activity and inactivity, as a function of the number of animals in each state. The data were obtained by continuously monitoring small groups of different sizes and sexes in small areas, with food evenly distributed and available to all individuals, thus minimizing the possibility that synchronization would be controlled by environmental cues. Sampling individual behaviour every second allowed us to study the process of synchronization in continuous time, at both the individual and group level.

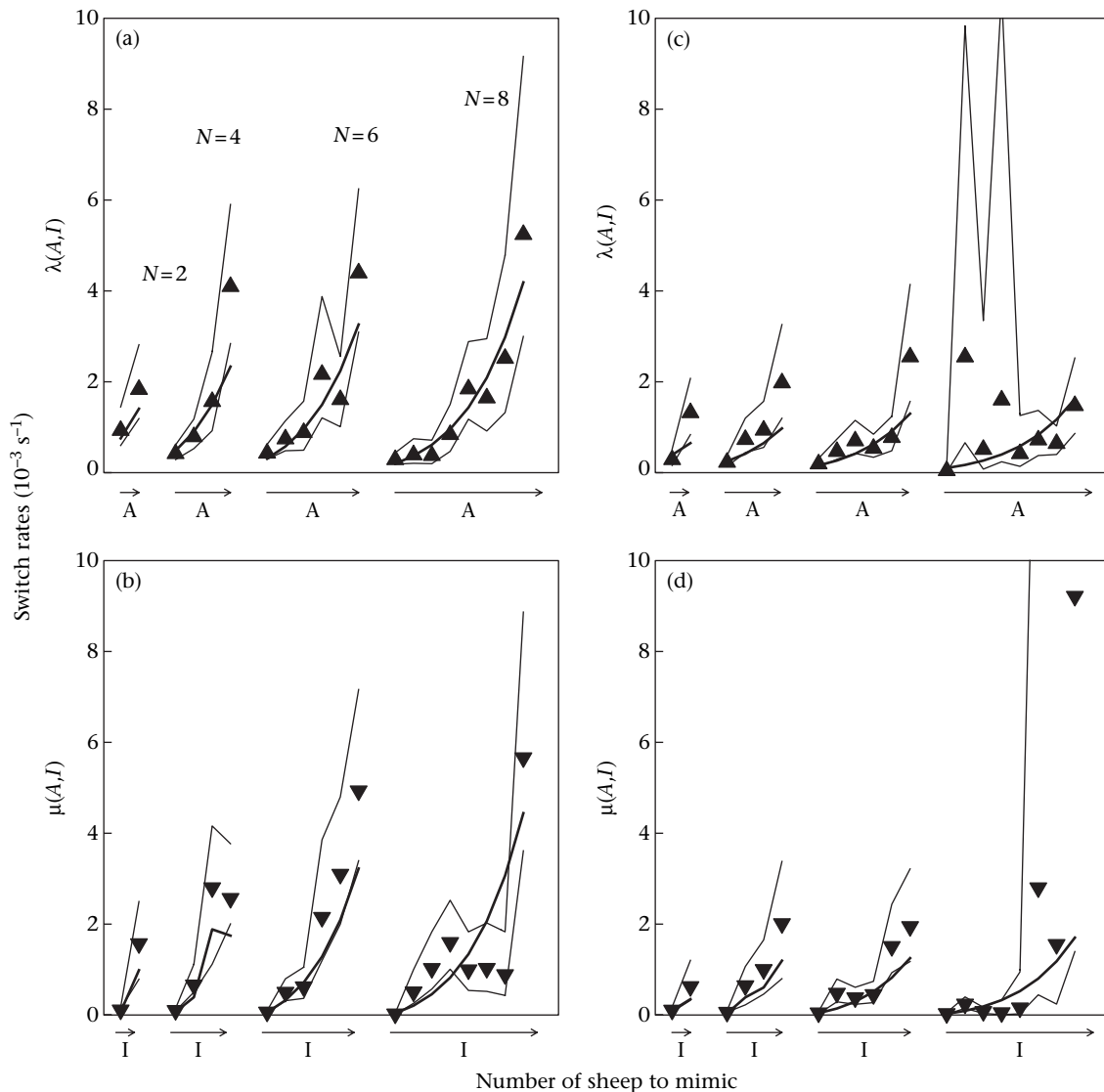


Figure 5. Mean individual activation rates $\lambda(A, I)$ in (a) males and (c) females and inactivation rates $\mu(A, I)$ in (b) males and (d) females, as a function of (a, c) the number of conspecifics in the active state ($A = 0 \dots N - 1$), or (b, d) in the inactive state ($I = 0 \dots N - 1$), for group sizes $N = 2, 4, 6$ and 8 (presented side by side, with number of conspecifics increasing from left to right). Plain lines denote 95% confidence intervals. Bold lines correspond to the fitted model (see text).

The process of switching between activity and inactivity appeared to be intrinsically stochastic. We focused on the synchrony of behavioural states (active and inactive) rather than events, such as interacting or vigilance head-up, described as phasic activities by Rook & Penning (1991a), since social cohesion relies more on individuals being active and inactive at the same time, than on synchronizing their phasic activities. This justified using a CTMC framework for quantifying individual switch rates, whereas synchronization of events would have required other tools, such as a Phase Response Curve, for example Ramirez-Avila et al. (2003) for the synchronization of pulse-like flashings among fireflies and Cole (1991a, b) for short-term activity cycles in ants. This also justified adopting the CI for quantifying synchrony. The CI is not corrected for chance synchronization, but this is

appropriate since social cohesion will depend on all the occasions that synchrony occurs within the group, whether they are due to chance.

Synchronization Process

Obviously, individual animals will switch between activity and inactivity in the absence of conspecifics, and, in the absence of external influences, the rate of switching must be governed by physiological factors such as energy requirements and time taken to process food within the gut. The so-called spontaneous switching, seen when the first animal in a group became active or inactive, is likely to have been induced by such factors. However, the decrease in the spontaneous switch rate with

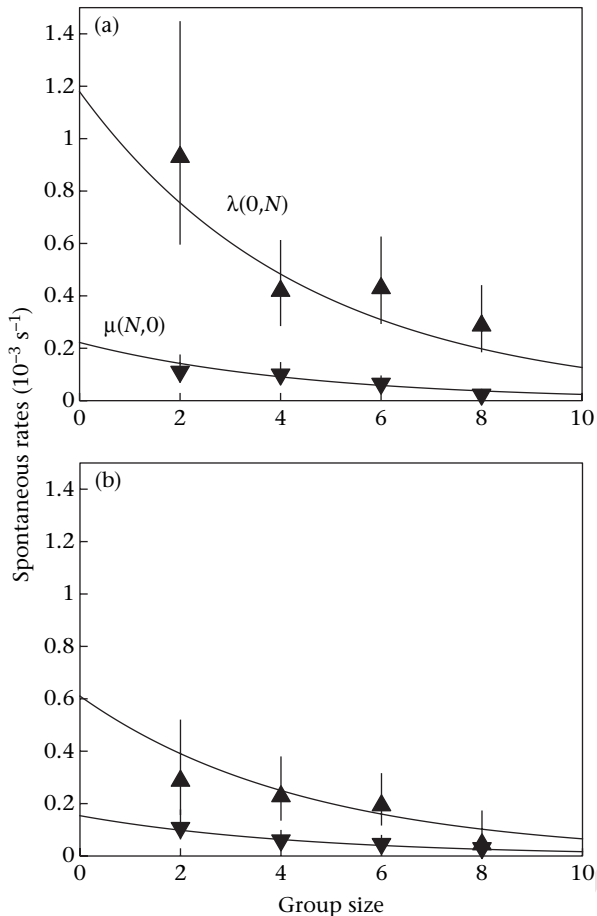


Figure 6. Estimated spontaneous activation $\lambda(0, N)$ and inactivation $\mu(N, 0)$ rates in (a) males and (b) females as a function of group sizes two, four, six and eight. Lines correspond to the fitted model (see text).

increasing group size suggested that switching is slowed down by an increasing number of individuals in the same state. Evidence of a social influence was further confirmed after the first individual had switched, as the probability per unit time of the other group members doing the same increased as a function of the number of individuals in the new state. This social influence was quantified in an individual-based model of the behavioural decision process. The proposed model meets the two basic requirements for self-organization, namely random fluctuations, embodied by spontaneous switches to activity or inactivity, and positive feedback loops, embodied by the allelomimetic enhancement of switch rates. Allelomimetic processes can produce widely different collective behaviours, depending on the parameters and the environmental conditions (Deneubourg & Goss 1989; Camazine et al. 2001). Allelomimetic has been used to explain collective decisions in social insects, such as pheromone-based path selection in ants, where the choice of only one path drives all the workers towards the same food source (Detrain et al. 1999), or the choice of a single aggregation site by cockroaches (Jeanson et al. 2005). Allelomimetic has also been found to be widespread in vertebrates, for

example schooling fishes (Grünbaum et al. 2004). When behaviours are markedly stochastic, allelomimeticism is a highly efficient mechanism for coordinating and synchronizing activities, since mixtures of states are very unstable.

Model Features

Analysis of the data did not lead to rejection of the Markovian hypothesis that switching rates would stay the same if the conditions did not change, in this case the states of the conspecifics. In their study of behavioural synchronization in sheep, in similar experimental conditions to ours, Rook & Penning (1991b) also found that a discrete time Markov model generally performed better than an age-dependent model to describe the time course of behaviours. Similarly, Dutilleul et al. (2000, Fig. 4), also using sheep, reported an apparently monotonous decay of the probability of leaving the current state, consistent with an exponential decay, although they wrongly attributed their survival curves to an age-dependent process. Such Markovian property is at odds with the structuring of activity into well-defined bouts, generally recognized as equivalent to meal and nonmeal periods by intake control theory. The concepts of hunger and satiety imply that the probability of an animal initiating a meal is a function of the duration of the previous nonmeal interval, that is age dependent (Tolkamp et al. 1998). However, the binary classification of behaviour in the present study is likely to mask any effects of this time dependency, since it combines ingestive behaviour with all other activities and all rumination behaviour with resting. Although hunger and satiety effects are likely to be responsible for the occurrence of so-called spontaneous switching, collective switching thereafter appears to be largely driven by allelomimeticism in the short term.

As far as the individual decision-making process is concerned, the model suggests that individuals have to make a trade-off between maintaining the behaviour of conspecifics in the same state and adopting the behaviour of conspecifics in the opposite state. At present, the cognitive processes involved are unclear. The model assumes that all individuals are aware of the states of all conspecifics at any time, which is reasonable for the small groups and arenas used in this study. However, the assumption may not hold for large groups, or groups dispersed over wider areas. Sibbald et al. (2000) found that mean grazing time in small groups of sheep ($n = 10$) increased with increasing space allowance, and suggested that the cause could have been a decrease in synchronization at low space allowances, since lying sheep would not have had to move around in order to stay close to their grazing companions. However, synchronization was quantified as the overall proportion of time spent grazing together, and could simply have been a by-product rather than a cause of the differences in grazing time. An analysis of the switching rates at the beginning and ending of grazing bouts, as described in this paper, would be necessary to determine whether space allowance affected switching rates and hence the process of synchronization.

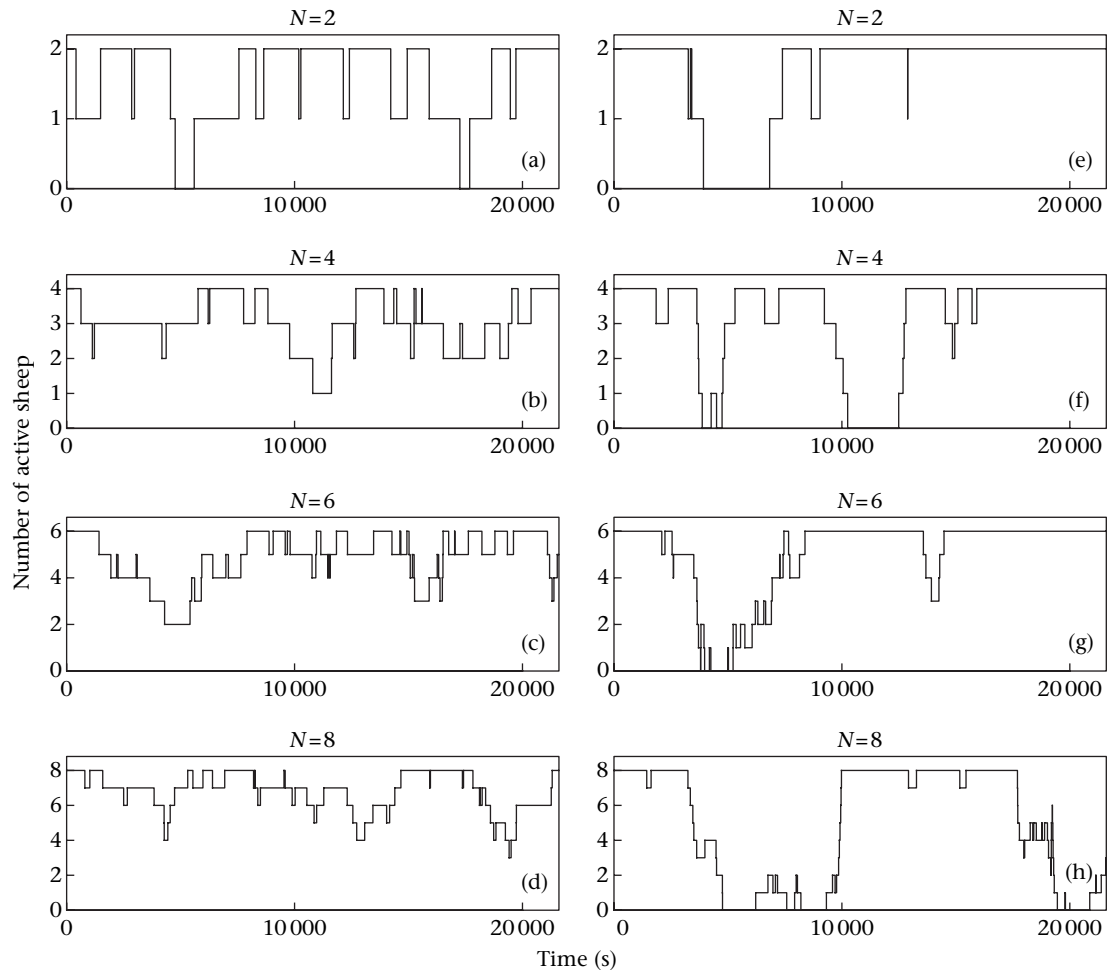


Figure 7. Examples of predicted numbers of active individuals (y -axis) in groups of $N = 2, 4, 6$ or 8 male sheep, evolving in continuous time (x -axis), in the absence (a–d) and in the presence (e–h) of allelomimeticism.

Furthermore, the tendency for animals to remain associated and match their activities with one another may vary with social relationships and between species. In the present study, for instance, males were more likely to mimic other males than females were to mimic other females, leading to greater synchrony amongst the males (Michelena et al. 2006). A previous analysis of these data showed that the mixed-sex groups were the least synchronized (Michelena et al. 2006), suggesting differential mimicking tendencies based on sex. Finally, in both sexes, inactive sheep were more effective in stimulating active sheep to become inactive (α_{ii}) than were active sheep in stimulating inactive sheep to become active (α_{li}), suggesting differential mimicking tendencies based on state. This may indicate that individual responsiveness is under selective pressure, since group cohesion will be helped more by a mechanism which favours the synchronization of inactivity than activity. This is because inactivity occupies a smaller place in an individual's time budget and therefore synchrony has a lower probability of occurring by chance. One would predict that such selective pressure should result in the reverse situation in animals whose time devoted to synchronized activity is shorter than to inactivity.

CONCLUSION

Cohesion is a prerequisite of group living, and activity synchrony is considered to be crucial for social cohesion. The analysis presented in this paper indicates that activity synchrony in grazing sheep arises from an allelomimetic synchronization process. It should be emphasized that the mechanisms involved do not require individuals to have intrinsic rhythms in order to produce an oscillating and collective synchrony. Allelomimetic modulation of switch rates is sufficient to build up oscillations between activity and inactivity concurrences at the group level, from the coupling of Markovian decisions at the individual level. It is the first ethological model, to our knowledge, to show how synchronized oscillations at the group level can emerge from nonoscillating stochastic behaviours at the individual level. These oscillation patterns might be more robust with the addition of other behavioural components known to be widespread in the animal kingdom, such as the delayed responsiveness (refractory period), often seen immediately after a switch in behaviour or as the result of satiety. Such a framework could prove fruitful for quantifying and modelling a large variety of collective oscillating behaviours, when individual stochasticity is high.

Acknowledgments

We thank the staff of the Domaine du Merle for technical assistance and access to facilities. We are also indebted to C. Boléat and V. Michelena who participated in the data collection and S. Noël who further contributed to the video analyses.

Pablo Michelena and Jacques Gautrais were supported by the Leurre project sponsored by the Future and Emerging Technologies programme of the European Community (IST-2001-35506).

Animal care and experimental manipulations were in accordance with the rules of the French committee of animal experimentation ethics.

References

- Bon, R., Deneubourg, J.-L., Gérard, J.-F. & Michelena, P. 2005. Sexual segregation in ungulates: from individual mechanisms to collective patterns. In: *Sexual Segregation in Vertebrates* (Ed. by K. Ruckstuhl & P. Neuhaus), pp. 180–199. Cambridge: Cambridge University Press.
- Camazine, S., Deneubourg, J.-L., Franks, N. R., Sneyd, J., Theraulaz, G. & Bonabeau, E. 2001. *Self-Organization in Biological Systems*. Princeton, New Jersey: Princeton University Press.
- Clayton, D. A. 1978. Socially facilitated behavior. *Quarterly Review of Biology*, **53**, 373–392.
- Cole, B. J. 1991a. Short-term activity cycles in ants: generation of periodicity by worker interaction. *American Naturalist*, **137**, 244–259.
- Cole, B. J. 1991b. Short-term activity cycles in ants: a phase-response curve and phase resetting in worker activity. *Journal of Insect Behavior*, **4**, 129–137.
- Conradt, L. 1998. Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London, Series B*, **265**, 1–5.
- Conradt, L. & Roper, T. J. 2005. Consensus decision making in animals. *Trends in Ecology and Evolution*, **20**, 449–456.
- Coté, S. D., Schaefer, J. A. & Messier, F. 1997. Time budgets and synchrony of activities in muskoxen: the influence of sex, age and season. *Canadian Journal of Zoology*, **75**, 1628–1635.
- Deneubourg, J.-L. & Goss, S. 1989. Collective patterns and decision making. *Ethology, Ecology and Evolution*, **1**, 295–311.
- Detrain, C., Deneubourg, J.-L. & Pasteels, J. 1999. *Information Processing in Social Insects*. Basel: Birkhäuser-Verlag.
- Dudzinsky, M. L. & Arnold, G. W. 1979. Factors influencing the grazing behaviour of sheep in a Mediterranean climate. *Applied Animal Ethology*, **5**, 125–144.
- Dumont, B., Boissy, A., Achard, C., Sibbald, A. M. & Erhard, H. W. 2005. Consistency of animal order in spontaneous group movements allows the measurement of leadership in a group of grazing heifers. *Applied Animal Behaviour Science*, **95**, 55–66.
- Dutilleul, P., Deswysen, A. G., Fisher, V. & Maene, D. 2000. Time-dependent transition probabilities and the assessment of seasonal effects on within-day variations in chewing behaviour of housed sheep. *Applied Animal Behaviour Science*, **68**, 13–37.
- Engel, J. & Lamprecht, J. 1997. Doing what everybody does? A procedure for investigating behavioural synchronization. *Journal of Theoretical Biology*, **185**, 255–262.
- Fernández-Juridic, E., Gilak, N., McDonald, J. C., Pithia, P. & Valcarce, A. 2006. A dynamic method to study the transmission of social foraging information in flocks using robots. *Animal Behaviour*, **71**, 901–911. doi:10.1016/j.anbehav.2005.09.008.
- Focardi, S. & Pecchiol, E. 2005. Social cohesion and foraging decrease with group size in fallow deer (*Dama dama*). *Behavioural Ecology and Sociobiology*, **59**, 84–91. doi:10.1007/s00265-005-0012-0.
- Grünbaum, D., Viscido, S. & Parrish, J. K. 2004. Extracting interactive control algorithms from group dynamics of schooling fish. In: *Lecture Notes in Control and Information Sciences* (Ed. by V. Kumar, N. E. Leonard & A. S. Morse), pp. 103–117. Springer-Verlag.
- Haccou, P. & Meelis, E. 1992. *Statistical Analysis of Behavioural Data. An Approach based on Time-Structured Models*. Oxford: Oxford University Press.
- Holm, S. 1979. A simple sequentially rejective Bonferroni test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.
- Jackson, C.H. 2005. msm: Multi-state Markov and hidden Markov models in continuous time. R package version 0.6. <http://cran.cict.fr/doc/packages/msm.pdf>.
- Jackson, C. H., Sharples, L. D., Thompson, S. G., Duffy, S. W. & Couto, E. 2003. Multistate Markov models for disease progression with classification error. *Journal of the Royal Statistical Society, D*, **52**, 1–17.
- Jeanson, R., Rivault, C., Deneubourg, J.-L., Blanco, S., Fournier, R., Jost, C. & Theraulaz, G. 2005. Self-organized aggregation in cockroaches. *Animal Behaviour*, **69**, 169–180.
- Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford University Press.
- Maier, J. A. K. & White, R. G. 1998. Timing and synchrony of activity in caribou. *Canadian Journal of Zoology*, **76**, 1999–2009.
- Mayer, E. & Duncan, P. 1986. Temporal patterns of feeding behaviour in free-ranging horses. *Behaviour*, **96**, 105–129.
- Michelena, P., Noël, S., Gautrais, J., Gérard, J.-F., Deneubourg, J.-L. & Bon, R. 2006. Sexual dimorphism, activity budget and synchrony in sheep group. *Oecologia*, **148**, 170–180. doi:10.1007/s00442-005-0347-2.
- van Oort, B. E. H., Tyler, N. J. C., Gerkema, M. P., Folkow, L., Blix, A. S. & Stokkan, K.-A. 2005. Circadian organization in reindeer. *Nature*, **438**, 1095–1096.
- Palestis, B. G. & Burger, J. 1998. Evidence for social facilitation of preening in the common tern. *Animal Behaviour*, **56**, 1107–1111.
- R Development Core Team. 2005. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna: Austria. ISBN 3-900051-07-0. <http://www.R-project.org>.
- Rajaratnam, S. M. W. & Redman, J. 1999. Social contact synchronizes free-running activity rhythms of diurnal palm squirrels. *Physiology and Behaviour*, **66**, 21–26.
- Ramirez-Avila, G. M., Guisset, J. L. & Deneubourg, J.-L. 2003. Synchronization in light-controlled oscillators. *Physica*, **182**, 254–273.
- Roden, C. & Wechsler, B. 1998. A comparison of the behaviour of domestic chicks reared with or without a hen in enriched pens. *Applied Animal Behaviour Science*, **55**, 317–326.
- Rook, A. J. & Penning, P. D. 1991a. Synchronisation of eating, ruminating and idling activity by grazing sheep. *Applied Animal Behaviour Science*, **32**, 157–166.
- Rook, A. J. & Penning, P. D. 1991b. Stochastic models of grazing behaviour in sheep. *Applied Animal Behaviour Science*, **32**, 167–177.
- Ross, J. V., Taimre, T. & Pollett, P. K. 2006. On parameter estimation in population models. *Theoretical Population Biology*, **70**, 498–510.
- Ruckstuhl, K. E. 1999. To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour*, **136**, 805–818.
- Ruckstuhl, K. E. & Neuhaus, P. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews*, **77**, 77–96.

Scott, J. P. 1956. The analysis of social organization in animals. *Ecology*, **37**, 213–221.

Sibbald, A. M., Shellard, L. J. F. & Smart, T. S. 2000. Effects of space allowance on the grazing behaviour and spacing of sheep. *Applied Animal Behaviour Science*, **70**, 48–62.

Stirzaker, D. 2005. *Stochastic Processes and Models*. Oxford: Oxford University Press.

Tolkamp, B. J., Allcroft, D. J., Austin, E. J., Nielsen, B. L. & Kyriazakis, I. 1998. Satiety splits feeding behaviour into bouts. *Journal of Theoretical Biology*, **194**, 235–250.

Watts, D. P. 2000. Mountain gorilla habitat use strategies and group movements. In: *On the Move. How and Why Animals Travel in Groups* (Ed. by S. Boinski & P. A. Garber), pp. 351–374. Chicago: University of Chicago Press.

Wechsler, B. & Brodman, N. 1996. The synchronization of nursing bouts in group-housed sows. *Applied Animal Behaviour Science*, **47**, 191–199.

Appendix

Group behaviour can be quantified at time t by the instantaneous probability density function $\Pi(A, t) = (P(A) = \Pr\{S(t) = A\}, A = 0 \dots N)$ of the probabilities $P(A)$ that the group comprises A active animals at time t .

$\Pi(A, t)$ is a function of time because it depends on the initial value $S(0)$. If, for example, the group starts with no active individual: $\Pi(0, 0) = (1, 0, \dots, 0)$, that is $P(0) = 1$ and $P(A > 0) = 0$. As time goes on, this probability density function evolves because transitions to higher values $1 \dots N$ accumulate, so that the probability $P(A > 0)$ of finding some individuals active increases, and the probability $P(0)$ finding the group still in the initial condition declines. Under the null hypothesis that all individuals switch states independently and at the same rate, $\Pi(A, t)$ would tend to the binomial distribution as time goes to infinity. In the short term, however, starting with all the individuals inactive would lead to a higher probability of finding few animals active than when starting with all the individuals active. Because of this sensitivity to initial conditions, an analytical expression for $\Pi(A, t)$ is impossible to formulate and its value at future time t , starting from a given value $S(0)$, is better computed by numerical integration.

If the process is time homogeneous, $\Pi(A, t)$ can be estimated over the observed time T by the relative proportion of time that the group spent with each value of A , $0 \leq A \leq N$ (summing the sojourn times in A) and it has a unique equilibrium value $\Pi^*(A) = \lim_{t \rightarrow \infty} \Pi(A, t)$, to which it will converge whatever the initial conditions: at the limit of infinite time, the impact of the initial

conditions vanishes, so that $\Pi(A, t)$ becomes independent of them. $\Pi(A, t)$ approaches Π^* exponentially with respect to time, and the rate of convergence depends on the set of transition rates. This equilibrium distribution is such that $d\Pi^*(A, t)/dt = 0$, and it can be derived from the master equation governing the evolution of $\Pi(A, t)$. The master equation balances for every value of A , the transitions at time t leading to A (from $A - 1$ and $A + 1$) and the transitions departing from A (to $A - 1$ and $A + 1$) conditionally to the probabilities $P(A)$ of finding the system in the state the transitions depart from:

$$\frac{dP(A)}{dt} = +\text{Transitions to } A - \text{Transitions from } A$$

where

$$\begin{aligned} \text{Transitions to } A &= \lambda_{A-1}P(A-1) + \mu_{A+1}P(A+1) \\ \text{Transitions from } A &= \mu_A P(A) + \lambda_A P(A) \end{aligned}$$

This master equation is known as the forward Chapman–Kolmogorov equations and reads

$$\frac{d\Pi(t)}{dt} = \begin{cases} \frac{dP(0)}{dt} = -(\lambda_0)P(0) + \mu_1 P(1) \\ \frac{dP(A)}{dt} = \lambda_{A-1}P(A-1) - (\lambda_A + \mu_A)P(A) + \mu_{A+1}P(A+1) \\ \frac{dP(N)}{dt} = \lambda_{N-1}P(N-1) - (\mu_N)P(N) \end{cases}$$

At the equilibrium, $dP^*(A, t)/dt = 0 \quad \forall A$. Since Π is a probability density function, we also have: $\sum_{A=0}^N P(A) = 1$. Hence, we can solve recursively and find

$$\Pi^* = \begin{cases} P^*(0) &= \frac{1}{1 + \sum_{A=1}^N S(A)} \\ P^*(A) &= P^*(0) S(A) \\ \text{with } S(A) &= \frac{\prod_{i=0}^{A-1} \lambda_i}{\prod_{i=1}^A \mu_i} \end{cases}$$

Note that in the case of an isolated individual ($N = 1$),

$$\Pi^* = \begin{cases} P^*(0) = \frac{\mu_1}{\lambda_0 + \mu_1} \\ P^*(1) = \frac{\lambda_0}{\lambda_0 + \mu_1} \end{cases}$$

with λ_0 denoting the spontaneous activation rate, μ_1 denoting the spontaneous inactivation rate, $P^*(1)$ denoting the mean proportion of time spent active Pa. Corresponding theoretical CI = $P^*(0) + P^*(1) = 1$, as expected.

Further details about stochastic processes can be found in Stirzaker (2005) and Ross et al. (2006).