# Behavioural synchronization in a multilevel society of feral horses

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**SUMMARY**

Behavioural synchrony among individuals is essential for group-living organisms to maintain their cohesiveness necessary to get information and against predation. It is still largely unknown how synchronization functions in a multilevel society, a nested assemblage of multiple social levels between many individuals. Our aim was to build a model to explain the synchronization of activity in a multilevel society of feral horses. We used multi-agent based models based on four hypotheses: A) independent model: horses do not synchronize, B) anonymous model: horses synchronize with any individual in any unit, C) unit-level social model: horses synchronize only within units and D) herd-level social model: horses synchronize across and within units, but internal synchronization is stronger. We simulated each model 100 times and compared simulations to the empirical data obtained from drone observations. The hypothesis D best supported empirical data. This result suggests that synchronization occurred at an intra- and inter-unit level.

## Introduction

Synchronization of behaviour is essential for animals to maintain a group's functioning (e.g. access to information, decrease in predation). The patterns of synchronous activity have been found in various behaviours of many animals, from Placozoa to humans (Couzin, 2018). The common property of this collective behaviour is that relatively simple interactions among the members of the group can explain a global pattern of behaviour (Couzin and Krause, 2003). For example, a pattern of fission-fusion in some ungulate species could be simply explained by the dynamic tension between the advantages of aggregation and the disagreement among individuals, mainly between female and males, due to the variation in resource demand (Bonenfant et al., 2004; Mooring et al., 2005).

Many studies on synchronization were done on cohesive, single-layered group, either in natural or experimental setup (Bialek et al., 2014; Kastberger et al., 2008; King et al., 2011; Torney et al., 2018). In many social animals, social networks often have a considerable effect on the propagation of behaviour (Centola, 2010; Couzin, 2018; King et al., 2008; Papageorgiou and Farine, 2020; C. Sueur et al., 2011; Sueur and Deneubourg, 2011). Socially central individuals can give greater influence on group behaviour than subordinate individuals (Sueur et al., 2012, 2009). Also, it is widely observed that socially affiliated dyads more intensely synchronize their behaviours (Briard et al., 2015; King et al., 2011). However, most of these studies taking account social network effect were conducted on small cohesive groups (but see Papageorgiou and Farine, 2020) whilst studies with large groups of individuals were based on anonymous mechanisms because of the difficulty in identifying and following all members.

Multilevel societies composed of nested and hierarchical social structures are considered to be among the most complex forms of social organization for animals (Grueter et al., 2020, 2017, 2012). In a multilevel society, the fundamental component is called as a 'unit', and these units gather to form larger groups. It is often reported that the different units also forage and sleep together (Papageorgiou et al., 2019; Swedell and Plummer, 2012). The most famous example of multilevel society is the troop, a third or fourth level social organization, of hamadryas baboons sleeping together in a cliff (Schreier and Swedell, 2009). It is highly likely that synchrony occurs not only among the same units but also in a higher-level of social organization, but studies on their synchronization mechanisms and functions are quite limited (but see Ozogány and Vicsek, 2014).

Multilevel society is characterized by a different association pattern in each social level. Usually, members of a unit stay close together, while the extent of cohesion become smaller as

the social level becomes higher (Grueter et al., 2012; Maeda et al., 2021; Papageorgiou et al., 2019; Qi et al., 2014; Snyder-Mackler et al., 2012). Some studies have found that different units keep an intermediate distance from each other; farther than the inter-individual distance within units (Bowler et al., 2012), but closer than random distribution (Maeda et al., 2021). It is argued that this differentiation of social relationships has evolved to balance the advantages of being a large-group and the disadvantages of resource competition with other units (Moscovice et al., 2020; Rubenstein and Hack, 2004; Cédric Sueur et al., 2011). For example, a study on Asian colobine suggested that harem unit aggregation could reduce a risk of inbreeding and bachelor threat, but being a large group may cause intense competition for food, so their aggregation pattern changes according to the seasonal prevalence of resources (Qi et al., 2014). We assumed that this fission-fusion patterns balancing between units' competition and cooperation could be also applied to the behavioural synchronization. It is unknown but important to investigate whether the mechanisms of the synchronization could be described in a simple model even in such complex society with many individuals for the further understandings of collective feature of animal groups.

New technologies enable more wide ranging and accurate data collection in societies with hundreds of individuals (Charpentier et al., 2021; Inoue et al., 2019; Schroeder et al., 2020). For instance, our use of drones succeed in obtaining positional and behavioural data of more than a hundred of feral horses in Portugal, which formed multilevel society with a two-layered structure with units—a group of individuals which stayed closer than 11.5m more than 70% of the time—and a herd—an aggregation of units (Maeda et al., 2021). In the current study, we further apply this data collection to create a model of behavioural synchronization.

We hypothesize that (1) horses synchronize their behaviour both at an intra- and inter-unit level, and (2) the extent of synchronization in a dyad is correlated to its social relationships. In this current study, we develop different models based on hypotheses ranging from no synchronization between individuals and units to full synchronization, with intermediate mechanisms based on social networks. In this way, we develop a stochastic multi-agent based model where the probability of an individual to change stage (resting versus moving) depends on different hypotheses: (A) Independent: horses do not synchronize and are socially independent. This hypothesis is used as the null model. (B) Anonymous: horses synchronize with any individual in any unit. This hypothesis does not include the importance of stable social relationships in trade-off between group-living advantages and competition. (C) Unit-level social: horses synchronize only within units, not considering the herd-level association and

without advantages of large societies. (D) Herd-level social: horses synchronize across and within units, but internal synchronization is stronger (Figure 1). Hypothesis D could achieve the best balance between the intra and inter-unit level associations. Finally, we compared these models to the empirical data in order to assess which models best explain synchronization in our population of feral horses.

## Method

### (a) Data collection

We conducted observations from June 6th to July 10th, 2018 in Serra D'Arga, Portugal, where approximately 150 feral horses were living without human care (Ringhofer et al., 2017). We used drones (Mavic Pro: DJI, China) to accurately measure distances between all individuals in the observation area of two zones covering approximately 1 $km^2$ each. The flights were performed under clear sky conditions at an altitude of 30–50 m from the ground and we took successive aerial photographs of the horses present at the site in 30-minute intervals from 9:00–18:00 (for more detailed explanation see Maeda et al., 2021). The average duration of each flight was 4 minutes 24 seconds ± 3 minutes 5 seconds.

Orthomosaic imaging was conducted using AgiSoft PhotoScan Professional software. The software connected successive photos and created orthophotographs in the GeoTIFF format under the WGS 84 geographic coordinate system. We first identified all horses from the ground and made an identification sheet for all individuals, recording their physical characteristics such as colour, body shape, and white markings on the face and feet (Fig. 2). All horses in the orthophotographs were identified accordingly. We positioned the heads of the horses and recorded whether they were resting or not. The horses were considered to be resting if they did not move in the successive photos and showed resting posture, i.e., laying down or standing still with their neck parallel to the ground. Otherwise, we considered them to be moving. All locations were stored in shapefile formats. The coordinate system was converted to a rectangular plain WGS 84 / UTM Zone 29N and we then calculated the distances between all pairs of individuals in the same zone. In total, 243 observations were conducted in 20 days and a total of 23,716 data points of individual positions were obtained. A total of 126 non-infant horses (119 adults: 82 females and 37 males, 7 young individuals: 6 females and 1 male) and 19 infants (11 females and 8 males) were successfully identified. They belonged to 23 units (21 harems and 2 AMUs), along with 5 solitary males. We eliminated infants from the subsequent analysis because their position was highly dependent on their mothers. We also eliminated three

solitary males whose availability rate were less than 50%.

**b) Herd social network**

To create a social network, we first decided the threshold distance which defines the association. We created a histogram from the distance data to the shape under the R environment. The bin width was decided based on the method of Wand (1999) using R package 'KernSmooth' (Wand, 2015). As shown in the Figure 2, the distance had two peaks. The bin width was 0.92 m and the two peaks were on the 2nd (0.9–1.8 m) and 55th bin (49.7–50.6 m). The minimum frequency between these two peaks was observed on the 12th bin (10.1–11.0 m). We decided the threshold as the distance between two peaks with the lowest frequency (11.0 m), because it represents the threshold that divides the intra- and inter-unit association (Maeda et al., 2021).

To obtain the social relationships for each dyad $a_{ik}$, networks were generated for each sampling period (i.e., each flight of drones), where edges were scaled to 1 when the inter-individual distance was smaller than 11m (the distance between two peaks with the lowest frequency; Fig. 2), or otherwise scaled to 0. When a pair of individuals were in the same unconnected component of the graph, they were considered to be associated. In the total of all flights of drones, we detected 658 temporarily isolated individuals who had no association with any other individuals. If the distance from the nearest individual was smaller than $p_2$ (the second peak of the histogram), we presumed that they had an association with the nearest neighbour, otherwise we eliminated them from the analysis. 643 out of 658 isolated points were within 50.6 m (the second peak of histogram) from the nearest individual. A social network was created from this co-membership data using the simple ratio index (Cairns and Schwager, 1987). This calculates the probability that two individuals are observed together given that one has been seen, which is widely used in animal social network analysis. The edge weight was normalized so that the sum of $a_{ik}$ ($k=1,2,\ldots, N; k\neq i$) became N.

**c) Synchronization data scoring and calculation of modelling parameters**

*Population synchronization rate:* We scored at each time step (in our case, a scan of 30 minutes) the number N of horses and their identities in each state ($S_r$ for resting and $S_m$ for moving). As explained in (a), resting is standing still or laying down, and moving is the other behaviour, mainly grazing. We only used the observation with more than 90% (21 or more, as

the total number of units was 23) of units were available in the field. We defined a synchronization rate of a dyad as a proportion of the observation when two individuals were in the same activity state, i.e., we scored 1 when two individuals were in a same state (e.g., resting or moving respectively) in an observation and 0 when not, and then calculated its average.

*Individual synchronization/state phase latency:* We defined a synchronization phase $P_{r:m}$ as a 'resting → moving' event as the continuous decrease of resting individuals from the rest from the minimal of resting individuals to the maximal, and a phase $P_{m:r}$ 'moving → resting' event as the opposite. We excluded the increase/decrease from the first observation or to the last observation of the day. We observed 21–23 units in 8 days during July 14$^{th}$–28$^{th}$. One AMU was not observed on 15$^{th}$ and 16$^{th}$, and one harem and one AMU on 28$^{th}$. In total, we found 21 moving → resting events and 18 resting → moving events. We calculated the state phase latency $\Delta T_{01s}$ as the time elapsed between the end of a previous state phase and the beginning of a new one. This phase latency corresponds to the departure latency on an individual to change state in previous works (Bourjade et al., 2009; Sueur et al., 2010, 2009; Sueur and Deneubourg, 2011). $\Delta T_{01r}$ corresponds to the resting phase latency and $\Delta T_{01m}$ to the moving phase latency (Table 1, Figure S1). For explanations of modelling self-organisation and collectives, see also Sueur and Deneubourg (2011).

*Individual refractory period:* Many synchronization processes in animal groups imply a refractory period (Couzin, 2018, 2009). Theoretical studies showed that this period is necessary for animals to not be stuck in a state (Couzin, 2018, 2009). Preliminary works on our model showed that this refractory period is necessary to not observe agents being stuck in a state. According to the observed data, the mean refractory periods for moving was 50 minutes and that for resting is 25 minutes (Figs. S3, S4). We used these values as well as lower and higher values of the refractory period to check the fitness of simulations to the empirical data (see supplementary material and section (d)). We then scored the changing state latency $\Delta T_{j-1,j,s}$ of each horse j changing state s corresponding to the time elapsed between the state change of the individual j - 1 (i.e., the previous individual changing state s1 to s2, and the state change of the horse j (changing also from s1 to s2). The expected value of $\Delta T_{j-1,j,m}$ and $\Delta T_{j-1,j,}$ were 2.3 and 1.3 minutes respectively (Table 1, Figure S2).

**(d) The models**

Our aims were to understand the synchronization process of horses between two states—moving and resting—throughout the day. In order to do this, we created a model in

which different hypotheses were tested.

According to the preliminary analysis, the horses' resting/moving was independent of the time of day (see Supplementary Appendix for detailed explanation), so we did not consider the effect of time in the following models.

*Model setup:* At the group level, the collective state S(t) can be described at time t by the number $n_m$ of individuals which are moving at that time (for a given group size N, the number $n_r$ of resting individuals is always N - $n_m$).

The number of individuals, individual identities, and social relationships of the observed herd were included in the model. Thus, the number of agents N was fixed to 123. The model is time-dependent with each time-step representing one minute. At the start of simulation, 30% of the agents were resting ($n_r$ = 37). This 30% came from the average percentage of resting horses through observation. This value was consistent with the other studies of feral horses (Boyd and Keiper, 2005). We implemented the probability of changing state $\lambda_i$ of each agent. We assumed in the model that all agents were aware of the state (resting or moving) of all other agents at any time.

*Model design:* The overall design of the models is shown in Figure 1. The model is stochastic and individualistic (Couzin, 2009; Sueur and Deneubourg, 2011), meaning that we consider the probability of each individual to change state, and not the collective probability or state. We followed this concept as we introduced the selective mimetism (mimetism based on social relationships) as a hypothesis and this can be done only with calculating probabilities per individuals (Sueur et al., 2009; Sueur and Deneubourg, 2011). This bottom-up approach is also better than the top-down one in understanding individual decision processes. We obtained probability of individuals to change states, mimetic-coefficient and refractory time period of resting/moving and social relationships from the data set (Table 1, details about calculations are given below). The probability $\Psi_1$ ($N\lambda$), mimetic coefficient C, and refractory time period$\Delta T_{01}$ (=1/$\Psi_1$) of moving were calculated as 0.04, 0.796 and 25 minutes, and those of resting were 0.02, 0.426 and 50 minutes, respectively (Table 1, Figure S1 and S2). We also tested different mimetic coefficients and refractory periods to assess the exactitude of the values we implemented in the model from the observed data (Supplementary). We ran a simulation (one day) extending 9 hours (540 minutes) with 18 observations, and we repeated the simulations 100 times for each hypothesis. We also tested the model with different parameter sets to investigate its robustness (Supplementary).

*Individual probability of changing state:* As the distribution of the state latencies corresponded to an exponential distribution (figure S3), the probability of an individual changing its state was the log gradient of this exponential distribution, that is, the inverse of the mean state latency (Sueur et al., 2009):

$$\Psi_{1,s} = \sum_{i=1}^{N} \lambda_{i,s}$$

We assumed that all individuals may have the same mean latency while their probability of changing their state might differ. The mean latencies to start event are equal whatever the individual:

$$\Delta T_{01,s} = \frac{1}{\Psi_{01,s}}$$

as explained above, we also defined $\Delta T_{01}$ as a refractory time period in the simulations.

*Mimetic coefficient:* In a mimetic process where the probability of changing state is proportional to the number of individuals already in this state, the probability per unit time that individual i changes state is:

$$\psi_{i,s} = \lambda_s + Cn_s$$

where C was the mimetic coefficient per individual and $j_s$ is the number of individuals in the state s, either R for resting or M for moving. As $\psi_i$ is same for all the individuals in the herd, the mimetic coefficient C could be obtained from the inverse of the average $T_{j,j-1}$, $1/E[\Delta T_{j,j-1}]$ (j=2,3,…). We calculated the parameters C and $\Delta T_{01}$ using survival analysis (figures S3 and S4 respectively) and quadratic functions (see results and figures 4 and 5 respectively).

*Models based on the different hypotheses:* We tested different sub-models (Figure 1) based on each hypothesis, presented here for i to iii. Overall, we tested seven models: (A) independent, (Ba) absolute anonymous, (Bb) proportional anonymous, (Ca) unit-level absolute social, (Cb) unit-level proportional social, (Da) herd-level absolute social, and (Db) herd-level proportional social model.

(i) Independent hypothesis (model A)

The first hypothesis assumed that horses were independent: the probability of an individual changing their state is not influenced by the state of any other members. Under this

hypothesis, the probability that one of the agents (e.g., individual i) changes state per unit time was $\lambda_{i,s}$. Considering the refractory period, the probability $\psi_i$ is equal to $\lambda = \Psi_{01}/N$ when $\Delta t_i < \Delta T_{01,s}$ and is equal to 1 when $\Delta t_i = \Delta T_{01,s}$.

This model corresponds to a null model.

(ii) Anonymous hypotheses (model Ba and Bb)

The second hypothesis specified that horses synchronize with all the herd members anonymously. In the absolute anonymous model (model Ba), individuals will change state s according to the absolute (i.e., not proportional) number of herd members in this state s (respectively number R for state r and number M for state m). To test this hypothesis, we added a mimetic coefficient C in the independent model, which indicated the strength of the collective process.

Considering the refractory time period, the n resting agents became the joiner j+1 under the model Ba was obtained from equation:

$$\psi_{i,s} = min\,\{\frac{1}{\Delta T_{01,s} - \Delta t_i}\,,\ \lambda_s + Cn_s\}$$

when $\Delta t_i < \Delta T_{01,s}$. It is equal to 1 when $\Delta t_i = \Delta T_{01,s}$ (this is same for all the models, so we only refer to the probability when $\Delta t_i < \Delta T_{01,s}$). The equation shows that when $\Delta t_i$ is small, that is, soon after an individual changed its state (beginning of a refractory period), it is less likely to be influenced by the states of other individuals.

We also created another model based on proportional number of individuals in this state s, where the probability of changing state s1 depends on the number of individuals in this state s1 divided by the number of individuals in the second state s2 (model Bb). The probability of individuals in s2 to go in state s1 is:

$$\psi_{i,s1} = min\,\{\frac{1}{\Delta T_{01,s1} - \Delta t_i}\,,\ \lambda_{s1} + C\frac{n_{s1}}{n_{s2}}\}$$

As $n_{s1} = N - n_{s2}$, the response of individuals become reciprocal, not linear like the anonymous model.

(iii) Social hypothesis (model Ca, Cb, Da and Db)

In these hypotheses, we tested the influence of the social relationships between units or herd members on the decision to join. Unit-level social hypothesis (model Ca and Cb) assumed the synchrony happened only among unit members, while herd-level social hypothesis (models

Da and Db) considered both intra- and inter-unit sociality. Within these two social hypotheses, we tested two models: one taking the absolute numbers of individuals in each state (model Ca and Da), another one taking the proportion as described for the anonymous mimetic models (Cb and Db).

Models Ca and Da took into an account of the individual identities and the social relationships of each dyad. Each observed social relationship of the study herd was implemented in the model allowing us to consider social relationships differences between dyads. The probability per unit time that one of the $n_{s2}$ individuals to change state to $n_{s1}$ differed between the resting agents with respect to their social relationships with agents already in s1, and inversely. The probability of an individual i to change state under the social hypothesis was:

$$\psi_{i,s} = \min\{\frac{1}{\Delta T_{01,s} - \Delta t_i}, \lambda_s + C \sum_{k \in s, k \neq i} a_{ik}\}$$

where $k \in s$ means that individual k is in the state s. We simulated two types of the social index $a_{ik}$; 'unit-level' (only intra-unit) in model Ca, and 'herd-level' (both intra- and inter-unit) association network in the model Da to investigate whether individuals made decisions based only on the members of the same unit or on all herd individuals.

In models Cb and Db, again the proportion of the joiner to the non-joiner mattered. The probability of an individual i becoming a joiner j+1 under the social hypothesis was:

$$\psi_{i,s1} = min\{\frac{1}{\Delta T_{01,s1} - \Delta t_i}, \lambda_{s1} + C \frac{\sum_{k \in s1, k \neq i} a_{ik}}{\sum_{k \in s2, k \neq i} a_{ik}}\}$$

**(e) Statistical analyses**

To evaluate the fitness of models, we compared the number of horses changing states and synchronization rate of simulated data to those of observed data.

For both $P_{m:r}$ and $P_{r:m}$, we plotted how many individuals changes state after the synchronization phase started in each 30 minutes (e.g. 0–30, 30–60, 60–90 min…). We refer to this number as $\Delta n_s$ ($\Delta n_r$ is for $P_{m:r}$ and $\Delta n_s$ for $P_{r:m}$). We fitted the observed data to quadratic function that cross (0,0), i.e., $ax^2+bx$, using linear regression method under R environment. We evaluated the models by comparing the simulated data to observed data using Kolmogorov-Smirnov (K-S) test.

We calculated the correlation between the synchronization rate per dyad of simulated data and that of observed data and tested its significance using Mantel test and K-S test. We evaluated the similarity of the intra-unit synchronization rate distribution to that of the observed

data using the K-S test. Indeed, the synchronization rate across units were mostly the same among models and never became better than independent, so we eliminated it from the evaluation. A Mantel test was performed under R environment with the 'vegan' package (Oksanen et al., 2019). We used a function 'ks.test' in R for K-S test.

Being a social species, horses live in multilevel society, and we supposed them to be cohesive and to synchronize. So, we expected the mimetic model, either anonymous or social to do better than the independent model (model Aa). Thus, we defined the model Aa as a null model and compared other models to it. We calculated the proportion of the model showing better results than the independent one, i.e., when the model had lower D in K-S tests, and higher r in Mantel tests than those of independent model. We calculated a score which showed the model fitting the best with empirical data.

## Results

### (a) Empirical data

The average number of individuals changing states are shown in Figures 4 ($P_{m:r}$) and 5 ($P_{r:m}$) (in blue, repeated in all graphs for comparison). Both showed a positive correlation with the quadratic function (adjusted $R^2 = 0.79$ in $P_{m:r}$, $R^2 = 0.81$ in $P_{r:m}$, see table S4 for the detailed results), indicating a mimetic or synchronization process with an increase of the number of horses in a state followed by a decrease (Sueur et al., 2009; Sueur and Deneubourg, 2011).

The average ± SD synchronization rate of each pair was 0.93 ± 0.03 within unit and 0.63 ± 0.06 across units in observed data, which showed a strong synchronization based on the social network of horses. The correlation of the social network and synchronization rate of observed data was 0.69 (Mantel test, permutation: 9999, $p<0.001$), indicating a synchronization process based on social relationships but a part of the process (at least 31%) was not based on these relationships.

### (b) Simulations

Models are supposed to confirm previous results on empirical data indicating a synchronization process based on the social network.

Concerning the states' synchronization, four models showed parabolic shape correlated to observed data (table 2) in moving to resting phase (absolute anonymous: Figure 4Ba, proportional anonymous: 4Bb, herd level absolute social: 4Da, and herd-level proportional social: 4Db ) and resting to moving phase (absolute anonymous: Figure 5Ba, proportional

anonymous: 5Bb, herd level absolute social: 5Da, and herd-level proportional social: 5Db). Agents merely changed their states in the other three models (independent: Figure 4A and 5A, unit-level absolute social: 4Ca and 5Ca, and unit-level proportional social: 4Cb and 5Cb).

The histogram of synchronization score comparing models to empirical data is showed in Figure 6. The results of the Mantel test and K-S tests were shown in Table 2. As a matter of course, the intra and inter-unit synchronization rate largely overlapped when we did not consider social effects (model: independent: Figure 6A, absolute anonymous: 6Ba, proportional absolute anonymous: 6Bb) which do not fit to observe data with intra and inter-unit synchronization being well separated. So, unit-level (model Ca and Cb) and herd-level hypotheses (model Da and Db) better explained synchronization score.

Overall, the herd-level social (model Da) and the herd-level proportional social (model Db) always had better scores than the independent (null) model, while the others did not. K-S tests for $\Delta n_m$ and $\Delta n_r$ were better in the herd-level social model, and the K-S test and the Mantel test were better in the herd-level proportional social model (Table 2).

**Discussion**

We compared seven models to find which one best explains the dynamics of behavioural states in horses' multilevel society. The herd-level absolute social model (model Da) and the herd-level proportional social model (model Db) always showed better results than the null model (model A), while other models did not. Considering the simplicity of the model, which does not contain any environmental effect and temporal changes of agents' positions, and the fact that the model is based on the temporally sparse data with 30 minutes intervals, we argue that these two models were quite fitted to the empirical data. These models indicate that synchronization in a multilevel society of horses can be largely explained by their internal rhythm plus the social network. Model Da (herd-level absolute) was better at explaining the number of horses changing states, while model Db (her-level proportional) more successfully explained the synchronization rate distribution, thus the mechanism most likely lies somewhere between them (for instance, these two mechanisms switch at a certain threshold). It is also possible that we could not evaluate the fitness of two models accurately enough because of the sparse observed data. Although a multilevel society is considered among the most complex social structures in animals (Grueter et al., 2017), our study suggested that the collective behavioural pattern could be represented by simple mathematical models.

The observation data had higher intra- and inter-unit synchronization rate and also the number of individuals changes state after the synchronization phase started ($\Delta n_s$) was higher in both $P_{m:r}$ and $P_{r:m}$ (moving to resting, and resting to moving synchronization phase) in the herd-level hypothesis (models Da and Db), suggesting the speed of behavioural transmission and the stability of synchronization is stronger than that in simulation and explaining why social relationships explained 69% of the synchronization process. According to the models with different parameter sets, the fittiness to $\Delta n_s$ value and to synchronization rate was negatively correlated with each other, suggesting the trade-off between them (Figure S2). $\Delta n_s$ represents the speed of the behaviour spread, and synchronization rate corresponds to the stability of the state. Indeed, the higher the speed of synchronization, the lower the stability. To further improve the fitness of the model, we may need to consider a parameter sets and/or equations which establish compatibility between the speed and the stability. For example, in the current model, shorter refractory time period could enhance the speed but lower the stability, because agents will definitely wake up after the refractory time passes. We may need to either change the equation of refractory time period or enhance the speed without changing the refractory time period.

Most previous studies of non-multilevel societies suggested local interaction within a few body lengths or the several nearest neighbours (Couzin and Krause, 2003). However, our result showed that inter-individual interaction also occurred among spatially separated individuals. According to Maeda et al., (2021), the average nearest unit distance was 39.3 m (around 26.2 times a horse's body length) and the nearest individual within the same unit was 3.2 m. It is still not sure whether horses actually have a global view or they just respond to the several nearest units, but either way this is a notably large distance compared to other studies. Horses usually did not create any significant cue (e.g. vocalization) when they start moving/resting, thus it is likely that horses have an ability to recognize the behaviour of horses of the same units and others simultaneously. In a multilevel society, it is important to keep the inter-unit distance moderate, not too close but not too far. This avoids competition between units while keeping the cohesion of the higher-level group to obtain the benefits of being in a large group, such as protection from bachelors or predators (Swedell and Plummer, 2012), and may have led to the evolution of such cognitive ability. As our data was too sparse in time scale, it was difficult to observe how behaviour propagated across units and finer-scaled observation will be needed for the further investigation on the underlying mechanism in herd-level synchronization.

Because of the simplicity of our model, our methodology is highly applicable to other species. The spatial structure of multilevel societies is still poorly understood, but it may vary among species and contexts. For example, a migrating herd of Prezewalski's horses (*Equus ferus przewalskii*) was relatively aggregated (Ozogany and Vicsek, 2014), but a higher level group of Peruvian red uakari (*Cacajao calvus*) was much more sparsely distributed, like the horses in our study (the nearest unit distance was 10–15 m or more) (Bowler et al., 2012). It is important to discover whether the association index could also explain the behavioural decision of other multilevel social animals with various special structures to generalize our knowledge of behavioural synchronization in multilevel societies.

Overall, our study provides new insights into the behavioural synchronization process and contributes to the understanding of collective behaviours in complex animal societies. The organization of multilevel societies has become a topic of great interest recently, but studies have so far usually focused on social relationships and many questions are still unresolved. We hope that our study on collective synchronization will contribute to an understanding of the evolution and functional significance of multi-level animal societies.

**Limitations of the study**

Our model could not consider the temporal changes in position of horses including concurrent inter-individual and inter-group distances, although it is highly likely that the behaviour of units is more affected by closer units. While horses are in moving state, also their movement is likely to be synchronized with each other, so we may need to consider movement synchronization in a model as well as behavioural state synchronization. Developing inter-individual and intergroup distances in the model can be done indirectly through giving variance using stochasticity to relationships implemented in the model. For the calculation of the parameter on stochasticity, more temporally fine scaled data may be needed. Orthomosaic data has an advantage of obtaining the accurate and identified positions of individuals in a wide-ranged group, but it could obtain only temporally sparse data. Optimizing the data collection method, such as combination of the video recording from drones, should be needed to further develop the model. In addition, the variations of parameter sets we tested were limited, thus it was difficult to make a detailed discussion on the function of the paramteres.

**Author Contributions**

SH and SY managed the project. TM collected data. CS designed the models and, TM and CS conducted the analysis and interpreted the results. TM wrote the manuscript with help from CS, SH, and SY. All authors have approved the final version of the manuscript and agree to be accountable for all aspects of the work related to the accuracy and integrity of any part of the work.

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**Data availability**

The relevant data and models are available at the following link: https://doi.org/10.5061/dryad.c866t1g3b

**Declaration of Interests**

The authors declare no competing interests.

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**Figure and Tables Legends**

**Figure 1.** A graphic representation of synchronisation models. The dots represent individual agents and the cluster of dots represent units. When agents/units were connected with lines, it

means that their states were affected by each other. The width of the lines represents the strength of synchronisation.

**Figure 2.** Overall procedure of the research. (a)We took aerial photos of horses using drones. (b) These successive photos were stitched together to create an orthomosaic. (c) Individuals in orthomosaics were identified, and the positional and behavioural data of horses were obtained. We then constructed the social network using inter-individual distance data. The photograph is also used in Maeda et al., (2021) published in Scientific Reports.

**Figure 3.** Histogram of inter-individual distances showing clear bimodality. The distance of the first peak and the second peak could be considered as the most frequent value of inter-individual distances within a unit and between units, respectively. The trough between two peaks represents the threshold that divides the intra- and inter-unit association. This figure is reprinted from Figure 2(a) in Maeda et al., (2021).

**Figure 4**. The change of the number of resting individuals in $P_{m:r}$. The pink points are data obtained from simulation and blue are those from the observation. Data was fitted to quadratic function that cross (0,0), i.e., $ax^2+bx$. $R^2$ is the coefficient of determination of the regression for simulated data. Aa: independent, Ba: absolute anonymous, Bb: proportional anonymous, Ca: unit-level absolute social, Cb: unit-level proportional social, Da: herd-level absolute social, and Db: herd-level proportional social models.

**Figure 5**. The change of the number of resting individuals in $P_{r:m}$. Same as Figure, 4.

**Figure 6.** Histograms of the synchronisation rate. White and grey bars represent the observed value of synchronisation rate across units and within units, respectively. Pink and blue bars represent those of simulated data across units and within units, respectively. Aa: independent, Ba: absolute anonymous, Bb: proportional anonymous, Ca: unit-level absolute social, Cb: unit-level proportional social, Da: herd-level absolute social, and Db: herd-level proportional social models.

Table 1. The explanation and values of parameters. The value of the parameter was written when it is a constant. See also supplementary appendix for the detailed explanation of how to obtain the parameter value. '-' means that the value can change dynamically.

Table 2. The result of the evaluation of Δn and the synchronisation rate obtained from the simulations. "Eval" (evaluation) is "+" when the result it better than independent model and "-" when not. The model with smaller D and larger r is considered as the better. Score is the percentage of the tests which showed better results than independent (null) model.

**Figures and Tables**

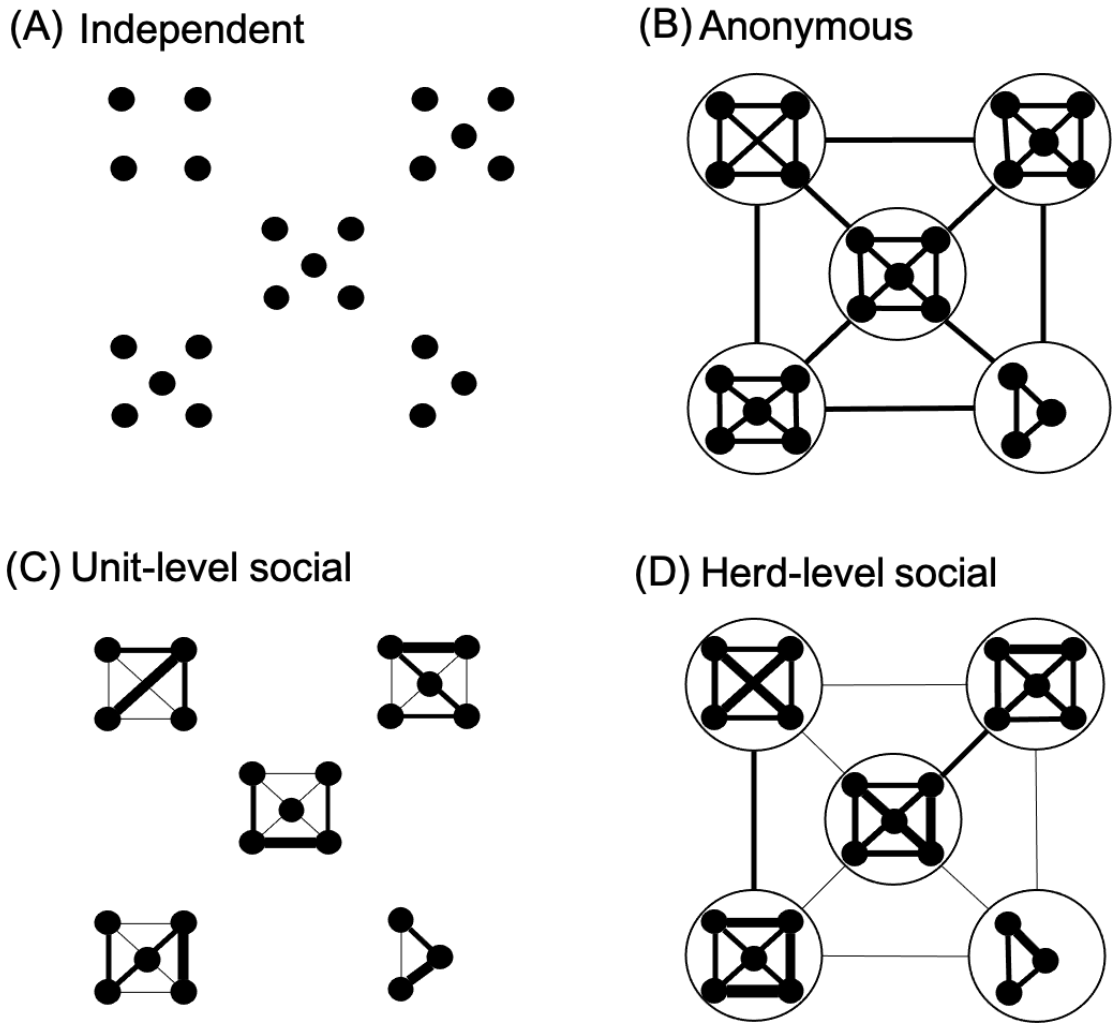


**Figure 1**

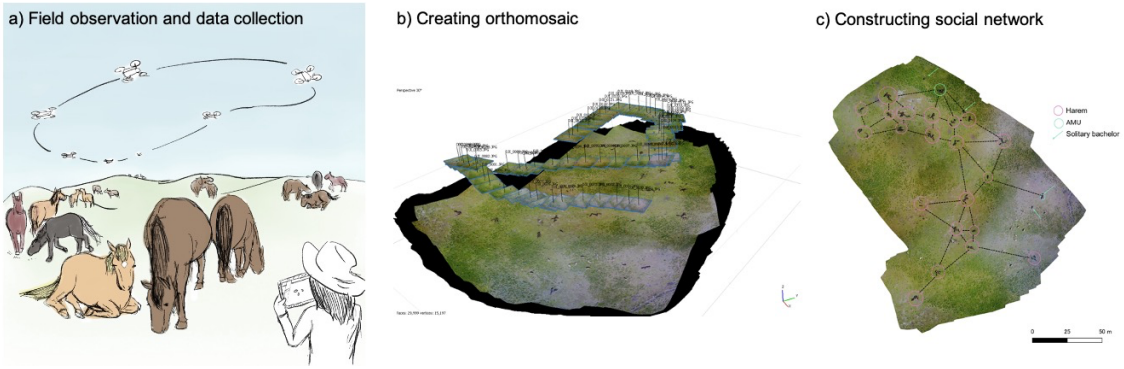
a) Field observation and data collection
b) Creating orthomosaic
c) Constructing social network
Harem
AMU
Solitary bachelor
0
25
50 m

**Figure 2**

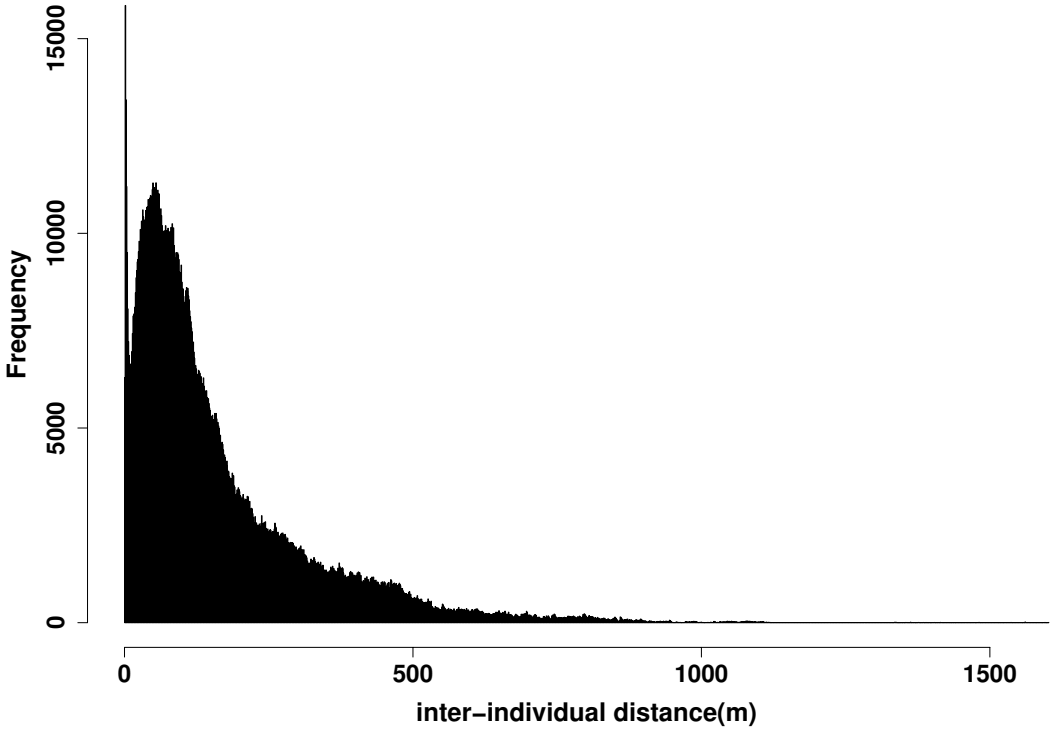
Frequency
0
5000
10000
15000
0
500
1000
1500
inter−individual distance(m)

**Figure 3**

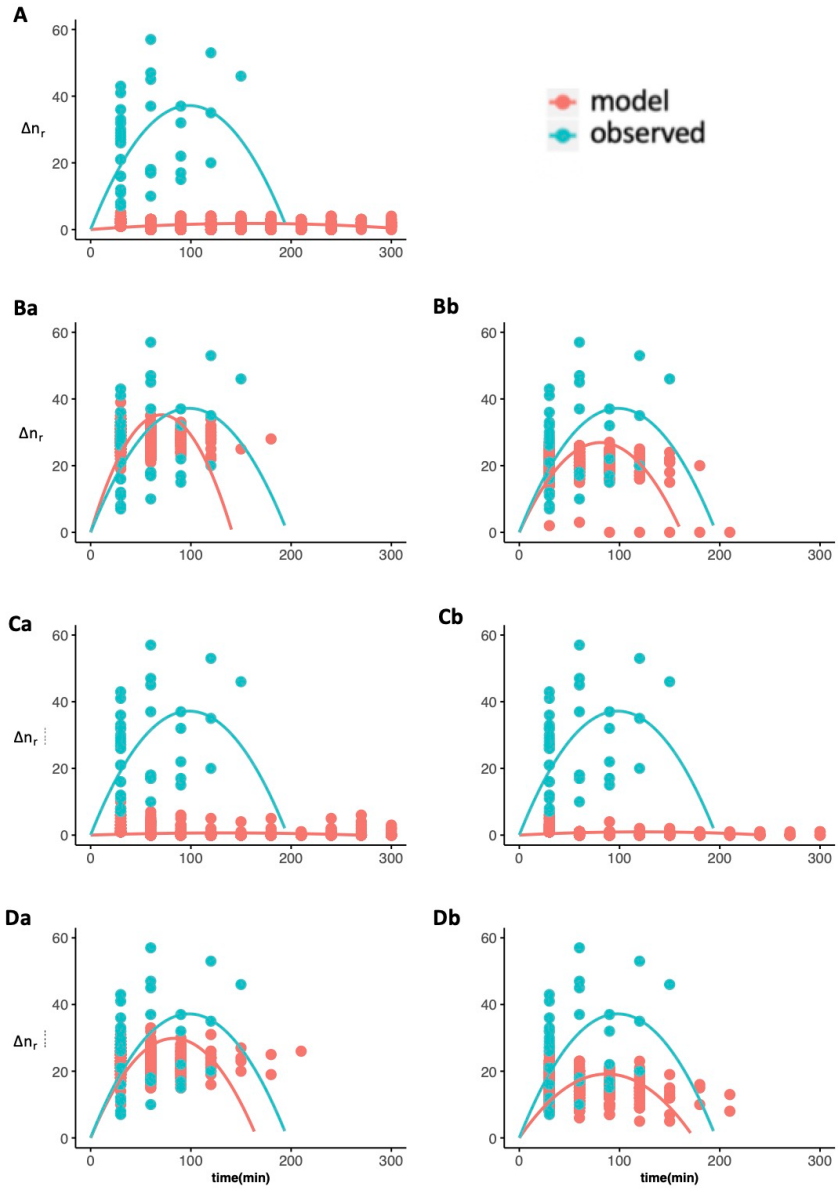
A
Ba
Bb
Ca
Cb
Da
Db
model
observed
Δn_r
time(min)
0
20
40
60
100
200
300

**Figure 4**

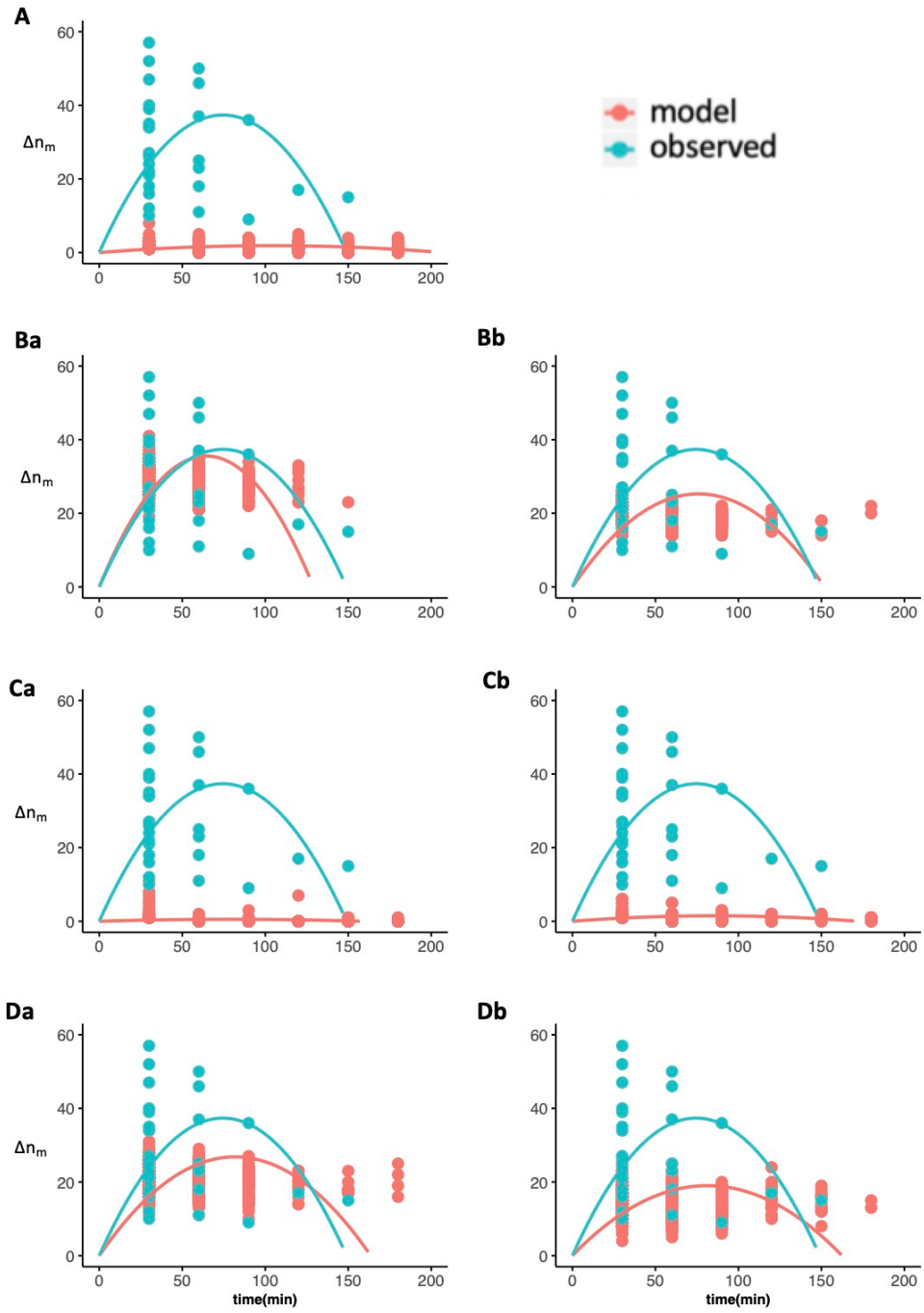
A
Ba
Bb
Ca
Cb
Da
Db
model
observed
Δn_m
time(min)
0
20
40
60
0
50
100
150
200

**Figure 5**

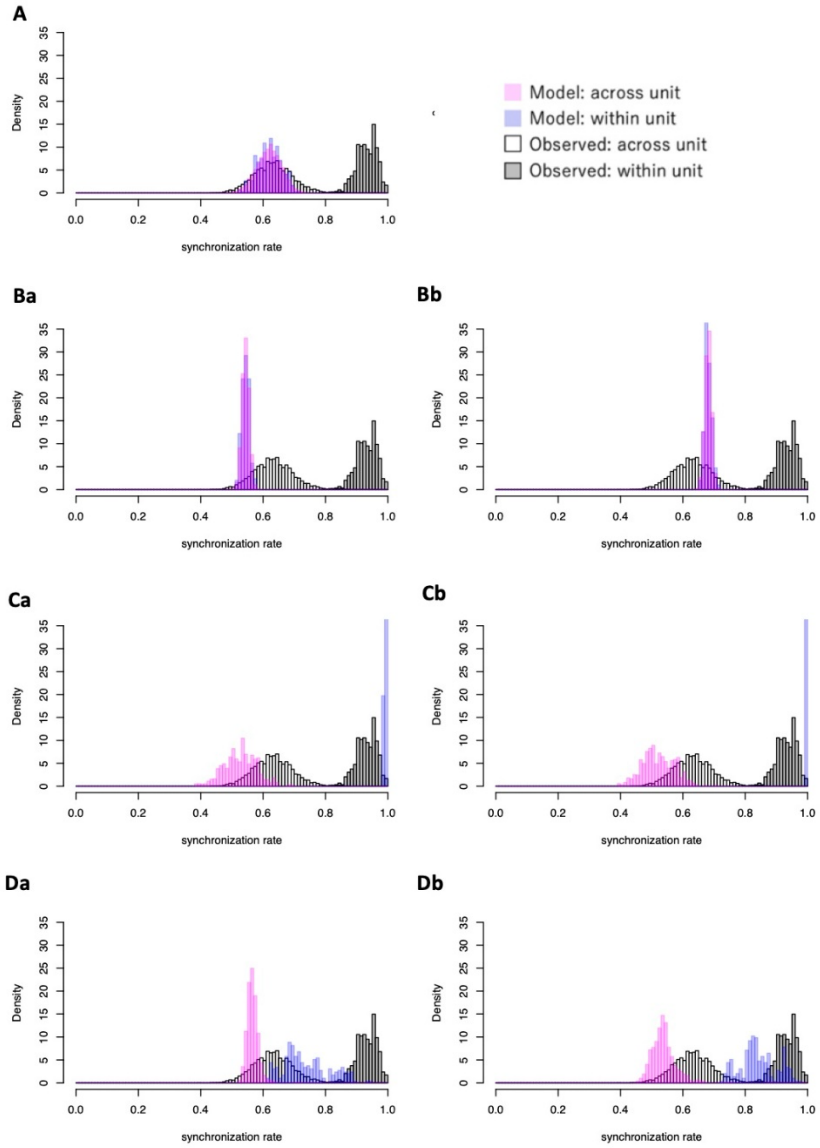
A
Ba
Bb
Ca
Cb
Da
Db
Density
synchronization rate
Model: across unit
Model: within unit
Observed: across unit
Observed: within unit

**Figure 6**

| parameter | value (resting) | value (moving) | Definition |
|---|---|---|---|
| $a_{ki}$ | social network | | social network weight between individuals *k* and *i*. |
| C | 0.426 | 0.796 | mimetic coefficient |
| $\Psi_1$ | 0.030 | 0.040 | A probability of starting resting/moving. Equal to $N\lambda_i$ |
| $\Psi_j$ | - | - | Probability per unit time that one of the n agents became the jth joiner (corresponding to the hypothesis where the identities of individuals are not taken into an account) |
| $\psi_{i,s}$ | - | - | Probability per unit time of an individual *i* changing the state s (the refractory time period and the identities of individuals are taken into an account.) |
| $\lambda_{i.s}$ | 0.00016 | 0.00033 | The average probability per unit time of an individual i changing the state s. |
| $\Delta T_{01,s}$ | 50 (min) | 25 (min) | Refractory time period. time elapsed from the end of the previous event. |
| $\Delta T_{j,\,j-1,s}$ | 2.3 (min) | 1.3 (min) | time elapsed between the state change of the joiner j-1 and the state change of the joiner j. The inverse of C. |
| $\Delta t_i$ | - | - | time elapsed from the previous state change of individual *i* |
| N | 123 | | number of individuals in a herd |
| $n_s$ | - | - | Number of the individuals in the state s (resting/moving). |

**Table 1**

| | K-S test ($\Delta n_m$, $P_{r:m}$) | | | K-S test ($\Delta n_r$, $P_{m:r}$) | | | K-S test (sync rate of intra-unit) | | | Mantel test (sync rate) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| model | D | p | eval | r | p | eval | D | p | eval | r | p | eval | **score** |
| independent (null model) | 0.980 | 0.010 | | 0.980 | 0.010 | | 1.000 | <0.001 | | 0.367 | 0.010 | | |
| anonymous | 0.215 | 0.989 | + | 0.306 | 0.989 | + | 1.000 | <0.001 | - | -0.050 | 0.989 | - | **0.50** |
| proportional anonymous | 0.564 | 0.947 | + | 0.561 | 0.947 | + | 1.000 | <0.001 | - | -0.057 | 0.947 | - | **0.50** |
| unit-level | 0.993 | <0.001 | - | 0.995 | <0.001 | - | 0.973 | <0.001 | + | 0.572 | <0.001 | + | **0.50** |
| unit-level proportional | 0.980 | <0.001 | - | 0.980 | <0.001 | - | 0.993 | <0.001 | + | 0.627 | <0.001 | + | **0.50** |
| herd-level | 0.537 | <0.001 | + | 0.577 | <0.001 | + | 0.915 | <0.001 | + | 0.601 | <0.001 | + | **1** |
| herd-level proportional | 0.698 | <0.001 | + | 0.714 | <0.001 | + | 0.714 | <0.001 | + | 0.634 | <0.001 | + | **1** |

**Table 2**