

All Together Now: Activity Synchrony and Social Cohesion in Group-Living Animals

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A central problem all group-living animals face is how to maintain group cohesion during the course of the day in the face of forces that drive animals apart. When activity schedules become desynchronised, groups will inevitably fragment as animals drift apart. To explore the impact that individual differences in activity scheduling might have for group cohesion, we here explore the consequences having different activity schedules has for social cohesion. By modeling a group as a set of semi-coupled oscillators, we show that, all else equal, the members of the group will become less and less coupled across the active day until the group devolves and breaks apart, setting an upper limit on the size of group that can be maintained as a coherent entity given a particular level of correlation in members' activity schedules. We then show that when social bonding creates a stickiness, or gravitational pull, between pairs of individuals, fragmentation is reduced. We argue that large, stable social groups are only possible when some form of social bonding has evolved.

Keywords: Animal Synchrony, agents' segregation

I. INTRODUCTION

During their waking day, animals forage, rest and socialise in varying quantities determined both by their species-typical physiological demands and by their own individual physiological cycles. Each day, they must ingest sufficient nutrients both to keep alive and to fuel their particular reproductive activities [1]. When individuals have cycles of different length or structure, their schedules will inevitably become desynchronised, causing them to drift apart [4],[24]. In the limit, this will cause groups to fragment, ultimately placing an upper limit on social group size. For species that require to live in stable social groups, this inevitably creates a problem, since, in the absence of any mechanisms to keep animals together, it will be impossible for groups of any size to maintain any kind of temporal coherence.

This problem is exemplified more strongly by herding ungulates, which broadly lack mechanisms to maintain social cohesion during foraging. In large-bodied species characterised by sexual dimorphism, this is reflected in a striking tendency for sexual segregation outside the breeding season. Even when animals start the day together, the greater foraging demands of large-bodied males necessitates that they carry on feeding, and hence moving, when females, with their smaller rumens, have to go to rest in order to clear their full rumen by the processes associated with rumination [9]-[12]. The mechanisms that drive this phenomenon have been extensively studied both behaviourally [4]-[8] and mathematically [2],[3]. Conradt [20], for example, used an agent-based coupled model to study the decision making processes in sexual segregation in herd-forming deer and feral sheep [2]. In such settings, members of the group decide on a

direction of travel and whilst each agent has a preferred angle, they are gradually influenced by the position of other agents. As time passes, the agents move along a circle to the angle they desire, and at the end of the process, all the agents either agree on one angle or congregate in multiple groups that want to move in different directions, in which case the group breaks up into sub-groups.

Most of these approaches have focussed on how animals coordinate movements when travelling in groups and on finding explanations for why groups fragment during foraging. However, that has not often been considered is how animals *prevent* fragmentation occurring.. This issue is important because it may impose limits on the size of group that animals manage to create the kind of stable social groups of the kind found in primates and many other mammals (notably equids, camelids, delphinids and elephantids) [3, 4]. Understanding how failure of coordination imposes constraints on the size of stable groups thus goes beyond the kind of joiner/leaver models [21] that have dominated classic behavioural ecology. In these kinds of groups, bonded relationships between individuals create complex networks that create a form of gravitational drag that holds individuals in defined orbits with respect to each other [22]. In the present paper, we expand on the work in [2] by creating a model which allows for both different activities and different types of agents within the group to be factored in. For present purposes, we shall simply consider these agent categories to be male and female, but any biological phenotype that influences activity schedules would be appropriate.

We begin by introducing the background from [2] for defining our new model in [section II](#). Then, in [section III](#),

we modify the agent-based coupled model to study synchrony as animals cycle through various daily activities such as feeding, grooming, and resting. These activity categories account for different proportions of the day, which we represent as an arc on a circle (where the whole circumference represents the complete active day – 12 hours of daylight in the case of diurnal primates, 24 hours in the case of cathemeral ungulates) Figure 1. An individual must satisfy the full time demands expressed in its activity schedule circle because time is not compressible (i.e. it is not possible to do two of these core activities at the same time in order to create savings via time-sharing) [1]. In the setting illustrated in Figure 1, an agent being in a given range represents it doing the activity defined by that arc (i.e. it is *NOT* to be confused with a direction of travel). Within our model, we assign each agent an activity schedule to perform, such as eating for 800 units of time and then resting for 700. When an agent moves from one activity to another, we set its desired angle to a randomly selected value in the appropriate range defined by the arc of the circle. We further divide our group into two categories (Female and Male agents) who move through the activities at different times as a group. After describing the essentials of the model, we study the model under different conditions in section IV, using two, three, or five sectors as well as the effect of different parameter values on the behavior of the agents. The implications of our model are considered in section V. First, we use Conradt’s [20] established segregation index to show that:

- the segregation index is periodic, and
- the period is similar to the least common multiple of the female and male cycles.

Second, we study a coupling value a_{jl} between individuals which takes on values between 0 and 1, for 0 corresponding to the case where agents completely disregard each other. This parameter controls how much agent j cares about information from agent l , allowing us to measure female/male segregation by considering the average of a_{jl} where j and l are two different members of the group. In particular, we show that by changing the distance at which agents can detect each other, we cause the group to slowly decouple.

II. BACKGROUND

We here give a short overview of some of the background which will be important for developing our synchrony model. Conradt’s [2] agent-based coupled model is based on the Kuramoto [23] model of coupled oscillators, and describes a group of animals making a decision about what direction to head in. The basic premise of this model is that there are three groups of individuals N_1 , N_2 and N_3 which have different preferences. Individuals in N_1 and N_2 are ‘informed’, meaning that they have

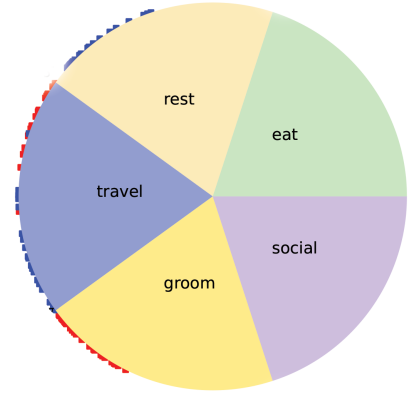


FIG. 1: An example of a divided disc with five activity categories, showing male (blue dots) and female (red dots) agents doing different activities.

a preference (1,2) for which direction the group should move in, while individuals in N_3 have no preference (‘uninformed’). These models derive from the classic disease propagation models of Kermode & McKendrick [25] where individuals in class N_3 are in this case equivalent to the ‘susceptible’ category who are vulnerable to infection by individuals from either of the other two classes (representing the classes of infected and recovered individuals). At every iteration, the angle of every agent is given by the following equations:

$$\frac{d\theta_j}{dt} = \sin(\bar{\theta}_1 - \theta_j(t)) + \quad (1)$$

$$\frac{K_1}{N} \sum_{l=1}^N a_{jl}(t) \sin(\theta_l(t) - \theta_j(t)), \text{ for } j \in N_1,$$

$$\frac{d\theta_j}{dt} = \sin(\bar{\theta}_2 - \theta_j(t)) + \quad (2)$$

$$\frac{K_1}{N} \sum_{l=1}^N a_{jl}(t) \sin(\theta_l(t) - \theta_j(t)), \text{ for } j \in N_2,$$

$$\frac{d\theta_j}{dt} = \frac{K_1}{N} \sum_{l=1}^N a_{jl}(t) \sin(\theta_l(t) - \theta_j(t)), \quad (3)$$

for $j \in N_3$.

The parameter K_1 gives the amount an agent cares about other individuals’ directions overall versus the direction it wants. The function $a_{jl}(t)$ describes how much individual j cares about individual l and how much that influences its overall direction. Thus, K_1 can be thought of as controlling the overall influence of other individuals while $a_{jl}(t)$ controls the influence of a single individual (in effect, the stickiness created by social bonding between specific individuals that causes an individual to move towards a neighbour’s preference). In primates, this stickiness is created by social grooming [20].

Following [2], the values of the function $a_{jl}(t)$ are then adjusted in every iteration according to the following:

$$\begin{aligned} \frac{da_{jl}}{dt} &= K_2(1 - a_{jl}(t))a_{jl}(t)(\rho_{jl}(t) - r) \\ \rho_{jl} &= \left| \cos\left(\frac{1}{2}(\theta_j - \theta_l)\right) \right|, \end{aligned} \quad (4)$$

where we introduce the parameter K_2 which controls how fast a_{jl} changes, and r represents the distance at which agents can sense each other. In other words, the value of r gives the maximum of the distance that the agents can be apart and still be aware of each other: if two agents are more than r apart, they cannot sense each other. In effect, r indexes the limit at which the stickiness, or gravitational pull, between pairs of individuals can function – their likelihood of remaining spatially close enough to each other to be able to determine which activity phase the other individual is in. In these equations, ρ_{jl} represents how aligned the motion of agent j and l are.

Using a computational agent-based model, it was shown in [24] that a group of animals moving together can make a collective decision on direction of travel. The same authors later considered the impact of having informed and uninformed individuals in [2] and showed how the dynamics of this system can be modeled analytically. They found that adding uninformed individuals improves the stability of collective decision making, where such stability corresponds to most of the group moving in one of two alternative preferred directions. In particular, they showed that this stability depends explicitly on the magnitude of the difference in the preferred directions of each subgroup.

In what follows we shall study a setting not encompassed in [2], namely social groups where two sets of people have more than two activities available, as a result of which the group could decouple. We are interested in the extent to which decoupling might be prevented by the extent to which individuals care about each other's preferences.

III. FEED-REST CYCLE VIA A COUPLED MODEL

Expanding on the model [2], we consider a system where sectors of the circle represent different activities. For example, an angle between 0 and π could represent feeding, while an angle between π and 2π represents that the animal is currently resting. We shall consider two groups of agents, with all agents being informed individuals with a desired heading. These two categories of agents could be any phenotype or social subnetwork within a group (e.g. a kinship group or a grooming clique) that have different activity schedules., but for convenience (and to relate our analysis directly to the literature on sexual segregation in ungulates) we shall refer to these two groups as males and females.

For analytical convenience, the desired heading of an agent changes to a randomly selected angle within the bounds of the preferred sector. For example, at time 20, males might all desire to switch from resting to eating, at which point they would be randomly assigned a desired heading between π and 2π . Hence, agents are only randomly assigned a heading when they first move sectors, not every single iteration. In the model, an agent's current angle can be thought of the activity it is currently performing while its heading is the activity that it would like to be performing. In our model, the *desired angle* is randomly assigned within a specific range associated with the current activity sector for an agent. For example, if an agent is currently in the "eating" sector, the desired angle might be randomly assigned within the range corresponding to the "eating" sector.

We build the model following Equations (1)-(3) but without any non-informed agents, and adding the separation of the disc into equal parts as a new parameter, which we shall begin by setting it to 3. We implement this model in Python and our code is available in a public github repository [28]. We configure our code to create images of the agents using matplotlib as well as CSV files of the various statistics such as M-F, F-F, M-M, group, and different group coupling. Inputs to this model include parameters such as K_1 , K_2 , r , $g_{starting}$, and $group_{boosted}$. These parameters and their effects shall be described in the following sections.

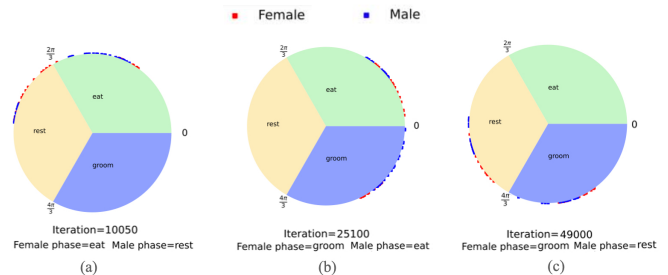


FIG. 2: Evolution in a simple three-activity system. Sectors identified with sectors for eating, resting, and grooming. 50 males, 50 females. Males spent 400 units of time eating, 600 resting, and 300 grooming. Females spent 300 eating, 700 resting, and 400 grooming. $K_1 = 2$, $K_2 = 0.5$.

Consider a case where there are two types of agents (males and females) who engage in three activities (rest, eat and groom, between them summing to 100% of the waking day) for different periods Figure 2. We initialise the model with all animals at rest (defined by their individual angles lying between π and 2π). After a certain amount of rest time m , the males move into feeding phase, in which case their desired angle is randomly set to a value between 0 and π . After f rest time, the females also move into the feeding phase. At the end of the day, all animals' desired angle moves back to the resting phase.

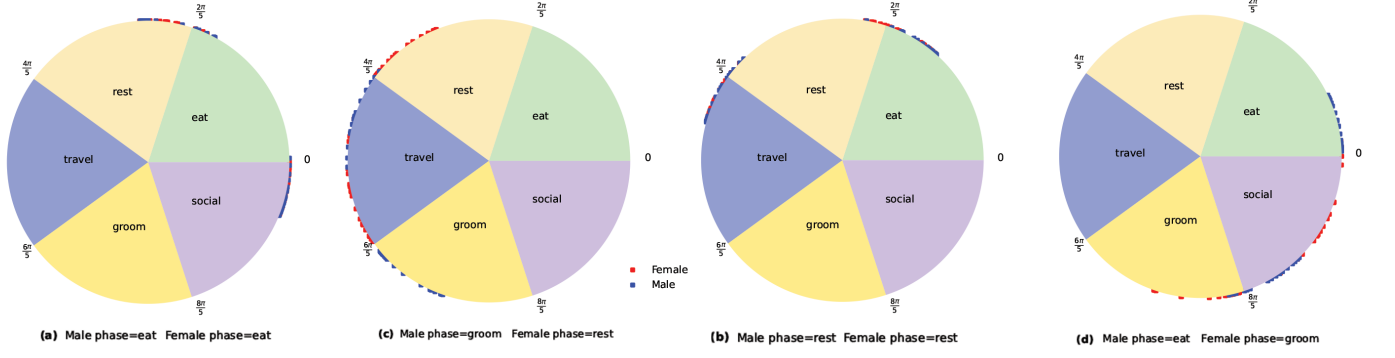


FIG. 3: Values of $K_1 = 2$, $K_2 = 0.25$ seen in different phases and iterations: (a) 50 iterations, (b) 750 iterations, (c) 4550 iterations, and (d) 13100 iterations.

When females and males spend a fixed amount of time on each activity before moving to a different activity, agents of the two types will move progressively between sectors (i.e. activities) in ways that cause them to pass through phases of within-type and between-type synchrony and asynchrony (when some individuals are in different sectors) [Figure 2\(a\)-\(c\)](#).

To understand the impact of considering 5 sectors, we study the behaviour of 50 males and 50 females within sectors representing eating, resting, traveling, grooming, and socializing. We shall set males to spend 400 units of time eating, 600 resting, 300 traveling, 200 grooming, and 100 socializing and females shall be set to spend 300 eating, 700 resting, 400 traveling, 300 grooming, and 200 socializing, each performing their cycle sequentially (see [\[28\]](#)). This schedule is constant and agents continuously cycle between activities in this order and spend the specified amount of iterations in that activity. In order to illustrate the role that the parameter K_2 plays, we consider different values of K_2 from those used in [Figure 2](#).

Recall that K_1 governs the collective influence of other agents on an individual, $a_{ji}(t)$ represents the specific interaction strength between two individuals, and K_2 determines the rate at which these interaction strengths evolve over time. With $K_1 = 2$ and $K_2 = 0.25$, a new

pattern emerges in which the two classes of agents oscillate between being distributed in two distinct clumps in different activity states and being so widely scattered that there is no consistent activity [Figure 3](#). Even so, the two classes (sexes) of agents are intermingled, even if sometimes there is a degree of segregation by sex, see [Figure 3\(b\)](#). The described pattern emerges due to the combined effects of sequential activity schedules, high influence of other individuals (K_1), and moderate rate of change in interaction strengths (K_2). These factors lead to oscillatory behavior and the intermingling of agent classes, despite occasional segregation by sex.

With $K_2 = 0$, we find that although all the agents initially (and lastly, see [Figure 4\(d\)](#)) cluster towards the center of the sector ([Figure 4\(a\)](#)), the males move to resting while the females stay eating and the agents seem to cleanly move towards the same sector with no agents in the wrong sector ([Figure 4\(b\)](#)). We see the same oscillatory pattern in [Figure 4\(c\)](#), the males move to grooming while the females are now resting. There are still some agents in the sector between them (travel) but overall it looks much more clean.

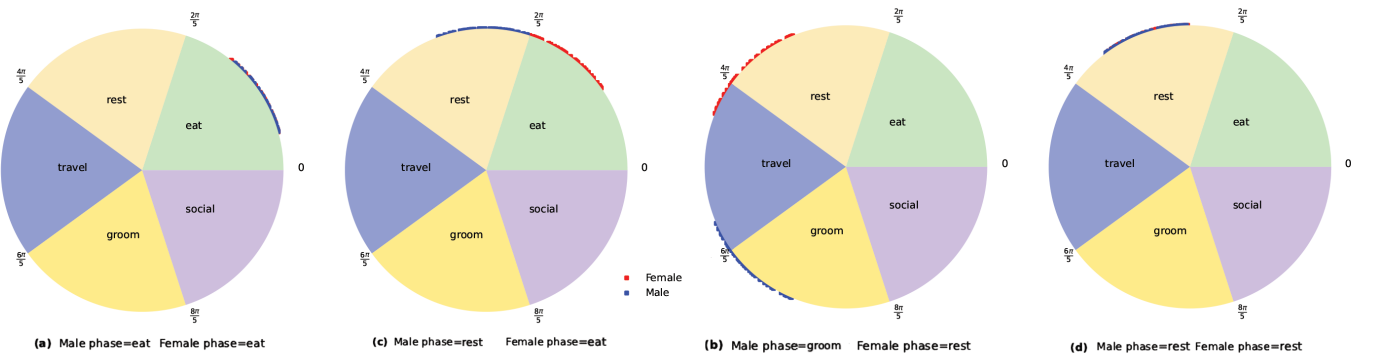


FIG. 4: Values of $K_1 = 2$, $K_2 = 0$ seen in different phases and iterations: (a) 50 iterations, (b) 4050 iterations, (c) 6300 iterations, and (d) 12100 iterations.

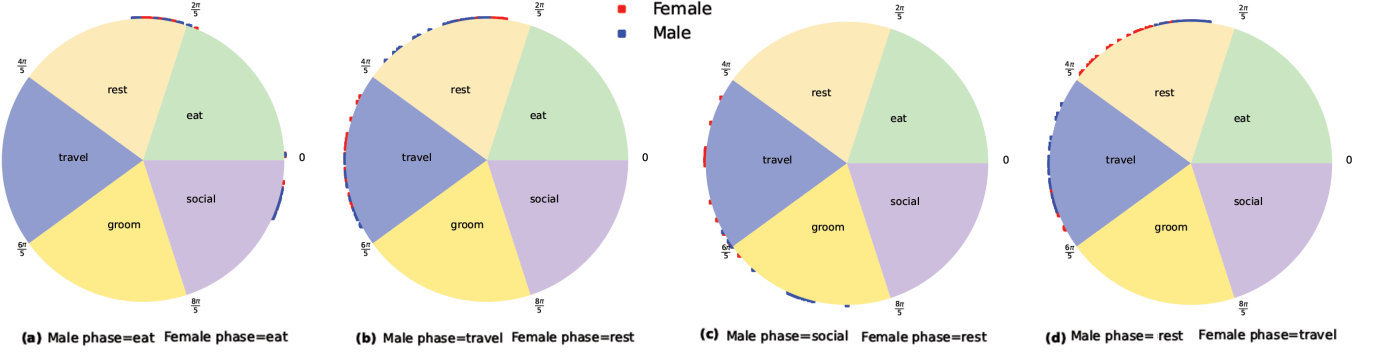


FIG. 5: $K_1 = K_2 = 2$, iteration (a) 1950, (b) 2850, (c) 6400, and (d) 7100.

Following the same line as before, in Figure 5, we consider 50 males and 50 females, with Males assigned to spend 400 units of time eating, 600 resting, 300 traveling, 200 grooming, and 100 socializing; and Females to spend 300 eating, 700 resting, 400 traveling, 300 grooming, and 200 socializing, and K_2 set to a high value of 2 (agents care a great deal about the group of agents they are around). It should be noted that the times we have assigned to each activity were inspired by the literature of activity budget studies on a wide range of animals, see for example [19].

In Figure 5(a), there are two clumps that are so far apart that most agents are in the wrong sector. In Figure 5(b), the males and females are in different sectors but there appears to be more males than females in the sector the females are actually supposed to be in. In Figure 5(c), the females are supposed to be in rest while the males are in social, but all of them are clumped in the two sectors between rest and social with no agent in the right sector. In Figure 5(d), they are again supposed to be in different sectors but the travel sector where the females are supposed to be is almost completely filled with males, and in further iterations, there were once again no agents in the right sector as they are all in the sectors between them.

From the above analysis, we can see that when K_2 is set to 0, indicating no change in interaction strengths over time, as agents transition between activity states, they cleanly move towards the corresponding sector without significant overlap or mixing between sectors. This behavior suggests that without changes in interaction strengths, agents exhibit predictable and orderly movement between activity sectors. Moreover, with a high value of K_2 ($K_2 = 2$), indicating rapid changes in interaction strengths, the behavior of agents becomes more erratic and less predictable. Despite sequential activity schedules, agents form two distinct clumps that are far apart, with most agents occupying the wrong sector and there is a tendency for agents to cluster in sectors between the intended activity states, leading to misallocation of agents across sectors. This behavior indicates that high

sensitivity to changes in interaction strengths can lead to increased mixing and disorganization within the system.

The observed patterns highlight the importance of parameter selection in influencing the dynamics of the agent-based model. Specifically, the choice of K_2 significantly impacts the organization and coherence of agent behavior within the system. A low or zero value of K_2 results in more orderly and predictable behavior, with agents smoothly transitioning between activity states. In contrast, a high value of K_2 leads to erratic and disorganized behavior, with agents clustering unpredictably and often occupying incorrect sectors.

Based on these findings, it is evident that the rate of change in interaction strengths plays a crucial role in shaping the emergent behavior of the model. Therefore, in the next section, we will explore adjustments to the model design to better capture the desired patterns of behavior and improve the model's fidelity in simulating real-world scenarios.

IV. SUBGROUPS

In order to understand how female and male groups interact throughout the course of time, in what follows we create multiple groups of females and males (5 groups with 10 females each and another 5 groups of 10 males). To accommodate our groups, we tweak the model in two ways:

- the initial value between members of the same group ($g_{starting}$), and
- adding $g_{boosted}$ to create an initiator who makes the first move that others then follow:

$$\begin{aligned} \frac{d\theta_j}{dt} &= \sin(\bar{\theta}_1 - \theta_j(t)) \\ &+ \frac{K_1}{N} \sum_{j \in N_1, l=1}^N (a_{jl}(t) + group_{boosted}) \sin(\theta_l(t) - \theta_j(t)) \end{aligned} \quad (5)$$

From a visual perspective, we use differently shaded dots to represent different groups. We take the average of a_{jl} for all agent type combinations of j and l , and use *group_starting* in our code [28] to represent a parameter that determines the initial value assigned to the interaction strength between agents belonging to the same group. In Figure 6, we see that the same group average goes very quickly to 1 which is to be expected given that we are boosting it and starting it higher. In contrast, the values for the overall correlation between the two sexes and the correlation between different groups of the same sex undergo a series of very distinct oscillations as they go through phases of synchrony and desynchrony, while undergoing a long slow steady decline.

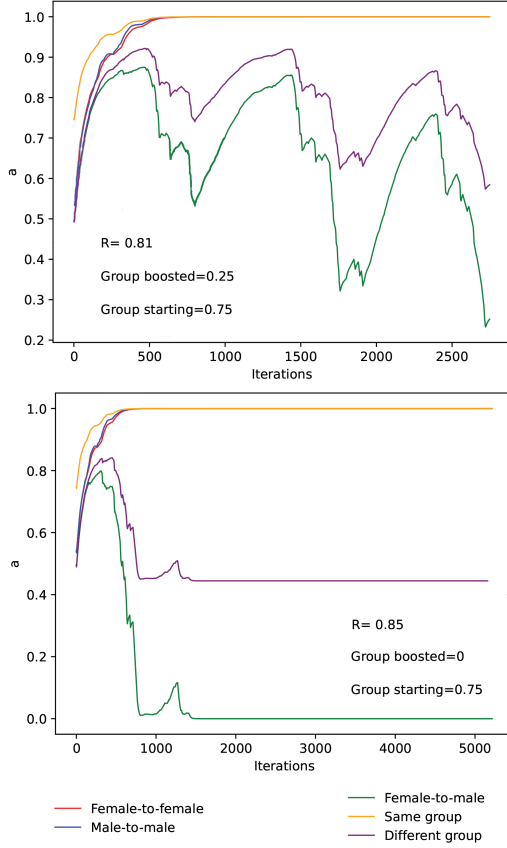


FIG. 6: Top: graph of all a averages with $r = 0.81$, group boosted = 0.25, group starting = 0.75. Bottom: $r = 0.85$, boosted = 0, group starting = 0.75.

In order to measure how close together a given group is, we use a spatial version of standard deviation where we first convert the agents' positions into rectangular coordinates, compute the midpoint, and then use the distance from each point to the midpoint. We first examine the effect of the r value on the standard deviation (Figure 7), and see that a higher r value of 0.85 and 0.81 results in a lower standard deviation (although the effect takes longer to evolve in the latter case); in contrast, there is less of a visible change between $r = 0.79$ and $r = 0.75$.

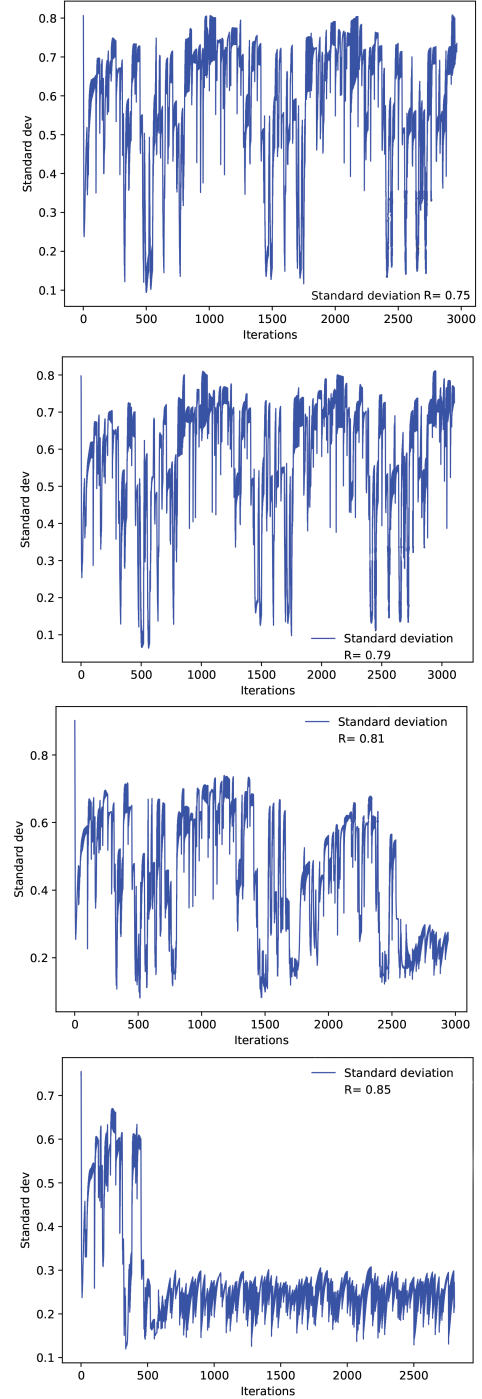


FIG. 7: Graph of standard deviation with varying r values. Boosted = 0.5, starting = 0.75 for all trials.

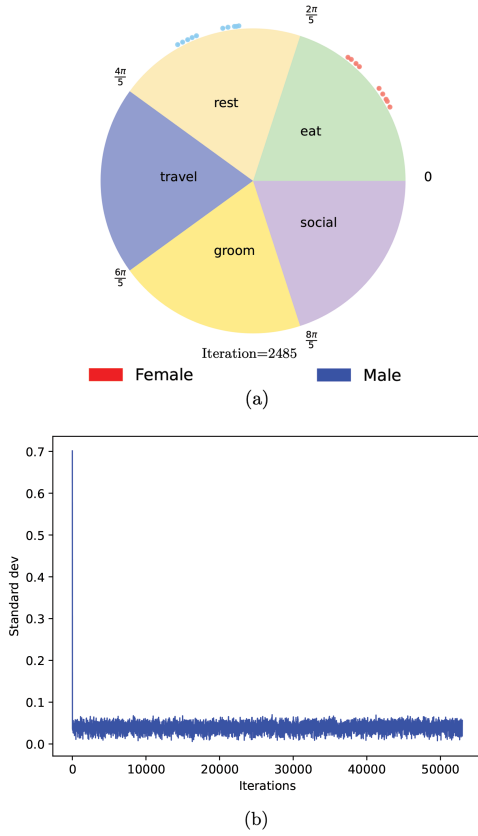


FIG. 8: Study of model for $K_0, K_1, K_2 = 0.1$. (a) Female phase=eat and Male phase=rest; $R=0.85$, Boosted= 40, starting= 1. (b) Graph of standard deviation, MF average=0.00011244701793142417, Std dev average=0.04071990250949034.

Within the model we introduced above, the desired angle θ (which represents the angle at which an agent aims to move towards in the circular space) is assigned to a random number in the sector range; as a result, there is a large range of desired angles and this was keeping agents from the same group apart. To explore this effect further, we modified Equation (5) to introduce another parameter, K_0 , allowing us to decrease the importance of the desired angle. In this modified model, K_0 must strike a balance between still keeping agents going to the correct sectors/activities but also allowing them to group:

$$\frac{d\theta_j}{dt} = K_0 \sin(\bar{\theta}_1 - \theta_j(t)) + \frac{K_1}{N} \sum_{l=1}^N (a_{jl}(t) + group_{boosted}) \sin(\theta_l(t) - \theta_j(t)). \quad (6)$$

In order to understand the relevance of K_0 , we begin by considering 2 groups of females and 2 groups of males with only 5 agents per group. An additional adjustment we make is the balance between K_1 and boosted. By decreasing the values of K_1 and proportionally increasing

boosted, we can decrease the influence of agents outside the group while keeping the influence of agents within the group the same. We see the agents stick to their own groups (Figure 8), and we also see in the line chart that the standard deviation of the agents is much lower than in Figure 7.

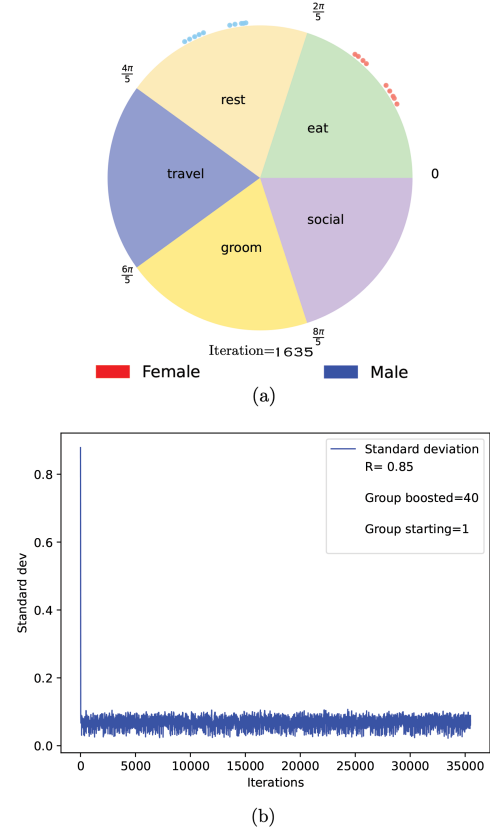


FIG. 9: Study of model for $K_0, K_1, K_2 = 0.1$. (a) Female phase=travel and Male phase=eat; $R=0.85$, Boosted= 40, starting= 1. (b) Graph of standard deviation, MF average= $1.1304 \cdot 10^{-4}$, Std dev average=0.068705.

The effect of making both the number of subgroups and their sizes larger is shown in Figure 9, where we consider 4 groups of each gender and 40 total agents. Notice that the male agents form distinct groups but the female groups seem to overlap rather more with each other. This suggests that groups being visually close might be dependent on their randomly chosen desired angle. Finally, comparing the results shown in Figure 8 and Figure 9, it should be noted that by considering the standard deviation values one can see that groups are overall much closer to each other, as shown in Figure 8.

We conclude this section by comparing the standard deviation between members of a group and randomly selected members of the same gender. For the randomly selected members, each sample consists of the same number of individuals as the group size. We compared the variance within groups with the variance between the same number of agents randomly selected from different groups.

As we can see from Figure 10, there is a large difference between the standard deviation of members in the same group and those who were not: in other words, the individual groups have drifted out of synchrony with each other. In what follows, we briefly discuss the implications both of our original model as well as the extension model which allows for subgroups of agents of the same type.

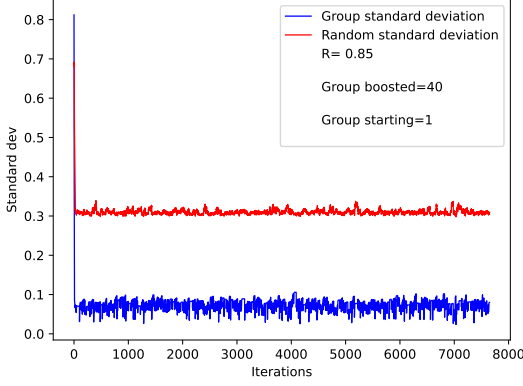


FIG. 10: Standard deviations for $K_0 = 0.1, K_1 = 0.1, K_2 = 0.1$. boosted= 40, starting= 1.

V. SYNCHRONY AND SEGREGATION

The spatial segregation index is a commonly used metric in animal behaviour studies [20]. In what follows, we analyze the spatial segregation within our model by computing the index in every iteration using the number of males and females in each given sector of the circle. Graphing the spatial segregation index, we find that it appears to be periodic and have a similar period to the least common multiple of the female and male cycles.

The coupling parameter a_{jl} between individuals is then introduced in the framework of our model, which controls how much agent j cares about information from agent l . This value measures female/male segregation. For this, we took the average of a_{jl} where both same sex and mixed sex groupings, referring to these as the MM, MF, and FF average values. In particular, we show that changing r , the distance agents can detect each other, can cause the MF average to slowly decouple.

In order to study the properties of our model further, we shall consider the segregation index defined as:

$$SC := 1 - \frac{C}{A \cdot B} \cdot \sum_{i=1}^r \frac{a_i \cdot b_i}{c_i - 1}, \quad (7)$$

where a_i is the number of males in the i -th circle sector, b_i is number of females in i -th sector, $c_i = a_i + b_i$, and A is number of males, B is number of females, the value of $C = A + B$ and we exclude animals in their own sector. The values of SC can be between 0 to 1, where 0 represents no segregation and 1 represents complete seg-

regation. By calculating SC over many iterations and graphing it as a scatterplot (Figure 11), we can see from the upper pair of images that it always seems to hit certain SC values as the points appear to be in “rooms”. In the lower pair of images, we can see a line plot where SC appears to be periodic, possibly due to the different length of female and male cycles, or how their cycles are offset.

The distribution of points in the upper pair of panels of Figure 11 suggests that the points are more likely to appear in rows that are either close to a SC value of 1.0 or close to 0.0, with the former being more common. Figure 11 also suggests that there is a tendency for a periodicity in the distribution of the data points. In the lower pair of panels, SC appears to suddenly spike up to 1.0 before falling again, creating a distinctly W-shaped line. This is due to males and females moving into and out of phase, causing SC to change abruptly. In this version of the model, males have a 1600 unit cycle while females have a 1900 unit cycle. The Least Common Multiple of 1600 and 1900 is 30400 which closely matches the periodicity of the graphs in Figure 11.

In Figure 12 we considered 50 males and 50 females as before. Males are set to spend 400 units of time eating, 600 resting, 300 traveling, 200 grooming, and 100 socializing. Females set to spend 300 eating, 700 resting, 400 traveling, 300 grooming, and 200 socializing. In Figure 12 (a), we see that the females and males do a better job of converging on the same sector due to the lower K_1 value, and observe much higher SC values than in Figure 12 (b), (c) and (d).

A. The impact of the coupling value

Recall that the coupling value a_{jl} measures of how much weight individual j places on information from individual l , where a_{jl} takes on values between 0 and 1, for 0 corresponding to the case where agents completely disregard each other. Using the definition of a_{jl} in Equation (8), one can deduce how to adjust the parameter r :

$$\frac{da_{jl}}{dt} = K_2(1 - a_{jl}(t))a_{jl}(t)(\rho_{jl}(t) - r). \quad (8)$$

We test for various values of r and examine its impact on a_{jl} by computing the average value for all male-male, female-female and male-female agent groupings.

Looking at the decoupling process, one can see that $r = 0.817$ leads to the longest decoupling process, and thus we consider this setting in Figure 13 (a). We start all runs at $r = 0.5$, and see the male-male and female-female average increases to 1 quickly, as is expected. Moreover, we see the female-male average initially grows to above 0.8 before decreasing and increasing in cycles as their phases go in and out of synchrony. At approximately 6000 iterations, we see the male and female groups completely decouple.

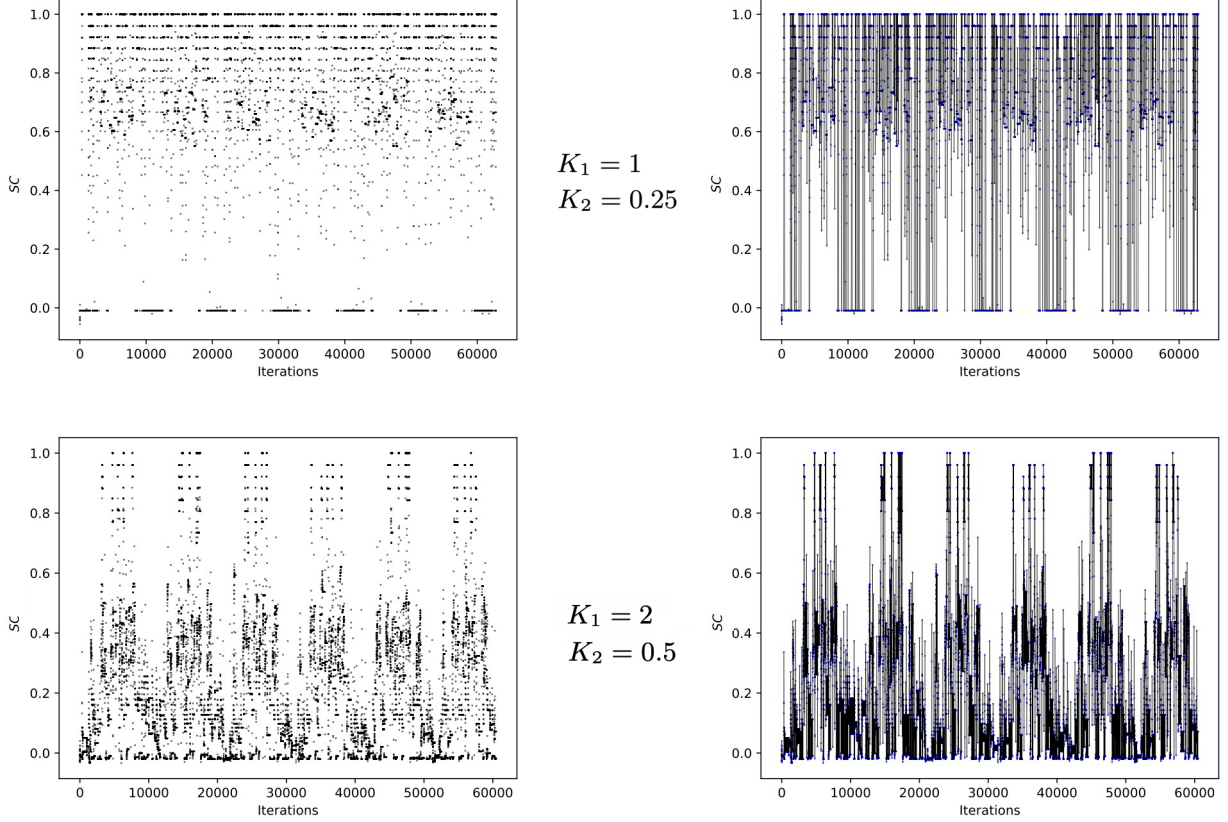


FIG. 11: Plots done for 50 males, 50 females. Males spent 400 units of time eating, 600 resting, 300 traveling, 200 grooming, and 100 socializing. Females spent 300 eating, 700 resting, 400 traveling, 300 grooming, and 200 socializing. Top: $K_1 = 1$, $K_2 = 0.25$. Bottom: $K_1 = 2$, $K_2 = 0.5$

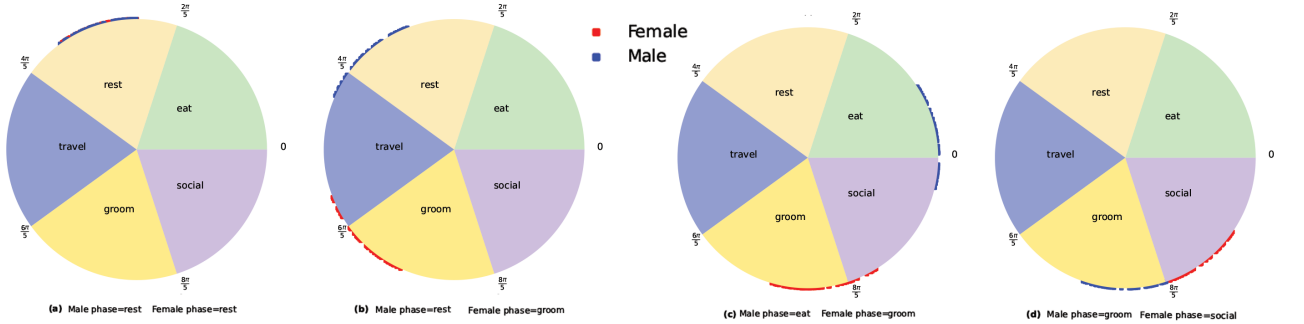


FIG. 12: Values of $K_1 = 1$, $K_2 = 0.5$ seen at different iterations: (a) 500 iterations with $SC = -0.010101$, (b) 7350 iterations with $SC = 0.749565$, (c) 13100 iterations with $SC = 0.7312$, and (d) 18950 iterations with $SC = 0.92157$.

In Figure 13 (b), we use $r = 0.81$ and see a gradual increase in the average coupling value for females-to-males. The coupling value appears to increase rapidly in the beginning as $(1 - a_{jl})a_{jl}$ is maximized with $a_{jl} = 0.5$ and in the beginning the phases of males and females are relatively in synchrony. We then see periodic dips and in-

creases except with much smaller amplitude and period (Figure 13 (a)). Overall, there is an upwards trend that begins to approach 1.0. Based on additional trials with r , we can conclude that values of r less than or equal to 0.81 will not result in decoupling but will instead result in convergence to 1.

In Figure 13 (c), we use a value of $r = 0.85$. We see the female-to-male average increase to slightly below 0.8, which is lower than in Figure 13 (a). We then see it quickly decouple to an average 0. Although there are some dips, there does not appear to be a clear cycle. In addition, it is worth noting that the female-female as well as male-male averages take longer to converge to 1. Using information from other trials, we conclude that the greater r gets, the faster the female-male average decouples to 0.

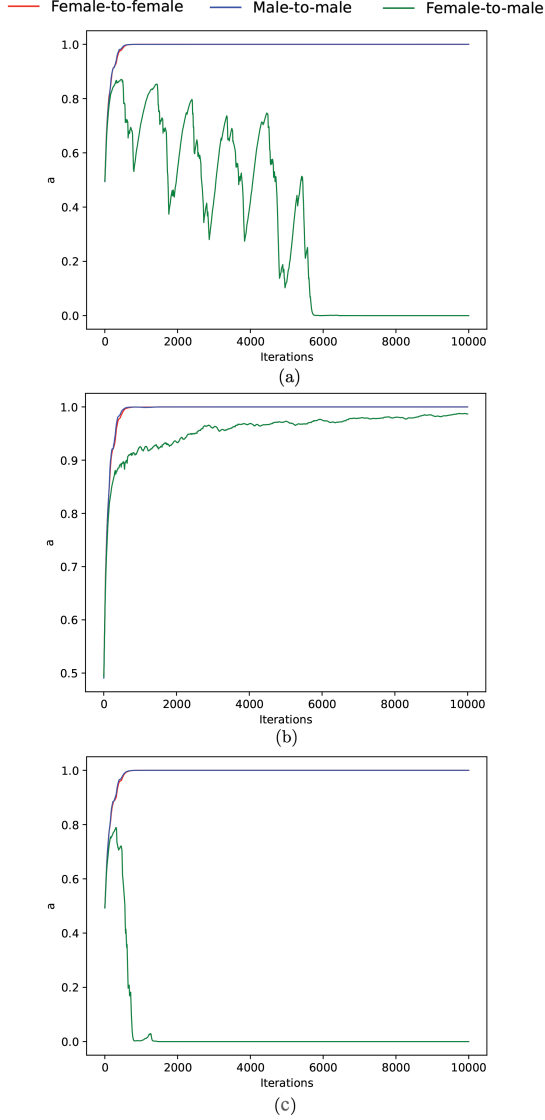


FIG. 13: A long, cyclic decoupling process. As before, we have 50 males and 50 females. Males spend 40 units of time eating, 60 resting, 30 traveling, 20 grooming, and 10 socializing. Females spend 30 units of time eating, 70 resting, 40 traveling, 30 grooming, and 20 socializing. Note that this is scaled down by 10 from previous experiments to save computational time. Values of $K_1 = 2, K_2 = 0.1$ for (a) $r = 0.817$, (b) $r = 0.81$ and (c) $r = 0.85$.

To understand our model better, we focus on a two-state setting, with just rest and forage with an average ratio of approximately 20 move and 80 stay. For this, we consider a model where males spend 19 units eating and 81 units rest, while females spend 21 units eating and 79 units resting. This setting results in the same cycle length for both males and females (Figure 14).

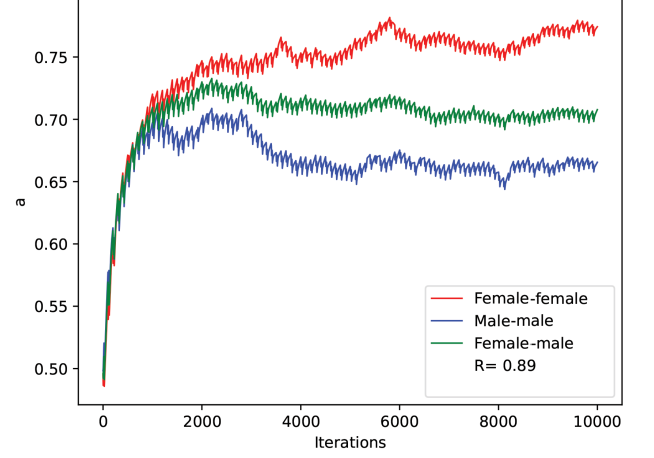


FIG. 14: Males spend 19 units of time eating and then 81 resting while females spend 21 eating and then 79 resting. Parameters set to $K_1 = 2, K_2 = 0.1$ and $r = 0.89$.

Notice that the synchrony in female-male groupings is higher than that of the male-male synchrony groups. For only two iterations, males and females in the same grouping are not all in the same sector, so one would expect FF, MM, and MF to all have the same synchrony.

Since in this simplified case the sectors are large, it is possible for two agents that are in different sectors to be more in synchrony than those who are in the same sector. To model this behaviour, we consider a multiplier m in Equation (9), in such a way that if the agents are not in the same sector, m is lower, leading to the following:

$$\frac{da_{jl}}{dt} = K_2(1 - a_{jl}(t))a_{jl}(t)(m\rho_{jl}(t) - r). \quad (9)$$

In Figure 15 (top), we successfully have the female and male groups decoupling while male-male and female-female stay coupled. It is worth noting that the male and female lines appear to hover around 0.7. It seems unlikely that they will ever completely couple to 1.0 considering that each sector is so large. In Figure 15 (bottom), we use the same parameters (but not the same seed) as in Figure 15 (top) but run it for 10 times as long, and see that, after initially peaking, MM and FF synchrony decreases.

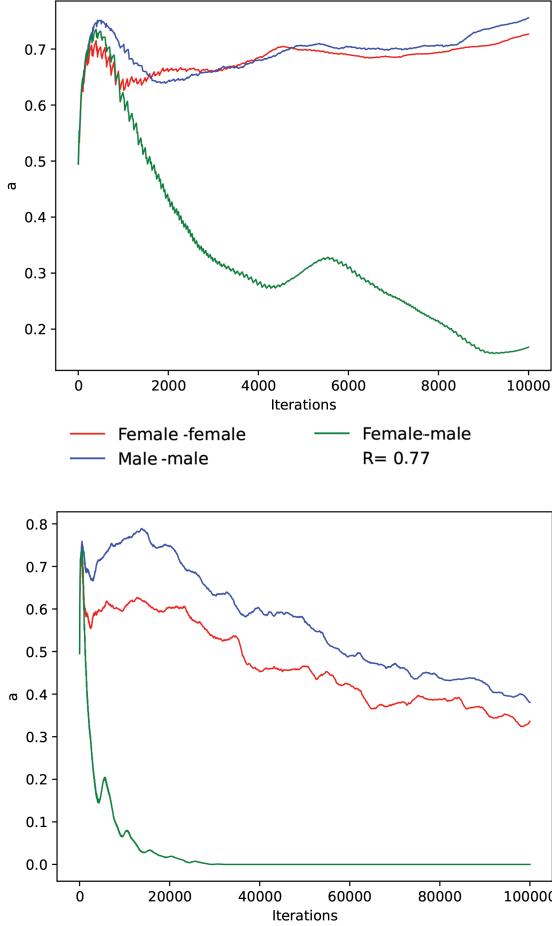


FIG. 15: (Top) $r = 0.77$. Males spend 21 units of time eating and then 80 resting while females spend 19 eating and then 80 resting. $K_1 = 2, K_2 = 0.1$. $m_{\text{same sector}} = 1, m_{\text{different sector}} = 0.8$; (Bottom) $r = 0.77$. Males spend 21 units of time eating and then 80 resting while females spend 19 eating and then 80 resting. $K_1 = 2, K_2 = 0.1$. $m_{\text{same sector}} = 1, m_{\text{different sector}} = 0.8$.

VI. CONCLUSIONS

In natural primate social groups, animals risk the fragmentation of groups if individuals' activity schedules become desynchronised during daily foraging. To avoid this, species need strategies that increase the stickiness, or gravitational pull [27], that causes individuals to coordinate their activities. Failure to do so results in groups fragmenting and hence the loss of the benefits gained from living in large social groups. Through the synchrony model introduced in our paper, we are able to see key features of social behaviours:

- (I) The impact of disparate activity schedules and stickiness (as represented by the parameter t) on group cohesion;
- (II) The existence of thresholds for group fragmentation;

- (III) The relevance of synchrony models to natural systems and social bonding mechanisms.

Our analyses indicate that the more disparate the activity schedules of group members (here simplified to just two phenotypes, conveniently labelled males and females, but they could be lactating versus non-reproductive females, or adults versus immatures that differ in body size and hence energetic demand), the more likely groups are to fragment. Furthermore, this tendency is exacerbated by lower values of r , the stickiness between individuals. The study demonstrates that disparate activity schedules among group members, coupled with lower stickiness, can lead to group fragmentation.

Although we have focused on establishing proof of principle rather than finding exactly what magnitude of these values causes a phase transition between a cohesive group and a fragmented one, our analysis reveals that there is a critical threshold, around $r = 0.75$, where groups transition from being cohesive to fragmented. Indeed, through our model one can see that the transition between a single coherent group and a fragmented one occurs quite suddenly in a distinct phase transition when the stickiness variable reaches such value. This is rather high, and implies that the average degree of stickiness between individuals (however that is measured in practice) needs to be quite substantial.

Since differences in activity schedules are usually determined by differences in body mass or reproductive state (e.g. pregnant and lactating females have higher feeding demands than non-reproductive females), the one parameter that animals can manipulate in order to reduce the risk of group fragmentation is r , the stickiness. This they can do increasing bonding activities like social grooming that create attraction between individuals [4, 22]. Our findings here thus reinforce the suggestion that some mechanism to underpin social bonding becomes necessary for animals to be able to live in large stable social groups.

We have not, at this point, explored the consequences of either the full range of values of a_{jl} or r , or of group size. Rather, our aim here has been to establish the principle that uncoupled activity schedules causes fragmentation of groups, and that this can be counteracted by increasing the stickiness, or gravitational pull, between individuals. Finally, it should be noted that in our model we have not attempted to encode day/night preferences, which leads to the animals not aligning their sleep schedule with the day/night cycle. Since this would, in the limit, result in different subsets of animals in the group sleeping at opposite times of the 24h cycle, we may presume that this is unlikely to occur with any frequency if animals want to live in stable social groups. It would therefore be very interesting to extend our model to include further parameters which influence animal cycles, such as the constraints arising from day/night cycles in regions where those are considerable, and to further consider the influence of group size.

Data Availability. No live vertebral animal was used in our study and no animal data was used. All the datasets were generated. The datasets generated and/or analysed during the current study are available in the Github repository [28] found in <https://github.com/sher222/Animal-Synchrony>.

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