

Inferring influence and its localizability in a baboon troop with an information-theoretic approach

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Abstract:

Inferring the differential influence that animal groupmates have on their group's decision-making process has important implications for the evolution of sociality. However, tools for inferring causal relationships from observational data remain elusive. In this project, I used newly developed information-theoretic approaches to quantify influence in a troop of wild olive baboons in Kenya. I found an interesting characteristic of the non-stationary influence flow wherein the rate of influence flow increases simultaneously with an increase in the quantity of influence flowing. I also found that influence is temporally dynamic and surprisingly non-hierarchical, indicative of a shared decision-making process. Most importantly, I found that up to 84% of influence over groupmates is non-localizable. These substantial polyadic dependencies demonstrate that influence is socially and temporally context-dependent. Thus, as context continuously varies, so too does influence. With highly variable influence, consensus costs are ultimately shared, which helps explain how sociality could evolve despite the often conflicting interests of groupmates.

Introduction

Motivation:

Social animals receive a variety of benefits from living in a group, including dilution of predation risk, improved resource defense capabilities, and increased access to social information (Krause & Ruxton 2002). Unlike their solitary counterparts however, group-living organisms face the challenge of having to collectively decide on where and when to move in their environment (Conradt & Roper 2005), with severe costs of failure to reach consensus and maintain cohesion (Krause & Ruxton 2002). After several decades of research, the process by which animals make these collective decisions is still an area of active research.

Group members likely have differential ability to influence their group's decision-making process in most animal groups, and this heterogeneity has significant consequences for a group's movement dynamics (del Mar Delgado et al. 2018). With conflicts of interest essentially unavoidable in animal groups (Shen et al. 2013), groupmates also often have different preferred destinations, or direction and timing of travel due to within-group variation in physiological capabilities, nutritional requirements, predator vulnerabilities, or reproductive opportunities. Therefore, differential influence over group movement fundamentally affects the way each individual experiences group life and the costs and benefits that sociality confers upon it. Because natural selection acts on individual agents, and rarely the group as a whole, understanding the costs and benefits of sociality to *each* group member, and not the *average* group member, will be key to understanding how sociality evolved (Strandburg-Peshkin et al. 2018). Furthermore, the evolution of sociality offers several parallels to the evolution of multicellularity (Shen et al. 2013). Therefore, an investigation of the influence structure of complex animal groups, with implications for how within-group conflicts of interest are resolved, will shed light on essential questions in biology: how and why did multicellularity and sociality evolve?

Due to theoretical differences in the spatial targets of groupmates, the leadership structure of animal groups also affects our predictions of where and when animals will move in their environment (King et al. 2011). These predictions lie at the heart of collective movement ecology and can be used not only to understand how animals interface with the natural world, but also to develop critical conservation and management policies (Allen & Singh 2016). Therefore, understanding the flow of influence in animal groups could help maintain healthy animal populations.

Despite its instrumentality to our understanding of collective movement ecology and, more generally, the evolution of sociality, the investigation of influence and leadership in animal groups remains underdeveloped. This can be partially attributed to a historical lack of data sufficient to explore complex dynamics in animal groups. With recent technological advances

that allow for continuous and simultaneous monitoring of all, or at least most, group members (Cagnacci et al. 2010, Kays et al. 2015), a dearth of data is no longer the problem. Our data has surpassed the tools and intuition that we have to analyze it. I believe this problem can be solved with an information-theoretic approach, presented herein, aimed at quantifying and localizing the flow of influence through a complex network.

Synopsis:

In this project, I set out to infer the influence structure of an olive baboon (*Papio anubis*) troop, using information-theoretic measures to analyze time-series data of each troop member's position and acceleration. Data was collected on each baboon simultaneously using animal-mounted bio-loggers. The goal was to analyze the flow of causation entropy in the baboon troop to determine an influence hierarchy and assess the stability and linearity of this hierarchy. This goal eventually led me to use intrinsic mutual information to localize the influence flow in the baboon network and to quantify polyadic dependencies in the influence network. While I did not discover an overt influence hierarchy, several more interesting results, stemmed from this objective.

As I searched parameter space for an appropriate sampling rate of the time series, I found a statistically significant direct relationship between the quantity of influence flow at a given time and the sampling rate that optimizes the influence flow at that time, suggesting that when influence flows at high quantities, it also flows quickly. These spikes of the rate and quantity of influence flow correspond temporally to major decision-making time periods in the baboons' day. There was also a highly symmetrical structure to the causation entropy flow; when an individual has a strong influence over another individual, it is also often highly influenced by that other individual. This may indicate that while no individual is consistently more influential than its groupmates, certain individuals partake in the group's decision-making process more than their peers.

An intrinsic mutual information approach reveals that up to 84% of an individual's influence over its groupmates, as determined by causation entropy, actually cannot be attributed exclusively to that particular individual. Rather, polyadic dependencies appear to comprise a non-trivial component of the baboon influence network. These influence synergisms reveal that leadership in a baboon troop is highly context-dependent. The lack of hierarchical structure of the causation entropy flow could therefore be a result of a continuously varying social and temporal context.

Background

Definitions:

To provide context for the rest of this report, I provide here the definitions of the information-theoretic measures to which I refer throughout the report. Each definition is taken from the reference cited after it.

Definition 1: Shannon entropy

Let X be a random variable that assumes the values $x \in \mathcal{X}$, where \mathcal{X} 's a finite set. We denote the probability that X assumes the particular value x by $\Pr(x)$. The Shannon entropy of X is defined by:

$$H[X] \equiv - \sum_{x \in \mathcal{X}} \Pr(x) \log_2 \Pr(x)$$

The Shannon entropy of X is non-negative, and its units are bits. The entropy of a random variable measures its uncertainty (Crutchfield & Feldman 2003).

Definition 2: Conditional entropy

$$H[X|Y] \equiv - \sum_{x \in \mathcal{X}, y \in \mathcal{Y}} \Pr(x, y) \log_2 \Pr(x|y)$$

The conditional entropy measures the average uncertainty of associated with one variable, X , given that we know another variable Y (Crutchfield & Feldman 2003).

Definition 3: Mutual information

$$I[X; Y] \equiv H[X] - H[X|Y]$$

The mutual information is the average reduction of uncertainty of one variable, X , given the knowledge of another variable, Y . The mutual information is non-negative (for the two-variable mutual information), and $I[X; Y] = 0$ when X and Y are independent or when either $H[X] = 0$ or $H[Y] = 0$. (Crutchfield & Feldman 2003)

Definition 4: Transfer entropy

$$T_{X \rightarrow Y} = I[Y_t : X_{0:t} \mid Y_{0:t}]$$

$$T_{X \rightarrow Y} = H[Y_t \mid Y_{0:t}] - H[Y_t \mid Y_{0:t}, X_{0:t}]$$

The transfer entropy from time series X to time series Y is the mutual information between X 's past and Y 's present state, conditioned on Y 's past (James et al. 2016). The second definition explicitly shows that transfer entropy measures the amount of uncertainty of Y 's present state that is reduced by knowing X 's past state, given that we already knew Y 's past state.

Definition 5: Causation entropy

$$C_{X \rightarrow Y \mid (Y, Z)} = I[Y_t : X_{0:t} \mid Y_{0:t}, Z_{0:t}]$$

$$C_{X \rightarrow Y \mid (Y, Z)} = H[Y_t \mid Y_{0:t}, Z_{0:t}] - H[Y_t \mid Y_{0:t}, Z_{0:t}, X_{0:t}]$$

The causation entropy is similar to the transfer entropy, but conditions on the past of a third (or more) time series, represented here by Z , that might also affect the uncertainty of time series Y 's present state. The causation entropy *aims* to determine Y 's direct dependence on X (James et al. 2016).

Definition 6: Intrinsic mutual information

$$I[X_{0:t} : Y_t \downarrow Y_{0:t}] = \min_{p(\bar{y}_{0:t} \mid y_{0:t})} I[X_{0:t} : Y_t \mid \bar{Y}_{0:t}]$$

The intrinsic mutual information represents the information that X 's past and Y 's present state share that is inaccessible to Y 's past. It correctly fulfills the aim of causation entropy: quantifying Y 's direct dependence on X (James et al. 2018). The intrinsic mutual information is derived from the secret key agreement rate (Maurer 1993). Applied to the variables presented here, the secret key agreement rate is the rate at which X 's past and Y 's present can agree upon a secret key with Y 's past eavesdropping. The intrinsic mutual information provides a measure of the influence on Y 's present state that came exclusively from X 's past. Conditioning on further variables, here represented as Z , provides a measure of the influence that X intrinsically has on Y , independent of Y 's past and Z 's past. Therefore, I will be using the following form of intrinsic mutual information for my analysis.

$$I[X_{0:t} : Y_t \downarrow Y_{0:t}, Z_{0:t}]$$

Relevant information:

The study of collective decision-making has deep roots in the field of animal behavior. The first studies of collective animal behavior, dating back to the early 20th century, readily recognized that groups of animals often outperform solitary animals when faced with a decision (Wheeler 1910). This phenomenon of collective intelligence has since received thorough investigation, revealing the mechanisms by which some complex animal societies collectively reach decisions (Sasaki & Pratt 2012, Seeley 2010, Couzin et al. 2011). Most of this research, however, has focused on eusocial insect societies, in which high within-group genetic relatedness and heavy dependence on indirect fitness renders conflicts of interest among groupmates essentially non-existent. Without conflicts of interest, these decisions are often highly democratic (i.e. shared decisions, Conradt & Roper 2005). While the information acquisition, information sharing, voting mechanisms and high levels of coordination that these shared decisions necessitate are impressive, they lack a fundamental challenge that most animal groups face: conflicts of interest among group members.

Conflicts of interest are pervasive in most animal groups (Shen et al. 2013). When conflicts of interest occur within animal groups with stable group membership, some individuals are destined to experience consensus costs – the cost foregoing a preferred destination or activity in order to remain with the group (King et al. 2008). Based on optimality theory, every groupmate is theoretically inclined to direct the group towards their own preferred destination in order to eliminate consensus costs (Conradt & Roper 2009). A differential ability to exert this influence over one's groupmates results in differential contributions to the group's final decisions. Therefore, within-group heterogeneity creates the opportunity for unshared decision-making; a single group member or subset of group members make a decision by which the rest of the group abides (Conradt & Roper 2005). The resulting differential influence over the group's decisions has significant biological implications (see Introduction).

Olive baboons are an ideal organism in which to investigate differential influence, as significant variation in personality, relatedness, social dominance, and physiology within a troop produces a high degree of inter-individual heterogeneity (Cheney & Seyfarth 2008, Seyfarth et al. 2012, Seyfarth et al. 2014). This heterogeneity creates significant conflicts among groupmates in their optimal activity budgets and movement dynamics (Conradt & Roper 2000).

Several existing theories predict when and why an individual should be more likely to exert its influence over the group's decision-making process (Couzin et al. 2005, Conradt et al. 2009, King et al. 2009). While many of these theories have been validated with agent-based models, their predictions remain largely untested empirically. This is no doubt due to the difficulty associated with inferring causal relationships from (often imperfect) observational data. Animal groups are recognized as complex systems (Koorehdavoudi & Bogdan 2016), and discovering the causal structure of any complex system is a challenging task (Sun et al. 2015).

Several methods have been used to try to infer influence in animal groups. Within-group spatial positioning is often used to infer leadership, with individuals at the front of the group assumed to be leading the group (Smith et al. 2015). An individual's probability of being followed after initiating a movement has also been used to infer influence (Strandburg-Peshkin et al. 2015). Past studies have inferred influence from the final destination of a group, based on the assumed spatial goals of different individuals (King et al. 2008). Essentially, the group member whose preferred destination was achieved by the group is assumed to have had the most influence. Studies of fish and birds often used time-lagged directional correlations to determine influence (Nagy et al. 2010). While each of these methods has its own inherent challenges and issues, they all leave a more direct measure of causality to be desired and provide only a weak quantification of the influence they aim to infer. Moreover, studies using these methods find conflicting results. In baboon troops, studies inspecting the probability of being followed and inferring influence from final destinations suggest that dominant, highly social individuals have a disproportionately large influence over collective decision-making (King et al. 2011), but a more thorough study using high-frequency locational monitoring of baboons used the probability of being followed to find that decisions are largely shared (Strandburg-Peshkin et al. 2015).

Information-theoretic measures offer promising methods to reliably quantify influence flow between time series of observational data, including data on animals' positions and movements (Garland et al. 2018, Strandburg-Peshkin et al. 2018). Several previous attempts to use information theory to determine influence in animal groups employed transfer entropy to infer the influence that a member of a dyad has over its counterpart (Butail et al. 2014, Butail et al. 2016). However, as Butail et al. note (2016), transfer entropy conflates correlation with causation in systems with more than two interacting individuals. Specifically, transfer entropy measures cannot distinguish between the follow situations: 1) individual A follows B and B follows C, and 2) individuals A and B both exclusively follow C, but B does so first. Because of this conflation, transfer entropy is not an appropriate measure to determine causal relationships complex systems that, by definition, are composed of more than two components. Despite this shortcoming, a transfer entropy analysis not specifically aimed at inferring causation can shed light on the general characteristics of influence flow in a network, such as the rate of influence flow (Borge-Holthoefer et al. 2016).

Causation entropy presents a much truer measure of causality in complex animal networks, by conditioning on every other component of the network when determining the flow of influence between a dyad (Garland et al. 2018, Lord et al. 2016, Sun et al. 2015). Causation in a dyad can be entirely disentangled from correlation when one conditions all over potentially influential variables (note: I do not mean to imply that this is a simple task, as the *potential* influences can enumerate to a countable infinity). While perfectly conditioned causation entropy can quantify causal influence, it cannot, however, localize the influence to its source (James et al.

2016). Due to the potential for conditional dependence, causation entropy (and transfer entropy) from one individual to another represents both the influence that the first individual has on the second *and* any polyadic influence on the second individual in which the first individual is involved. Using causation entropy to infer influence in an animal group may therefore attribute influence to one individual, even if that influence depends entirely on the past states of other individuals in the group (i.e. it is social context-dependent). Thus, causation entropy can determine the influence over groupmates to which an individual contributes but cannot actually quantify the influence that the individual directly imposes on its groupmates. Fortunately, James et al. recently developed a measure, the intrinsic mutual information, that uncovers this quantity (2018). In doing so, they also developed a method to quantify, but not necessarily localize, the polyadic dependencies (also referred to as synergisms henceforth) in the network of influence.

My study aims to use causation entropy to quantify causal influence flow through the complex system of a baboon troop. I also aim to perform a partial information decomposition, enabled only by the recent development of the intrinsic mutual information (James et al. 2018), to attempt to understand the influence structure and localizability of influence in the baboon troop. Together, these analyses will shed light on how animals reach a consensus concerning where and when to move in their environment.

System

I am focusing my investigation on a troop of olive baboons at Mpala Research Centre in Kenya (Fig. 1). Olive baboons are highly social, living in large, stable groups that sometimes contain over 100 individuals (Cheney & Seyfarth 2008). Baboons exhibit male-biased dispersal with female philopatry and thus, groups consist of several matriline. Genetic relatedness is high within matriline, but relatedness between baboons of different matriline (in the same group) is quite low; it is roughly equivalent to the relatedness between baboons in completely different groups. Baboons have strong linear dominance hierarchies, and female rank is maternally inherited and highly stable. Males are dominant to females, but their rank is unstable and tightly correlated with competitive ability. Baboons exhibit extreme sexual dimorphism, with males about twice the size as females, creating high variation in body size within the group. Groupmates also have distinct personalities that are not always correlated with their dominance (Silk et al. 2012). Significant inter-individual variation in physiology, dominance, relatedness, and personality create considerable conflicts of interest amongst baboon groupmates.

A baboon's state space is $N*(2+K)$ dimensional, where N is the number of baboons in the troop, and K represents the dimensionality of their internal state. The remaining dimensionality derives from the baboon's current two-dimensional positional location (note: baboons are largely terrestrial, so we do not need to consider a third positional dimension). Examining the structure

and complexity of the baboon's internal state to quantify K will certainly inform how baboon's make decisions as a group. While I plan to complete this examination in the future, it is beyond the scope of the current project. The quantity of K is likely substantial, as baboon's have significant cognitive capabilities (Forster 2002). The high dimensionality of the system, mostly due to the N interacting components of the system, causes it to have non-linear and complex dynamics.

The baboon's alphabet, for this analysis, is binary; it can choose to either move or remain stationary. Several factors influence this decision, including the baboon's internal state, the states of its groupmates, other biotic factors (e.g. heterospecific predators or conspecific competitors), and abiotic factors (e.g. weather, temperature). Of these potential influences, I only have data on the states of the baboon's groupmates, and thus this potential influence will be the focus of the project. A future project will investigate baboons' internal states by analyzing their movement using computational mechanics.

The flow of influence in a baboon troop is non-stationary. Theory suggests that self-organized leadership can result from heterogeneity of groupmates' internal states, referred to as "leading according to need" (Conradt et al. 2009). Even in systems, like baboon troops, where a structural component likely compliments an self-organized component of leadership (King et al. 2011, Strandburg-Peshkin et al. 2018), temporally varying internal states likely causes the influence network to be non-stationary. Despite this complexity and non-stationarity, baboon troops still invariantly reach a consensus when making decisions as a group. This feat makes the system particularly worthy of investigation.

Methods

Data:

I obtained my data from Strandburg-Peshkin et al. (2015). This data consisted of the GPS locations (sampled at 1 Hz) and the tri-axial accelerations (sampled at 10 Hz) of 26 members of a troop of wild olive baboons at Mpala Research Centre in Kenya. The bio-logging collars took data every day from 6:00 to 18:00 for roughly 30 days. These 26 baboons represent over 80% of the adults and subadults in their troop (Table 1). For this project, I discretized the accelerometer data to a binary alphabet; at any given time, a baboon was either stationary or moving. I performed this discretization by setting a threshold on the overall dynamic body acceleration (ODBA) below which a baboon was very unlikely to be walking and above which a baboon was very unlikely to be stationary. I proceeded with the rest of the analysis using only the first day of data (2012-08-01) for the causation entropy analysis and seven minutes and ten seconds of data from a later date (2012-08-11) for the intrinsic mutual information and partial information decomposition analysis.

Causation Entropy Analysis:

I first divided the day into ten identical length time periods (each 72 minutes long). For each time period, I created a probability distribution of each individual's past and current stop-go states from its time series for that time period using the *dit* package in Python (James 2017). I decided on a history length (number of past states considered) for this distribution by choosing the maximum history length that did not overwhelm my computer's random-access memory (RAM) within 24 hours. For the whole group analysis, this history length was one. Using the distribution, I calculated the causation entropy from one group member to another group member for every dyadic permutation (not combination, as causation entropy is not inherently symmetric) in the group for each time period separately. In words, the causation entropy represents the mutual information between one individual's past and another individual's present state, conditioned on the past of every other group member. I represented the outcome of these calculations as an $n \times n$ matrix, with the individual imparting influence represented by the rows of the matrix and the individual being influenced represented by the columns of the matrix, where n is the number of individuals included in the analysis; n equals 26 for this analysis.

Downsampling the original data was necessary, as I do not know that a baboon can even respond to another baboon's potential influence within a tenth of a second. Intuition did not provide an appropriate *a priori* sampling rate, and so I carried out the preceding calculations with several different sampling rates. I calculated a causation entropy matrix with a sampling interval of every integer second between 1 and 15, inclusive. I summed the causation entropy for each matrix and kept the matrix for analysis that had the highest total causation entropy flow as determined by the sum of its elements. This process occurred once for each 72-minute time period.

Once I had the maximized causation entropy matrix for each time period, matrices were ordered by their row sums, so that the most influential individuals were at the top of the matrix and the least influential individuals were at the bottom. The hierarchical structure of the matrix, σ , was then determined by dividing the upper right triangle of the matrix by the lower right triangle of the matrix. I then calculated the *net* causation entropy between each dyad by subtracting the transpose of each causation entropy matrix from the original matrices. I ordered the net causation entropy matrices by their row sums as well, with individuals at the top having a high total net causation entropy and individuals at the bottom having a low total net causation entropy.

My analysis for the group as a whole stopped here. I learned from my experience with this project that these information-theoretic measures are highly sensitive to history length. Thus, to more realistically measure the influence flowing between groupmates, I chose to focus my calculations on a subset of the whole group, which allowed me to increase the history length to two. I chose to analyze the eight adults in the group. An attempt to measure causal influence

necessitates conditioning on every other potentially influential variable. In choosing to analyze only eight individuals, I recognize that I have not appropriately conditioned to necessarily infer causality. However, my subsetting is biologically informed, as older individuals are typically more likely to be involved in the group's collective decision-making (Brent et al. 2015, McComb et al. 2001, Seeley 2010). I therefore continue with my analysis of this subset, henceforth called the adult group.

I repeated the same analysis described above for the whole group with the adult group, with some additions. When determining the appropriate sampling interval at which to measure causation entropy, I recorded the highest total causation entropy sum and the sampling interval that produced it. I then tested for a relationship between the causation entropy flow at a given time period and the sampling rate (in Hz) that maximized this total flow using a generalized linear model. I also tested for a correlation between the speed of the group's movement, as a proxy for when the group might have to make collective decisions, and total causation entropy flow using a generalized linear model. I similarly tested for a correlation between the speed of the group's movement and the sampling rate that maximized causation entropy flow. (Note: I wish I had done this analysis for the whole group, but I did not think to record the optimizing sampling interval when I carried out the calculations).

I then combined the adult group's causation entropy matrix from each time period into a dynamic network to visualize the temporal dynamic of influence flow in the baboon troop. I produced this dynamic network using `networkDynamic` and `ndtv` packages in R (Allaire et al. 2017, Bender deMoll 2018, R Core Team 2018). In the network, vertex size represents the individual's total causation entropy at a given time, and edge weights represent the net causation entropy between the dyad that the edge connects. Negative net causation entropies were set to zero, as negative edge weights are not possible.

Localizing the influence:

Intrinsic mutual information calculations were not possible for the adult group or the whole group, given my computing power. To avoid ignoring variables that could be influencing the system (as I did for my adult group analysis), I focused this analysis on two subgroups that were spatially isolated from the rest of the group during the time on which this analysis focuses. Thus, these subgroups were unlikely to be influenced by other groupmates on which I did not condition. One subgroup, referred to as the small subgroup, consisted of three individuals, and the other subgroup, referred to as the large subgroup, consisted of five individuals. My computing power allowed for a history length of three for the small subgroup and a history length of two for the large subgroup. As the duration of the data on these subgroups is only about seven minutes, I did not separate the time series of each baboon into several time periods, as I did above.

A causation entropy matrix for each subgroup was calculated using the same methods used for the whole group and adult group. Because the calculations ran fastest on the small subgroup, I created a causation entropy matrix for every sampling interval from 0.1 seconds to 20 seconds, by 0.1 second increments. The sampling interval that maximized the total causation entropy flow was two seconds. I arbitrarily used this same sampling interval for the large subgroup, because the observations for each subgroup were concurrent, and I thought it to be a safe assumption that influence would flow at relatively similar rates in two subgroups of the same total group, if the observations were concurrent. (Note: computation time was a limiting factor for many of these analyses).

Intrinsic mutual information matrices were calculated using the sampling rate and history lengths as that used for the causation entropy matrices. I used the IMI function in *dit* to calculate the *intrinsic* mutual information between one individual's past and the present state of another individual, given every other individual's past (this includes the past of the individual receiving influence). This quantity represents the minimum information that one individual's past shares with another individual's present, given all possible functions of other individuals' pasts.

Using the intrinsic mutual information, I performed a partial information decomposition. In doing so, synergism matrices were calculated by subtracting each subgroup's intrinsic mutual information matrix from its causation entropy matrix. These matrices represent any influence that cannot be localized to the influencing individual. They depict influence that an individual has on another individual that is dependent upon any other individual, or combinations of individuals, in the group and/or dependent upon the past of the individual receiving influence. I also calculated the amount of shared information between dyads (= time-delayed mutual information - intrinsic mutual information) to complete the partial information decomposition, but I do not present the results here as it is outside of the scope of this report. I then quantified the proportion of influence flow between each dyad that is not localizable, by dividing the synergism matrix by the causation entropy matrix for each subgroup.

In an attempt to isolate the component of synergy that exists between two groupmates in influencing a third groupmate (i.e. remove the possibility that the synergy involves the past of the individual receiving influence), I also calculated a transfer entropy matrix and intrinsic mutual information matrix that did not condition on other individuals, for the small subgroup. The transfer entropy matrix represents mutual information between an individual's past and another individual's present state conditioned on the past of only the individual receiving influence (not all other groupmates). I subtracted from this matrix the intrinsic mutual information between one individual's past and the other individual's present state, again conditioned only on the second individual's past state (not all other groupmates). I then believed I had a synergy matrix that represented the synergy between an influencing individual and the past of the individual receiving influence. I subtracted this two-party synergism matrix from the

non-isolated three-party synergism matrix generate previously. (Note: two party matrices are not presented in the Figures sections). I hoped to have removed the component that the past of the individual receiving influence contributed to the total synergy in influence from the total synergism matrix to produce a synergism matrix that denoted the synergy between an individual and its groupmate in influencing their third groupmate.

Results and Discussion

Causation entropy analysis:

As displayed in Fig. 2-5, the influence hierarchy of the baboon troop appears non-existent, or at least highly unstable. Fig. 2 suggests that individual 2457 has a disproportionate influence over the whole group's movement decisions and Fig. 4 suggests that 2457 and 2447 have a strong influence over the adult group's movement, as these individuals are the source of a relatively high amount of causation entropy in several time periods throughout the day. However, as represented by the amount of symmetry in these matrices, even though these individuals have a strong influence over their groupmates, they are also strongly influenced by their groupmates. This phenomenon is more explicitly represented in Fig. 3 and Fig. 5, which shows that these individuals do not have a disproportionate *net* influence over their groupmates. Because the causation entropy matrices were so highly symmetric, I believe that the analysis of the net entropy matrices underrepresents some interesting results.

The symmetry of the causation entropy matrices itself is worth discussing. As these measures are not spatially explicit, I would have expected some symmetry in the matrix, where individuals in proximity influence and are influenced by their neighbors more often than non-neighbors. A comparison of the causation entropy matrices to a spatial cluster analysis could inform this hypothesis. However, this explanation of the symmetry does not explain the symmetries that are not locally isolated in the matrix. For example, the individual that has the most influence at any given time is also highly influenced by almost all other individuals. This influential individual cannot possibly be a neighbor to all of its groupmates. My best interpretation is that, even though an individual may not be particularly influential over the group's decision (as determined by *net* causation entropy), it may be especially active in the decision-making process. Over time, this individual would influence others more than the average group member, but it would also be influenced by others more than average. This interpretation is consistent with reports of baboons that do not have higher success rates of initiating group movements *per se*, but persistently attempt to influence their groupmates nonetheless (Dr. Meg Crofoot, personal communication).

The dynamic network (Vid. 1) shows the temporal dynamics of influence and net influence flow amongst the adults of the baboon troop. This provides a visual to confirm the

result that the structure of influence flow is unstable. As Vid. 1 depicts, the amount of influence that a given individual has (represented by vertex size) consistently varies throughout the day and the net flow of influence between dyads (represented by edge width) is highly dynamic. Even the direction of net influence between dyads is not static. Although the visual analysis presented to this point seems reliable, I will confirm this analysis with statistical methods at a later date.

An interesting result arose from the process of finding the sampling interval that optimized the total amount of causation entropy flow amongst the adult group (see Methods). There was a strong correlation between the total causation entropy flow and the sampling rate that optimized its flow (Fig. 6). This correlation had strong statistical significance ($p < 0.005$). Thus, when influence flows at high quantities through the baboon troop, it also flows faster.

Increases in the quantity and speed of causation entropy flow appear to correlate with times of the day when baboons have to make collective decisions. As Fig. 7 attempts show (the projection of a three-dimensional scatter plot onto two-dimensions complicates visual inspection), during time period 2 and 3, the baboon troop decides to leave its sleep site and then stop for a rest. During time period 4, they make the significant decision of where they are going to forage for the day. At time period 5, they are exclusively foraging and have no decision to make. In time period 6, 7, and 8, they are in the process of deciding to return back to their sleep site. During times 9 and 10, they are on the road to their sleep site (they follow a literal road to their sleep site) and then resting in their sleep site, and thus do not require consensus decision-making. I attempted to capture the correlation between influence flow and collective decision-making, but there was no statistical significance between the speed of group travel and the total influence flow or rate of influence flow in the troop. I attribute this lack of significance to speed of group travel being a poor proxy for group decision-making. Some of the most significant decisions occur before the group is moving, and they may not be making any decisions while in transit.

The hierarchical structure, σ , of the causation entropy matrices at each time period in the adult group is also plotted in Fig. 6. Values of σ less than or equal to one indicate a lack of any hierarchical structure to the flow of influence, while values approaching infinity represent a completely linear hierarchy of influence (if A influences B which influences C, both B and C *never* influence A). Throughout the day, σ is regularly less than or equal to one, in both the adult group (Fig. 6) and the whole group (Fig. 8). This finding shows that at any given time, there is no hierarchical structure to the flow of influence. This is intuitively consistent with the temporal instability of the influence structure across the day. This result contrasts with previous findings that a baboon's ability to influence its group's movement correlates with its social dominance (King et al. 2008) but supports a more recent discovery that collective decisions in baboon groups are highly democratic (Strandburg-Peshkin et al. 2015). Results from the latter study and

this project are surprising, given the strength of the linear social dominance hierarchy in baboon troops.

Localizing the influence:

As mentioned in the Background, while causation entropy can provide interesting metrics of information flow through a network, it cannot appropriately localize the source of influence due to the potential for conditional dependence. Fortunately, the intrinsic mutual information can quantify the influence on one random variable that came exclusively from another random variable. Fig. 9 and Fig. 10 show that in both the small and large subgroups, the causation entropy is *not* equivalent to the intrinsic mutual information between dyads, which indicates that influence in the baboon group is indeed conditionally dependent. The newly developed intrinsic mutual information measure allows for a partial information decomposition, which enabled me to quantify the polyadic dependencies in the influence structure of each subgroup. Fig. 11 depicts these quantities and shows that the amount of synergism of influence in both subgroups is substantial. (I also quantified the amount of shared information between each dyad of baboons to complete the partial information decomposition, but its presentation is beyond the scope of this report). I have also quantified the proportion of an individual's influence over a groupmate that can be attributed to these synergies (i.e. the proportion of non-localizable influence) in Table 2 and 3. The non-localizability of influence in both subgroups is extraordinary. In several cases, over 50% of the influence that one individual has over another is critically dependent on the pasts of other individuals in the group and/or the past of the individual receiving the influence. In one case, almost 85% of an individual's influence depends on these synergies.

These results have significant implications for the study of collective animal behavior, and the study of complex systems more generally. Here, I have specifically quantified the non-localizability of causal influence in a complex network. In a baboon troop, an individual can influence its groupmates intrinsically or through synergistic influence relationships. These synergies are highly non-trivial and can occur within any component of the network that involves the influencing individual. These components can consist of any other groupmate or any other combination of groupmates. The synergism can even involve the past states of the individual being influenced (biological interpretation: individual B will follow A, but only after B has remained stationary for a given amount of time). Thus, influence in a baboon group is highly context-dependent, both on temporal context, as this affects the past states of each individual potentially being influenced, and on social context, as this affects the potential for polyadic influence relationships. It therefore seems that the search for leadership in animal groups has been vastly oversimplified, and fundamental theories and questions in the field are in desperate need of reassessment.

Directions forward and challenges ahead

This project potentially raises more questions than it answers, and so there are many opportunities for further research. First, a thorough biological interpretation of influence synergies requires an identification of the polyadic relationships that produce the synergisms (i.e. localizing the polyadic dependencies). Using the small subgroup, I attempted to isolate the synergy between two groupmates, X and Z, in influencing the third groupmate, Y, from the component that Y's past contributes to the synergism. This attempt (shown in Fig. 12) ultimately failed, producing some negative values of influence. Negative values resulted from finding that the synergy between X's past and Y's past in influencing Y's present could be a greater quantity than the synergy between X, Y, and Z's pasts in influencing Y's present. This confusing outcome occurred because when I ignored Z to calculate the synergy between X and Y's past in influencing Y's present, I incidentally ascribed some of the influence to the synergy between X and Y's pasts that in reality was an intrinsic influence of the Z's past. This mistake alone explains why two individuals could appear to have a greater synergy than they have when a third individual (that was present for the entire duration of interaction) is entered into the calculation. I attempted to isolate the synergy using:

$$I [X_{0:t} : Y_t | Y_{0:t}, Z_{0:t}] - I [X_{0:t} : Y_t \downarrow Y_{0:t}, Z_{0:t}] - (I [X_{0:t} : Y_t | Y_{0:t}] - I [X_{0:t} : Y_t \downarrow Y_{0:t}])$$

But what I think that I actually need to isolate the synergy is:

$$\min_{p(\bar{y}_{0:t} | y_{0:t})} I [X_{0:t} : Y_t | \bar{Y}_{0:t}, Z] - \min_{p(\bar{y}_{0:t}, \bar{z}_{0:t} | y_{0:t}, z_{0:t})} I [X_{0:t} : Y_t | \bar{Y}_{0:t}, \bar{Z}_{0:t}]$$

Clearly, the next step is to develop this measure, so that I can localize polyadic dependencies in the flow of influence and test these dependencies for correlations with known polyadic affiliative relationships in the baboon troop. Unfortunately, the number of potential polyadic relationships experiences exponential blow-up when this method is scaled to the whole group. My solution to this problem is to only search for polyadic relationships within a biologically-informed potential set. This set can be determined by kinship or strong affiliative relationships, of which each baboon in the troop only has a few.

Another obvious next step is to increase my computing power. My analyses were severely limited by computing power. As mentioned in the Methods, I was never able to calculate the intrinsic mutual information for the whole group, even for one time point with a history length of one. I also was also never able to calculate the intrinsic mutual information for the adult group at a history length of two (the history length I used for the causation entropy analysis for this group). I would have liked to complete a partial information breakdown for these larger groups as well, but it was not possible without the intrinsic mutual information. A partial information breakdown of the whole group could shed light on the possibility that the

instability we see in the influence network is purely a result of a continuously varying social context. If this possibility is realized, we would expect the intrinsic mutual information matrices to be stable over time, unlike the causation entropy matrices.

My computing power also severely limited my potential history lengths. I would have done my causation entropy analysis exclusively with the whole group, but I did not trust that I accurately representing information flow with a history length of one. I would like to increase the history lengths for all of the analyses presented herein to at least five. I plan to proceed with future calculations in this analysis to be performed on a computing cluster.

Lastly, I plan to enrich the alphabet of my random variables. Ultimately, I am interested not only in how one baboon influences another's decision to stop or move, but in how it influences another's speed and direction of motion as well. This goal can be achieved by allowing each random variable (representing a baboon) to take on a discrete alphabet that represents potential options for a baboon's step length and turning angle at every time step. Eventually, I aim to allow each variable to realize a continuous alphabet, representing the baboon's movement vector. Cafaro et al. showed that the specific partition chosen, when using symbolic partitioning to discretize the tent map, can affect the Markov order and causal structure of the time series output, even the partitions are generating (2015). This result reminds us that discretizing a continuous state space can impact our interpretations of the system. Thus, if I can perform these measurements with continuous random variables I will. Unfortunately, the calculations to obtain the intrinsic mutual information for continuous variables do not yet exist, and I do not have a suggested direction forward here.

Conclusion

Although I did find evidence of a structure or hierarchy to the flow of causal influence in a baboon troop, as I expected to find, the results I found have more significant implications than my original objectives could have hoped to produce. First, there is statistically significant correlation between the amount of influence flowing through an animal network and the rate at which this influence flows. This finding suggests that we may be able to use information-theoretic measures to infer the timing and magnitude of decision-making in animal groups from observational data.

The influence structure of a baboon troop appears surprisingly unstable over time and does not appear to be dominated by any particular individual or subset of individuals. At any given time, the flow of influence appears remarkably disordered (i.e. non-hierarchical). Statistical analysis has yet to confirm these results, but they suggest that, in accordance with

Strandburg-Peshkin et al. (2015), collective decision-making in baboon groups is largely shared; a remarkable finding, given the strong linear social dominance hierarchies of baboon troops.

Most importantly, this study reveals that causal influence in a complex biological system is highly non-localizable. Not only are polyadic dependencies in the flow of influence common and non-trivial, but they often outweigh the intrinsic influence that an individual has on its groupmates. In fact, these synergisms can account for almost 85% of the flow of influence from one baboon to another. The focus on dyadic relationships in animal behavior and other fields is clearly insufficient to capture the full dynamic of the complex system. Our study of animal behavior, and the study of causal inference more generally, should adjust approaches to reflect the importance of polyadic relationships. In terms of how these results shed light on the evolution of sociality, I posit that because differential influence is so highly context-dependent and temporally unstable, it is unlikely that any one individual can exert a disproportionately large influence over the group with any consistency. Consequently, conflicts of interests are likely resolved dynamically, spreading the consensus costs over several, if not all, group members over time, therefore fostering the evolution of sociality.

Figures

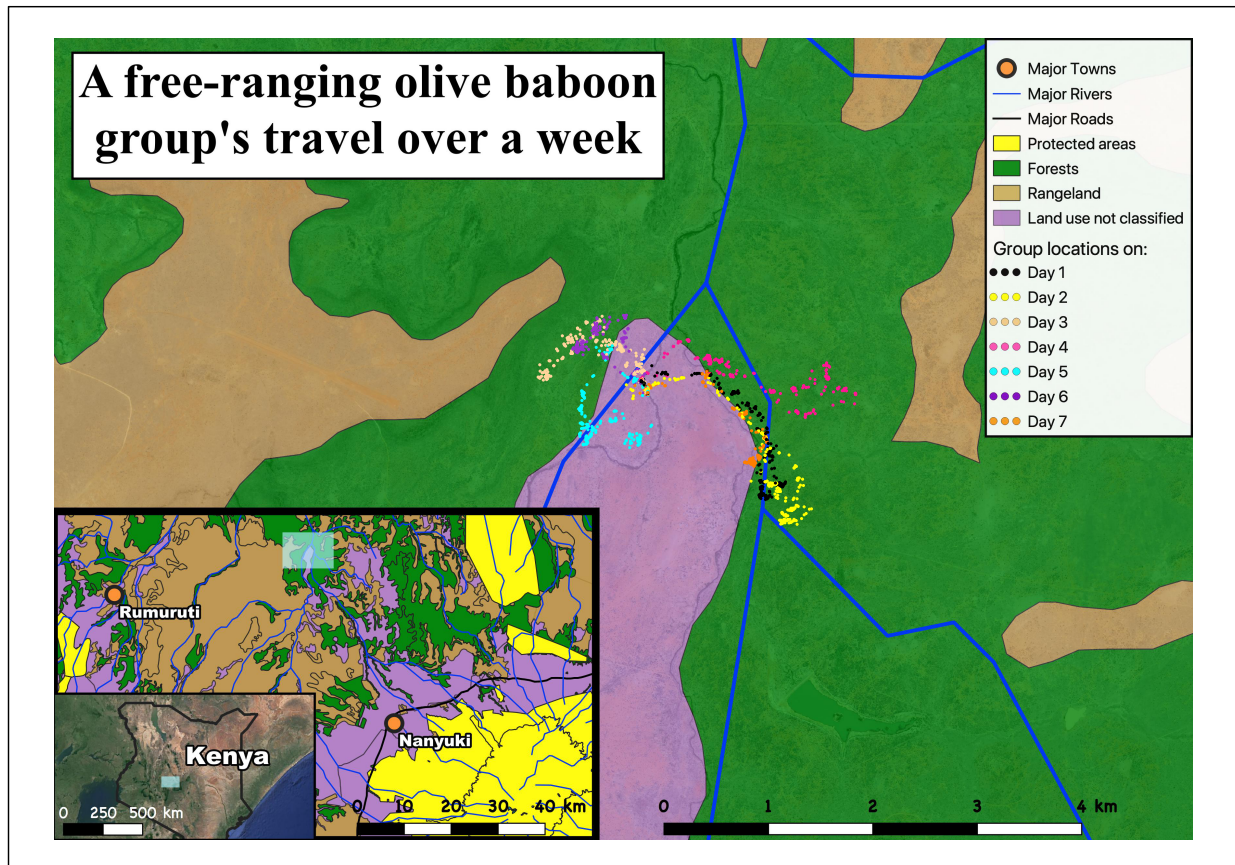
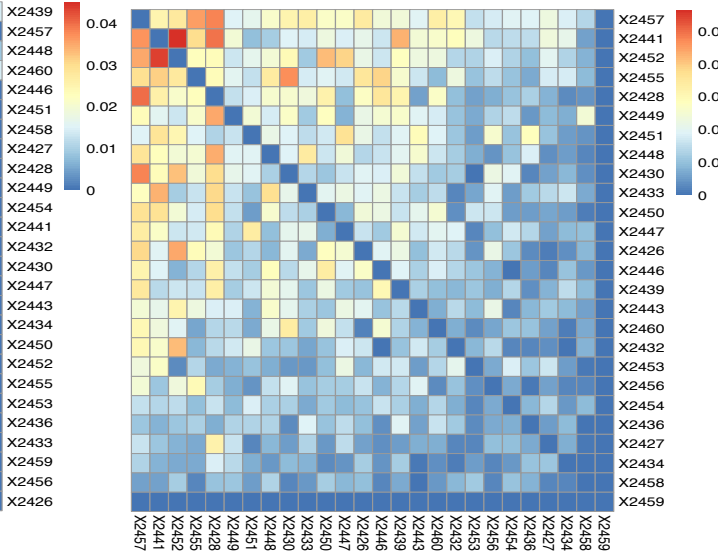
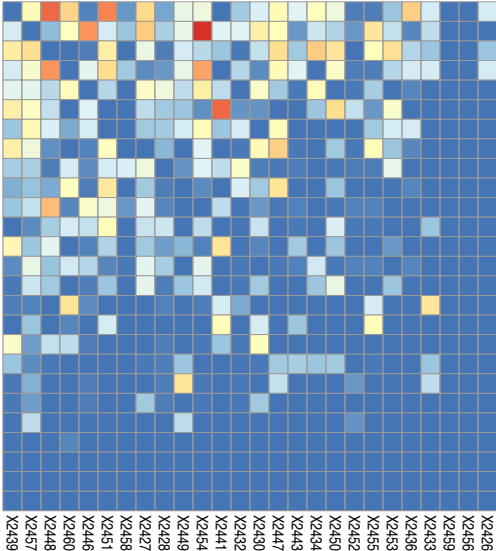
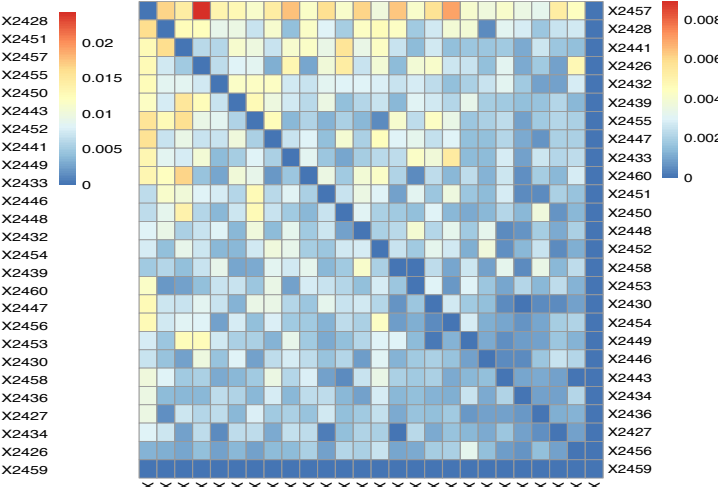
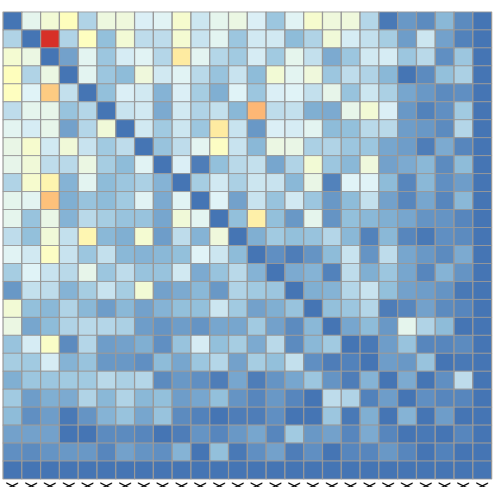
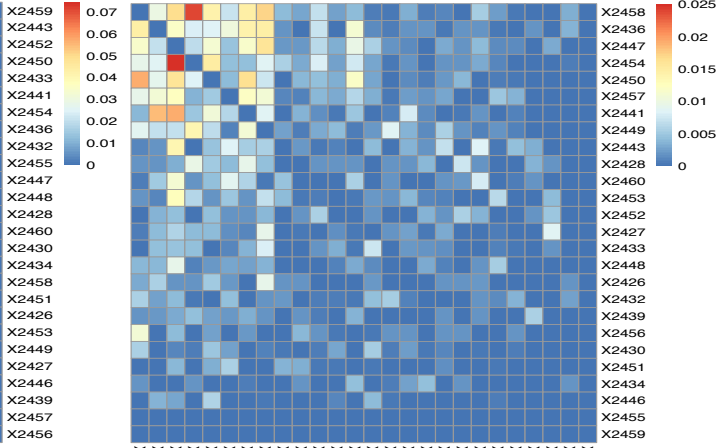
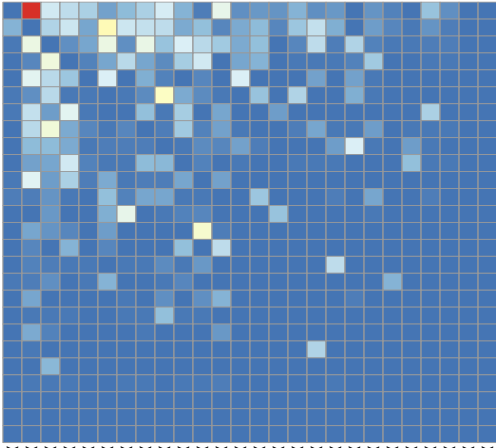


Figure. 1. A map of the baboon troop's habitat with the GPS data of the troop's location over a one-week duration overlaid. The week represented here is 2012-08-01 to 2012-08-07.



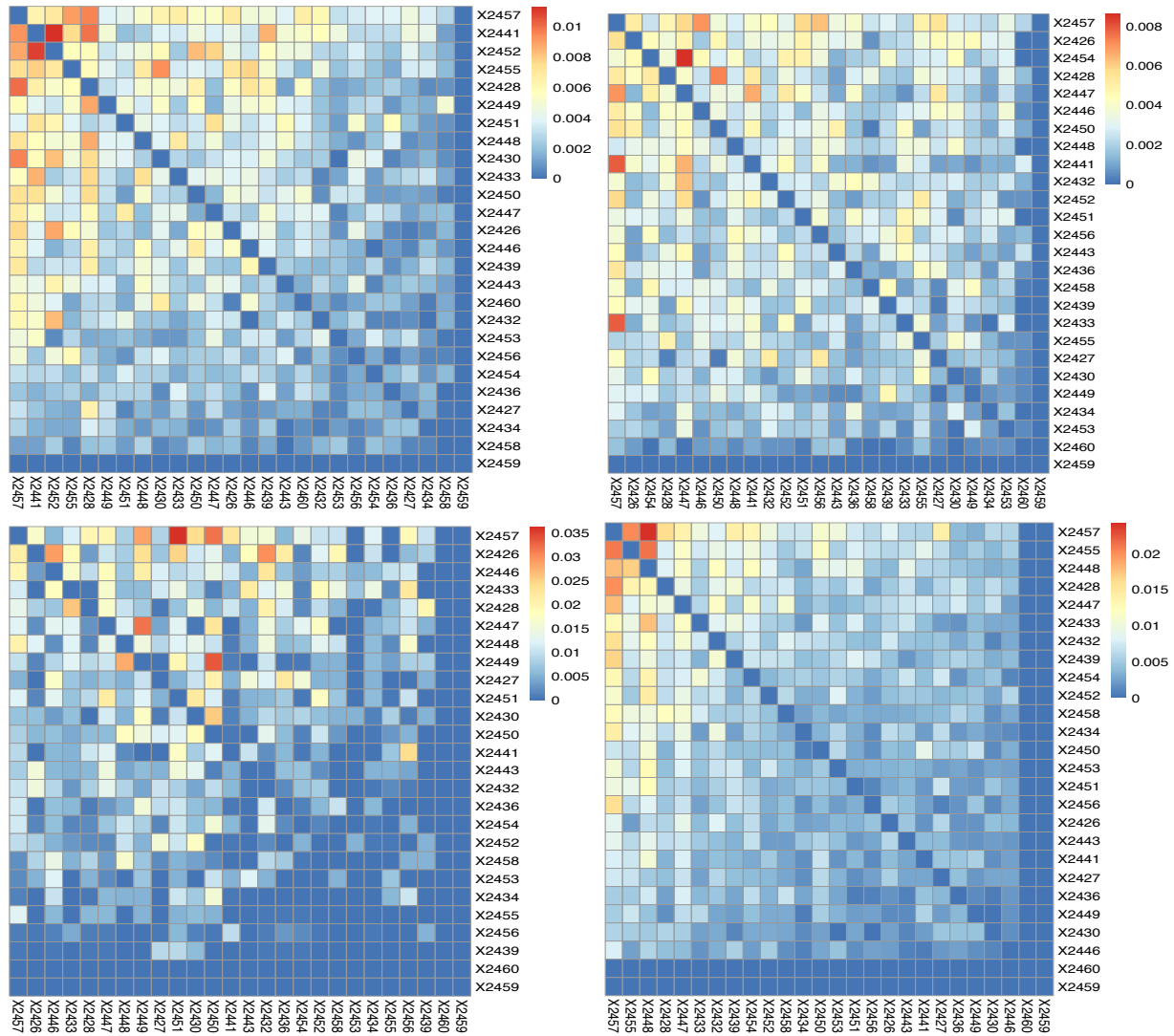
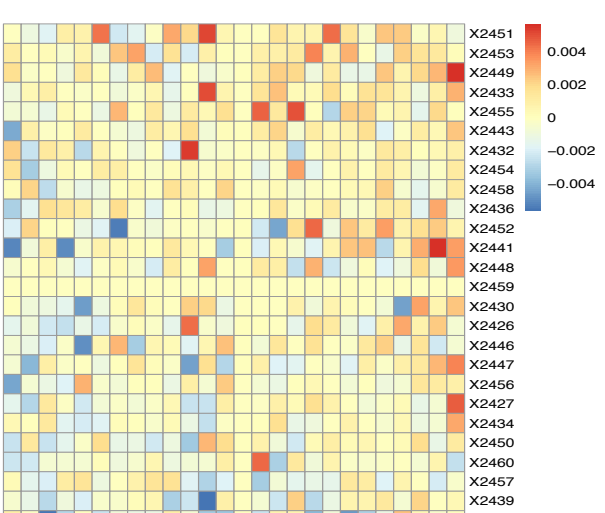
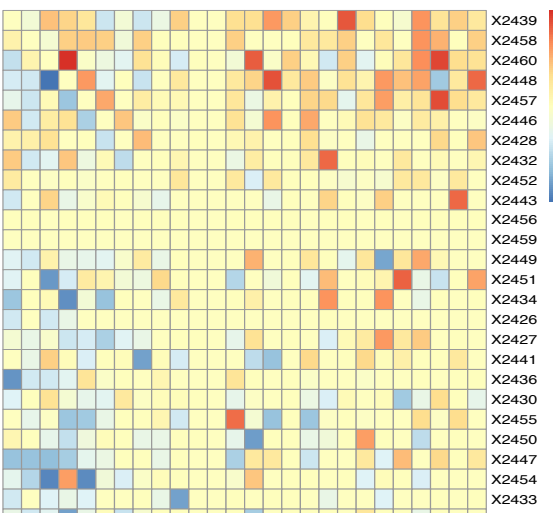
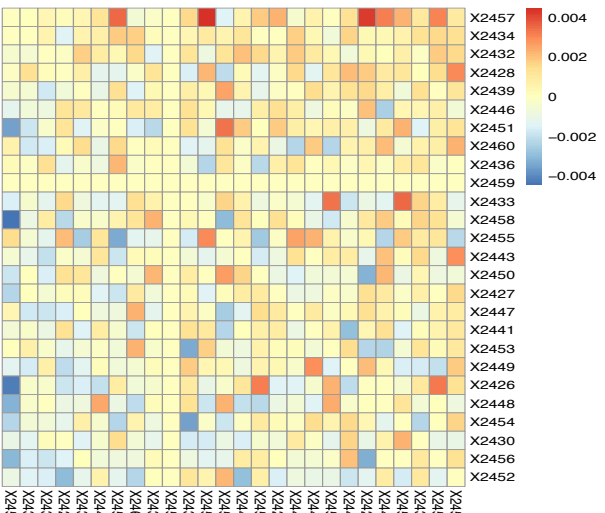
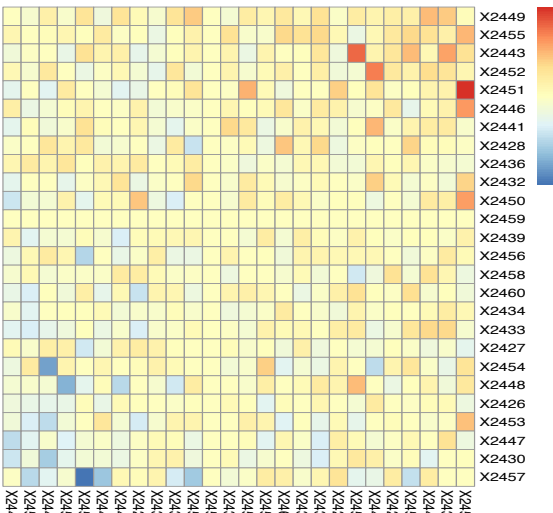
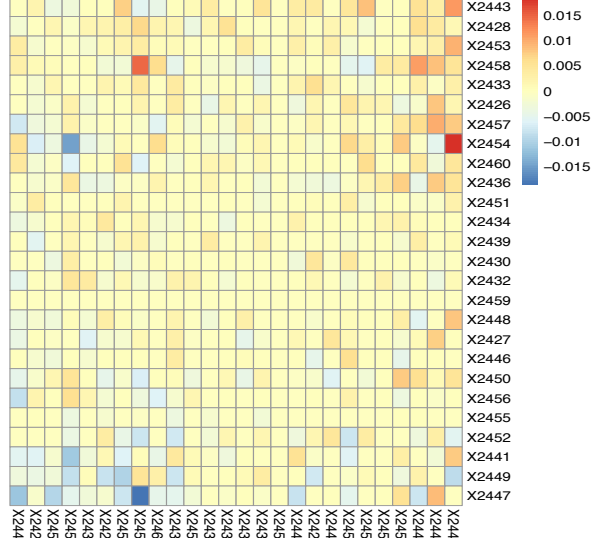
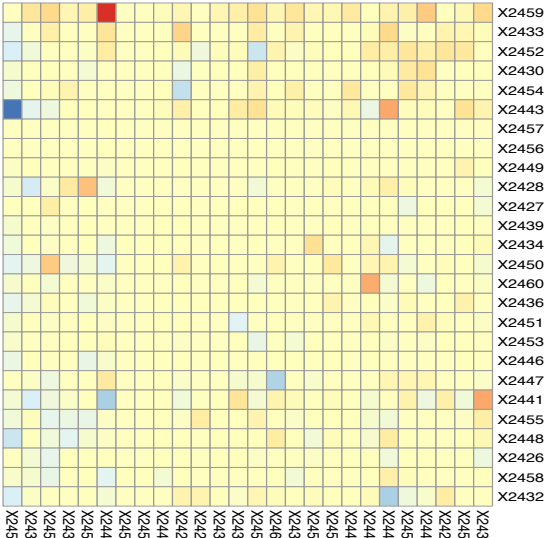


Figure 2. Causation entropy matrices for the whole group over a one-day duration. Each matrix represents the causation entropy flow in the group for a 72-minute period. This figure and subsequent figures are temporally ordered by row, and from left to right (i.e. to view them in order from the beginning of the day to the end of the day, read them in the direction you would read text). Rows and column names represent individual identification numbers of the baboons. Rows represent the influencing individual and columns represent the individual receiving influence. Note that the collars on ID 2459 and ID 2460 malfunctioned at some point during the day, and results from these individuals past the point of malfunction should not be interpreted.



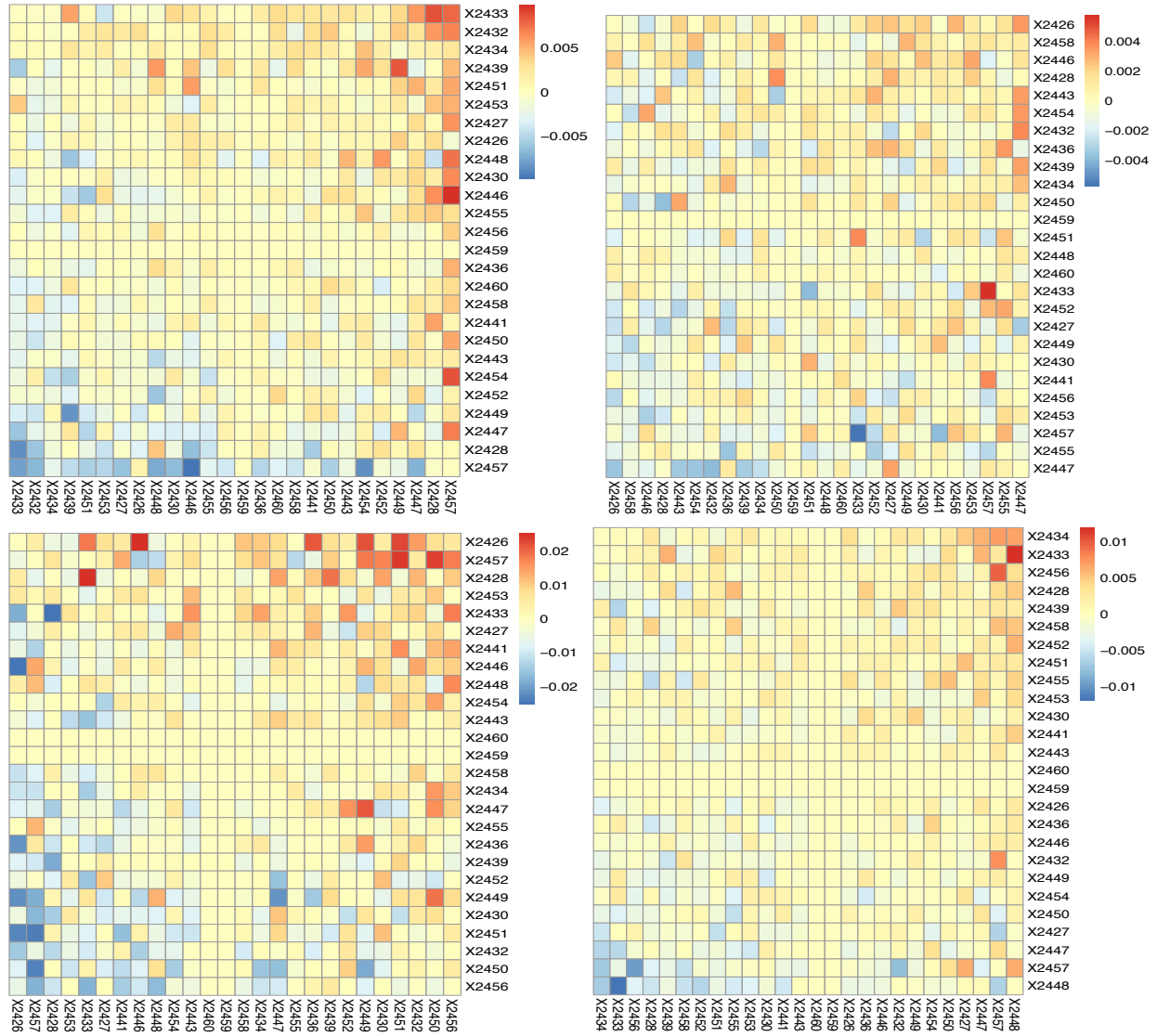


Figure 3. Net causation entropy matrices for the whole group over a one-day duration. Each matrix represents the net causation entropy flow in the group for a 72-minute period. The absolute values of these matrices are, by definition, symmetric across the diagonal.

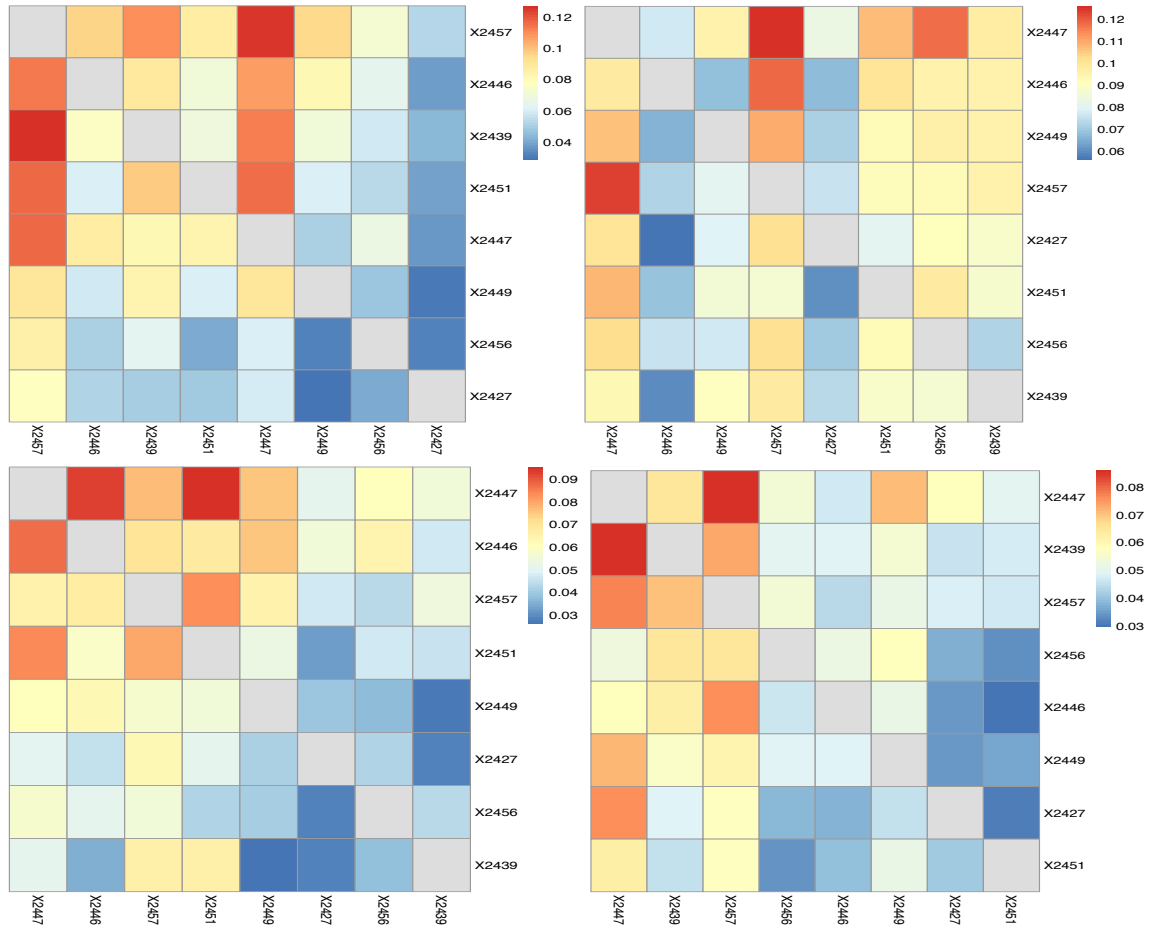


Figure 4. Causation entropy matrices for the adult group over a one-day duration. Each matrix represents the flow of causation entropy over 72 minutes.

Characteristics of influence flow throughout the day

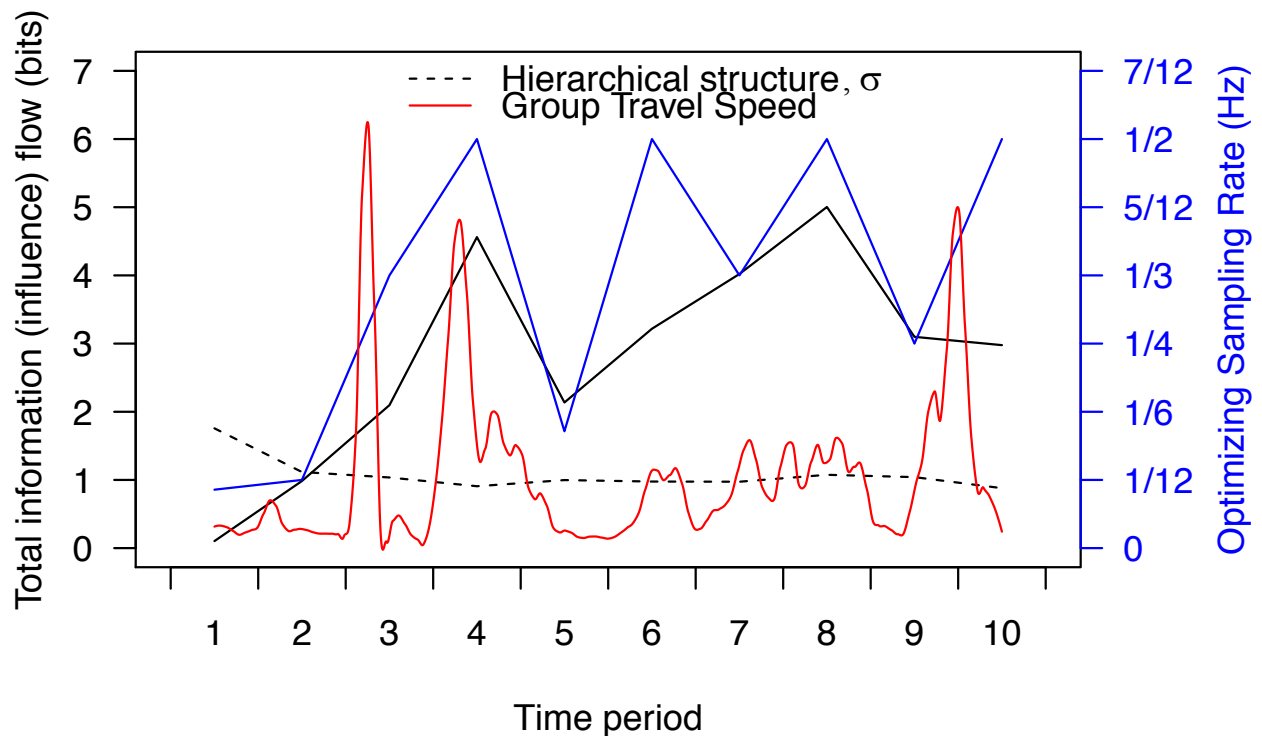


Figure 6. A plot showing the dynamic of total causation entropy flow in the adult group and the sampling rate that optimizes this total causation entropy flow throughout the day. These values are tightly correlated, with causation entropy flowing faster as it flows in higher quantities through the group. The hierarchical structure of the causation entropy matrix, σ , in each time period is plotted according to the left y-axis. Group travel speed throughout the day is also plotted here. No axis provides a reference to quantify group travel speed, but only the *relative* speed is relevant to this analysis.

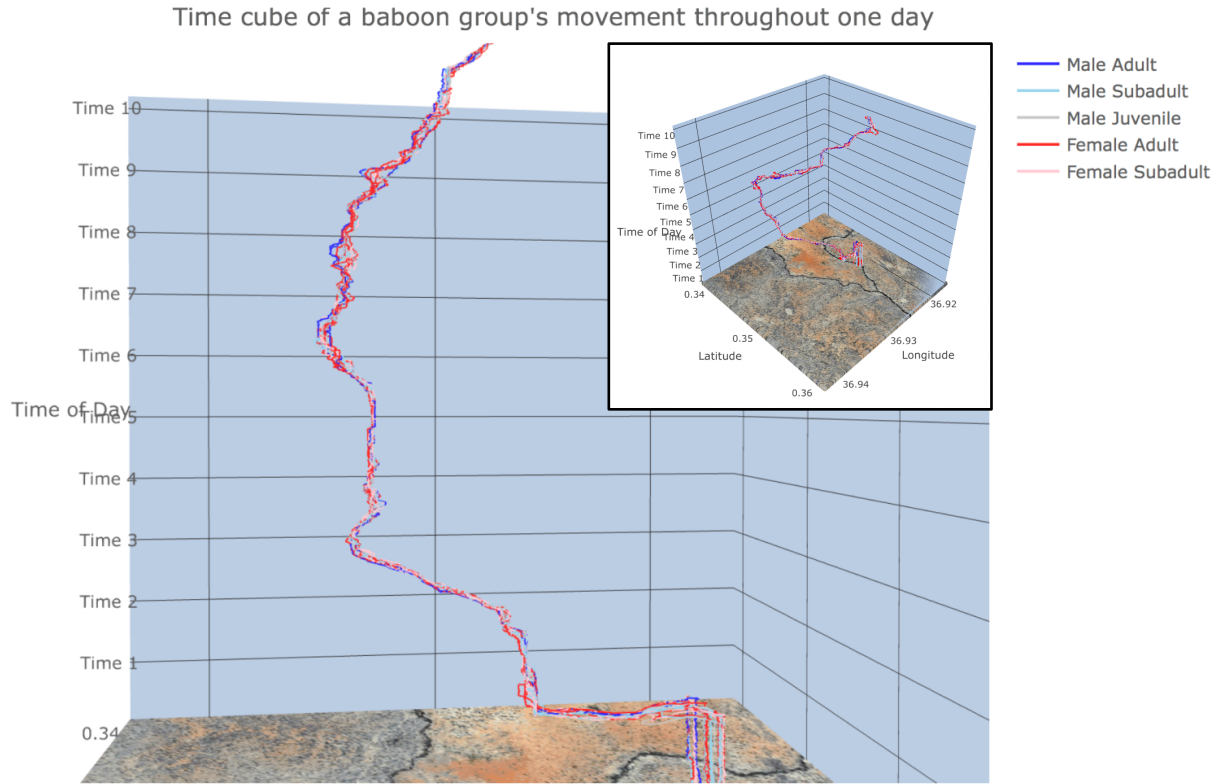


Figure 7. The GPS coordinates for each member of the baboon group on 2012-08-01 plotted as a line. GPS data is only collected from 6:00 to 18:00. The color of the line shows the individual's age-sex class. A satellite map is plotted on the x-y plane for georeferencing. As the inset displays, longitude and latitude are plotted on the x and y axes respectively, and time is plotted on the z-axis. Here, values on the z-axis correspond to the time periods represented by each causation entropy matrix. For orientation to the time cube, a line perpendicular to the x-y plane indicates that the baboon is not moving while a line almost parallel to the x-y plane indicates that the baboon is moving quickly.

Hierarchical structure of influence flow in the whole group throughout the day

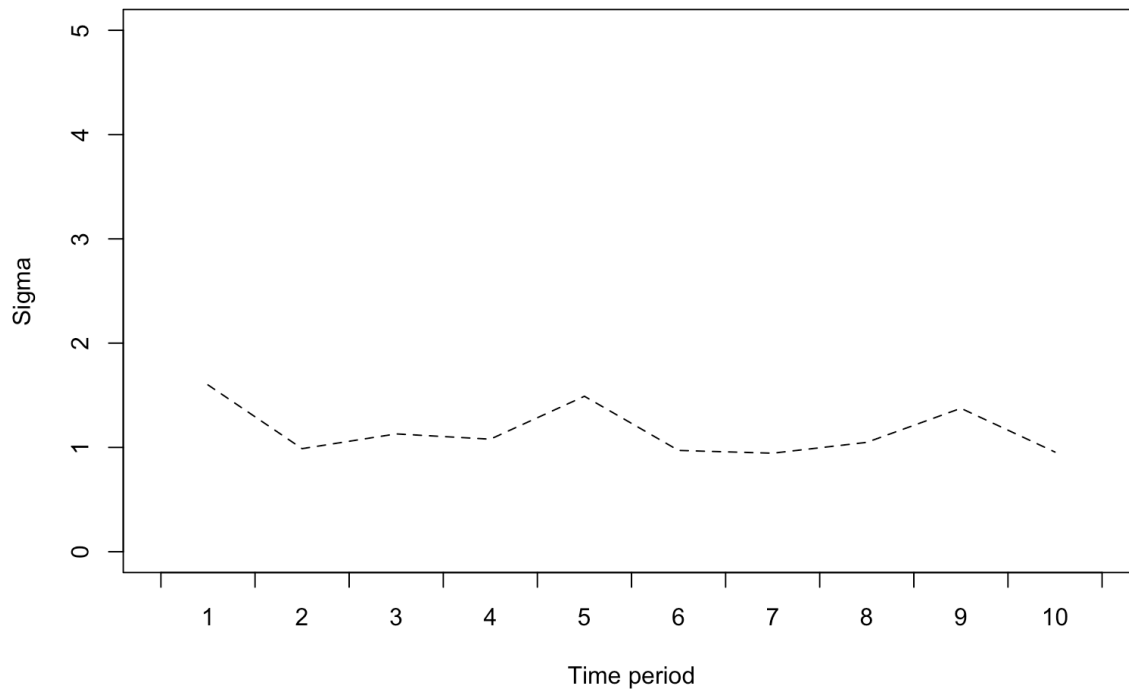


Figure 8. The hierarchical structure of the whole group causation entropy matrix, σ , for each time period throughout the day. This plot is analogous to that displayed for the adult group, depicted by a dotted line in Fig. 6.

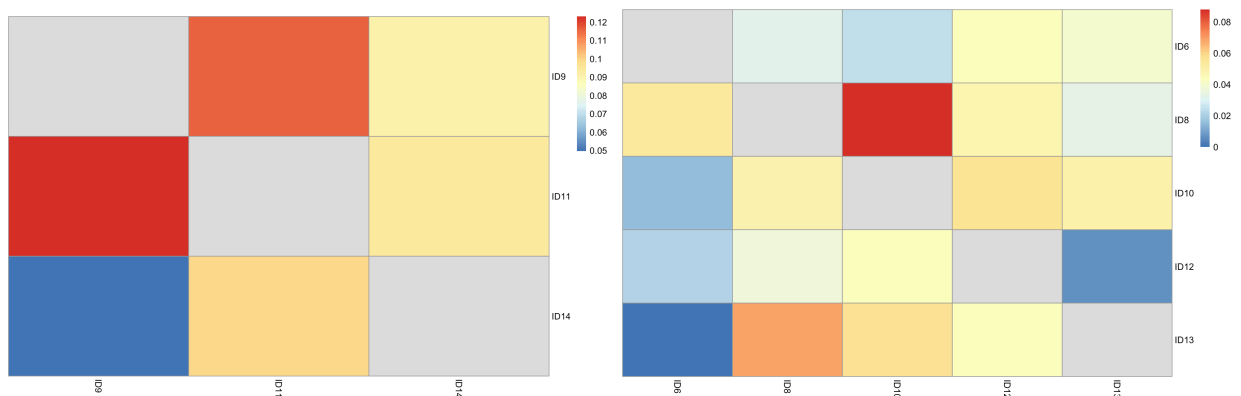


Figure 9. Causation entropy matrices for the small subgroup and large subgroups. Each matrix is generated from approximately 7 minutes and 10 seconds of data, using a sampling rate of 2 seconds and a history length of 3 and 2 for the small subgroup and large subgroup respectively. The same data and history lengths were used to generate the matrices in Fig. 8 and Fig. 9. (Sorry, these are individuals that are also part of the whole group analysis presented above, but the naming scheme is inconsistent with previous figures. At a later date, I will rename the row and columns here to be consistent with previous figures, as I currently don't have information on who they actually are).

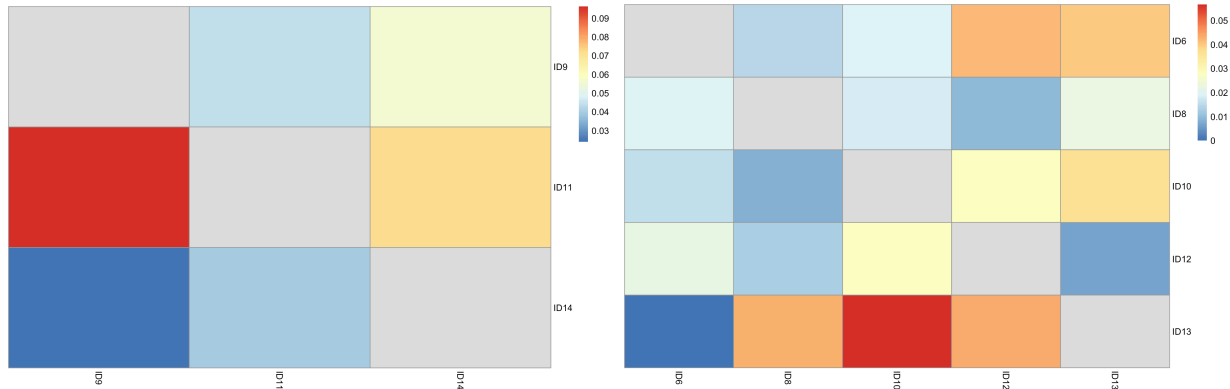


Figure 10. Intrinsic mutual information matrices for the small subgroup and large subgroups.

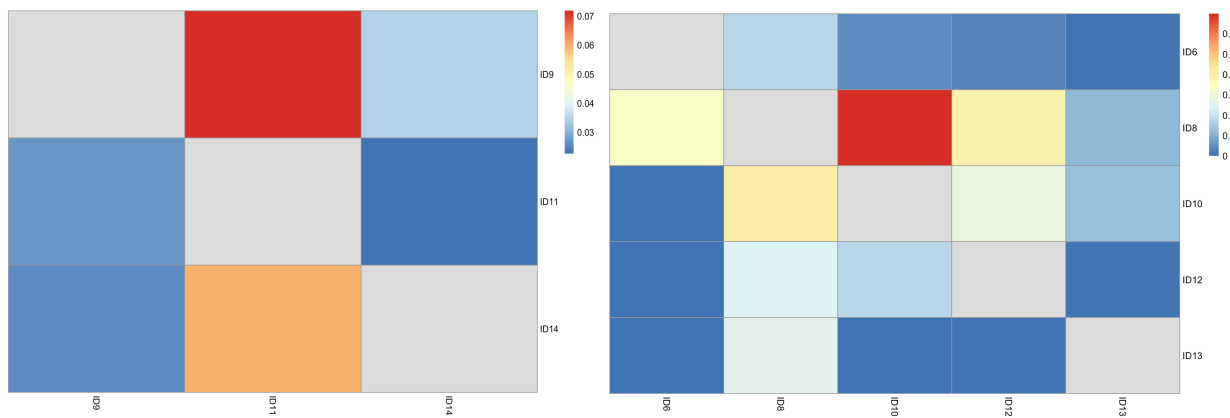


Figure 11. Synergism matrices for the small and large subgroups. These represent the non-localizable influence in which one individual (represented by the rows) is involved that impacts another individual (represented by the columns).

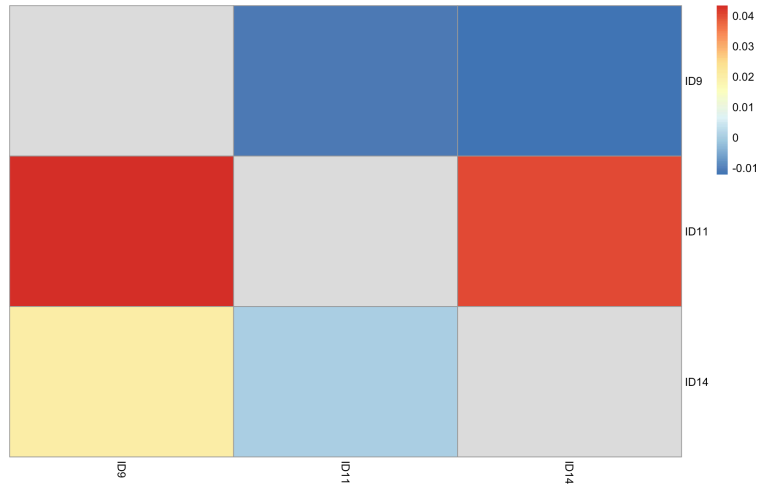


Figure 12. An attempt to isolate the component of synergism that comes from two baboons in influencing their third groupmate from the synergism component that comes from the third groupmate's past. Note the negative values in the matrix.

<http://rpubs.com/jcl273/396852>

(Click link above or copy and paste URL into web browser to view video)

Video 1.

A dynamic network of influence amongst eight adults in the baboon group from 6:00 to 18:00 on 2012-08-01. Each frame of the dynamic network represents the flow of influence amongst the eight baboons, as determined by causation entropy, for a 72-minute duration. The size of the vertex indicates the total causation entropy of the individual it represents (the row sum of the causation entropy matrix), with the size of each vertex normalized to the maximum total causation entropy at that given time period. The edge weights indicate the net causation entropy flow between the dyad of baboons that the edge connects. Edge direction shows the direction of net causation entropy flow. In other words, baboons represented by the vertex on the end of the edge with the arrowhead are being influenced by the baboon represented by the vertex on the opposite end of the edge. Clicking on the vertices reveals the identity of each baboon. Note that an individual can have a high amount of total influence, without having positive net influences. This is represented in the network by large vertices that are on the receiving end of all of its edges (i.e. next to the arrowheads).

Collar #	Sex	Age
2426	M	SA
2427	M	A
2428	F	SA
2430	F	A
2432	M	SA
2433	M	SA
2434	M	A
2436	M	SA
2439	F	A
2441	F	SA
2443	M	SA
2446	F	A
2447	F	A
2448	M	J
2449	F	A
2450	F	SA
2451	F	A
2452	M	SA
2453	F	A
2454	M	J
2455	F	SA
2456	F	A
2457	M	A
2458	F	A
2459	F	SA
2460	F	A

Table 1. Metadata of each baboon. M = males, F= female, A = adult, SA = subadult, J = Juvenile.

	ID 9	ID 11	ID 14
ID 9	--	0.62	0.38
ID 11	0.22	--	0.24
ID 14	0.52	0.61	--

Table 2. The proportion of influence that an individual has over its groupmate (as determined by causation entropy) that cannot be attributed exclusively to the influencing individual (i.e. the proportion of non-localizable influence) for the small subgroup. The table should be read in the same way as the matrices above are read.

	ID 6	ID 8	ID 10	ID 12	ID 13
ID 6	--	0.55	0.19	0.07	0
ID 8	0.63	--	0.79	0.80	0.34
ID 10	0	0.84	--	0.51	0.25
ID 12	0	0.65	0.39	--	0
ID 13	0	0.38	0	0	--

Table 3. The proportion of influence that an individual has over its groupmate (as determined by causation entropy) that cannot be attributed exclusively to the influencing individual (i.e. the proportion of non-localizable influence) for the large subgroup.

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