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Detecting social (in)stability in primates from their temporal co-presence network

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The stability of social relationships is important to animals living in groups, and social network analysis provides a powerful tool to help characterize and understand their (in)stability and the consequences at the group level. However, the use of dynamic social networks is still limited in this context because it requires long-term social data and new analytical tools. Here, we studied the dynamic evolution of a group of 29 Guinea baboons, *Papio papio*, using a data set of automatically collected cognitive tests comprising more than 16 million records collected over 3 years. We first built a monthly aggregated temporal network describing the baboon's co-presence in the cognitive testing booths. We then used a null model, considering the heterogeneity in the baboons' activity, to define both positive (association) and negative (avoidance) monthly networks. We tested social balance theory by combining these positive and negative social networks. The results showed that the networks were structurally balanced and that newly created edges also tended to preserve social balance. We then investigated several network metrics to gain insights into the individual level and group level social networks' long-term temporal evolution. Interestingly, a measure of similarity between successive monthly networks was able to pinpoint periods of stability and instability and to show how some baboons' ego-networks remained stable while others changed radically. Our study confirms the prediction of social balance theory but also shows that large fluctuations in the numbers of triads may limit its applicability to study the dynamic evolution of animal social networks. In contrast, the use of the similarity measure proved to be very versatile and sensitive in detecting relationships' (in)stabilities at different levels. The changes we identified can be linked, at least in some cases, to females changing primary male, as observed in the wild.

The stability of social relationships is important to group-living animals and is a significant aspect of social structure (Hinde, 1976). In primate societies for instance, stable and long-lasting relationships can increase individuals' fitness (Silk, 2007; Silk et al., 2010; Alberts, 2019) through offspring survival (Silk, Alberts, & Altmann, 2003, 2009) and reproduction (Schülke, Bhagavatula, Vigilant, & Ostner, 2010). There is also evidence that disruption of social stability can have negative consequences, in zebra finches, *Taeniopygia guttata*, for instance (Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby, & Farine, 2018). Despite the benefits of stability in relationships, natural processes such as demography naturally bring changes in social relationships (Shizuka & Johnson, 2019): individuals thus adapt and flexibly change their social strategies on different timescales depending on context, from a daily basis (Sick et al., 2014), to seasonal (Henzi, Lusseau, Weingrill, Van Schaik, & Barrett, 2009) to several years (Silk et al., 2010). The changes in relationship, which can be based, for instance, on factors such as genetic relatedness (Beisner, Jackson, Cameron, & McCowan, 2011) and personality (McCowan et al., 2011), can in turn give rise to stability or instability at the group level.

Social network analysis is a powerful tool to better understand the dynamic changes in social relationships because it provides a conceptual framework that uses dyadic interactions to infer social relationships and group level properties (Croft, James, & Krause, 2008; Hinde, 1976; Hobson, Avery, & Wright, 2013; Krause, James, Franks, & Croft, 2015; Kurvers, Krause, Croft, Wilson, & Wolf, 2014; Webber & Wal, 2019; Wey, Blumstein, Shen, & Jordán, 2008; Whitehead, 2008). To go further and analyse the dynamic

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changes in social relationships and their consequences at the group level, a dynamic social network analysis (dynSNA) approach is needed. However, the use of a dynamic network approach is still limited for nonhuman animals (Pinter-Wollman et al., 2014). In many cases progress in this direction has been hampered by the nature of the techniques used to gather social information (Farine & Whitehead, 2015), although recent technological developments are starting to provide automatically collected high-resolution data (Hughey, Hein, Strandburg-Peshkin, & Jensen, 2018; Rutz et al., 2012).

The nature and evolution of each dyadic relationship could of course be studied by itself: it can, for instance, be positive, negative, appear or disappear, and its change during a social instability can be investigated. Studying each relation in isolation, however, is not sufficient, as the evolution of a dyadic relationship is most often related to the other dyads of the group. To understand the evolution of single dyads, the whole network evolution thus needs to be considered, as well as the structures formed by dyads at various scales, such as triangles. Few tools are available, however, to study network structures and their evolution at various scales, from individuals' dyadic relationships to intermediate scales and to the entire social network. In the present work, our goal was to contribute to bridging this gap by presenting analytical tools and a methodological framework to study the dynamics of animal temporal networks and, in particular, to detect periods of stability and instability.

The simplest social structures beyond dyadic associations involve three individuals, that is, triads, among which at most three links can exist. Triadic closure refers to the fact that, if only two links are known to be present in a triad (e.g. between three individuals A, B and C, only the links AB and BC are known to exist), the third link AC is predicted to exist as well or to appear in the future. This phenomenon helps to characterize and predict the development of ties within a network and the progression of its connectivity (Granovetter, 1973; Rapoport, 1953; Thurner, 2018). Evidence of triadic closure in primates has been reported by Borgeaud, Sosa, Bshary, Sueur, and Van de Waal (2016) in three groups of vervet monkeys, *Chlorocebus pygerythrus*, finding that two individuals are more likely to be associated if they are both linked with a mutual third-party associate. The notion of triadic closure is, however, limited to binary associations (a link is either present or not) and does not consider that links can be weighted or of different types (see, however, Brandenberger, Casiraghi, Nanumyan, and Schweitzer (2019) for a recent extension to multi-edge social networks).

Triadic structures become richer when it is possible to assign signs (positive or negative) to the links of a social network, to denote, on the one hand, positive associations such as friendship or trust, and, on the other, antagonistic relationships such as dislike, distrust or aggression. In this case, social balance theory (Heider, 1946, 1958; Wasserman & Faust, 1994; Cartwright & Harary, 1956) provides a theoretical framework to understand the dynamic (in)stability of signed social networks by studying the closed triangles, which have each either 0, 1, 2 or 3 negative links (see Fig. 1). In its strong formulation, social balance theory states that a triangle is balanced if all three links are positive (the three nodes are all 'friends'), or if two links are negative and one is positive (two 'friends' are 'nonfriends' with the third). The remaining two configurations (either three negative links or two positive links and one negative, see Fig. 1) are called unbalanced and are considered a symptom of tension and social stress. For instance, the configuration with two positive links and one negative is in contradiction with the common belief that 'a friend of a friend is a friend'. A network should thus tend towards more balanced configurations (KuŁakowski, Gawronski, & Gronek, 2005; Marvel, Kleinberg, Kleinberg, & Strogatz, 2011). In Heider's (1946, page 108) words, 'If no balanced state exists, then forces towards this state will arise'. Studying social balance is therefore an interesting direction for investigating the dynamics of social networks, as the numbers of balanced and unbalanced triads could be expected to be predictors of changes and instability.

Social balance theory has received a lot of theoretical attention (KuŁakowski et al., 2005; Marvel et al., 2011) but relatively little empirical validation in human social networks (Doreian & Mrvar, 1996, 2009; Leskovec, Huttenlocher, & Kleinberg, 2010; Szell, Lambiotte, & Thurner, 2010; Thurner, 2018). This is most probably due to the difficulty in defining signed social networks, that is, in having information on both affiliative (positive) and antagonistic (negative) ties between individuals. The study of social balance theory in nonhuman animals is even more difficult, as their social networks are often built using only information of a positive nature (such as proximity) and avoidance behaviour is difficult to observe and ascertain. We know of only one study that explicitly tested social balance in a wild, nonhuman system. In social rock hyrax, *Procavia capensis*, Ilany, Barocas, Koren, Kam, and Geffen (2013) considered two individuals that did not share a positive interaction within a year to be 'nonfriends' (negative link), and individuals that shared at least one positive interaction to be friends (positive link). By counting balanced and unbalanced triangles, the authors confirmed the predictions of social balance theory in its strong version. They also showed that unbalanced triangles tended to change to become balanced, as predicted by the theory, but that some level of imbalance remained in the network, mostly due to new individuals entering the group and forming unbalanced structures.

Social balance theory provides a very interesting framework as it formulates predictions both on the state of a social network and on the evolution of structures involving three individuals. However, it

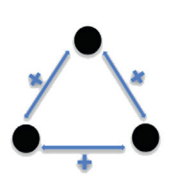
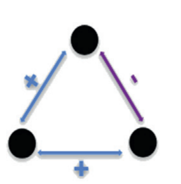
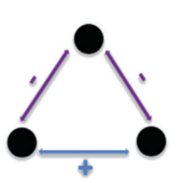
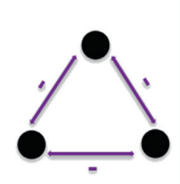
				
Weak	B	U	B	B
Strong	B	U	B	U

Figure 1. Principle of social balance theory. We show the four possible signed triads. In the original 'strong' formulation of the social balance theory, two triads are balanced (B) and two are unbalanced (U). In the 'weak' formulation put forward by Davis (1967), triangles with three negative edges are also considered balanced because such configurations can arise when more than two subgroups exist within the social network under consideration.

is limited to the smallest structures beyond dyads, namely triads. More flexible approaches to characterize dynamic changes across different levels of description of the social network (pairs, triads, subgroups of individuals, entire network) are thus needed and have started to be developed in the context of temporal networks (Croft, Darden, & Wey, 2016; Darst et al., 2016; Farine, 2018; Fournet & Barrat, 2014; Holme, 2015). Temporal networks representations of the evolution of social relationships are often composed of successive snapshots corresponding to the relationships observed or measured in successive time windows (e.g. successive weeks or months), and tools to detect changes between these time windows are typically based on measures of similarity between networks. Such measures can be used to detect the multiple timescales on which a network changes (Darst et al., 2016); they can highlight abrupt changes in the network structure, or, in contrast, periods during which the structure remains stable. They are also easily generalized to weighted networks (Fournet & Barrat, 2014) and quantify the amount of structural and weights change in the network.

To develop data-driven investigations of dynamic social networks in animals, primates are particularly useful because many nonhuman primates have highly developed social relationships. For instance, they can use deceptive tactics (Whiten & Byrne, 1988), be prosocial (Claidière et al., 2015), understand one another's intentions (Tomasello, Carpenter, Call, Behne, & Moll, 2005) and can evaluate the potential helpfulness of others (Anderson, Kuroshima, Takimoto, & Fujita, 2013). Moreover, these social relationships are both structured and flexible. In our study species for example, Guinea baboons, *Papio papio*, have complex social relationships and a multilevel social organization. The core unit of Guinea baboon's society is one primary male with one to four females and their offspring; several core units form parties, which form larger assemblies called gangs (Patzelt et al., 2014).

Males form strong bonds predominantly within parties; these bonds are not correlated with genetic relatedness and males are highly tolerant of one another (Patzelt et al., 2014). Moreover, a recent study found that the social structure was flexible, with half of the females of a group having changed primary male at least once in 17 months (Goffe, Zinner, & Fischer, 2016), a behaviour also observed informally in our study group. Overall, a single group of individuals is thus composed of multiple core units with a certain diversity of social structures, and the social network describing this social structure changes spontaneously. These characteristics make Guinea baboons ideal to study dynamic changes in social relationships.

In the present study, we leveraged a long-term data set with high temporal resolution collected automatically on a group of Guinea baboons. We developed general analytical tools that can be used to study the structure and temporal evolution of nonhuman animal networks, with an emphasis on detecting the periods of stability and instability in the social network evolution (both at the individual and the global level). We first put forward a systematic way to use the data to generate signed social networks among the individuals: to this aim, we defined both affiliative (positive) and antagonistic (negative) links between individuals, by comparing the data to a suitable null model (Bejder, Fletcher, & Bräger, 1998; Farine, 2017; Manly, 1997).

This allowed us to investigate social balance theory in the social network of these nonhuman primates. We then considered various methods to detect changes in the network structure, either using tools linked to social balance theory, such as counts of the numbers of triangles and triangle creations, or through quantitative similarity measures between networks built in successive periods. In particular, the similarity metrics we considered allowed us to investigate the rearrangements of the network at various scales. It can indeed be measured at the scale of the whole network but also at more detailed levels such as subgroups or for each single individual. We highlight, in particular, how the local ego-network of some individuals could be completely altered while others were left unchanged, with only partial rearrangements of the overall social network. Notably, some of the periods of interest and rearrangements of the ego-network of some individuals revealed by this analysis were confirmed by external observations.

METHODS

Participants

Between January 2014 and May 2017, 29 Guinea baboons belonging to a large social group of the CNRS Primate Centre in Rousset-sur-Arc (France) participated in cognitive tests using automatic learning devices for monkeys (ALDM). The size of the group varied from 19 to 24 individuals, because of several births and natural deaths during these years. The monthly average size was 21.8 individuals with 7.3 (range 7–9) males and 14.4 (12–17) females, with age ranging from 0 to 21 years old. The baboons were all marked by two biocompatible 1.2 × 0.2 cm RFID microchips injected into each forearm to individually identify each participant.

Ethical Note

The baboons lived in an outdoor enclosure (700 m^2) connected to an indoor area that provided shelter when necessary. The outside enclosure was connected to 10 testing booths freely accessible to the animals at any time where they could voluntarily perform ALDM tests. This procedure reduces stress levels (Fagot, Gullstrand, Kemp, Defilles, & Mekaouche, 2014). Water was provided ad libitum within the enclosure, and they received their normal ration of food (fruits, vegetables and monkey chow) every day at 1700 hours. The baboons were all born within the primate centre. This research was carried out in accordance with French standards and received approval from the national French ethics committee, the 'Comité d'Ethique CE-14 pour l'Expérimentation Animale' (approval number APAFIS#2717-2015111708173794). Procedures were also consistent with the ASAB/ABS guidelines.

ALDM Data

ALDM database

The data set analysed here contains all recorded cognitive tests performed by the group of baboons in a facility developed by J. Fagot (Fagot & Bonté, 2010; Fagot & Paleressompoulle, 2009). In this facility baboons can freely access 10 workstations installed in two trailers (five workstations in each trailer) connected to their enclosure. Each workstation consists of a test chamber with open rear side and transparent sidewalls. The front of the test chamber is fitted with a view port and two hand ports. By looking through the view port, participants can interact with an LCD touch screen installed at eye level and whenever a monkey introduces its forearm through one arm port, its RFID identity is recognized and triggers the presentation of the cognitive task on the touch screen. For each test, the date and time (with millisecond precision), the nature of the task, the name, age, sex and maternal family of the individual performing the test and the identification number of the workstation in which the individual performed the test are recorded. The system provides rewards (grains of dry wheat), delivered through a food dispenser, whenever the baboons succeed at the task.

Crucially, in the ALDM system the monkeys cannot see each other's screen (observational learning is thus impossible), but they have visual access to each other in neighbouring workstations through their transparent sides: they can thus approach booths together and see each other during the tests, meaning that co-presence may be interpreted as association. In fact, Claidière, Gullstrand, Latouche, and Fagot (2017) recently showed that the timings of cognitive tests could be used to construct a social network of baboons highly similar to that obtained from behavioural observations.

The data cover the period from January 2014 to May 2017. The facility was closed, however, in August 2014 and 2015, which are thus missing from the data. Furthermore, two individuals were born in May 2017, so do not appear in some of the analyses (e.g. in the measures of stability from one month to the next).

The data analysed here concern a total of 16 403 680 cognitive tests, representing an average of 13 186 records a day over 1244 days, and an average of 565 640 records per individual. The duration of a single bout of trials (i.e. a succession of trials of a given individual separated by less than 5 s) was on average 60 s.

Construction of the co-presence network: from raw data to monthly networks

Using the ALDM data set we built a temporal co-presence network based on the temporal and spatial proximity of the baboons (see Fig. 2). To this aim, we first aggregated the raw ALDM data in successive temporal windows of $\Delta t = 5$ s: this interval length was short enough to consider that the individuals performing tests in the same time window were in co-presence, and long enough to have a sufficient number of co-presence events. This interval length was also used by Claidière et al. (2017), and we show in the Appendix that our main results are robust with respect to changes in Δt. Note that a single co-presence event lasting, for instance, 1 min gave rise to 12 successive time windows in which the individuals were detected in co-presence.

For each time window, we built a proximity network in which nodes represented baboons, and a link was drawn between two individuals if their presence had been recorded in two adjacent booths. We then aggregated these proximity networks on a monthly timescale, shown by Claidière et al. (2017) to correspond to an adequate aggregation timescale: in each monthly network, nodes represented baboons and a weighted link between two baboons represented that they had been in co-presence at least once; the weight of the link corresponded to the number of time windows in which co-presence of these individuals had been recorded (i.e. the weight represented the total co-presence time, in units of 5 s).

Constructing a null model for the co-presence monthly network

We considered the ALDM data of each month, which consists of the list of tests performed in that month, with for each test the date, identity of the individual performing the test and identification of the workstation (see above). In this list, we reshuffled the identities of the individuals among the tests, swapping all observations at once and keeping the number of occurrences of each individual. This procedure ensured that the frequency of participation of each individual and the spatial and temporal organization of the trials were preserved for each month in the null model (Bejder et al., 1998; Farine, 2017; Manly, 1997). We then used the randomized data to create a weighted co-presence network as previously. We performed the randomization procedure 100 times. Comparison of the co-presence networks with these randomized data allowed us to build monthly signed networks from the ALDM data as described below in the Results.

Network Metrics and Evolution Measures

A large variety of metrics have been defined to describe the nodes of a network and the network as a whole. The simplest metric to characterize a node is given by its degree, i.e. the number of links to which it participates or in other words its number of neighbours. Going beyond dyads, the clustering coefficient of a node quantifies the cohesiveness of its neighbourhood; it is defined for node i as

$$C_i = \frac{\Delta_i}{k_i(k_i-1)/2}, \qquad (1)$$

where k_i is the degree of node i, Δ_i is the number of closed triangles ijk to which i participated (i.e. such that all links ij, ik and jk exist), and the denominator gives the maximum possible number of such triangles, ensuring that C_i is bounded between 0 and 1. The average clustering coefficient of a network is then simply the average of C_i over all the nodes. The transitivity of a network (Wasserman & Faust, 1994) is also often used and gives a global quantification of

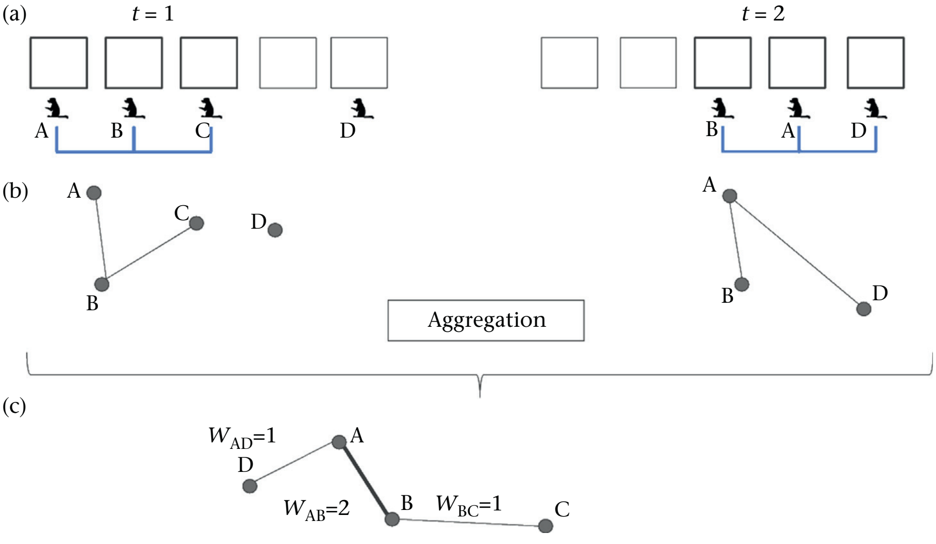


Figure 2. Sketch of the construction of the co-presence network. (a) Schematic of the network construction from the ALDM data set. In each time window of $\Delta t = 5$ s, links were created between individuals (nodes) if they were recorded in adjacent workstations, as depicted in (b): links AB and BC in the first time window and AB and AD in the second. (c) Afterwards, the instantaneous networks were aggregated to produce a weighted co-presence network.

its cohesiveness through the ratio of the number of closed triangles divided by the number of triads.

Balanced and unbalanced triangles

To validate social balance theory, we counted the triangles of each of the four possible types (see Fig. 1) in each monthly signed social network obtained from the ALDM data. Moreover, we compared the results in each case to a null model in which the signs were reshuffled among the links, to check whether the balanced triangles were overrepresented and the unbalanced ones underrepresented with respect to this null model.

Triadic closure events

In social networks, a group of three individuals A, B, C such that A and C are both friends of B are called a triad centred at B. The triad is open, forming a 'wedge', if the link from A to C is missing. The process of closing an open triad to create a triangle is called triadic closure and is a well-known mechanism of evolution of social networks (Rapoport, 1953; Granovetter, 1973). In signed networks with positive and negative links, there are three possible wedge types: $++$, $+-$ and $--$ (Thurner, 2018). To investigate the dynamic aspects of social balance, we considered the triadic closure events between successive months, in which an open 'wedge' in a month t became a closed triangle in the following month $t+1$. We thus counted, for each wedge type in month t, how many became triangles of each of the four possible types (Fig. 1) and thus whether closing wedges became preferentially balanced or unbalanced triangles (Szell et al., 2010).

Cosine similarity measure

The cosine similarity (Singhal, 2001) is a measure defined between two vectors. It is bounded between -1 and $+1$, taking a value of 1 if the vectors are identical, a value of -1 if they are opposite and 0 if they are perpendicular. In the case of temporal networks, let us consider a node i and two different months t_1 and t_2. We denote by $w_{ij}^{(t_1)}$ and $w_{ij}^{(t_2)}$ the weights of the links between individual i and its neighbours j in months t_1 and t_2, respectively. The local cosine similarity between months t_1 and t_2 is then defined for the ego-network of node i as:

$$CS_{t_1,t_2}(i)=\frac{\sum_j w_{ij}^{(t_1)} w_{ij}^{(t_2)}}{\sqrt{\sum_j \left(w_{ij}^{(t_1)}\right)^2}\sqrt{\sum_j \left(w_{ij}^{(t_2)}\right)^2}}$$

It is thus equal to 1 if i not only has the same neighbours at t_1 and t_2 but also divides its co-presence time between them in the exact same way. It is equal to 0 if i has disjoint sets of neighbours in months t_1 and t_2. Note that, if all links are positive, the cosine similarity is bounded between 0 and 1. Overall, an individual whose ego-network changes strongly between t_1 and t_2 will have a low cosine similarity, whereas individuals whose ego-network is similar in both months will be associated with a high cosine similarity. The cosine similarity values between months therefore follow the evolution of the (in)stability of the considered ego-network over time and we used the average value over all individuals as a global measure of the network's stability between 2 months.

We calculated the cosine similarity for every individual and for every pair of months. For each pair of months, we computed the average of the obtained values over all individuals present in both months, to obtain a first global characterization of the network rearrangements between two months. We then considered the whole histograms of the values for all nodes, to characterize the heterogeneity of the amount of changes observed in the ego-networks of different individuals. Finally, we considered 'trajectories' of change for each individual, by computing CSt,$t+1(i)$ for all t, i.e. by following for each individual the amount of change of its ego-network from one month to the next.

Behavioural Data

Observations

We used the behavioural observations described by Claidière et al. (2017) and recorded between 1 July and 29 July 2014. During that time, the group included 22 individuals, seven males (mean age = 62 months, SD = 33) and 15 females (mean age = 124 months, SD = 75) ranging from 24 to 226 months. Observations were carried out by four trained observers using scan sampling (Altmann, 1974). The data contained 210 behavioural observations per monkey per day during the study period, for a total of 79 380 observations for the 22 individuals. For our study, we decided to focus solely on grooming as it is known to be a bonding activity in primates and therefore to represent affiliative relationships accurately (Seyfarth, 1977). More details on the behavioural observations can be found in Claidière et al. (2017).

Construction of the grooming network

We used the number of grooming events observed between a pair of individuals during the observation month (July 2014) to build a weighted and undirected network. This network was then compared to the proximity network based on ALDM data of the same period. This network resulted in 216 links. A fully connected network with the same number of nodes would have had 231 links. The weights (i.e. number of grooming events per dyad) ranged from 1 to 778 and the average and the median were 60.7 and 23.0, respectively.

ANALYSIS AND RESULTS

Our first objective was to use the ALDM data to build a signed social network for the entire group. The co-presence network, however, contained only positive events (proximity events), so that we first transformed it by a comparison with a suitable null model. The definition of avoidance (negative) links made it possible to then analyse social balance and triadic closure events. We finally focused on the temporal evolution of the network using various network metrics and showed how to study it at various scales using similarity measures.

From Weighted Co-presence Networks to Affiliation and Avoidance Networks

A first analysis of the ALDM data revealed that the baboons' frequency of participation in cognitive tests was very heterogeneous (see Fig. 3a), as in Claidière et al. (2017). This difference in participation could result in biased estimates of link strength in the co-presence network defined in the Methods, for simple statistical reasons: individuals that are present more often in the ALDM have a higher probability of being found in co-presence simply by chance, compared to individuals that participate less frequently. To take this behavioural heterogeneity into account and to determine which links could be interpreted as socially meaningful, we compared the observed co-presence to a null model based on the random permutation of the baboons' names for each month analysed, as described in the Methods: this null model corresponds to the assumption that co-presence in the ALDM booths was independent from social relationships.

The results showed that some links had weights compatible with the null distribution, but others had observed weights that

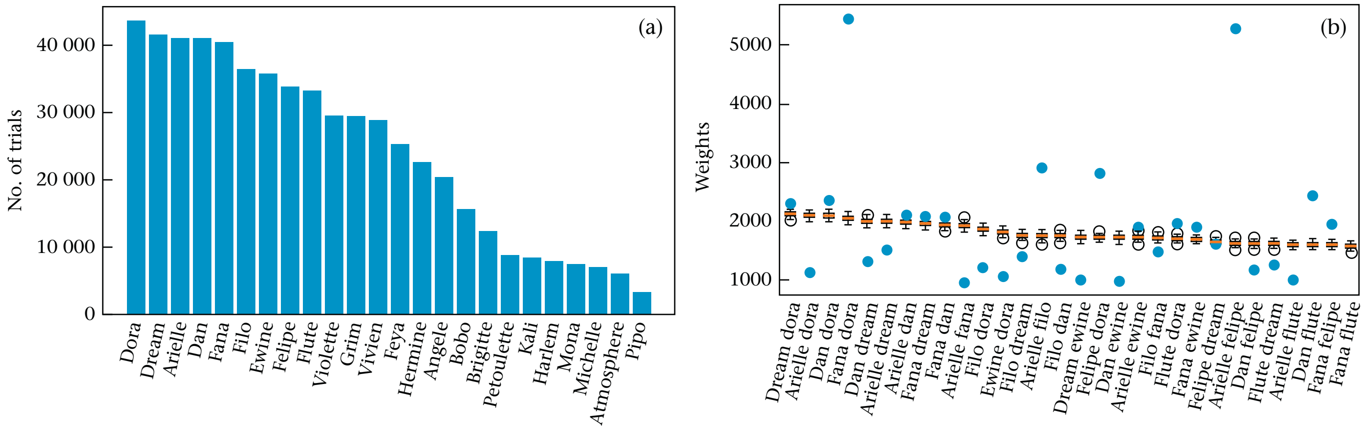


Figure 3. From the weighted co-presence network to the signed social network. (a) Bar plot representing the number of cognitive tests performed by each individual in January 2014. (b) For a sample of 30 pairs of individuals, weights of the January 2014 co-presence network (blue dots) and box plot showing the distributions of weights for the same pairs in networks resulting from the null model. In each box, the orange line marks the median and the extremities of the box correspond to the 25th and 75th percentiles; the whiskers give the 5th and 95th percentiles of each distribution.

were above the 95th percentile of the null distribution (see Fig. 3b for illustrative examples), showing that the corresponding baboons were found in co-presence much more frequently than expected by chance, suggesting that they affiliated with each other. Interestingly, some observed weights were significantly lower than expected by chance (below the 5th percentile of the null model distribution), showing that these baboons were in co-presence much less often than predicted by chance: it was then natural to assume that they were actively avoiding each other (see Bejder et al., 1998). Note that pairs with no co-presence events, i.e. that were not linked in the original co-presence network, could be considered as avoiding each other if they were often found in co-presence in the null model.

This comparison with a null model therefore allowed us to construct for each month a new signed weighted network with both positive (affiliative) and negative (avoidance) links. In this new network, the positive links were given by the co-presence links with weights above the 95th percentile of the null model distribution. The negative links, on the other hand, joined the pairs of baboons with weights below the 5th percentile of the null distribution. Moreover, the weight of each link in the new network was given by the *z* score value of the original weight with respect to the null model distribution (hence obtaining positive values for the affiliative links and negative values for the avoidance links). Finally, for each month we defined the set of positive links as the monthly affiliative network and the set of negative links as the monthly avoidance network.

Validation of the ALDM Network with the Grooming Network

To validate the network obtained through the ALDM system, we compared the network obtained from the ALDM data during July 2014 to that based on grooming behaviour (see Methods). Since grooming is an affiliative behaviour, we used as a measure of similarity the Pearson correlation coefficient between the weights of the affiliative network (i.e. using only the positive links) and the weights of the grooming network. In addition, as it is known that the choice of the aggregation timescale can impact the characteristics of the network (Ribeiro, Perra, & Baronchelli, 2013), we tested the robustness of the analysis by measuring the correlation between the affiliative and the grooming networks on various timescales, ranging from 3 to 25 days within the same period (1–29 July 2014).

Note that, for timescales *T* smaller than 14 days, we could define more than one observation period of this length within the period of interest (1–29 July 2014): we thus divided the total data set into successive time windows of duration *T* before building the affiliative and grooming networks, computing the correlation between their weights, and averaging over the time windows.

In addition, we compared the observed Pearson correlation to a null model based on the random reshuffling of the baboon names in the grooming network. We simulated for each time window 1000 such randomized networks, computed for each randomized network the correlation with the ALDM affiliative network, and built the distributions of these Pearson correlation coefficients. The results (Table 1) show that the observed Pearson correlation was well above the 95th percentile of the random distribution for all the timescales considered. We also observe that the correlation tends to increase for larger time windows, as also found by Claidière et al. (2017), since more observational data are included and thus a more complete view of the social network is obtained.

The correlation between the grooming and ALDM networks is an overall measure of network similarity. Another well-known aspect of a social network's organization, at an intermediate scale, is its community structure (Fortunato, 2010). We determined the community structure of the affiliative and grooming networks using the Louvain algorithm (Blondel, Guillaume, Lambiotte, & Lefebvre, 2008, p. P10008) implemented in the Gephi visualization software (www.gephi.org, see also Bastian, Heymann, &

Table 1
Pearson correlation coefficients between the grooming and co-presence networks calculated for various aggregation timescales

Timescale (days)	Empirical value	Mean of the random distribution (90% CI)
3	0.257	0.065 (0.045–0.085)
5	0.309	0.066 (0.048–0.086)
7	0.309	0.069 (0.047–0.091)
10	0.396	0.094 (0.076–0.113)
14	0.330	0.079 (0.053–0.111)
18	0.413	0.105 (0.087–0.122)
21	0.431	0.104 (0.085–0.123)
25	0.389	0.094 (0.065–0.124)
29	0.473	0.121 (0.103–0.138)

The last column gives the mean and 90% confidence interval of Pearson correlation coefficients computed between the co-presence affiliative network and 1000 randomized versions of the grooming network in which the baboon names were randomly reshuffled.

Jacomy, 2009). To compare the resulting partitions (see Fig. 4), we calculated the adjusted Rand index (ARI; Rand, 1971; Hubert & Arabie, 1985) implemented in the sklearn Python module (Pedregosa et al., 2011). The Rand index takes values between 0 and 1, with 1 indicating that the two partitions are the same and 0 corresponding to a case in which the two partitions disagree on all pairs of elements. The ARI is a version of the Rand index corrected for chance, i.e. yielding a value close to 0 when comparing two random partitions. Finally, we compared the observed ARI value with a distribution of ARI values obtained by randomizing the community structure of the grooming network, keeping the number and size of communities fixed but reshuffling individuals among communities. We observed an ARI value of 0.23, well above the null distribution with mean = 0.0001 (SD = 0.067), that is, very close to 0 as expected between random partitions.

Social Balance: Static and Dynamic Points of View

Negative interactions among animals such as avoidance behaviour are very difficult to observe. The construction described above, however, yielded a signed social network for each month, with both positive and negative links. This made it possible to study social balance theory in the baboons' social network. To this aim, we counted in each monthly network the triangles of each type, i.e. with 0, 1, 2 or 3 negative links. These numbers and the total number of triangles fluctuated between months, but in all months the balanced triangles were more numerous than the unbalanced ones. This was true for the strong and the weak versions of the social balance theory (see Fig. 1).

Moreover, we compared the numbers obtained in each month with a null model in which the monthly network structure was fixed but the signs of the links were shuffled. Fig. 5 shows that the triangles with three positive links were strongly overrepresented in each month (100% of the months) with respect to this null model. It also shows that the triangles with only one positive link (balanced in both weak and strong balance theory) were also overrepresented in most months (74% of the months), while the unbalanced triangles with two positive and one negative links were clearly underrepresented (95% of the months). Triangles with three negative links tended to be moderately underrepresented (82% of the months). We recall that these triangles are unbalanced in the strong version but balanced in the weak version of the social balance theory. Overall, balanced triangles were overrepresented and unbalanced ones were underrepresented with respect to the null model, showing that the signed monthly networks built from co-presence data did respect social balance theory.

In the union of the affiliative and avoidance networks, social balance theory implies that wedges (structures of two links AB and AC such that the link BC does not exist, see Methods) should preferentially close by forming balanced triangles. We thus calculated, for each pair of successive months (t, $t+1$), the number of wedges of each type at t ($++$ with two positive links, $+-$ with one positive and one negative and $--$ with two negative links) that became closed triangles at $t+1$ (Thurner, 2018). The results, summed over all values of t, showed that the total number of triadic closure events producing balanced triangles was larger than the total number of events producing unbalanced triangles, using either the strong or the weak version of the social balance (see Fig. 6). Note that we obtained a substantial number of events in which a $--$ wedge became a $---$ triangle, which is considered balanced only in the weak formulation of social balance theory.

Stability and Instability from Network Dynamics

The long-term nature of the data set makes it an ideal setting to study the evolution of the social network structure and to investigate tools able to detect periods of stability and instability. We first investigated the temporal evolution of the number of balanced and unbalanced triangles and the number of triadic closure events of each type. Indeed, given the interpretation of the social balance theory that unbalanced triangles are a sign of tension and social stress, one could expect (1) an increase in the number of balanced triangles and a decrease in the number of unbalanced ones during periods of stability, and (2) that a large number of unbalanced triangles could lead to an instability of the network and thus to important rearrangements in the following month. However, these numbers fluctuated widely from one month to the next (see Fig. A4 in the Appendix), and these variations showed no clear temporal signal or trend.

We therefore decided to conduct a different investigation considering only the affiliative links. To detect (in)stability in the resulting affiliative network, we measured the similarity between monthly networks using the cosine similarity measure (see Methods), which we calculated for every individual and for every

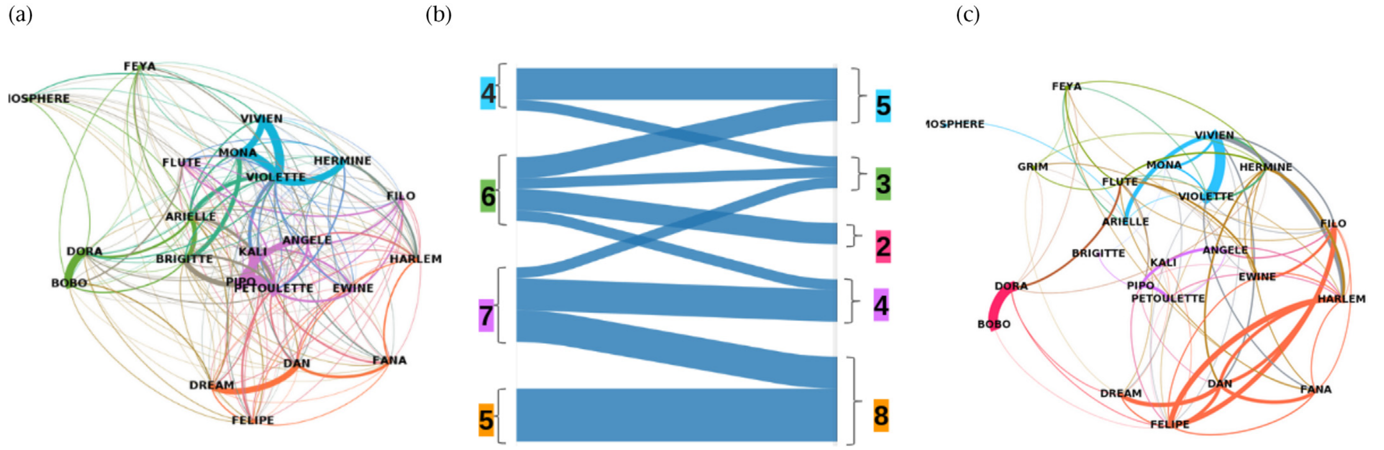


Figure 4. Affiliative network and grooming network. (a) and (c) Visualization, made using the Gephi software, of (a) grooming and (c) affiliative network in July 2014. The widths of the links are proportional to the weights of the networks (number of grooming events and z-scores of the number of co-presence events, respectively), reflecting the strength of the relationships between nodes. Each colour corresponds to a modularity class (i.e. a community) as assigned by the implementation (within Gephi) of the Louvain algorithm. The positions of the nodes were obtained by a Gephi layout implemented for the grooming network and kept fixed for the affiliative network to facilitate visual comparison. (b) Visualization of the differences in the community structures between the two networks by the flow of individuals across communities. Numbers give the community sizes and the widths of the lines are proportional to the number of individuals common to grooming and affiliative network communities.

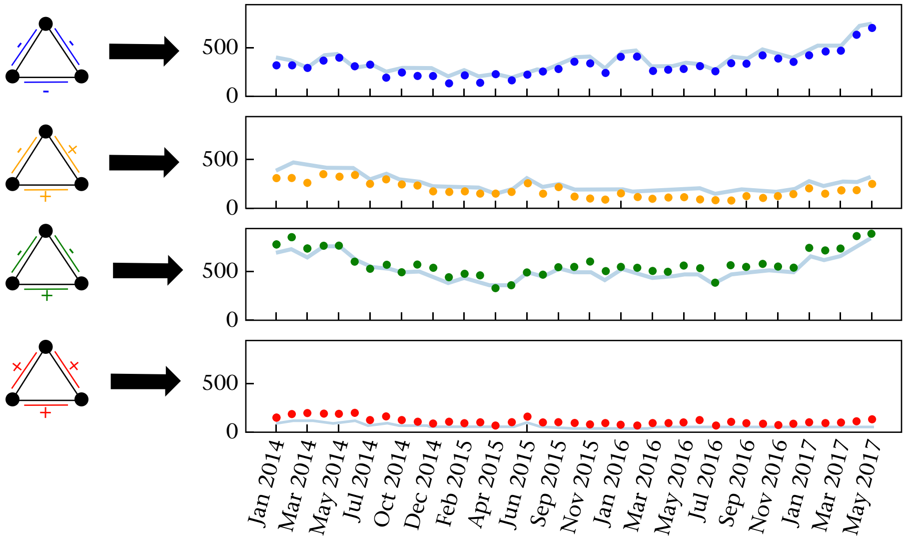


Figure 5. Evolution of the number of signed triangles through time. Coloured filled circles: number of triangles of each type (shown on the left) in the empirical monthly signed co-presence networks (union of affiliative and avoidance networks). Shadowed area: confidence interval (5th to 95th percentiles) of the distributions of numbers of triangles of each type in the randomized monthly networks. In the strong version of social balance theory, the triangle types in the bottom two panels are balanced, while those in the top two panels are unbalanced. In the weak version, triangles with three negative links (top panels) are also considered balanced.

pair of months. The cosine similarity values at the group level (averaged over all individuals) are shown in Fig. 7a. The figure clearly shows that the average cosine similarity between different months remained very high in certain periods (yellow blocks along the diagonal). For instance, the average of the values obtained between two different months between January and July 2014 was 0.794 (SD = 0.07). The average of the values over different months taken between September 2014 and May 2015 was 0.784 (SD = 0.054). These examples are shown as blocks 1 and 2 in Fig. 7b. Such large values of the average cosine similarity between different months imply that the ego-networks of the individuals did not change much, and therefore highlight periods of high network stability.

On the other hand, at some moments the average cosine similarity (CS) between successive months was lower, such as between July and September 2014 (CS = 0.577) and between July and September 2015 (CS = 0.65). These lower values indicate that the networks in these cases differed between the successive months, i.e. that some social network rearrangements took place, suggesting potential periods of network instability.

We also note that the average cosine similarity values tended to be progressively lower away from the diagonal, that is, for months separated by longer and longer times. For instance, block 4 in Fig. 7b corresponds to all pairs of months (t_1,t_2) with t_1 between January and July 2014 and t_2 between September 2014 and May 2015: the average of the values within this block was 0.61 (SD = 0.045). When considering instead block 5 in Fig. 7b, which corresponds to comparing a month between January and July 2014 to a month between September 2015 and December 2016, the average of the cosine similarity values was 0.454 (SD = 0.047). This is consistent with the fact that the social network became more and more different and did not come back to a previous structure during the period of study.

Fig. 8 sheds more light on these two types of periods by presenting the distributions of individual cosine similarity values for two periods corresponding to high and low group level similarity. When the similarity is high (Fig. 8a), the distribution is highly skewed with most individuals' cosine similarity values close to 1. This shows that the network global stability was the result of the stability at the individual's level. In contrast, when the average similarity is lower (Fig. 8b), the distribution of the individual cosine similarity values is broader with some individuals maintaining their ego-network (large value of the cosine similarity) while others changed dramatically (cosine similarity values close to 0).

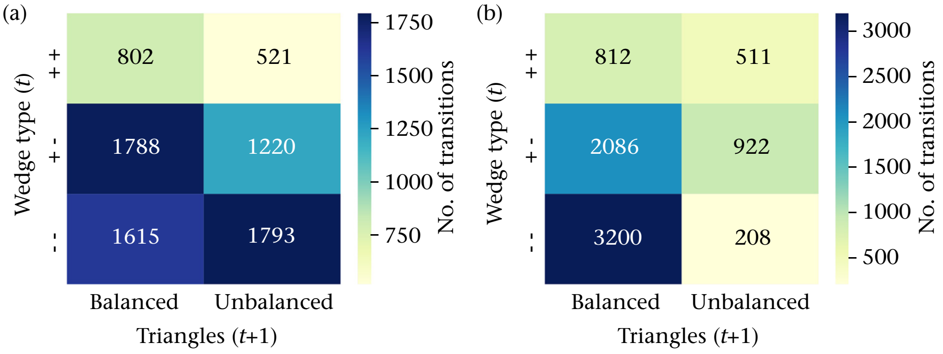


Figure 6. Social balance in the signed monthly networks. Total numbers of triadic closures of each type from a month t to the next one $t+1$, i.e. numbers of transitions from the various types of wedges (from bottom to top, −−, +−, ++) to balanced triangles (left column of each table) or unbalanced triangles (right column of each table). We present the numbers of transitions summed over all the period of investigation (39 months) and for both the (a) strong and (b) weak formulations of social balance. For instance, over the whole period there were 3200 transitions from a wedge −− to balanced triangles, and 208 to unbalanced ones, in the weak social balance formulation.

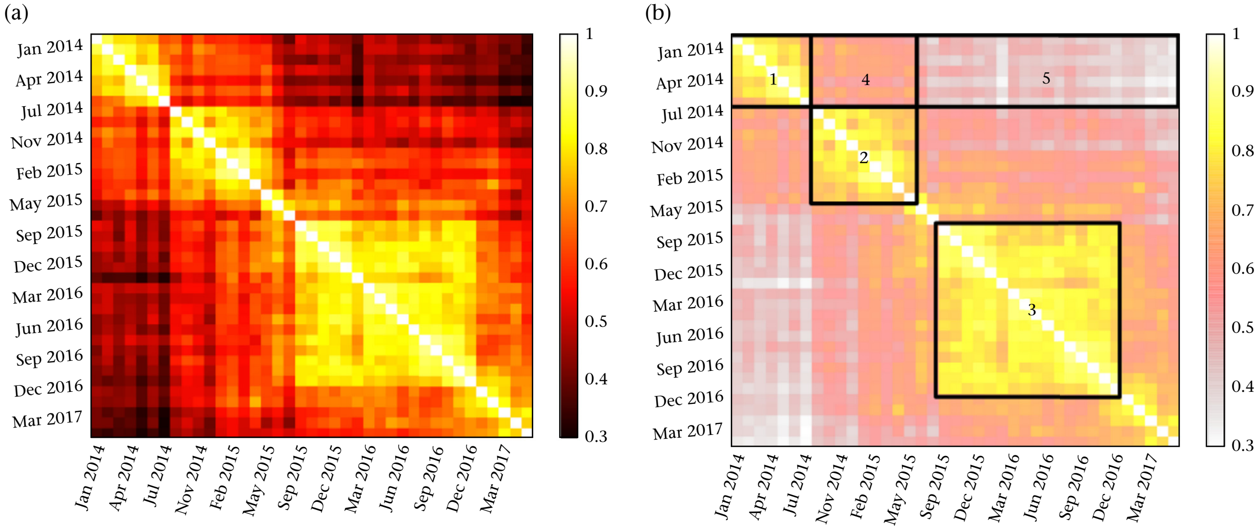


Figure 7. Dynamics of the social network at the group level. (a) Colour-coded matrix of the average cosine similarity (CS) values for all pairs of months. Several periods of strong structural stability clearly appear as blocks of lighter (yellow-white) colour. In contrast, the average CS between July and September 2014 was 0.577 and between July and September 2015 it was 0.65. (b) The same matrix is represented with periods of particular interest highlighted. The principal periods of stability are shown as block 1 (January–July 2014: the average of the average CS values, excluding the diagonal, was 0.794, SD = 0.07), block 2 (September 2014–May 2015: average of values 0.784, SD = 0.054) and block 3 (September 2015–December 2016: average of values 0.814, SD = 0.044). Note that values tended to be progressively smaller away from the diagonal, i.e. for months separated by longer and longer times. For example, block 4, which represents the average CS values between January–July 2014 and September 2014–May 2015, had a mean of 0.61 and a SD = 0.045, while in block 5, between January–July 2014 and September 2015–December 2016, the mean value was 0.454 and a SD = 0.047.

This implies that the instability of the network was not a global one but that some parts of the networks remained stable while others underwent important changes.

To better understand the network's dynamic, we studied the evolution of ego-networks independently. Fig. 9 shows the cosine similarity between the ego-networks of specific individuals in successive months. The resulting patterns differed greatly between individuals (we show the results for all individuals in the Appendix). For instance, as can be seen in Fig. 9a, Vivien (adult male) and Angele (adult female) had on average high cosine similarity values over the entire study (0.96 and 0.95, respectively), showing a strong stability of their ego-networks, but these averages hide an interesting pattern: in a synchronized way, these two baboons went through a strong rearrangement of their ego-networks, with cosine similarity values of respectively 0.23 and 0.01, between July and September 2014. Both individuals thus had very stable ego-networks before and after this period, but their ego-networks between the first and second stability periods differed strongly. In particular, between these two periods Angele lost her strong link with Pipo (adult male), the links between Vivien and most of his females became much weaker, and a strong link between Angele and Vivien appeared. On the other hand, both individuals kept a stable ego-network during other structural changes observed in the matrix of Fig. 7a, such as between March and June 2015: this highlights once again, as deduced also from Fig. 8b, that a low average cosine similarity between two different months can be the result of a large variation of some ego-networks while others remain completely unchanged. Fig. 9b shows that other individuals went through very different patterns of ego-network stability and instability: some kept a relatively stable ego-network throughout the whole period, with only small changes (for instance, Petoulette, adult female, in Fig. 9b), and some had much more important and frequent changes in their local ego-network (such as Brigitte, adult female). Fig. A6 in the Appendix displays the evolution of the ego-network cosine similarity values for all the individuals.

Finally, we sought to analyse in more detail the important change in the network between July and September 2014 (see Fig. 7a). Indeed, the average cosine similarity between these months was 0.577, while the average between May and July was 0.779, and 0.845 between September and November 2014. As

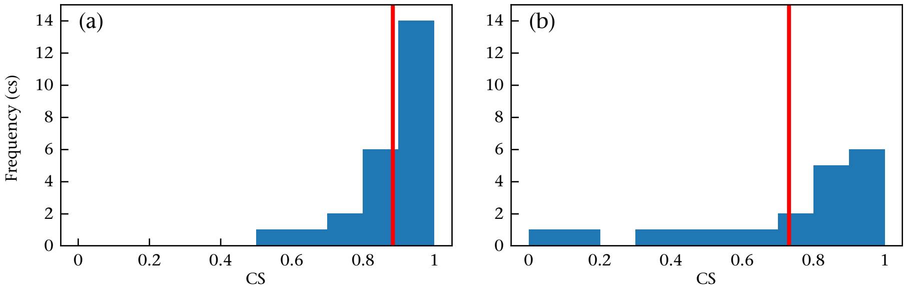


Figure 8. Histograms of the individual's cosine similarity values between weighted ego-networks for two different pairs of successive months: (a) April 2014, May 2014; (b) April 2015, May 2015. For each panel, the histogram corresponds to the cosine similarity values of all the ego-networks of the individuals present in both months. The vertical line gives the average value of the cosine similarity (i.e. the value shown in Fig. 7a), which corresponds to 0.884 and 0.731 for April 2014, May 2014 and for April 2015, May 2015, respectively.

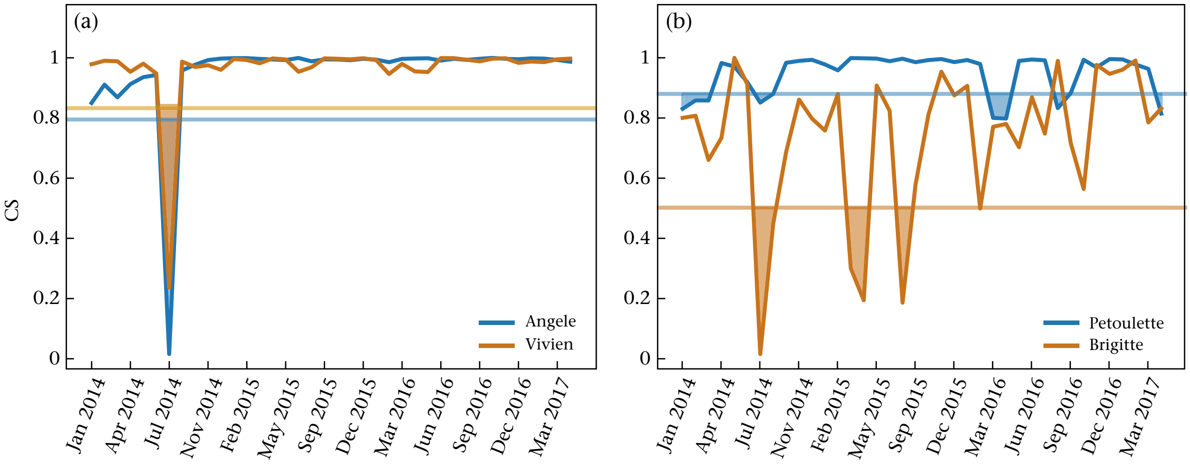


Figure 9. Dynamics of ego-networks. Evolution of ego-network cosine similarity (CS) values computed between one month and the next for several individuals $CS_{t,\,t+1}(i)$ for each month t). The lines give for each individual the average of its cosine similarity value over time, minus one standard deviation. The filled areas therefore correspond to very unstable periods, i.e. to periods where the ego-network cosine similarity between successive months is more than a standard deviation below the average. The two individuals in (a) showed a stable ego-network overall (Vivien: mean = 0.96, SD = 0.12; Angele: mean = 0.95, SD = 0.15) but displayed a sudden and synchronized change between July and September 2014. The two individuals in (b) had very different patterns of ego-network stability and instability both in terms of variability of values (Petoulette: mean = 0.94, SD = 0.12; Brigitte: mean = 0.71, SD = 0.06) and in terms of (absence of) synchronization: for instance in August 2016 while Brigitte's trajectory had a local maximum (0.93), Petoulette's trajectory underwent a local minimum (0.83).

already discussed above, these average values hide a heterogeneous amount of local rearrangements, as shown by the distributions of Fig. 8. Fig. 10 shows a visualization of the affiliative networks in these months, as well as the flux of individuals between communities obtained by the Louvain algorithm. The ARI between the resulting partitions in July and September was 0.16, while it was 0.67 between the partitions in communities of the September and November networks and 0.41 between partitions in communities of May and July networks.

The visualization reveals several important changes in the network. (1) Angele moved from one community to another. The strong link with Pipo disappeared and a new strong link with Vivien emerged. (2) Links between Vivien and other females of his community weakened as the link with Angele abruptly became very strong. (3) The number of individuals went from 23 to 22 because Grim was removed from the group for a medical reason unrelated to the experiment. The first two points are clearly related to the synchronization in the timelines of Fig. 9a. The visualization also made clear how certain parts of the network were in contrast very stable between these months, as discussed above in relation to Fig. 8b.

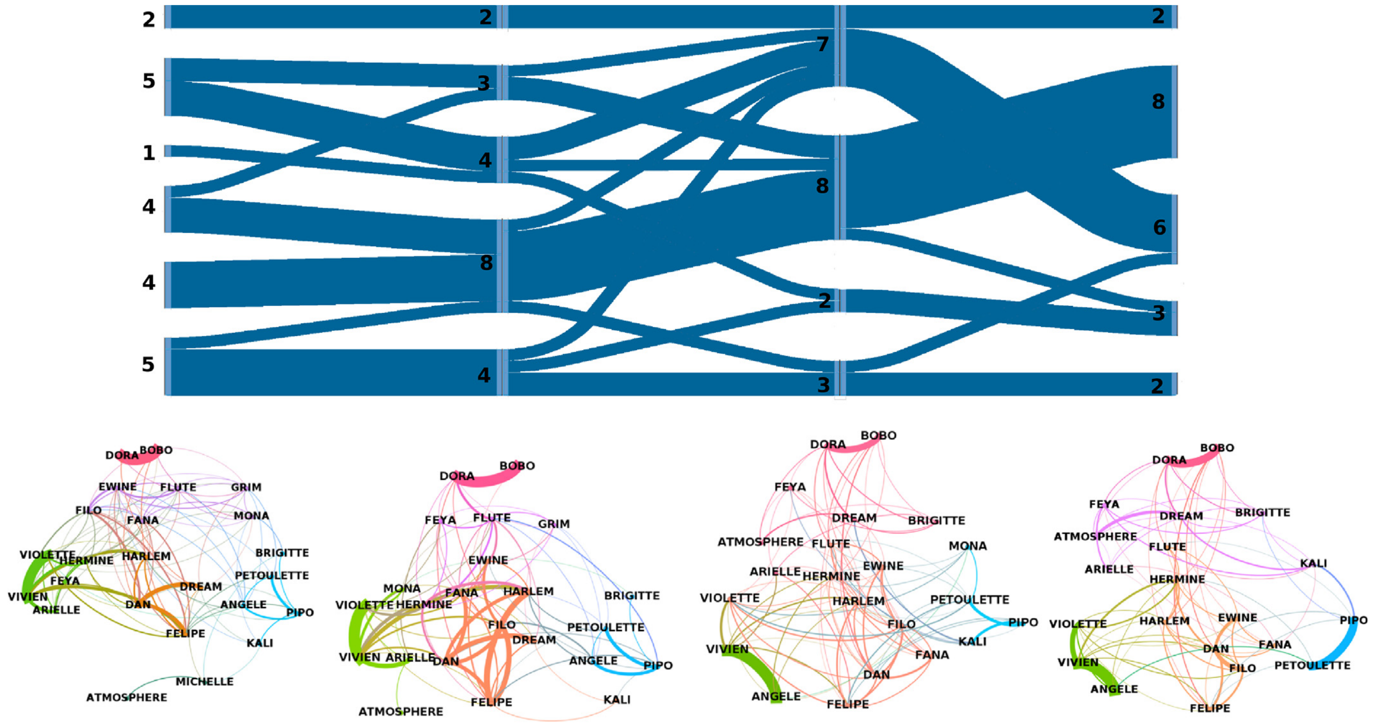
Note that all these points were deduced only from the study of the affiliative network built from the proximity in ALDM booths, without any external knowledge. Interestingly, it turned out that direct annotations of observations of the group in summer 2014 confirmed that two important changes occurred in July 2014, namely: (1) Grim died and (2) Angele changed primary male during that month.

DISCUSSION

In the present study, we analysed one of the largest (more than 16 million records) long-term (more than 3 years) high-resolution data sets collected on a group of nonhuman primates. We used this data set, composed of automatically collected cognitive tests performed by a group of Guinea baboons, to build a co-presence network. By comparing the observed co-presence to a random distribution generated under the assumption that the co-presence in neighbouring ALDM booths was due only to randomness and independent from the actual social relationships among the baboons (Bejder et al., 1998; Farine, 2017; Manly, 1997), we were able to establish a signed network representing both affiliative and avoidance relationships. This network-building procedure has two main advantages. First, it takes the heterogeneity in the number of records of different individuals into account, thus reducing potential biases in the estimation of bond strength. Heterogeneity in the number of observations of individuals is a common feature of social network analysis in animals and several association coefficients have been developed to limit common biases (see e.g. Whitehead, 2008). Developing a null model of social interaction to estimate link strength, however, has the second advantage of allowing the researcher to determine both affiliative and avoidance relationships from positive interactions simply by assuming that individuals that meet more than chance are actively seeking each other's company while individuals that meet less than chance are actively avoiding each other (Bejder et al., 1998). Notably, negative interactions are more difficult to study in nature than positive interactions because they are often less evident (such as avoidance) and/or less frequent (such as open fights). Consequently, little attention has been paid to agonistic social networks but according to social balance theory for instance, negative links are crucial to understand the social evolution of a group. Using the lack of positive interactions, compared to a null model, as an indicator of a negative relationship could therefore prove a useful general tool.

Indeed, in our study we were able to use the signed network to show that the networks followed the predictions of social balance theory (Heider, 1946). From a static point of view, the results showed that balanced triangles were overrepresented and unbalanced triangles underrepresented when compared to a null distribution based on random permutation of the networks' edge signs. Furthermore, from a dynamic point of view, we found that wedges (unclosed triangles) tended to close into balanced triangles more frequently than into unbalanced ones. Interestingly, we also observed many closure events towards triangles with three negative edges: this could be linked to the fact that the group of baboons was composed of more than two subunits, so that triangles with three avoidance links were not rare.

Our results are in line with two previous studies that aimed at testing social balance theory directly. Szell et al. (2010), in an online game with more than 300 000 participants, and Ilany et al. (2013),



May 2014 July 2014 September 2014 November 2014

Figure 10. Visualization of the co-presence networks and of the flow between communities across May, July, September and November 2014. Different colours correspond to different communities. In the flow diagram, the numbers specify the community size and the widths of the lines are proportional to the number of individuals common to the communities joined by the lines.

in a study of rock hyraxes, both found that their networks were generally balanced with an overrepresentation of balanced triangles (especially + + + triangles) and an underrepresentation of unbalanced triangles (especially + + − triangles). In these two studies, as in ours, there was substantially more support for the weak formulation of social balance theory (Davis, 1967), compared to its stronger alternative. Finally, Szell et al. (2010) also studied the triangle closure dynamic and found, like us, that more wedges (unclosed triangles) closed into balanced triangles than unbalanced ones. Based on these three studies with different species and in very different contexts, it is tempting to conclude that (weak) social balance theory may represent general principles of social organization, as envisaged by Heider (1946). Surprisingly, however, few studies have tested social balance theory, and, in our opinion, it deserves more scrutiny especially because it provides a clear static and dynamic theoretical framework to understand the structure of social networks and their evolution.

Unfortunately, the analysis of the temporal evolution of social balance measures (in proportion or number of balanced versus unbalanced triangles with both the weak and strong interpretation) did not yield clear insights into the temporal evolution of the structure of the social network (see Appendix). There were no clear changes in the different measures between periods of social stability and instability that were instead revealed by the analysis of the cosine similarity. One explanation could be that our analysis did not consider the correct timescale on which changes in social balance occur. For instance, there is some evidence in chacma baboons, *Papio ursinus*, that individuals adapt their social strategies on very different timescales (Henzi et al., 2009; Sick et al., 2014; Silk et al., 2010). If the social network we studied can be reorganized rapidly, going from balanced to unbalanced to balanced again on a scale of a few days, then we should expect to find a large difference in a similarity measure (the network has changed) but little difference in terms of the number of balanced−unbalanced triangles on a monthly timescale. This problem may not be easy to solve because networks established on shorter timescales are subject to imprecise estimates of link strengths, which in turn could mask changes in the network. In our study for instance, we found that the monthly timescale usually recommended (Whitehead, 2008) represented a good compromise between a precise estimate of link strength and the possibility to detect temporal changes. However, the best aggregation timescale is likely to change depending on the situation, study species, group and data-gathering technique (Davis, Crofoot, & Farine, 2018; Farine & Whitehead, 2015). The investigation of the cosine similarity measure also shows a limit of the social balance theory. We observed important changes in the structure of the network (Fig. 7) that were not reflected by changes in the social balance of the social network, probably because they were linked to changes occurring in the relationships of only some of the individuals (Fig. 8). This suggests that the measure of social balance through the counting of balanced and unbalanced triangles may be too coarse and too global a measure to be able to detect and follow changes in the relationships between individuals. In particular, social balance focuses on the sign of these links but does not take into account their weights and hence the relative importance of the relationships in the social network.

We were nevertheless able to study the social network's dynamics using the cosine similarity between the affiliative ego-networks in successive months. Cosine similarity is a very versatile measure and can be used to compare networks over different timescales but also across scales within the network, from single individuals to subgroups to the entire network. The group-averaged cosine similarity value allowed us to visualize periods of global stability, and to identify moments of instability (Fig. 7a). More detailed investigation of the cosine similarity values showed that the periods of stability corresponded to high stability (large similarity values) for almost all individuals, as could be expected. However, the instability revealed by the average did not necessarily come from an instability of the entire network, but rather from a mixture of locally stable and changing structures (Fig. 8). Following individual cosine similarities therefore allowed us to identify, for each period of interest, individuals with more, or less, stable ego-networks, as well as interesting patterns of synchronization of ego-network evolution (Fig. 9). The patterns we identified on a monthly timescale often suggested sudden and important changes that corresponded, at least in some cases, to adult females changing primary males, as observed in the wild (Goffe et al., 2016). We suspect that stronger perturbations of the network could be linked to high-ranking females changing males (such as Angele), whereas smaller perturbations could be linked to more peripheral females (such as Brigitte) changing principal male.

Importantly, if some individuals in a wild population have more stable ego-networks compared to other members of the group, we may expect these individuals to have higher fitness, with increased longevity and more offspring for instance, because stable social relationships have been associated with all these factors, especially in baboons (Silk et al., 2009, 2010, 2003; Alberts, 2019). However, this effect on fitness may be more difficult to study in captivity where food, health and reproduction are controlled.

Conclusions and Perspectives

Social interactions are an important fitness component of group-living animals (see e.g. Alberts, 2019) and social network analysis provides powerful tools to describe social interactions and analyse their evolution through time (Hinde, 1976). In fact, social network analysis has transformed research in ecology and evolution (for a review see Cantor et al., 2019). Here, we have analysed the temporal (in)stability of a social group of baboons using an automatically collected high-resolution long-term data set. We have developed general tools to construct a signed network and shown that our study group's social network respected the predictions of social balance theory. However, the use of a similarity measure proved to be more sensitive and more versatile to understand changes in the individuals' social relationships and their consequences at the group level. In particular, our results show that behind what, at first glance, looks like a stable social network, there is a complex and subtle mixture of stable and unstable ego-networks. In the future, long-term high-frequency data (see Krause et al., 2013 for a review of recent technological developments) could help determine the fitness consequences of individuals' social strategies.

Data Availability

The data analysed in this article are freely available on the Open Science Foundation website at DOI:10.17605/OSF.IO/NX2PJ.

Acknowledgments

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Appendix

Robustness of the analysis with respect to the ALDM aggregation time window

In the Methods, we described how we built a temporal co-presence network based on the temporal and spatial proximity of the baboons in the ALDM workstations: we aggregated the raw data in time windows of length $\Delta t = 5$ s and considered that the individuals performing tests in the same time window and in neighbouring workstations were in co-presence.

For the sake of completeness, we report here results obtained with a different value of the aggregating window, namely $\Delta t = 10$ s, to show the robustness of the observed phenomenology.

Fig. A1 and A2 show the results concerning social balance theory, and Fig. A3 displays the colour-coded matrix of the average individual cosine similarity values between the monthly affiliative networks for all pairs of months. In all cases, results very similar to those presented in the main text were obtained.

Temporal evolution of triadic closure events and of indicators linked to the numbers of triangles

Fig. 6 gives the global number of triadic closure events from one month to the next. These events are defined by the fact that a wedge in one month (a structure of two links AB and AC such that the link BC does not exist) becomes a triangle in the next month. We classified these events depending on the type of wedge and on the type of resulting triangle (balanced or unbalanced). In Fig. A4, we show the numbers of each type of event for each month.

Moreover, we mention in the main text that the number of triangles and the number of triadic closure events fluctuate widely, with no clear temporal signal or trend. This is illustrated both by Fig. A4 and by Fig. A5, which shows the average clustering coefficient and the transitivity of each monthly network.

Dynamics of individual ego-networks

Fig. 9 illustrates the evolution of individuals' ego-networks similarities between successive months. Fig. A6 displays the same information for all individuals.

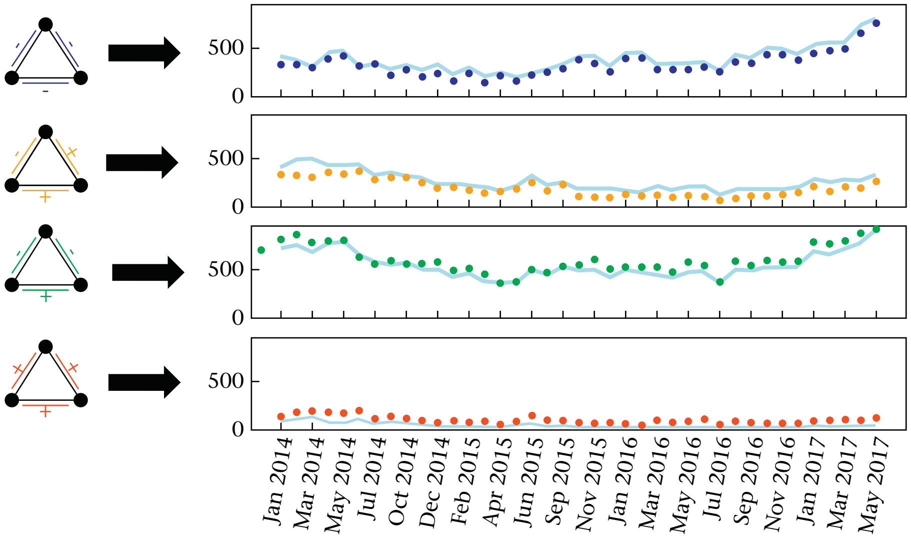

Figure A1. Evolution of the number of signed triangles through time: number of triangles of each type in the 39 monthly signed co-presence networks built using $\Delta t = 10$ s. As in the main text, the shadowed areas correspond to the confidence interval (5th to 95th percentiles) of the distributions of the numbers of triangles of each type in randomized monthly networks.

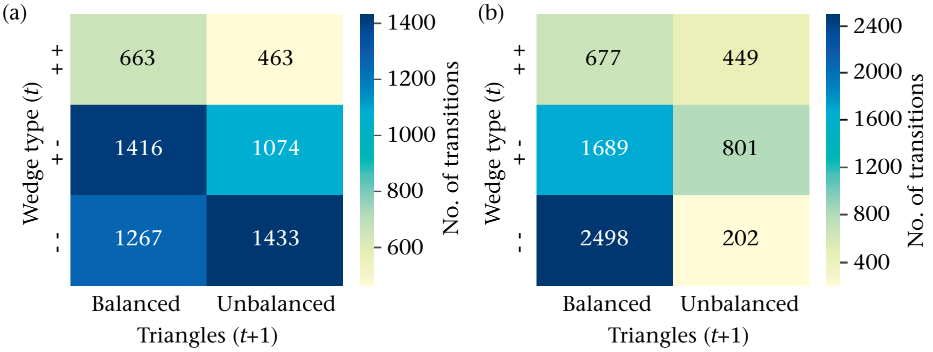

Figure A2. Social balance theory from the dynamical point of view in the signed monthly networks built with $\Delta t = 10$ s. Numbers of transitions from one month to the next, from the various types of wedges to balanced or unbalanced triangles, summed over the period of investigation (39 months) and for both (a) strong and (b) weak formulations of social balance.

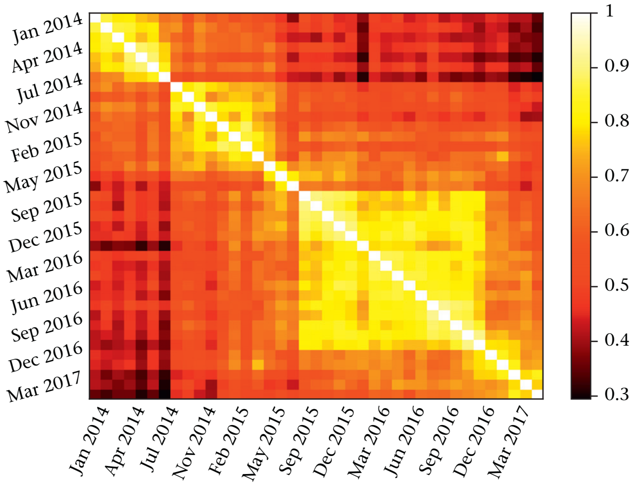

Figure A3. Group level dynamics for the monthly networks built using $\Delta t = 10$ s. Colour-coded matrix of the group cosine similarity values for all pairs of months. Patterns of stability and instability are the same as the case of $\Delta t = 5$ s shown in the main text.

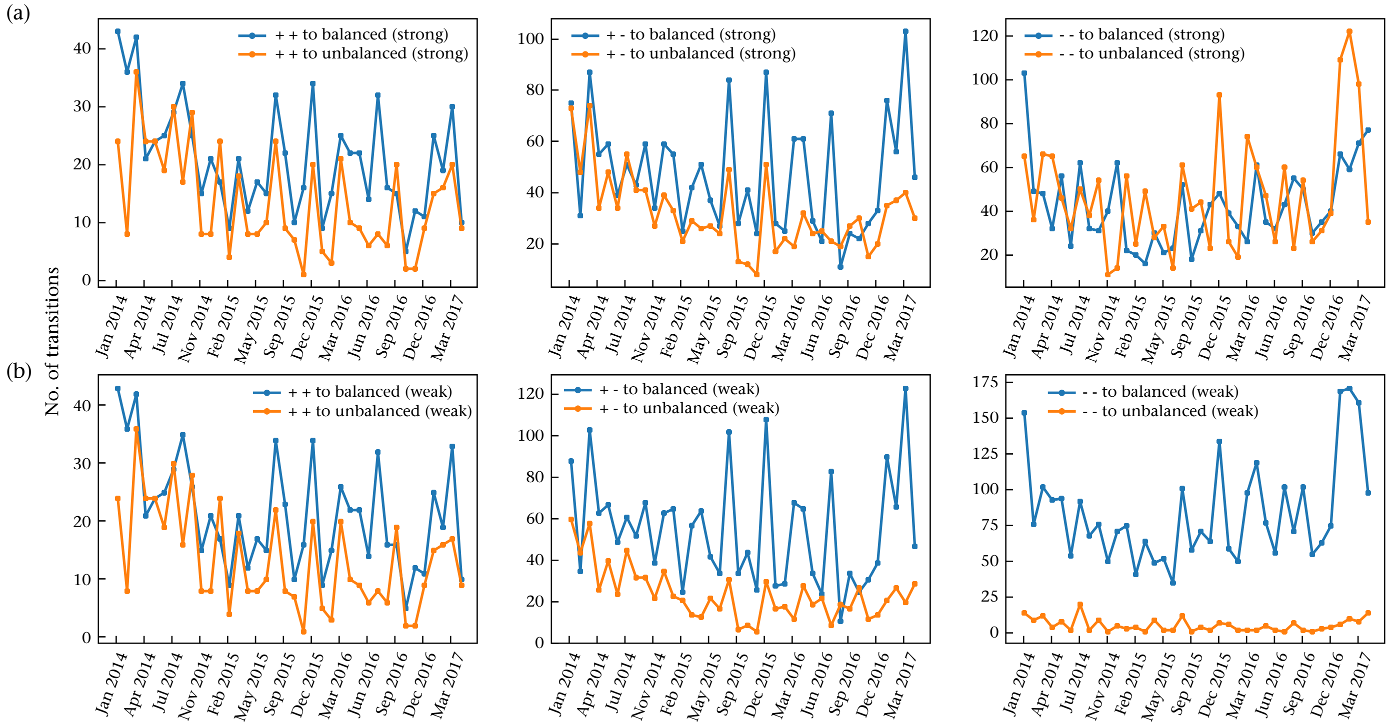

Figure A4. Numbers of transitions from one month to the next, from wedges of each type to balanced and unbalanced triangles, where balanced and unbalanced triangles are defined either according to the (a) strong or (b) weak version of social balance.

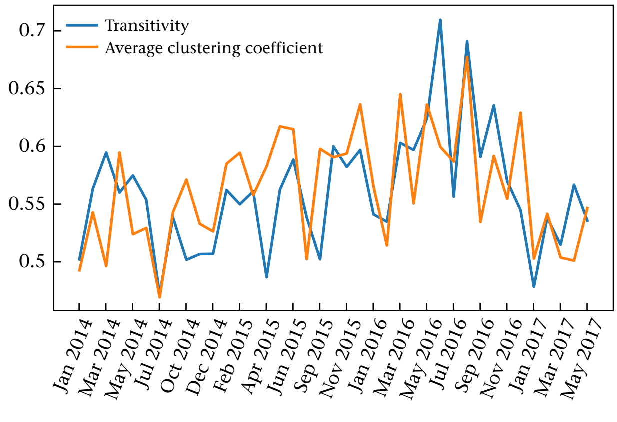

Figure A5. Transitivity and average clustering coefficient values during the 39 months of investigation.

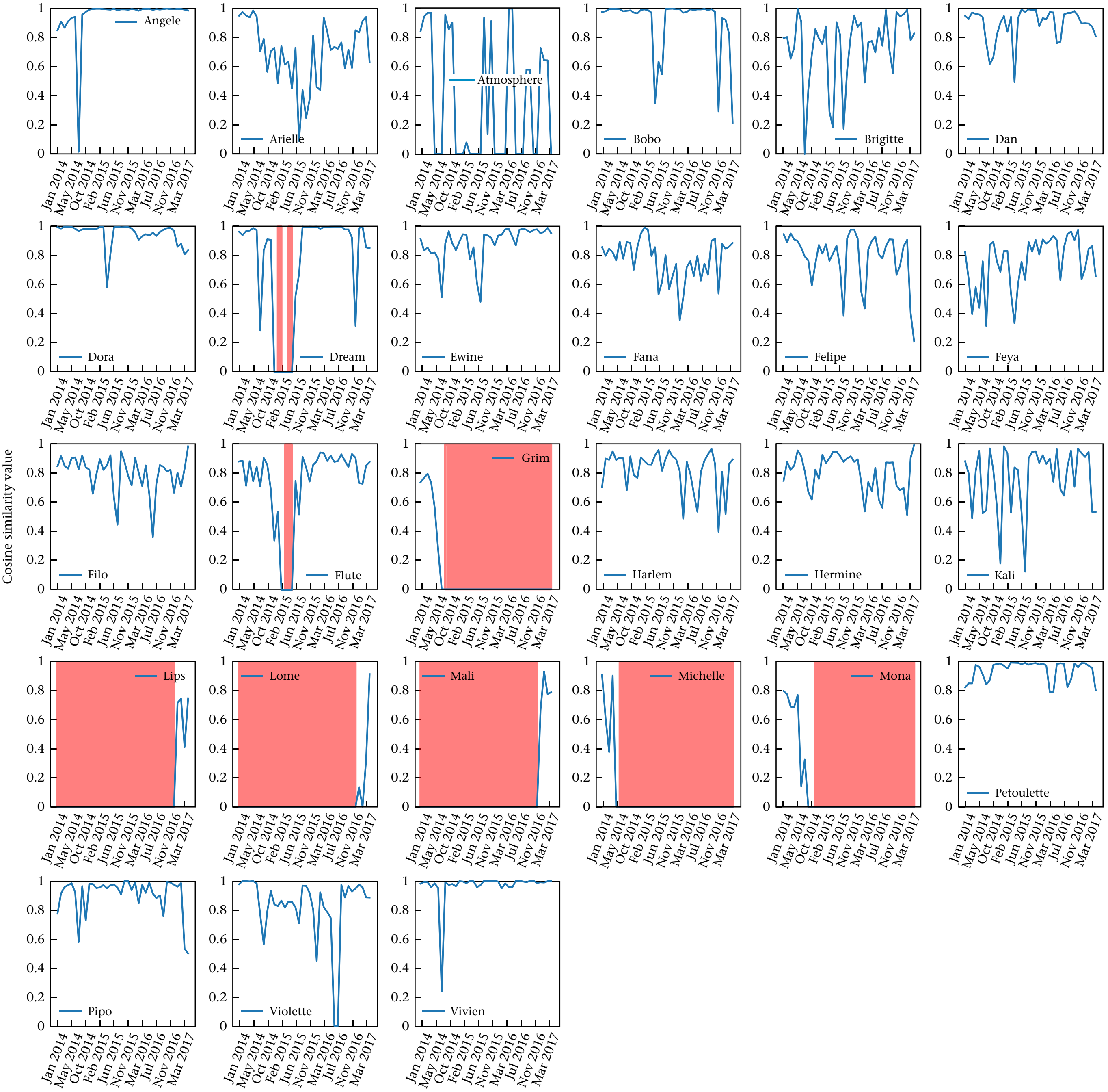

Figure A6. Evolution of ego-network cosine similarity values for all the individuals that were present in at least two successive months during the study. In each plot, the *x*-axis corresponds to the month and the *y*-axis gives the value of the cosine similarity between the ego-networks of the individual in one month and the next. Red vertical bars correspond to the period of absence of that individual from the enclosure.