Current Zoology 61 (1): 70–84, 2015

Detection of social group instability among captive rhesus macaques using joint network modeling

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Abstract Social stability in group-living animals is an emergent property which arises from the interaction amongst multiple behavioral networks. However, pinpointing when a social group is at risk of collapse is difficult. We used a joint network modeling approach to examine the interdependencies between two behavioral networks, aggression and status signaling, from four stable and three unstable groups of rhesus macaques in order to identify characteristic patterns of network interdependence in stable groups that are readily distinguishable from unstable groups. Our results showed that the most prominent source of aggression-status network interdependence in stable social groups came from more frequent dyads than expected with opposite direction status-aggression (i.e. A threatens B and B signals acceptance of subordinate status). In contrast, unstable groups showed a decrease in opposite direction aggression-status dyads (but remained higher than expected) as well as more frequent than expected dyads with bidirectional aggression. These results demonstrate that not only was the stable joint relationship between aggression and status networks readily distinguishable from unstable time points, social instability manifested in at least two different ways. In sum, our joint modeling approach may prove useful in quantifying and monitoring the complex social dynamics of any wild or captive social system, as all social systems are composed of multiple interconnected networks [*Current Zoology* 61 (1): 70–84, 2015].

Keywords Nonhuman primates, Network stability, Social network analysis, Dominance, Aggression, Status signaling

The persistence of stable social groups in many animal societies indicates that, despite the inherent costs (Alexander, 1974), group members gain a net benefit by living in a group. Regardless of the precise benefits of group-living, the inevitable competitive interactions among group members over similar resources (i.e., mates, food, alliance partners) has led to the evolution of mechanisms that maintain group stability. For example, cooperative foraging in bats (McCracken and Bradbury, 1981) conflict resolution and reconciliation in primates (de Waal, 2000), conflict management via conflict policing in primates and reproductive policing in social insects (Ratnieks, 1988; Flack et al., 2005), group composition such as the presence of keystone individuals versus problematic individuals (Dazey et al., 1977; Beisner et al., 2011b; Abell et al., 2013), and cohesive kinship structure (Beisner et al., 2011a) may all contribute to maintaining group stability, although the precise mechanisms are likely to vary across taxa.

Despite this large body of research, pinpointing when a group has become unstable is no easy task. In fact, the study of the resilience (and conversely, vulnerability) of complex social systems (such as banking networks) has received much research attention (Dorogovtsev and Mendes, 2001; Haldane and May, 2011; Hsieh et al., 2014) because identifying network instabilities and vulnerabilities may allow us to (a) minimize the potential costs if the system does collapse, and (b) prevent such instabilities from materializing in the future.

Group stability in animal societies

Among wild primate groups, reduced group stability or cohesion may lead to group fission (Malik et al., 1985; Dittus, 1988; Oi, 1988). In the confines of captivity however, group fission may not be possible, and instability may result in outbreaks of serious aggression and the dissolution of the primary organizational structure of the group, e.g., dominance hierarchy (Ehardt and Bernstein, 1986; Gygax et al., 1997; McCowan et al., 2008). Groups may reach a point of maximal instability through natural social processes, or it may be brought on by sudden absence of key individuals, such as the death or removal of alpha individuals (Gouzoules, 1984;

Received Sep. 10, 2014; accepted Dec. 9, 2014.

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Ehardt and Bernstein, 1986; Beisner et al., 2011a). It is possible, however, that sudden absence of key individuals will only result in maximal instability (i.e. social collapse) if the groups are already experiencing other forms of instability.

Joint network relationships as a method for detecting stability

Stability in a biological system is a higher-level outcome arising from interactions among lower-level components within the system. Social network theory is therefore an ideal method for investigating the emergence of stability from interactions among group members. Biologists have already used a number of social network approaches to detect such emergent properties (Palla et al., 2007; Wolf et al., 2007; Gustafsson et al., 2009), including group stability (Flack et al., 2006). Flack and colleagues (2006), found that removing key conflict policers (i.e. those that intervene to stop fights) changed the structure of numerous affiliation networks (i.e. grooming, play, social contact, and proximity) in a captive group of pigtail macaques. For example, groom and play networks showed reduced mean degree and proximity networks showed increased clustering. Flack and colleagues concluded that group stability had been temporarily reduced, because group members retracted their affiliation networks to focus on fewer social ties. Such network analyses, however, cannot distinguish between temporary reductions in stability, from which animals can recover, and more serious reductions in stability that will likely end in social collapse. Furthermore, it can be difficult to know which behavioral networks to examine and which measures to calculate to quantify group stability. An examination of the synergistic interaction among multiple networks is likely to yield better insight into the social dynamics of the group, and may therefore offer a better way to quantify group stability.

All social systems, regardless of their particular mechanisms of stability, are similar in having inter-connected behavioral, biological, and/or physical networks, and the synergistic interaction amongst these networks yield emergent properties of complexity and stability. Given this commonality, such inter-connections are likely to change under changing conditions of stability. Although separate behavioral networks are commonly constructed from a single target system, such as grooming and aggression networks in primate social groups (Flack et al., 2006; Wey and Blumenstein, 2010; Beisner et al., 2011b; Beisner et al., 2011a; Vander Waal et al., 2014) it has only been recently that joint modeling methodologies and computational algorithms have been developed that can examine interdependencies amongst multiple networks (Barrett et al., 2012; Chan et al., 2013).

A new network analytical technique developed by our research team, called joint network modeling (JNM) (Chan et al., 2013) has the potential to detect network instabilities. JNM is a data driven, iterative modeling approach that involves empirically constructing multiple networks to quantify the interdependence among them. This approach recreates the joint probabilities of two types of social relationships (e.g. groom and aggression) by first using the raw data to calculate expected probabilities of jointly observing groom and aggression for a given dyad. Under this null hypothesis, these behaviors are assumed to be independent. Constraint functions are then applied sequentially to adjust our expected probabilities (which began at independence) to match the observed network data based upon hypothesized interdependencies in the data (e.g. two behaviors covary in similar or opposite directions) (Chan et al., 2013). By using constraint functions to adjust expected probabilities of each type of dyad, we are essentially modeling the way in which a pair of networks are interdependent. Thus, the purpose of adding constraint functions is to determine which patterns of network interdependence are present in a given joint-network system, e.g. which constraint functions bring our expected probabilities more closely in line with observed network data. The joint network model is done once sufficient constraint functions are applied to match the observed data, meaning the expected frequencies under the model are not statistically different from observed frequencies, according to chi-squared values.

The social dynamics of a complex social group are played out through a wide variety of dyadic or even polyadic behavioral interactions (e.g. proximity, co-feeding, fighting, alliance support, avoidance). Although any set of networks may be useful in quantifying network interdependence as it relates to stability, the networks most relevant to social stability will vary by species' social structure. Therefore, it may be important to distinguish keystone networks from other more subsidiary networks. Keystone networks communicate animals' most fundamental relationships because they govern or influence the manner in which other networks interact (Hsieh et al., 2014). As such, the presence and direction of links in these networks are less likely to be influenced by situational variables (e.g., presence of kin, hunger/satiation) than other networks, which tends to

generate a more rigid structure.

Rhesus macaques live in large, multi-male/multi-female groups that average around 40 individuals, though groups can number in the hundreds in areas with high human food subsidization (Seth and Seth, 1986; Qu et al., 1993; Southwick and Siddiqi, 1994). Females remain in their natal groups while males disperse around sexual maturity (Berard, 1999). Females form dominance hierarchies according to matrilineal kinship (Sade, 1967; 1969) that remain relatively stable over time. Rhesus macaques are also a highly despotic species, showing intense and highly asymmetric patterns of aggression, well-defined dominance hierarchies, and strong preference for kin in affiliative interactions (Thierry, 2004).

Dominance relationships form the core of rhesus macaque social structure (Sade, 1967; Lindburg, 1971). Among the different types of dominance networks, the status signaling network (e.g., peaceful communication of subordinate status, such as displacements and silent-bared-teeth signals) is likely to be a keystone network because it communicates fundamental dominance relationships (Flack and de Waal, 2004; Beisner and McCowan, 2014; Hsieh et al., 2014). Choosing the second of the two networks is somewhat arbitrary, and we chose to examine aggression networks because aggressive behavior is well-studied in macaques (facilitating the generation of hypotheses that underlie the constraint functions) and we have a sufficiently large data set of aggressive interactions. We therefore examined status signaling and aggression networks with respect to stability. Despite the fact that we have chosen to examine two dominance behavioral networks, our goal was not to study dominance per se, but to examine inter-network dependence in relationship to stability.

Here we use our joint modeling technique to examine social stability in seven social groups of rhesus macaques, three of which experienced a social collapse. Our goal was two-fold: (1) to identify consistent patterns in the interdependence between aggression and status networks that are characteristic of stable social groups of rhesus macaques, and (2) to determine whether these characteristic patterns of interdependence change during unstable time periods, such that our JNM approach can readily distinguish between stable and unstable periods.

Although it is not entirely apparent *how* two different types of behaviors should interact synergistically, there should be some degree of coordination between aggression and status as opposed to independence. For example, we might see more dyads than expected that show unidirectional status with no aggression, because dyads that use subordination signals fight less frequently (Flack and de Waal, 2007; Beisner and McCowan, 2014). Further, in species with a clear dominance hierarchy, aggression and status signaling should typically show opposite directions, where if individual A is dominant to individual B, then A should threaten B and B should signal acceptance of subordinate status to A. Finally, we can expect that any interdependencies between aggression and status present at stable time points will likely change or disappear during unstable periods.

1 Materials and Methods

1.1 Study subjects and behavioral data collection

Seven large outdoor captive groups of rhesus macaques were studied at the California National Primate Research Center between June 2008 and July 2014. We performed network analyses on data available from two studies (UC Davis Institutional Animal Care and Use Committee protocol #s 11843, 16674, 16810). We coded group IDs as follows: (1) groups from the first study are referred to as “A” groups because they were observed under the same study design (six hours/day on four days/week on a weekly rotating schedule), (2) groups from the second study, “B” groups, were observed under a different study design (six hours/day on four days/week for 12 consecutive weeks, including an experimental removal of a high-ranking 3–6 year old natal male in the seventh week), and (3) stable groups are labeled with an “S” identifier, and unstable groups (i.e. those that eventually collapsed) are labeled with a “U” identifier (see Table 1 and Figure 1). We used an event sampling design to record all occurrences of aggressive and status interactions across all study groups, yielding a total of 50,110 dyadic aggressive interactions and 24,537 status interactions. Aggression was defined as one monkey threatening, lunging at, chasing, or biting another monkey, who typically responds with submission, such as moving away, running away, or screaming. We also included bidirectional aggression, in which a subordinate either responded to a dominant’s attack with aggressive behavior or, on a separate day, initiated a fight by directing aggression at a dominant. Mild protests by the subordinate (e.g. open mouth threat; head bob) in response to receiving aggression, however, were omitted because they likely do not represent true aggressive challenge. Furthermore, we focus on only dyadic interactions, because polyadic interactions may

Table 1 Study group characteristics

Group	Stability Code	Group Size (>2yr)	Observation period	Stability	Mean aggression network density	Mean status network density
5	A1-S	95	6/2/08 –4/24/09	Stable	0.16	0.21
8	A2-S	97	6/9/08 –4/3/09	Stable	0.14	0.16
14B	A3-U	68	6/16/08 –4/10/09; 4/27/11 –6/24/11	Social collapse 9/17/11	0.16	0.23
6C	B1-S	116	2/21/12 –5/11/12	Stable	0.17	0.09
19	B2-U	101	9/24/12 –12/13/12	Social collapse 12/14/12	0.24	0.08
16D	B3-S	68	9/3/13 –11/22/13	Stable	0.34	0.19
13B	B4-U	125	3/3/14 –7/17/14	Social collapse 7/18/14	0.19	0.10

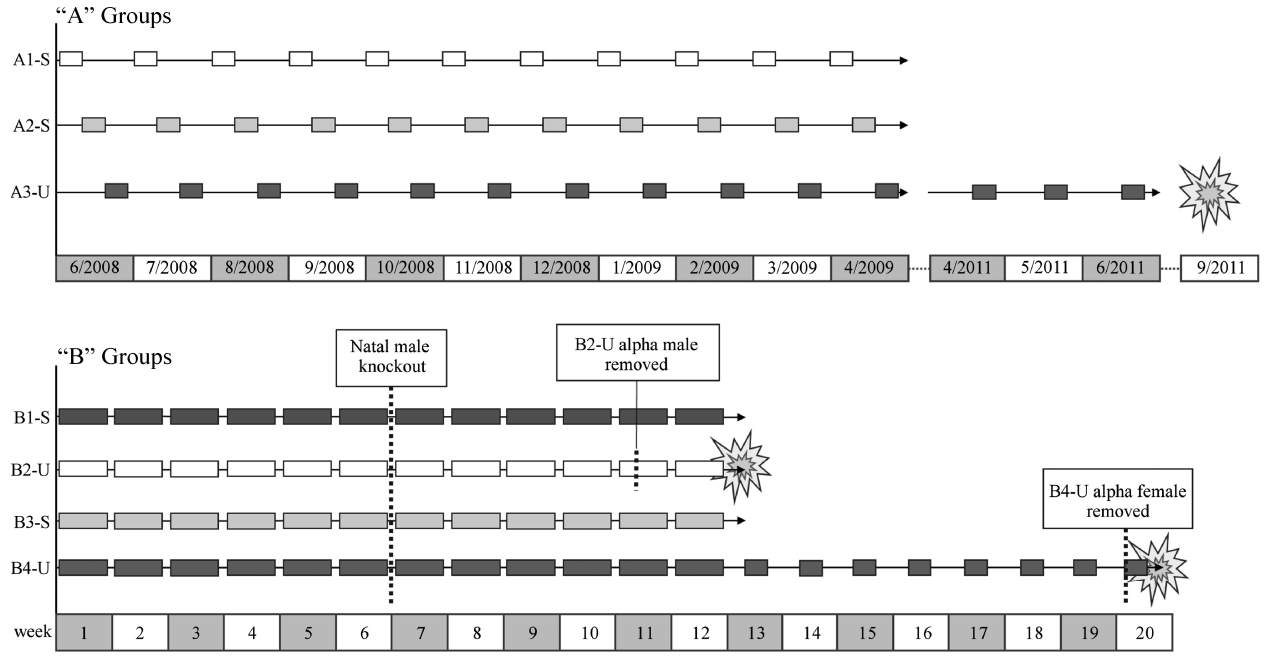

Fig. 1 Diagram of the sampling design for each of the seven study groups

The "A" groups were observed one week per month on a rotating schedule for an 11-month period. The "B" groups were each observed four days/week across 12 consecutive weeks, except B4-U, which was observed an additional eight weeks at half the sampling effort (two days/week) for a total of 20 weeks.

cloud the expected relationship between aggression and status signaling. Status signaling was defined as submission (i.e. silent bared teeth (SBT), move away, or non-sexual rump present) given in response to a peaceful approach (i.e. not in response to aggression).

Fig. 1 summarizes the study design and stability status of each group. Briefly, all "A" groups (A1-S, A2-S, and A3-U) were stable during their primary observation period in 2008–2009. These groups remained intact and experienced no major changes in their social hierarchy or group membership (i.e., same alpha males and females, same matrilineally structured hierarchy) several months before, during, and after their observation in 2008 and 2009. However, one "A" group became unstable in 2011. In early 2011 the male hierarchy in group A3-U was in flux – the previous alpha male was injured and deposed, after which time two males jockeyed for the alpha position. Our observers collected data on group A3-U from April-June 2011. The alpha male and alpha family were overthrown on September 17, 2011.

Among the "B" groups, two were stable (B1-S, B3-S) and two were unstable (B2-U, B4-U). As part of their original study design, each "B" group experienced experimental removal of a high-ranking 3–6 year-old natal male (primarily sons of the alpha female), because these males often instigate disproportionate amounts of severe

aggression, prematurely attain high individual rank as a result of female kin support, and may end up challenging the alpha male (Beisner et al., 2011b). In groups B1-S and B3-S, the targeted natal males were both 4-year-old sons of the alpha female, and both attained the position of beta male in their respective groups. Groups B1-S and B3-S represented stable groups because the alpha male and female both retained their positions following the experimental removal, and there were no major changes to group membership or the matrilineally structured hierarchy.

Groups B2-U and B4-U both socially collapsed at the end of scheduled observations (B2-U: during week 12; B4-U: during week 20; see Figure 1). While both represent unstable groups, their descent into instability was unclear, particularly whether the experimental removals during the seventh week influenced group stability. Unlike groups B1-S and B3-S, the two unstable "B" groups did experience major changes to the group hierarchy. In group B2-U, the alpha male was temporarily removed for dental treatment in the 11th week, and nine days later, the group had a social overthrow. Although it seems clear that the absence of the alpha male was the proximate cause of the social collapse, it is uncertain whether removal of the natal male reduced the stability of the group, priming it for collapse when the alpha male was removed one month later, or whether group B2-U was already unstable before the natal male was removed. Group B4-U was observed an additional eight weeks beyond the other "B" groups (weeks 13–20) according to a planned extension of observation effort, but at a lower observation frequency (2 days/week, rather than the 4 days/week during weeks 1–12. Observers noted a dramatic increase in fighting during weeks 13–20 between females from the alpha family and the fourth ranked family. The alpha female was removed for veterinary treatment in the 20th week due to a hand laceration , and the next day there was an outbreak of deleterious aggression and a major upset in the social hierarchy (i.e. very low-ranking females were collectively challenging the highest-ranking females).

1.1 Network construction

Aggression and status networks were constructed for each group across multiple time points. For "A" groups, each time point included eight 6-hr days of observation: June–July 2008, August–September 2008, October–November 2008, December–January 2008/2009, and February–April 2009. The final time point included 12 6-hr days of observation due to relatively low levels of activity (and thus lower rates of aggression and status) in early spring. Observation hours from April-June 2011 on group A3-U were matched to the stable time points. For "B" groups, each time point included 12 6-hr days of observation: weeks 1–3, weeks 4–6, weeks 7–9 and weeks 10–12. These 3-week time points maintained a separation between the 6-week baseline and 6-week post removal periods. Although these divisions combine eight days of observation for "A" groups and 12 days of observation for "B" groups, the temporal variance in behavior was lower for "B" groups. Eight days across a 5-week period had greater temporal variance (i.e., increased chance of recording rare behaviors, such as status signals or bidirectional aggression) than 12 days across a 3-week period. We initially examined "B" groups using 8-day observation periods, but found few dyads with rare behaviors (even in stable groups), such as dyads with status signals or bidirectional aggression. Combining data into non-adjacent sets of eight days (e.g., week 1 + week 4) increased joint network interdependence, but did not provide a simple method of combining data across the experimental knockout. We therefore decided to use sets of 12 consecutive days (e.g. weeks 1–3) to perform JNM.

Two exceptions were made for unstable groups. First, group B4-U had two additional time periods from a less-intensive observation period (2 days/week during weeks 13–20): weeks 13–17 and weeks 16–20. Data from weeks 16 and 17 contribute to networks for these last two time points to maintain similar hours of observation. Second, in group B2-U, data from the 9th week contribute to the networks for two time points: weeks 7–9 weeks 9–11 in order to examine the experimental removal of the natal male prior to the alpha male's absence. A final fifth time point was created (weeks 11–12) the final six days of observation after the alpha male was removed.

We constructed two binary networks (aggression and status) for each group at each time point. For each network, a node represents an individual monkey and an edge represents the directed behavioral relationship. In the aggression network, for example, an edge was drawn from A to B if, at any time during the observation period, A threatened, lunged at, chased, or bit monkey B. A bidirectional edge was drawn between A and B if, at any time during the observation period, monkey B also threatened, lunged at, chased, or bit monkey A. The same is true for the status network. For each pair of animals, we described their joint aggression-status relationship using a 4-digit binary code (aka 4-dimensional binary vector). The first two digits (i.e. dimensions)

code for the two possible directions of aggression – from A to B and from B to A. The second two digits code for the two possible directions of status – again, A to B and B to A. The 4-digit code is binary, because we use 1s and 0s to describe whether the behavior was present or absent. To make these 4-digit codes easier to interpret, we use the letter "A" to represent presence of aggression and "0" for absence, and the letter "S" to represent presence of status and "0" for absence (i.e. A000 refers to unidirectional aggression and no status; 00S0 refers to unidirectional status and no aggression). There are a total of 16 possible 4-digit codes; we show only the 10 biologically-distinct codes and omit those that are repeated (i.e. A000 and 0A00 both refer to unidirectional aggression and no status). All network matrices were constructed in R (R Core Team, 2013).

1.2 Joint network modeling

To recreate the observed joint probabilities of aggression and status relationships, we first used the raw data to calculate expected probabilities of jointly observing aggression and status for a given dyad, assuming aggression and status relationships were independent. The assumption of independence is the null model. A series of six constraint functions were then iteratively applied to calculate the number of expected relationships with each new constraint until the expected probabilities were not significantly different from the observed, according to chi-squared test. All steps in the joint modeling analyses were run in R using code written by members of our research team. R code is available upon request.

A complete description of the constraint functions can be found in (Chan et al., 2013). Briefly, constraint function 1 determined whether the two directions of the first behavior (i.e. aggression) were independent, by calculating the covariance of outward and inward aggression across all dyads. For example, if monkey A threatens B, are we more or less likely to see aggression from B to A. Constraint function 2 determined whether the two directions of the second behavior were independent. Constraint function 3 determined whether the direction of aggression affected the direction of status signaling (i.e. does monkey A both threaten and give signals of subordination to B). Constraint 4 determined whether it was more likely to see a status interaction (regardless of direction) if there was at least one aggressive interaction between two animals. Constraint 5 accounted for the covariance present when both behaviors occurred in both directions (i.e. code AASS). Finally, constraint 6 accounted for the covariance present when both behaviors were absent (i.e. code 0000).

The primary output from each joint modeling analysis is a table showing the total number of dyads observed for all 10 types of relationships (i.e. codes A000, AA00, 00S0, etc.) as well as the expected counts of each type of relationship under each constraint function, which allows us to see which constraints need to be added to bring the expected number of relationships in line with observed frequencies. For example, we observed 420 pairs of animals showing unidirectional aggression and no status signals (code A000) in group A1-S during June-July. If aggression and status interactions occurred independently, we should expect to see approximately 527 of these types of dyads. The chi-squared value for this relationship was 21.93, meaning that such dyads appeared less often than expected under independence. In these output tables, the numbers in parenthesis represent the chi-squared value for the difference between expected and observed; it generally decreases as we add more and better constraints. Given that the 16 different 4-digit codes represent only 10 biologically-distinct types of bivariate interaction, the appropriate degrees of freedom is 9 for the total Chi-squared calculation, and the 95% and 99%-percentiles are 16.92 and 21.67, respectively.

2 Results

2.1 Descriptive

All networks were sparsely populated, between 14 and 34% of the total possible dyadic relationships were present across all aggression networks with groups B2-U and B3-S having the highest densities (Table 1). Among status networks, between 8 and 23% of all possible dyadic relationships were present, with "A" groups showing the highest percentages, suggesting that differences in data collection protocol contributed to this pattern. Although network densities varied widely between aggression and status networks, as well as across groups, network densities remained highly consistent within a single group for a given behavior (SD of network density ranged from 0.009 to 0.054). Despite the differences in overall presence of edges in each network, however, JNM results were remarkably similar across groups.

The extent of interdependence between aggression and status networks was quite high. Across all joint aggression-status networks, all six constraint functions were required to bring expected dyadic frequencies in line with observed frequencies, such that total chi-squared values were less than 21.67 (Fig. 2, 3). However,

constraint function 3 (which determined whether the direction of aggression affected the direction of status signaling) accomplished the majority of this improvement, typically showing between 60%–75% of the reduction in total chi-squared. Reductions in total chi-squared by other constraint functions were: constraint 1: -2.4%–17.2% (mean=3.9%); constraint 2: 6%–20% (mean=10.6%), constraint 4: 0–4.9% mean=1.8%; constraint 5: 0–3.9% (mean=0.57%); constraint 6: 4.4%–9.4% (mean=6.8%). Overall, dyads with no interactions (i.e. 0000) were the most common, which is not surprising because in any large social group, many pairs of animals will not directly interact. The next most common dyads were those with unidirectional aggression and no status (i.e. A000) and unidirectional status and no aggression (i.e. 00S0). However, because the relative proportions of any two types of dyads depends upon how often aggression versus status interactions were sampled in that group, further examination of the frequencies of different types of dyads will be done using chi-squared values.

2.2 Opposite direction aggression and status is key for stability

The most obvious pattern across all joint aggression-status networks was that aggression and status occurred in opposite directions (e.g. monkey A threatens B and monkey B gives subordination signals to A). There were far more dyads with opposite direction aggression-

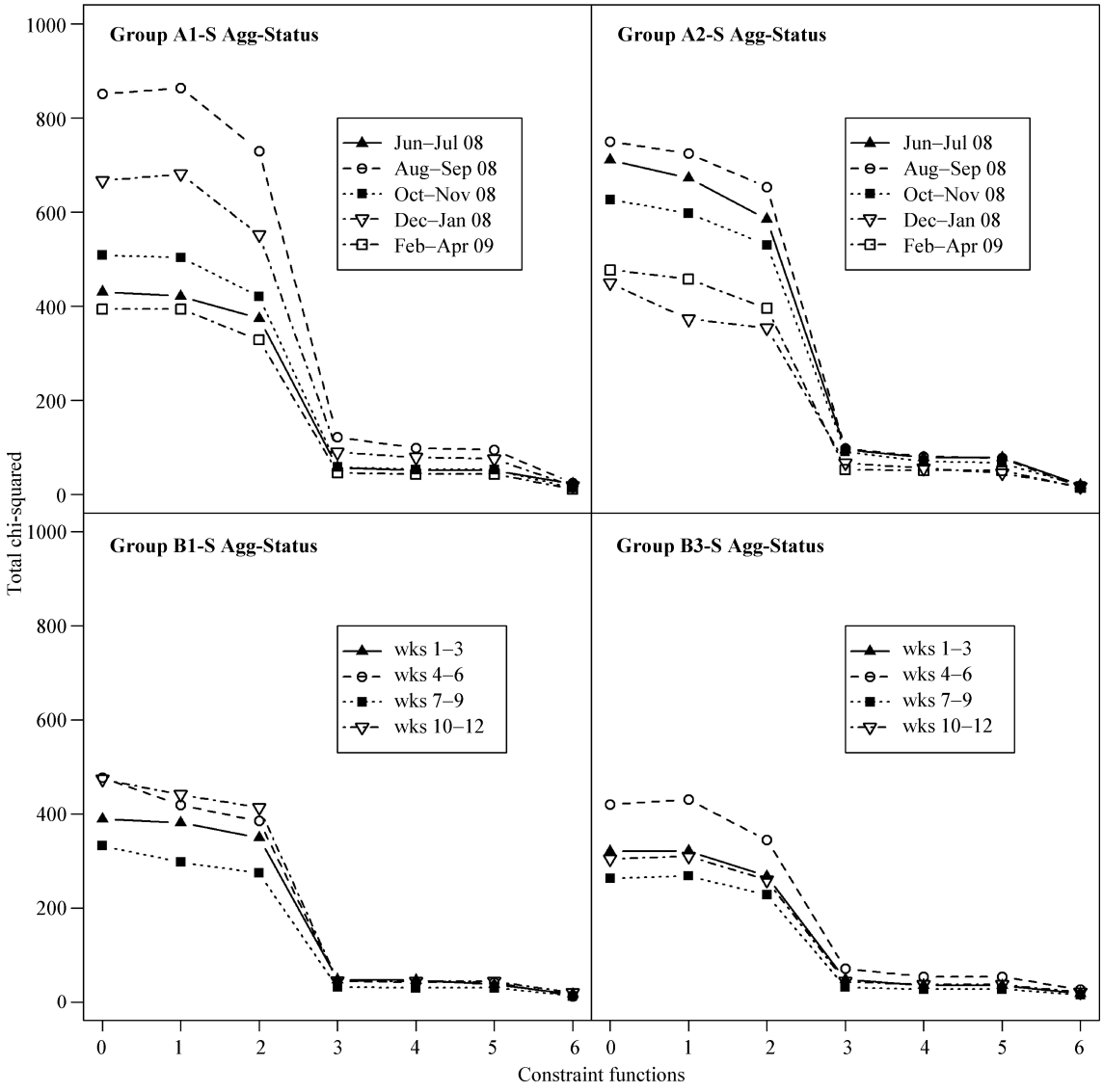

Fig. 2 Plots of the change in cumulative chi-squared upon application of constraint functions for aggression-status networks in four stable social groups (A1-S, A2-S, B1-S, B3-S) across multiple time points

Groups A1-S and A2-S were observed between June 2008 and April 2009. Groups B1-S and B3-S were observed for 12 consecutive weeks in spring 2012 and fall 2013, respectively.

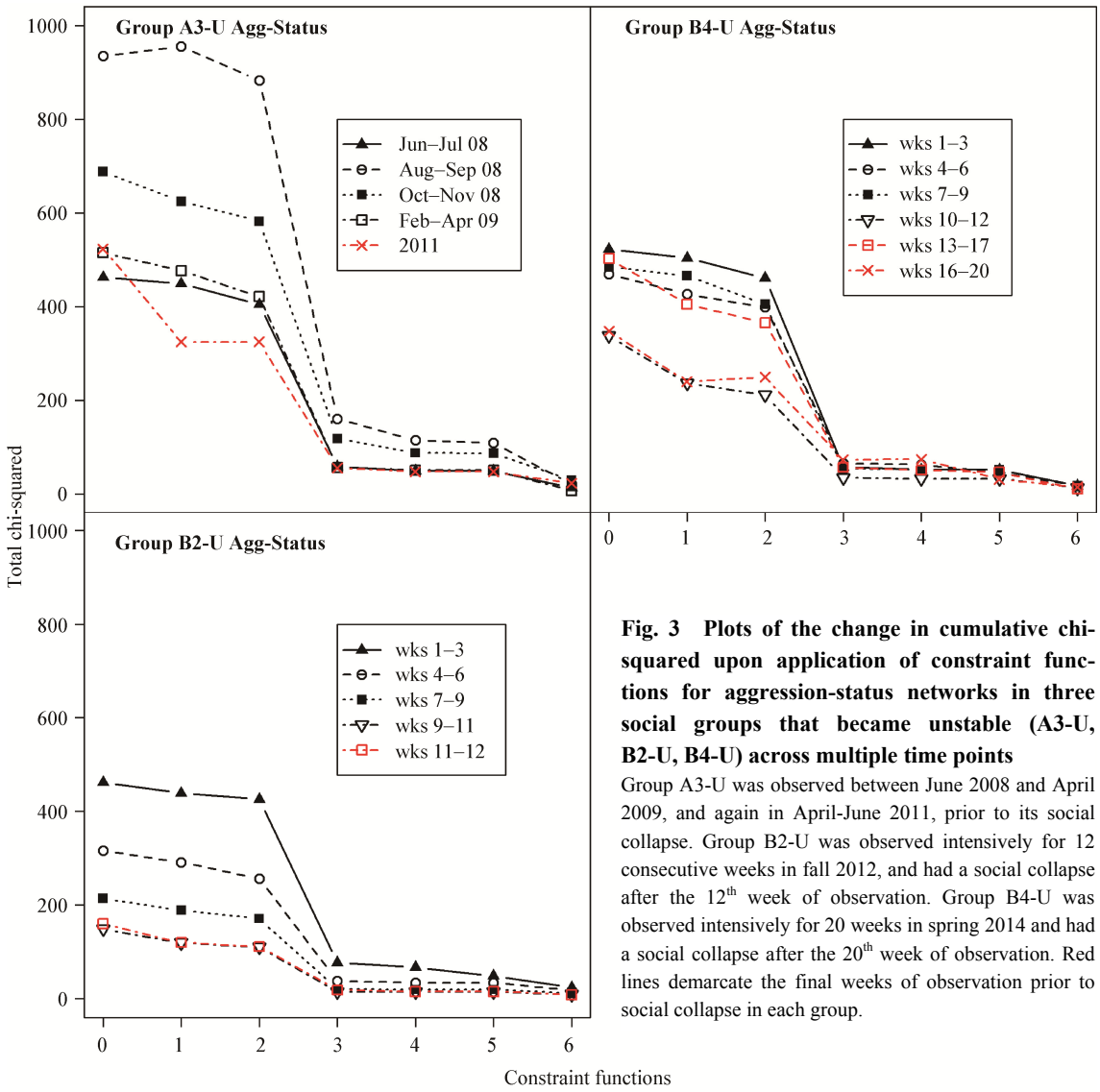

Fig. 3 Plots of the change in cumulative chi-squared upon application of constraint functions for aggression-status networks in three social groups that became unstable (A3-U, B2-U, B4-U) across multiple time points

Group A3-U was observed between June 2008 and April 2009, and again in April-June 2011, prior to its social collapse. Group B2-U was observed intensively for 12 consecutive weeks in fall 2012, and had a social collapse after the 12th week of observation. Group B4-U was observed intensively for 20 weeks in spring 2014 and had a social collapse after the 20th week of observation. Red lines demarcate the final weeks of observation prior to social collapse in each group.

status (code A00S) than expected under independence. The chi-squared values for opposite direction aggression-status ranged between 200 and 700 across all time points in all of the stable groups, accounting for 58%–76% (mean = 67.6%) of the total chi-squared. In comparison, chi-squared values for all other types of relationships ranged between 0 and 100. Table 2 shows the full joint modeling output for the June-July time period in group A1-S. The outputs for all other groups across all time points are shown in supplementary information Supplementary Tables S1–S31. Additionally, same direction aggression-status dyads (i.e. A0S0) showed consistently large chi-squared values under independence such that very few dyads (typically less than 10) showed both aggression and status from A to B. Furthermore, constraint function 3 (which determines whether the direction of aggression may affect the direction of status signaling) brought the expected counts of both of these types of dyads (A00S and A0S0) in line with observed counts. These results agree with our basic understanding of dominance relationships in a despotic society – many (if not most) dyads should have uncontested, clearly-communicated dominance relationships showing unidirectional aggression from dominant to subordinate as well as unidirectional signals of subordination from subordinate to dominant (Beisner and McCowan, 2014).

The most striking evidence of the importance of opposite direction aggression-status came from joint network analyses of the three groups that socially collapsed. First, we saw a loss of interdependence in the aggression-status relationship over time in groups B2-U and B4-U, both of which descended into social collapse shortly after the absence of alpha individuals. This decreased interdependence between aggression and status networks (as measured by a drop in total chi-squared under the null model of independence) was driven by a

Table 2 Observed versus expected counts of dyads for aggression and status networks for June–July for group A1-S

Agg-status	Total observed dyads	Expected dyads (independence)	F1	F2	F3	F4	F5	F6
A000	420	527.56 (21.93)	505.95 (14.60)	500.33 (12.90)	490.95 (10.25)	476.29 (6.65)	476.28 (6.65)	414.86 (0.06)
AA00	25	19.38 (1.63)	33.75 (2.27)	33.38 (2.10)	32.75 (1.83)	31.77 (1.44)	31.87 (1.48)	27.76 (0.27)
00S0	551	594.67 (3.21)	595.86 (3.38)	652.68 (15.84)	640.45 (12.49)	624.73 (8.70)	624.70 (8.70)	544.77 (0.07)
00SS	4	24.62 (17.27)	24.67 (17.32)	7.86 (1.90)	7.71 (1.79)	7.52 (1.65)	7.63 (1.73)	6.65 (1.06)
A00S	160	43.69 (309.65)	41.90 (332.89)	45.89 (283.69)	169.00 (0.48)	191.51 (5.18)	191.50 (5.18)	167.05 (0.30)
A0S0	3	43.69 (37.89)	41.90 (36.11)	45.89 (40.09)	12.00 (6.75)	13.60 (8.26)	13.60 (8.26)	11.86 (6.62)
AAS0	14	3.21 (36.27)	5.59 (12.65)	6.12 (10.13)	6.01 (10.63)	6.81 (7.60)	6.83 (7.53)	5.96 (10.86)
A0SS	3	3.62 (0.11)	3.47 (0.06)	1.11 (3.25)	1.08 (3.38)	1.23 (2.55)	1.25 (2.47)	1.09 (3.36)
AASS	0	0.13 (0.13)	0.23 (0.23)	0.07 (0.07)	0.07 (0.07)	0.08 (0.08)	0.01 (0.01)	0.01 (0.01)
0000	3671	3590.43 (1.81)	3597.7 (1.49)	3557.7 (3.61)	3491.0 (9.28)	3497.5 (8.61)	3497.3 (8.62)	3671.0 (0.00)
		429.91	421.01	373.58	56.96	50.73	50.63	22.62

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions. F1: whether the two directions of aggression were independent; F2: whether the two directions of status were independent; F3: whether the direction of aggression affected the direction of status; F4: whether any status interaction is more likely if there is an aggressive interaction; F5: accounts for covariance present when aggression and status occur in both directions [AASS]; and F6: accounts for covariance present when aggression and status were both absent [0000].

loss of dyads showing opposite direction aggression status (code A00S) just prior to collapse. Whereas A00S dyads accounted for 58%–76% of the total interdependence between aggression-status networks in stable groups, opposite direction aggression-status dyads accounted for only 38%–51% of the bivariate network interdependence in the final unstable time points of groups A3-U, B2-U and B4-U (B4-Uweeks 16-20: 38.7%; A3-U in 2011: 45.1%; B2-U weeks 9-11: 51.8%). In other words, unstable groups had fewer pairs of animals with well-defined dominance relationships in which aggression went from dominant to subordinate and status signals went from subordinate to dominant. Surprisingly, the number of well-defined dominance relationships showing opposite direction aggression-status during unstable time points remained significantly higher than expected under independence (B2-U weeks 9–11: chi-squared = 77.18; B4-U weeks 16-20: chi-squared = 134.5). Thus maintenance of stability in rhesus groups requires a far higher number of well-defined and clearly communicated dominance relationships than expected under the null model.

In B2-U, there was a persistent decrease in the overall interdependence between aggression and status networks. This decrease was driven by reduced interdependence in dyads with opposite direction aggression-status (A00S). Chi-squared for opposite direction aggression-status dyads, under independence, dropped from 288.5 to 191.9 to 126.3 to 77.2 in three-week increments, finally ending in an eruption of deleterious aggression and social overthrow at the end of the 12th week (Fig.3). Notably, total chi-squared and chi-squared for code A00S both show a decrease prior to experimental removal of the natal male, followed by continued decrease after removal. This suggests group B2-U may have been unstable before the experimental removal, and it certainly did not recover from this reduction in aggression-status network interdependence (Fig. 4). In contrast, we see only temporary decreases in chi-squared values after experimental removal of natal males in groups B1-S and B3-S (B1-S weeks 7–9: Δ total chi-squared = -144.6; B3-S weeks 7–9: Δ total chi-squared = -157.5), followed by a subsequent increase in both total chi-squared and chi-squared for opposite direction aggression-status (B1-S weeks 10–12: Δ total chi-squared = 141.6; B3-S weeks 10–12: Δ total chi-squared = 41.6; Fig. 2). Thus, the stable "B" groups show that although experimental removal of natal males caused a temporary reduction in the interdependent relationship between aggression and status networks, both groups recovered from this and regained the higher level of interdependence previously observed.

In group B4-U, joint modeling analyses showed two patterns that appear to be associated with instability: (a) two drops in the overall joint network interdependence, as measured by initial total chi-squared values, both of which were driven by fewer opposite direction aggression-status dyads, and (b) an increase in the extent to

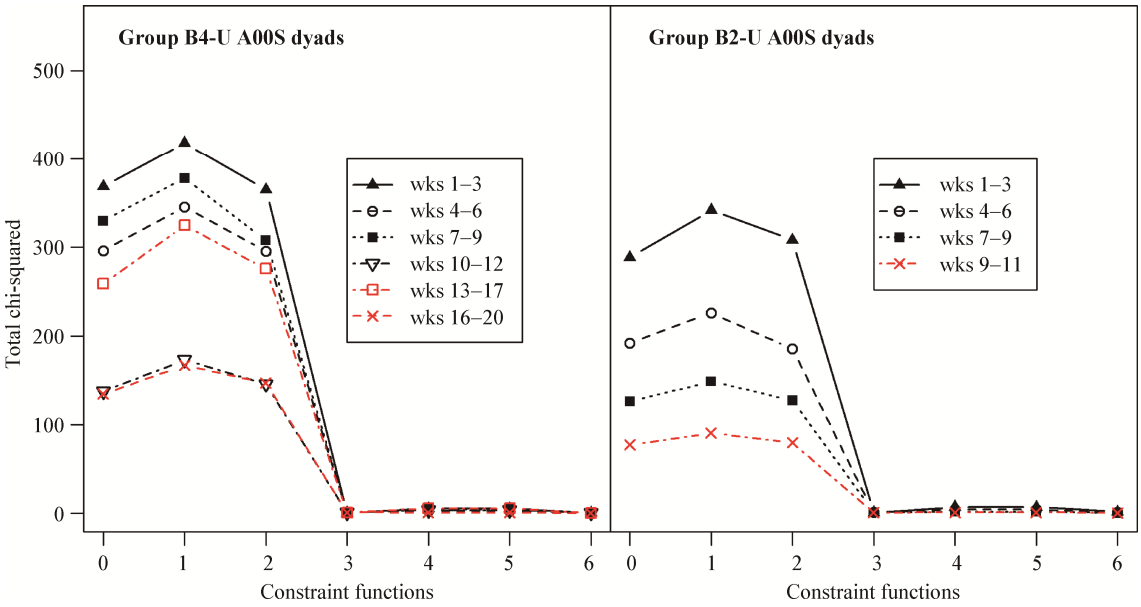

Fig. 4 Plot of the change in chi-squared for dyads with opposite direction aggression-status (code A00S) relative to application of all six constraint functions on aggression-status networks in two unstable groups B2-U and B4-U

which constraint function 1 improved the fit of expected counts during the last three time points (weeks 10–12; 13–17, and 16–20; see below). Unlike the stable "B" groups, B4-U did not show a decrease in aggression-status interdependence following experimental removal of the natal male during weeks 7–9. Instead, total chi-squared decreased during weeks 10–12 (from 484.4 to 337.7), increased (up to 502.5) during weeks 13–17, and finally decreased again (down to 347.5) during weeks 16-20, just before social collapse in the 20th week. Similar to B2-U, these two dramatic decreases in total chi-squared were largely driven by loss of opposite direction aggression-status dyads such that even though there were more A00S dyads than expected under independence (weeks 16–20: observed A00S dyads = 131, expected A00S dyads = 49.4, chi-squared = 134.5), the magnitude of this difference was lower than during stable time periods (e.g. weeks 1–3: observed A00S dyads = 195, expected A00S dyads = 53.9; chi-squared = 368.6; Fig. 4). Thus, the first decrease in aggression-status network interdependence was not closely associated with the experimental removal of the natal male, and although there was a recovery of aggression-status network interdependence during weeks 13–17, the level of interdependence decreased dramatically again in the final five weeks prior to social collapse.

2.3 Too much bidirectional aggression lowers stability

Unlike the unstable "B" groups, group A3-U did not show a drop in total chi-squared during its unstable time period in 2011. Two other patterns were apparent. First, there was seasonal variation in the complexity of the joint network relationship between aggression and status signaling in all "A" groups. In A3-U, the total chi-squared value from the unstable time point in 2011 fell within the range of seasonal variance observed in 2008–2009 (Fig. 3). Furthermore, approximately the same sort of seasonal variance was observed across all three of these groups – greater complexity in the aggression-status network interdependence during the breeding season (especially August–September) than at other times of year (Fig. 2,3).

Second, in A3-U, constraint function 1 reduced the total chi-squared value from 523.3 to 324.6 during the 2011 unstable time period, and this was largely driven by dyads with bidirectional aggression and no status signaling (chi-squared for code AA00 under independence = 137.8; chi-squared for AA00 after applying constraint 1 = 0.69; Fig. 5). Therefore, a key source of instability in 2011 was the presence of excessive bidirectional aggression between pairs of animals that were unwilling to use status signals, suggesting their dominance relationships were ambiguous. In all other stable groups and time points, constraint function 1 only slightly reduced (or sometimes increased) the total chi-squared, indicating that the number of dyads with bidirectional aggression and no status were closer to expected values under independence. An additional source of instability

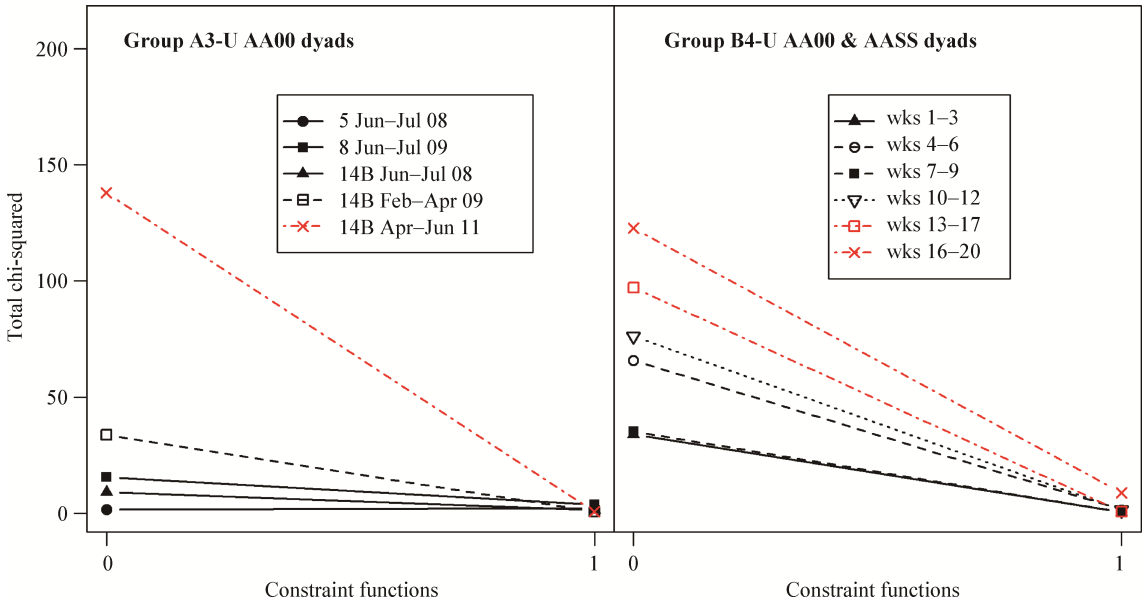

Fig. 5 Plot of the change in chi-squared for dyads with bidirectional aggression and no status signals (code AA00) in group A3-U, and for two types of dyads with bidirectional aggression (codes AA00 and AASS) in group B4-U before and after applying constraint function 1 on aggression-status networks

Red lines highlight time points just prior to social collapse.

in 2011 may have been the similar magnitude of reduction in total chi-squared accomplished by constraint functions 1 and 3, a pattern that was absent from the bivariate networks of all other stable time periods.

The social collapse in B4-U also appeared to coincide with problematic bidirectional aggression, showing a gradual increase over time in the joint aggression-status networks of this group. Similar to what we found in the 2011 unstable time period of A3-U, there was a consistent increase in the degree to which constraint function 1 accomplished a reduction in the total chi-squared in group B4-U (Fig. 5). However, unlike A3-U, this increase in total chi-squared was not driven by a single type of relationship, but rather by two types of relationships combined (bidirectional aggression and no status: AA00; bidirectional aggression and bidirectional status: AASS). The sum of the chi-squared values of these two linkage codes showed a steady increase across the bivariate aggression-status networks in group 13B, starting at a relatively low value of 33.9 in the first three weeks and ultimately increasing to 122.6 in the final five weeks before social collapse (Fig. 5). Both of these types of relationships represent ambiguous dominance. Dyads showing bidirectional aggression that are unwilling to use status signals likely have ambiguous relationships that are actively in flux. Dyads with bidirectional aggression and bidirectional status have either switched dominant-subordinate roles or alternate between aggressive challenge and active avoidance.

3 Discussion

Social stability in group-living animals is an emergent property of the system which arises from the synergistic interaction amongst the multiple behavioral networks. Although quite a bit of research has been done describing various mechanisms of stability and robusticity in animal societies, pinpointing when a social group is seriously unstable, such that social collapse is likely, remains difficult (as reviewed in the Introduction).

We used a joint network modeling approach to examine the interdependencies between aggression and status signaling networks from seven captive groups of rhesus macaques, three of which socially collapsed. Our findings showed that there is a clear and consistent pattern of interdependence between aggression and status signaling networks in rhesus macaques that was evident despite differences across groups, seasonal variation, and sampling methodology. During stable time points across all groups, the most prominent source of aggression-status network interdependence came from higher than expected frequency of dyads with opposite direction status-aggression (and lower than expected same direction aggression-status). Finally, our results also showed that this clear pattern of interdependence changed prior to social collapse, such that opposite direction aggression-status dyads decreased dramatically (but did not disappear) in unstable time points and/or dyads with

ambiguous/contested dominance relationships increased (e.g. bidirectional aggression and no status [AA00], bidirectional aggression and bidirectional status [AASS]).

First, stable rhesus social groups exhibited an exceptionally high frequency of dyads with opposite direction aggression and status such that chi-squared for A00S dyads was between 250 and 700. Further, these large chi-squared values accounted for 58%–76% of the total chi-squared, indicating that opposite direction aggression-status dyads comprise the largest component of the interdependence between aggression and status networks. This result may, at first, appear to be mundane, as any animal society with a readily identifiable dominance hierarchy should be expected to show an abundance of dyads whose dominance interactions reflect their dominant and subordinate roles. However, what was truly surprising was our finding that even our unstable groups, just days prior to collapse (i.e. B2-U and B4-U) also showed significantly more opposite direction aggression-status dyads than expected (Fig. 3). Thus, the stable pattern of interdependence between aggression and status networks reflects uncontested, well-communicated dominance relationships, which generate a blatantly obvious dominance hierarchy that is important to stability in despotic species.

Finding far more opposite direction aggression-status dyads than expected is reminiscent of the directional consistency index (DCI) (Vervaecke et al., 2000). Our JNM approach, however, reveals greater detail about such consistency. Three types of dyads have directionally consistent aggression and/or status interactions: A000, 00S0, and A00S. Across all time periods in all groups, one-way aggression and no status dyads (A000) were less common than expected and one-way status and no aggression dyads (00S0) were as common as expected (see Tables S1-S31). By jointly modeling aggression and status networks together, we found that a large portion of the directional consistency must come from a combination of these two behaviors (i.e., opposite direction aggression-status), rather than simply within a single behavior. Furthermore, the large number of dyads in our study groups with missing data (i.e, code 0000) present a problem for most traditional dominance hierarchy measures. Our JNM approach relies on comparing dyad frequencies to null expectations and handles missing data by tallying the frequency of such 'absent' relationships; it is thus applicable to both sparse and dense data sets.

Our examination of four stable groups across various time periods showed that there was quite a bit of natural variation in the precise degree of aggression-status network interdependence. Variance across seasons was greater than variance within season or even variance due to experimental perturbations (at least for groups that remained stable). Stable groups showed a higher degree of aggression-status network interdependence (i.e. higher chi-squared) during breeding season than during other seasons, and experimental perturbations caused temporary decreases in complexity. So how do we distinguish between natural variance in bivariate network independence and true instability? The "A" groups consistently showed 60%–75% of the total chi-squared was accounted for by A00S dyads, whereas the 2011 time point in A3-U shows a clear drop to 45.1% of total chi-squared. Thus, our analyses show that unstable groups show a decrease in the percent of total chi-squared that is due to opposite direction aggression-status dyads.

3.1 Multiple pathways of instability

The three groups that socially collapsed showed that social instability can manifest in different ways. The unstable "B" groups both experienced a loss of interdependence between aggression-status networks, as evidenced by dramatic decreases in total chi-squared, which were largely driven by fewer A00S dyads. However, group A3-U did not show this drop in overall bivariate network interdependence. Instead, we saw a change in the patterning of the interdependence between aggression and status networks such that (in addition to the above-described decrease in A00S dyads percentage of overall chi-squared) there was a large increase in the frequency of dyads with ambiguous dominance relationships – AA00 (bidirectional aggression, no status). Plots of the change in chi-squared values upon application of constraint function 1 (Fig. 5) highlight this change in the pattern of interdependence in A3-U. The social collapse in B4-U further demonstrates a variable pathway of instability, showing an increase in bidirectional aggression, but across two different types of dyads. Upon application of constraint function 1, we saw a decrease in chi-squared for AA00 dyads as well as AASS dyads, indicating that instability in this group emerged in the form of two different types of ambiguous/contested dominance relationships.

When talking about multiple pathways to instability, it is worth pointing out that the social collapse in group A3-U progressed naturally – there were no colony management removals that appeared to spark the group's collapse. Our 2011 observations began six months before social collapse, indicating that colony managers of

captive or managed free-ranging groups might be able to predict an eventual social collapse and take action before serious injuries occur.

The social collapses in B2-U and B4-U, however, did not progress naturally - both underwent experimental removal of a natal male followed by an unanticipated removal of the alpha male or female (for veterinary care). First, the fact that two stable "B" groups withstood the experimental removal of natal males, experiencing only temporary loss of aggression-status network interdependence, tells us that such social perturbations do not normally threaten the cohesion of groups with stable underlying aggression-status network dynamics. Group B2-U showed a steady decrease in its overall aggression-status network interdependence that preceded experimental natal male removal, suggesting that the group was becoming unstable prior to the knockout, which may have accelerated the progression toward maximal instability. Finally, it seems apparent that removal of the alpha male from B2-U was the final perturbation that caused its social collapse.

Carefully constructed binary data are sufficient to detect instability using JNM. Given the data are binary, the nature of ambiguity encoded in dyads with bidirectional aggression does not address the frequencies of aggression within a dyad. In constructing our data set, we chose to exclude mild agonistic protests by subordinates (e.g. open mouth threat, vocal threat), yielding a binary data set in which observations of bidirectional aggression always represent moderately to severely aggressive challenges by subordinates. Thus, even though relative frequencies of each direction of aggression are obscured, severity is not. Our finding that two unstable groups had more dyads with bidirectional aggression than expected indicates that the relative frequency of aggressive challenges by a subordinate within a given dyad matters less than knowing that such challenges occur in more dyads than expected.

3.2 Quantification of changes in social dynamics & health

Collecting network data and monitoring changes in network interdependence can be used to predict whether a social group is at risk of collapse. Advanced warning of risk of social collapse allows colony managers to take action before serious consequences arise. For example, managers can avoid removal of key individuals during periods of instability, to avoid triggering a collapse. When medical treatment of key individuals is necessary (as in B2-U and B4-U), veterinarians may treat animals in their social group, or expedite their care in the hospital. Conversely, knowledge that a social group is indeed stable is also valuable. Previous analyses of predictors of social collapse indicated that absence of the alpha female from the group was associated with matrilineal overthrow in univariate analyses, but multivariate analyses showed mixed support (Oates-O'Brien et al., 2010). Our joint modeling analyses suggest that temporary removal of such key individuals may only pose a risk of social collapse when groups show a loss in the interdependence of their joint network dynamics. In stable social groups, such temporary removals may pose no additional risk. The same may be true of other probable causal factors of social collapse, such as matrilineal cohesion (Beisner et al., 2011a), sex ratio (McCowan et al., 2008; Beisner et al., 2012), or presence of natal males (Beisner et al., 2011b) – a group may only be at risk of social collapse in the presence of these group composition factors if the group also shows a low degree of aggression-status network interdependence.

All social systems are composed of multiple interconnected networks, and our joint modeling approach can be used to quantify and monitor the complex social dynamics of any wild or captive social system. JNM may be of greatest utility in quantifying the impact of environmental, ecological, or social change on the underlying structure of a social group. For example, conservationists might use joint modeling to monitor the social health of reintroduced or trans-located social groups that are adjusting to unfamiliar environments, to determine whether the group has established a normal social dynamic (e.g. Ruiz-Miranda et al., 2006; Pinter-Wollman et al., 2009). The technique may prove equally useful in monitoring how social groups respond to anthropogenic change, because deforestation, urbanization and ecotourism can significantly impact animal behavior (e.g. Clarke et al., 2002; Lusseau and Higham, 2004; Davison et al., 2009). Even healthy groups that are not faced with such conservation issues experience major changes in their social and physical environments. For example, Sapolsky and Share (2004) reported a dramatic change in the tenor of social relationships when a set of aggressive resident male baboons died and were replaced by a set of more peaceful males. Such changes in the tenor of social interactions may have been accompanied by a shift in the interdependencies of their dominance behaviors. Similarly, the dramatic ecological changes associated with synchronous fruiting of dipterocarp trees, known as masting, (Curran and Leighton, 2000) might be expected to influence some aspects of the underlying network dynamics of social

groups living in those conditions. It would be equally interesting to discover that animal societies have developed ways of maintaining their patterns of behavioral network interdependence in spite of such dramatic social and ecological changes.

Many global patterns in biology arise from multiple interconnected networks. This joint modeling approach offers a new method of realistically and holistically extracting the dynamic processes involved in the emergence of social stability, and may further advance our understanding of a diverse array of other questions surrounding the complexity of other social systems.

Acknowledgments We thank Stephanie Chan for instruction on how to run the joint modeling code in R. We thank Eliza Bliss-Moreau, Darcy Hannibal, and Jessica Vandeleest for help with data, figures, and manuscript editing. We also thank our observation team: Allison Barnard, Tamar Boussina, Megan Jackson, Amy Nathman, Shannon Seil, and Alison Vitale. This research was funded by two NIH grants awarded to B. McCowan (R24-RR024396; R01-HD068335) as well as the CNPRC base grant (P51-OD01107-53).

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SUPPLEMENTARY TABLES

Table S1 Observed versus expected counts of dyads for aggression and status networks for August–September for group A1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	513	736.94 (68.05)	690.37 (45.57)	671.82 (37.54)	646.58 (27.60)	597.91 (12.06)	597.87 (12.05)	509.96 (0.02)
AA00	60	43.57 (6.20)	74.05 (2.67)	72.06 (2.02)	69.36 (1.26)	64.13 (0.27)	63.70 (0.22)	54.34 (0.59)
00S0	796	862.63 (5.15)	867.08 (5.83)	989.62 (37.88)	952.45 (25.70)	897.18 (11.41)	897.12 (11.40)	767.78 (1.04)
00SS	11	59.70 (39.73)	60.01 (40.02)	21.65 (5.24)	20.83 (4.64)	19.63 (3.79)	19.16 (3.48)	16.40 (1.78)
A00S	350	102.00 (602.95)	95.56 (677.53)	109.06 (532.30)	369.79 (1.06)	436.16 (17.02)	436.13 (17.01)	373.74 (1.51)
A0S0	10	102.00 (82.98)	95.56 (76.60)	109.06 (89.98)	29.79 (13.15)	35.14 (17.99)	35.14 (17.98)	30.11 (13.43)
AAS0	32	12.06 (32.96)	20.50 (6.45)	23.40 (3.16)	22.52 (3.99)	26.56 (1.11)	26.38 (1.20)	22.61 (3.90)
A0SS	7	14.12 (3.59)	13.23 (2.93)	4.77 (1.04)	4.59 (1.26)	5.42 (0.46)	5.29 (0.55)	4.53 (1.34)
AASS	2	0.83 (1.63)	1.42 (0.24)	0.51 (4.33)	0.49 (4.61)	0.58 (3.47)	2.11 (0.01)	1.81 (0.02)
0000	3269	3116.14 (7.50)	3132.23 (5.97)	3048.06 (16.01)	2933.59 (38.35)	2967.29 (30.68)	2967.10 (30.72)	3268.72 (0.00)
	6758	850.73	863.81	729.50	121.62	98.25	94.61	23.63

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S2 Observed versus expected counts of dyads for aggression and status networks for October–November for group A1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	446	586.62 (33.71)	553.92 (21.02)	542.76 (17.25)	529.72 (13.23)	511.01 (8.27)	510.97 (8.26)	446.36 (0.00)
AA00	41	26.07 (8.55)	48.59 (1.19)	47.61 (0.92)	46.47 (0.64)	44.83 (0.33)	45.05 (0.36)	39.35 (0.07)
00S0	721	749.09 (1.05)	751.40 (1.23)	846.69 (18.66)	826.35 (13.43)	805.30 (8.82)	805.23 (8.81)	704.65 (0.38)
00SS	10	42.51 (24.87)	42.65 (24.99)	14.03 (1.16)	13.69 (1.00)	13.35 (0.84)	13.59 (0.95)	11.89 (0.30)
A00S	220	66.59 (353.47)	62.87 (392.67)	70.85 (314.01)	234.40 (0.88)	260.18 (6.21)	260.16 (6.20)	227.82 (0.27)
A0S0	6	66.59 (55.13)	62.87 (51.45)	70.85 (59.36)	20.40 (10.16)	22.64 (12.23)	22.64 (12.23)	19.82 (9.64)
AAS0	18	5.92 (24.66)	11.03 (4.40)	12.43 (2.50)	12.13 (2.84)	13.47 (1.53)	13.53 (1.47)	11.85 (3.19)
A0SS	2	7.56 (4.09)	7.14 (3.70)	2.35 (0.05)	2.29 (0.04)	2.54 (0.12)	2.59 (0.13)	2.27 (0.03)
AASS	0	0.34 (0.34)	0.63 (0.63)	0.21 (0.21)	0.20 (0.20)	0.22 (0.22)	0.05 (0.05)	0.04 (0.04)
0000	3387	3299.72 (2.31)	3309.90 (1.80)	3243.23 (6.37)	3165.34 (15.52)	3177.46 (13.82)	3177.19 (13.86)	3386.94 (0.00)
		508.15	503.06	420.47	57.94	52.38	52.32	13.92

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S3 Observed versus expected counts of dyads for aggression and status networks for December–January for group A1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	461	612.49 (37.47)	590.64 (28.45)	571.98 (21.53)	553.15 (15.35)	524.31 (7.64)	524.27 (7.64)	447.73 (0.39)
AA00	40	32.51 (1.73)	45.45 (0.65)	44.01 (0.37)	42.56 (0.15)	40.34 (0.00)	40.13 (0.00)	34.27 (0.96)
00S0	682	719.40 (1.94)	721.63 (2.18)	846.71 (32.04)	818.83 (22.87)	786.28 (13.83)	786.22 (13.82)	672.99 (0.12)
00SS	3	44.85 (39.05)	44.99 (39.19)	11.32 (6.12)	10.95 (5.77)	10.51 (5.37)	10.29 (5.16)	8.81 (3.83)
A00S	273	76.37 (506.28)	73.64 (539.66)	86.41 (402.92)	290.07 (1.00)	329.79 (9.78)	329.77 (9.77)	282.48 (0.32)
A0S0	7	76.37 (63.01)	73.64 (60.31)	86.41 (72.98)	24.07 (12.11)	27.37 (15.16)	27.37 (15.16)	23.44 (11.53)
AAS0	16	8.11 (7.68)	11.33 (1.92)	13.30 (0.55)	12.86 (0.77)	14.62 (0.13)	14.54 (0.15)	12.46 (1.01)
A0SS	2	9.52 (5.94)	9.18 (5.62)	2.31 (0.04)	2.23 (0.02)	2.54 (0.12)	2.49 (0.10)	2.13 (0.01)
AASS	1	0.51 (0.48)	0.71 (0.12)	0.18 (3.80)	0.17 (3.99)	0.20 (3.31)	1.09 (0.01)	0.94 (0.00)
0000	2980	2884.87 (3.14)	2893.79 (2.57)	2802.37 (11.26)	2710.10 (26.88)	2729.04 (23.08)	2728.83 (23.12)	2979.75 (0.00)
		666.72	680.67	551.60	88.91	78.42	74.91	18.16

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S4 Observed versus expected counts of dyads for aggression and status networks for February–April for group A1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	441	547.41 (20.68)	522.91 (12.83)	513.61 (10.27)	504.10 (7.90)	492.12 (5.31)	492.12 (5.31)	425.09 (0.60)
AA00	35	22.30 (7.24)	38.51 (0.32)	37.83 (0.21)	37.13 (0.12)	36.25 (0.04)	36.25 (0.04)	31.31 (0.43)
00S0	487	519.08 (1.98)	520.36 (2.14)	597.25 (20.35)	586.19 (16.79)	573.61 (13.08)	573.61 (13.08)	496.36 (0.18)
00SS	0	20.05 (20.05)	20.10 (20.10)	3.07 (3.07)	3.02 (3.02)	2.95 (2.95)	2.95 (2.95)	2.56 (2.56)
A00S	154	42.29 (295.12)	40.39 (319.50)	46.36 (249.89)	162.72 (0.47)	180.00 (3.75)	180.00 (3.75)	155.78 (0.02)
A0S0	4	42.29 (34.67)	40.39 (32.79)	46.36 (38.71)	12.73 (5.98)	14.08 (7.21)	14.08 (7.21)	12.18 (5.50)
AAS0	9	3.44 (8.96)	5.95 (1.56)	6.83 (0.69)	6.70 (0.79)	7.41 (0.34)	7.42 (0.34)	6.42 (1.04)
A0SS	0	3.27 (3.27)	3.12 (3.12)	0.48 (0.48)	0.47 (0.47)	0.52 (0.52)	0.52 (0.52)	0.45 (0.45)
AASS	0	0.13 (0.13)	0.23 (0.23)	0.04 (0.04)	0.03 (0.03)	0.04 (0.04)	0.03 (0.03)	0.03 (0.03)
0000	3430	3359.74 (1.47)	3368.03 (1.14)	3308.17 (4.49)	3246.91 (10.32)	3253.03 (9.63)	3253.02 (9.63)	3429.82 (0.00)
		393.56	393.73	328.18	45.88	42.87	42.87	10.79

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S5 Observed versus expected counts of dyads for aggression and status networks in June–July for group A2–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	542	742.44 (54.11)	689.15 (31.42)	679.33 (27.76)	663.48 (22.24)	630.14 (12.33)	630.12 (12.32)	530.54 (0.25)
AA00	57	33.97 (15.60)	73.79 (3.82)	72.74 (3.40)	71.04 (2.77)	67.47 (1.62)	67.58 (1.66)	56.90 (0.00)
00S0	594	675.63 (9.86)	677.87 (10.38)	757.07 (35.12)	739.41 (28.60)	704.67 (17.38)	704.65 (17.37)	595.19 (0.00)
00SS	5	28.14 (19.02)	28.23 (19.11)	7.04 (0.59)	6.88 (0.51)	6.55 (0.37)	6.67 (0.42)	5.63 (0.07)
A00S	233	61.83 (473.80)	57.40 (537.26)	64.10 (445.02)	241.24 (0.28)	291.54 (11.75)	291.53 (11.75)	246.33 (0.72)
A0S0	8	61.83 (46.87)	57.40 (42.51)	64.10 (49.10)	16.25 (4.19)	19.63 (6.89)	19.63 (6.89)	16.59 (4.45)
AAS0	27	5.66 (80.48)	12.29 (17.60)	13.73 (12.83)	13.41 (13.78)	16.20 (7.20)	16.23 (7.15)	13.71 (12.87)
A0SS	0	5.15 (5.15)	4.78 (4.78)	1.19 (1.19)	1.16 (1.16)	1.41 (1.41)	1.43 (1.43)	1.21 (1.21)
AASS	0	0.24 (0.24)	0.51 (0.51)	0.13 (0.13)	0.12 (0.12)	0.15 (0.15)	0.05 (0.05)	0.04 (0.04)
0000	4205	4056.10 (5.47)	4069.58 (4.51)	4011.57 (9.33)	3918.00 (21.02)	3933.23 (18.78)	3933.10 (18.80)	4204.86 (0.00)
	7075	710.60	671.90	584.48	94.68	77.88	77.84	19.61

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S6 Observed versus expected counts of dyads for aggression and status networks in August–September for group A2–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	460	655.26 (58.18)	610.87 (37.26)	604.08 (34.36)	588.75 (28.16)	557.63 (17.09)	557.60 (17.08)	464.74 (0.05)
AA00	47	27.27 (14.28)	60.99 (3.21)	60.31 (2.94)	58.78 (2.36)	55.68 (1.35)	55.47 (1.29)	46.23 (0.01)
00S0	597	686.67 (11.71)	688.53 (12.17)	751.96 (31.93)	732.88 (25.19)	699.49 (15.02)	699.44 (15.00)	584.52 (0.27)
00SS	7	29.94 (17.58)	30.03 (17.66)	10.50 (1.17)	10.23 (1.02)	9.77 (0.78)	9.56 (0.68)	7.99 (0.12)
A00S	231	57.15 (528.87)	53.28 (592.83)	58.19 (513.26)	238.49 (0.24)	289.33 (11.76)	289.31 (11.75)	241.91 (0.49)
A0S0	6	57.15 (45.78)	53.28 (41.95)	58.19 (46.81)	13.48 (4.15)	16.36 (6.56)	16.36 (6.56)	13.68 (4.31)
AAS0	22	4.76 (62.52)	10.64 (12.13)	11.62 (9.27)	11.32 (10.06)	13.74 (4.97)	13.69 (5.05)	11.44 (9.74)
A0SS	2	4.98 (1.79)	4.65 (1.51)	1.63 (0.09)	1.58 (0.11)	1.92 (0.00)	1.88 (0.01)	1.57 (0.12)
AASS	1	0.21 (3.03)	0.46 (0.62)	0.16 (4.33)	0.16 (4.48)	0.19 (3.40)	1.03 (0.00)	0.86 (0.02)
0000	4087	3936.61 (5.75)	3947.27 (4.95)	3903.36 (8.64)	3804.31 (21.01)	3815.90 (19.26)	3815.67 (19.29)	4087.06 (0.00)
		749.47	724.29	652.79	96.78	80.20	76.72	15.12

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S7 Observed versus expected counts of dyads for aggression and status networks for October–November for group A2–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	552	738.94 (47.29)	689.14 (27.29)	680.41 (24.23)	665.01 (19.20)	628.08 (9.22)	628.04 (9.21)	536.11 (0.47)
AA00	54	36.16 (8.80)	71.52 (4.29)	70.62 (3.91)	69.02 (3.27)	65.19 (1.92)	64.98 (1.86)	55.47 (0.04)
00S0	561	641.55 (10.11)	644.01 (10.70)	711.29 (31.75)	695.18 (25.90)	657.42 (14.14)	657.37 (14.13)	562.84 (0.01)
00SS	4	27.26 (19.85)	27.36 (19.95)	8.08 (2.06)	7.90 (1.92)	7.47 (1.61)	7.27 (1.47)	6.22 (0.79)
A00S	225	62.79 (419.00)	58.56 (473.02)	64.68 (397.37)	230.35 (0.12)	283.83 (12.20)	283.81 (12.19)	243.10 (1.35)
A0S0	12	62.79 (41.09)	58.56 (37.02)	64.68 (42.91)	17.35 (1.65)	21.38 (4.11)	21.38 (4.11)	18.31 (2.17)
AAS0	27	6.15 (70.76)	12.16 (18.13)	13.43 (13.72)	13.12 (14.68)	16.17 (7.26)	16.12 (7.35)	13.81 (12.61)
A0SS	2	5.34 (2.09)	4.98 (1.78)	1.47 (0.19)	1.44 (0.22)	1.77 (0.03)	1.72 (0.04)	1.48 (0.19)
AASS	1	0.26 (2.09)	0.52 (0.45)	0.15 (4.71)	0.15 (4.86)	0.18 (3.63)	1.05 (0.00)	0.90 (0.01)
0000	3918	3774.76 (5.44)	3789.19 (4.38)	3741.19 (8.36)	3656.49 (18.70)	3674.52 (16.13)	3674.27 (16.17)	3917.78 (0.00)
		626.50	597.01	529.21	90.52	70.24	66.52	17.64

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S8 Observed versus expected counts of dyads for aggression and status networks for December–January for group A2–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	466	609.21 (33.67)	565.86 (17.62)	562.78 (16.64)	555.15 (14.32)	537.90 (9.61)	537.84 (9.59)	464.98 (0.00)
AA00	46	21.44 (28.12)	58.09 (2.52)	57.78 (2.40)	56.99 (2.12)	55.22 (1.54)	55.07 (1.49)	47.61 (0.05)
00S0	461	514.86 (5.63)	515.66 (5.79)	549.50 (14.25)	542.04 (12.12)	524.80 (7.76)	524.74 (7.74)	454.55 (0.09)
00SS	2	15.32 (11.58)	15.34 (11.60)	5.12 (1.90)	5.05 (1.85)	4.89 (1.71)	4.75 (1.59)	4.12 (1.09)
A00S	133	36.25 (258.28)	33.67 (293.09)	35.88 (262.94)	137.13 (0.12)	164.13 (5.91)	164.11 (5.90)	142.19 (0.59)
A0S0	5	36.25 (26.94)	33.67 (24.41)	35.88 (26.57)	9.13 (1.87)	10.93 (3.22)	10.93 (3.22)	9.47 (2.11)
AAS0	16	2.55 (70.88)	6.91 (11.95)	7.37 (10.12)	7.27 (10.50)	8.70 (6.13)	8.67 (6.19)	7.51 (9.58)
A0SS	2	2.16 (0.01)	2.00 (0.00)	0.67 (2.65)	0.66 (2.72)	0.79 (1.85)	0.77 (1.98)	0.66 (2.68)
AASS	1	0.08 (11.25)	0.21 (3.07)	0.07 (12.63)	0.07 (12.83)	0.08 (10.41)	1.02 (0.00)	0.88 (0.02)
						4257.56	4257.09	
0000	4433	4326.89 (2.60)	4333.59 (2.28)	4309.97 (3.51)	4251.51 (7.75)	(7.23)	(7.27)	4433.02 (0.00)
		448.95	372.32	353.62	66.18	55.36	44.98	16.22

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S9 Observed versus expected counts of dyads for aggression and status networks for February–April for group A2–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	503	649.17 (32.91)	605.49 (17.35)	597.85 (15.05)	586.48 (11.88)	578.69 (9.90)	578.68 (9.90)	498.29 (0.04)
AA00	59	27.01 (37.90)	60.11 (0.02)	59.35 (0.00)	58.22 (0.01)	57.45 (0.04)	57.48 (0.04)	49.50 (1.82)
00S0	517	556.10 (2.75)	557.61 (2.96)	622.88 (18.00)	611.03 (14.47)	603.08 (12.29)	603.07 (12.28)	520.55 (0.02)
00SS	2	19.82 (16.02)	19.87 (16.07)	3.93 (0.95)	3.86 (0.89)	3.81 (0.86)	3.84 (0.88)	3.31 (0.52)
A00S	170	46.27 (330.86)	43.16 (372.81)	48.21 (307.69)	182.27 (0.83)	193.53 (2.86)	193.53 (2.86)	167.08 (0.05)
A0S0	0	46.27 (46.27)	43.16 (43.16)	48.21 (48.21)	12.27 (12.27)	13.03 (13.03)	13.03 (13.03)	11.25 (11.25)
AAS0	8	3.85 (4.47)	8.57 (0.04)	9.57 (0.26)	9.39 (0.21)	9.97 (0.39)	9.98 (0.39)	8.61 (0.04)
A0SS	0	3.30 (3.30)	3.08 (3.08)	0.61 (0.61)	0.60 (0.60)	0.63 (0.63)	0.64 (0.64)	0.55 (0.55)
AASS	0	0.14 (0.14)	0.31 (0.31)	0.06 (0.06)	0.06 (0.06)	0.06 (0.06)	0.03 (0.03)	0.03 (0.03)
0000	3994	3901.07 (2.21)	3911.65 (1.73)	3862.32 (4.49)	3788.82 (11.11)	3792.75 (10.68)	3792.72 (10.68)	3993.83 (0.00)
		476.83	457.51	395.31	52.32	50.73	50.73	14.33

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S10 Observed versus expected counts of dyads for aggression and status networks for June–July for group A3–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	323	440.15 (31.18)	414.95 (20.38)	410.80 (18.77)	402.44 (15.68)	385.61 (10.16)	385.60 (10.16)	321.88 (0.00)
AA00	28	15.94 (9.12)	34.89 (1.36)	34.54 (1.24)	33.83 (1.01)	32.42 (0.60)	32.47 (0.61)	27.10 (0.03)
00S0	373	428.82 (7.27)	429.71 (7.48)	471.45 (20.56)	461.86 (17.10)	444.24 (11.42)	444.23 (11.42)	371.58 (0.01)
00SS	1	15.13 (13.20)	15.16 (13.23)	3.88 (2.14)	3.80 (2.06)	3.65 (1.93)	3.70 (1.97)	3.10 (1.42)
A00S	134	31.06 (341.15)	29.28 (374.47)	32.13 (323.02)	137.22 (0.08)	166.29 (6.27)	166.28 (6.27)	139.12 (0.19)
A0S0	4	31.06 (23.58)	29.28 (21.83)	32.13 (24.63)	7.22 (1.44)	8.75 (2.58)	8.75 (2.58)	7.32 (1.51)
AAS0	11	2.25 (34.03)	4.92 (7.50)	5.40 (5.80)	5.29 (6.16)	6.41 (3.28)	6.42 (3.26)	5.37 (5.89)
A0SS	2	2.19 (0.02)	2.07 (0.00)	0.53 (4.10)	0.52 (4.24)	0.63 (3.00)	0.64 (2.92)	0.53 (4.05)
AASS	0	0.08 (0.08)	0.17 (0.17)	0.04 (0.04)	0.04 (0.04)	0.05 (0.05)	0.01 (0.01)	0.01 (0.01)
0000	3129	3038.31 (2.71)	3044.56 (2.34)	3014.10 (4.38)	2952.78 (10.52)	2956.95 (10.01)	2956.89 (10.02)	3128.98 (0.00)
		462.32	448.76	404.66	58.31	49.31	49.23	13.10

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S11 Observed versus expected counts of dyads for aggression and status networks for August–September for group A3–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	381	613.04 (87.83)	570.58 (62.99)	563.11 (58.90)	539.81 (46.72)	480.86 (20.74)	480.79 (20.71)	386.12 (0.07)
AA00	52	35.17 (8.05)	63.98 (2.24)	63.14 (1.97)	60.53 (1.20)	53.92 (0.07)	53.56 (0.05)	43.02 (1.88)
00S0	462	591.24 (28.25)	594.26 (29.44)	647.64 (53.21)	620.84 (40.64)	558.61 (16.71)	558.52 (16.68)	450.61 (0.29)
00SS	5	32.71 (23.48)	32.88 (23.64)	14.62 (6.33)	14.02 (5.80)	12.61 (4.59)	12.26 (4.30)	9.89 (2.42)
A00S	285	67.84 (695.16)	63.14 (779.58)	68.81 (679.21)	286.20 (0.01)	379.65 (23.60)	379.59 (23.57)	306.68 (1.53)
A0S0	14	67.84 (42.73)	63.14 (38.24)	68.81 (43.66)	15.20 (0.10)	20.17 (1.89)	20.16 (1.88)	16.29 (0.32)
AAS0	23	7.78 (29.74)	14.16 (5.52)	15.43 (3.71)	14.79 (4.55)	19.62 (0.58)	19.49 (0.63)	15.75 (3.34)
A0SS	9	7.51 (0.30)	6.99 (0.58)	3.11 (11.18)	2.98 (12.17)	3.95 (6.45)	3.84 (6.93)	3.10 (11.21)
AASS	2	0.43 (5.72)	0.78 (1.89)	0.35 (7.83)	0.33 (8.31)	0.44 (5.47)	2.03 (0.00)	1.64 (0.08)
0000	2862	2671.44 (13.59)	2685.10 (11.66)	2649.97 (16.96)	2540.30 (40.74)	2565.16 (34.35)	2564.75 (34.45)	2861.90 (0.00)
		934.85	955.77	882.96	160.23	114.45	109.20	21.12

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S12 Observed versus expected counts of dyads for aggression and status networks for October–November for group A3–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	292	469.46 (67.08)	427.52 (42.96)	423.58 (40.87)	410.64 (34.28)	374.45 (18.15)	374.33 (18.11)	303.03 (0.40)
AA00	38	21.72 (12.21)	56.14 (5.86)	55.62 (5.58)	53.92 (4.70)	49.17 (2.54)	49.71 (2.76)	40.24 (0.12)
00S0	412	500.28 (15.58)	501.77 (16.06)	538.11 (29.56)	521.67 (23.06)	482.35 (10.26)	482.20 (10.22)	392.01 (1.02)
00SS	7	24.66 (12.65)	24.73 (12.71)	11.88 (2.00)	11.52 (1.77)	10.65 (1.25)	11.23 (1.60)	9.13 (0.50)
A00S	185	46.28 (415.76)	42.15 (484.16)	45.20 (432.37)	189.15 (0.09)	249.29 (16.58)	249.22 (16.55)	202.83 (1.57)
A0S0	6	46.28 (35.06)	42.15 (31.00)	45.20 (34.00)	10.15 (1.70)	13.38 (4.07)	13.38 (4.07)	10.89 (2.19)
AAS0	27	4.28 (120.54)	11.07 (22.93)	11.87 (19.28)	11.51 (20.86)	15.17 (9.23)	15.33 (8.87)	12.48 (16.89)
A0SS	6	4.56 (0.45)	4.16 (0.82)	2.00 (8.04)	1.93 (8.54)	2.55 (4.67)	2.69 (4.07)	2.19 (6.63)
AASS	0	0.21 (0.21)	0.55 (0.55)	0.26 (0.26)	0.25 (0.25)	0.33 (0.33)	0.02 (0.02)	0.01 (0.01)
				2521.28	2444.26			
0000	2682	2537.26 (8.26)	2544.77 (7.40)	(10.24)	(23.12)	2457.66 (20.48)	2456.89 (20.63)	2682.19 (0.00)
		687.80	624.45	582.20	118.36	87.56	86.88	29.34

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S13 Observed versus expected counts of dyads for aggression and status networks for February–April for group A3–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	333	464.56 (37.26)	431.95 (22.67)	427.62 (20.94)	420.07 (18.05)	407.04 (13.47)	407.04 (13.47)	331.76 (0.00)
AA00	38	15.27 (33.81)	43.73 (0.75)	43.29 (0.65)	42.53 (0.48)	41.21 (0.25)	41.21 (0.25)	33.59 (0.58)
00S0	332	388.07 (8.10)	388.53 (8.22)	433.29 (23.68)	425.64 (20.60)	412.46 (15.70)	412.46 (15.70)	337.08 (0.08)
00SS	0	10.66 (10.66)	10.67 (10.67)	1.36 (1.36)	1.34 (1.34)	1.30 (1.30)	1.30 (1.30)	1.06 (1.06)
A00S	122	25.52 (364.76)	23.73 (407.01)	26.46 (344.94)	125.39 (0.09)	149.29 (4.99)	149.29 (4.99)	122.02 (0.00)
A0S0	2	25.52 (21.68)	23.73 (19.90)	26.46 (22.61)	5.39 (2.13)	6.42 (3.04)	6.42 (3.04)	5.24 (2.01)
AAS0	9	1.68 (31.95)	4.80 (3.66)	5.36 (2.48)	5.26 (2.65)	6.27 (1.19)	6.27 (1.19)	5.12 (2.93)
A0SS	0	1.40 (1.40)	1.30 (1.30)	0.17 (0.17)	0.16 (0.16)	0.19 (0.19)	0.19 (0.19)	0.16 (0.16)
AASS	0	0.05 (0.05)	0.13 (0.13)	0.02 (0.02)	0.02 (0.02)	0.02 (0.02)	0.02 (0.02)	0.01 (0.01)
0000	3629	3532.27 (2.65)	3536.42 (2.42)	3500.97 (4.68)	3439.20 (10.47)	3440.80 (10.29)	3440.80 (10.29)	3628.94 (0.00)
		512.31	476.73	421.51	55.99	50.43	50.43	6.83

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S14 Observed versus expected counts of dyads for aggression and status networks for April–June 2011 for group A3–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	287	406.40 (35.08)	376.53 (21.29)	376.54 (21.29)	373.80 (20.16)	367.89 (17.79)	367.88 (17.78)	298.90 (0.47)
AA00	42	8.26 (137.84)	47.74 (0.69)	47.74 (0.69)	47.40 (0.61)	46.65 (0.46)	46.73 (0.48)	37.97 (0.43)
00S0	190	234.58 (8.47)	234.13 (8.32)	234.09 (8.31)	232.40 (7.73)	227.29 (6.12)	227.29 (6.12)	185.02 (0.13)
00SS	1	2.75 (1.12)	2.75 (1.11)	2.76 (1.13)	2.74 (1.11)	2.68 (1.06)	2.77 (1.13)	2.25 (0.70)
A00S	57	9.53 (236.29)	8.83 (262.62)	8.83 (262.67)	57.34 (0.00)	71.21 (2.83)	71.20 (2.83)	57.97 (0.02)
A0S0	1	9.53 (7.64)	8.83 (6.95)	8.83 (6.95)	1.34 (0.09)	1.67 (0.27)	1.67 (0.27)	1.36 (0.09)
AAS0	6	0.39 (81.28)	2.24 (6.31)	2.24 (6.31)	2.22 (6.41)	2.76 (3.80)	2.77 (3.78)	2.25 (6.24)
A0SS	2	0.22 (14.10)	0.21 (15.51)	0.21 (15.38)	0.21 (15.52)	0.26 (11.81)	0.27 (11.36)	0.22 (14.75)
AASS	0	0.00 (0.00)	0.03 (0.03)	0.03 (0.03)	0.03 (0.03)	0.03 (0.03)	0.00 (0.00)	0.00 (0.00)
0000	5085	4999.32 (1.47)	4989.70 (1.82)	4989.72 (1.82)	4953.52 (3.49)	4950.56 (3.65)	4950.43 (3.66)	5085.07 (0.00)
		523.28	324.63	324.56	55.15	47.81	47.40	22.83

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S15 Observed versus expected counts of dyads for aggression and status networks for weeks 1–3 for group B1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	1067	1223.42 (20.00)	1156.56 (6.94)	1148.74 (5.82)	1130.49 (3.57)	1124.04 (2.89)	1123.95 (2.89)	1027.02 (1.56)
AA00	120	81.84 (17.79)	122.83 (0.07)	122.00 (0.03)	120.06 (0.00)	119.38 (0.00)	119.17 (0.01)	108.90 (1.13)
00S0	467	512.69 (4.07)	515.59 (4.58)	557.73 (14.76)	548.87 (12.21)	543.33 (10.72)	543.28 (10.71)	497.70 (1.89)
00SS	1	14.37 (12.44)	14.45 (12.52)	3.41 (1.70)	3.36 (1.66)	3.32 (1.62)	3.16 (1.48)	2.89 (1.24)
A00S	204	68.59 (267.31)	64.84 (298.64)	70.14 (255.44)	220.60 (1.25)	227.67 (2.46)	227.65 (2.46)	208.57 (0.10)
A0S0	5	68.59 (58.96)	64.84 (55.23)	70.14 (60.50)	21.60 (12.76)	22.29 (13.41)	22.29 (13.41)	20.42 (11.65)
AAS0	14	9.18 (2.53)	13.77 (0.00)	14.90 (0.05)	14.66 (0.03)	15.13 (0.08)	15.11 (0.08)	13.84 (0.00)
A0SS	1	3.85 (2.11)	3.64 (1.91)	0.86 (0.02)	0.84 (0.03)	0.87 (0.02)	0.83 (0.04)	0.76 (0.08)
AASS	1	0.26 (2.14)	0.39 (0.98)	0.09 (9.06)	0.09 (9.24)	0.09 (8.90)	1.04 (0.00)	0.95 (0.00)
0000	4675	4572.21 (2.31)	4598.08 (1.29)	4566.99 (2.55)	4494.43 (7.25)	4498.88 (6.90)	4498.52 (6.92)	4673.94 (0.00)
		389.66	382.14	349.95	47.99	47.01	37.98	17.64

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S16 Observed versus expected counts of dyads for aggression and status networks for weeks 4–6 for group B1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	903	1128.09 (44.91)	1025.62 (14.66)	1020.62 (13.56)	1004.73 (10.30)	991.09 (7.83)	991.07 (7.83)	880.25 (0.59)
AA00	141	69.48 (73.62)	143.82 (0.06)	143.12 (0.03)	140.89 (0.00)	138.98 (0.03)	139.06 (0.03)	123.51 (2.48)
00S0	369	427.15 (7.92)	429.77 (8.59)	460.00 (18.00)	452.84 (15.52)	441.84 (12.01)	441.83 (12.00)	393.95 (1.58)
00SS	1	9.96 (8.06)	10.02 (8.12)	2.25 (0.69)	2.21 (0.67)	2.16 (0.62)	2.23 (0.68)	1.99 (0.49)
A00S	176	52.62 (289.33)	47.84 (343.36)	51.20 (304.17)	185.68 (0.51)	201.71 (3.28)	201.71 (3.28)	179.86 (0.08)
A0S0	4	52.62 (44.92)	47.84 (40.17)	51.20 (43.51)	13.68 (6.85)	14.86 (7.94)	14.86 (7.94)	13.25 (6.46)
AAS0	11	6.48 (3.15)	13.42 (0.44)	14.36 (0.79)	14.14 (0.70)	15.36 (1.24)	15.37 (1.24)	13.70 (0.53)
A0SS	1	2.45 (0.86)	2.23 (0.68)	0.50 (0.50)	0.49 (0.52)	0.54 (0.40)	0.55 (0.36)	0.49 (0.52)
AASS	0	0.15 (0.15)	0.31 (0.31)	0.07 (0.07)	0.07 (0.07)	0.08 (0.08)	0.02 (0.02)	0.02 (0.02)
0000	4722	4579.00 (4.47)	4607.12 (2.86)	4584.67 (4.11)	4513.26 (9.65)	4521.39 (8.90)	4521.30 (8.91)	4720.98 (0.00)
		477.38	419.25	385.44	44.78	42.32	42.28	12.75

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S17 Observed versus expected counts of dyads for aggression and status networks for weeks 7–9 for group B1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	976	1150.48 (26.46)	1062.76 (7.08)	1058.22 (6.39)	1044.99 (4.56)	1034.75 (3.34)	1034.74 (3.34)	943.87 (1.09)
AA00	129	74.92 (39.04)	133.76 (0.17)	133.19 (0.13)	131.53 (0.05)	130.24 (0.01)	130.27 (0.01)	118.83 (0.87)
00S0	310	355.20 (5.75)	357.53 (6.32)	382.43 (13.72)	377.65 (12.12)	369.71 (9.64)	369.70 (9.64)	338.21 (2.35)
00SS	0	7.14 (7.14)	7.19 (7.19)	1.30 (1.30)	1.28 (1.28)	1.25 (1.25)	1.28 (1.28)	1.17 (1.17)
A00S	144	46.26 (206.49)	42.74 (239.96)	45.71 (211.33)	153.29 (0.56)	164.40 (2.53)	164.40 (2.53)	150.40 (0.27)
A0S0	4	46.26 (38.61)	42.74 (35.11)	45.71 (38.06)	13.29 (6.50)	14.26 (7.38)	14.26 (7.38)	13.04 (6.27)
AAS0	12	6.03 (5.92)	10.76 (0.14)	11.51 (0.02)	11.36 (0.04)	12.19 (0.00)	12.19 (0.00)	11.15 (0.06)
A0SS	1	1.86 (0.40)	1.72 (0.30)	0.31 (1.54)	0.31 (1.58)	0.33 (1.38)	0.34 (1.31)	0.31 (1.56)
AASS	0	0.12 (0.12)	0.22 (0.22)	0.04 (0.04)	0.04 (0.04)	0.04 (0.04)	0.02 (0.02)	0.01 (0.01)
0000	4529	4416.72 (2.85)	4445.60 (1.56)	4426.58 (2.37)	4371.26 (5.69)	4377.84 (5.22)	4377.80 (5.22)	4528.00 (0.00)
		332.78	298.05	274.89	32.40	30.79	30.73	13.67

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S18 Observed versus expected counts of dyads for aggression and status networks for weeks 10–12 for group B1–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	988	1192.89 (35.19)	1098.46 (11.11)	1094.82 (10.42)	1076.93 (7.34)	1069.66 (6.23)	1069.63 (6.23)	960.63 (0.78)
AA00	147	79.67 (56.89)	143.23 (0.10)	142.75 (0.13)	140.42 (0.31)	139.47 (0.41)	139.56 (0.40)	125.34 (3.74)
00S0	305	364.86 (9.82)	367.38 (10.59)	387.88 (17.71)	381.54 (15.35)	376.10 (13.44)	376.09 (13.44)	338.97 (3.40)
00SS	2	7.45 (3.99)	7.51 (4.04)	1.93 (0.00)	1.90 (0.00)	1.88 (0.01)	1.96 (0.00)	1.76 (0.03)
A00S	173	48.74 (316.81)	44.88 (365.74)	47.38 (333.01)	182.88 (0.53)	191.24 (1.74)	191.24 (1.74)	172.37 (0.00)
A0S0	2	48.74 (44.82)	44.88 (40.97)	47.38 (43.47)	11.88 (8.22)	12.42 (8.74)	12.42 (8.74)	11.20 (7.55)
AAS0	4	6.51 (0.97)	11.70 (5.07)	12.36 (5.65)	12.15 (5.47)	12.71 (5.97)	12.72 (5.98)	11.46 (4.86)
A0SS	0	1.99 (1.99)	1.83 (1.83)	0.47 (0.47)	0.46 (0.46)	0.49 (0.49)	0.51 (0.51)	0.46 (0.46)
AASS	0	0.13 (0.13)	0.24 (0.24)	0.06 (0.06)	0.06 (0.06)	0.06 (0.06)	0.01 (0.01)	0.01 (0.01)
0000	4595	4465.01 (3.78)	4495.88 (2.19)	4480.96 (2.90)	4407.76 (7.95)	4411.97 (7.59)	4411.86 (7.60)	4593.80 (0.00)
		474.40	441.87	413.82	45.71	44.68	44.64	20.84

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S19 Observed versus expected counts of dyads for aggression and status networks for weeks 1–3 for group B4–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	839	1035.09 (37.15)	961.78 (15.67)	955.58 (14.22)	938.48 (10.54)	918.28 (6.84)	918.27 (6.84)	806.15 (1.34)
AA00	104	59.25 (33.80)	109.36 (0.26)	108.66 (0.20)	106.71 (0.07)	104.42 (0.00)	104.48 (0.00)	91.72 (1.64)
00S0	398	471.38 (11.42)	473.79 (12.13)	512.84 (25.72)	503.66 (22.17)	486.50 (16.10)	486.49 (16.10)	428.49 (2.17)
00SS	0	12.29 (12.29)	12.35 (12.35)	2.59 (2.59)	2.54 (2.54)	2.45 (2.45)	2.51 (2.51)	2.21 (2.21)
A00S	195	53.96 (368.62)	50.14 (418.52)	54.27 (364.91)	203.93 (0.39)	230.22 (5.39)	230.21 (5.39)	202.79 (0.30)
A0S0	5	53.96 (44.43)	50.14 (40.64)	54.27 (44.73)	13.93 (5.73)	15.73 (7.32)	15.73 (7.32)	13.85 (5.66)
AAS0	14	6.18 (9.91)	11.40 (0.59)	12.34 (0.22)	12.12 (0.29)	13.68 (0.01)	13.69 (0.01)	12.06 (0.31)
A0SS	2	2.81 (0.24)	2.61 (0.14)	0.55 (3.86)	0.54 (3.98)	0.61 (3.20)	0.62 (3.07)	0.55 (3.87)
AASS	0	0.16 (0.16)	0.30 (0.30)	0.06 (0.06)	0.06 (0.06)	0.07 (0.07)	0.02 (0.02)	0.02 (0.02)
0000	4659	4520.92 (4.22)	4544.12 (2.90)	4514.84 (4.60)	4434.03 (11.41)	4444.05 (10.40)	4443.98 (10.40)	4658.16 (0.00)
		522.22	503.50	461.11	57.18	51.77	51.65	17.51

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S20 Observed versus expected counts of dyads for aggression and status networks for weeks 4–6 for group B4–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	882	1085.33 (38.09)	996.28 (13.11)	989.40 (11.66)	973.57 (8.61)	963.64 (6.92)	963.53 (6.90)	856.49 (0.76)
AA00	129	65.56 (61.39)	128.29 (0.00)	127.41 (0.02)	125.37 (0.11)	124.09 (0.19)	123.94 (0.21)	110.17 (3.22)
00S0	394	445.22 (5.89)	447.82 (6.47)	488.28 (18.20)	480.47 (15.56)	472.14 (12.93)	472.08 (12.91)	421.13 (1.75)
00SS	0	11.03 (11.03)	11.10 (11.10)	1.84 (1.84)	1.81 (1.81)	1.78 (1.78)	1.66 (1.66)	1.48 (1.48)
A00S	180	53.79 (296.18)	49.37 (345.61)	53.83 (295.69)	190.72 (0.60)	202.47 (2.49)	202.45 (2.49)	180.61 (0.00)
A0S0	4	53.79 (46.08)	49.37 (41.70)	53.83 (46.13)	14.71 (7.80)	15.62 (8.64)	15.62 (8.64)	13.93 (7.08)
AAS0	7	6.50 (0.04)	12.72 (2.57)	13.86 (3.40)	13.64 (3.23)	14.48 (3.87)	14.47 (3.85)	12.91 (2.70)
A0SS	0	2.67 (2.67)	2.45 (2.45)	0.40 (0.40)	0.40 (0.40)	0.42 (0.42)	0.40 (0.40)	0.35 (0.35)
AASS	1	0.16 (4.37)	0.32 (1.49)	0.05 (17.23)	0.05 (17.54)	0.05 (16.41)	1.05 (0.00)	0.93 (0.00)
0000	4619	4491.97 (3.59)	4518.28 (2.25)	4487.08 (3.88)	4415.27 (9.40)	4421.31 (8.84)	4420.82 (8.88)	4618.00 (0.00)
		469.34	426.73	398.45	65.06	62.49	45.94	17.34

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S21 Observed versus expected counts of dyads for aggression and status networks for weeks 7–9 for group B4–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	833	1020.67 (34.51)	945.96 (13.49)	935.69 (11.27)	918.48 (7.96)	903.07 (5.44)	903.07 (5.44)	795.60 (1.76)
AA00	109	62.31 (34.98)	112.84 (0.13)	111.61 (0.06)	109.56 (0.00)	107.72 (0.02)	107.72 (0.02)	94.91 (2.09)
00S0	425	481.37 (6.60)	484.15 (7.23)	541.89 (25.22)	531.93 (21.49)	518.38 (16.82)	518.38 (16.82)	458.36 (2.43)
00SS	0	13.86 (13.86)	13.94 (13.94)	1.82 (1.82)	1.79 (1.79)	1.75 (1.75)	1.75 (1.75)	1.55 (1.55)
A00S	198	58.78 (329.77)	54.47 (378.15)	60.97 (307.96)	210.97 (0.80)	229.70 (4.38)	229.70 (4.38)	203.12 (0.13)
A0S0	4	58.78 (51.05)	54.47 (46.77)	60.97 (53.23)	16.98 (9.92)	18.49 (11.35)	18.49 (11.35)	16.35 (9.33)
AAS0	14	7.18 (6.49)	13.00 (0.08)	14.55 (0.02)	14.28 (0.01)	15.55 (0.15)	15.55 (0.15)	13.75 (0.00)
A0SS	0	3.38 (3.38)	3.14 (3.14)	0.41 (0.41)	0.40 (0.40)	0.44 (0.44)	0.44 (0.44)	0.39 (0.39)
AASS	0	0.21 (0.21)	0.37 (0.37)	0.05 (0.05)	0.05 (0.05)	0.05 (0.05)	0.05 (0.05)	0.04 (0.04)
0000	4303	4179.47 (3.65)	4203.66 (2.35)	4158.03 (5.05)	4081.56 (12.01)	4090.86 (11.00)	4090.86 (11.00)	4301.94 (0.00)
		484.49	465.63	405.09	54.43	51.39	51.39	17.71

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S22 Observed versus expected counts of dyads for aggression and status networks for weeks 10–12 for group B4–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	880	1088.22 (39.84)	976.34 (9.51)	970.23 (8.39)	959.85 (6.64)	947.57 (4.82)	947.56 (4.82)	858.41 (0.54)
AA00	141	68.75 (75.93)	153.10 (0.96)	152.14 (0.82)	150.51 (0.60)	148.58 (0.39)	148.62 (0.39)	134.64 (0.30)
00S0	380	409.34 (2.10)	411.96 (2.48)	447.22 (10.10)	442.43 (8.81)	432.16 (6.30)	432.16 (6.30)	392.95 (0.43)
00SS	0	9.73 (9.73)	9.79 (9.79)	1.65 (1.65)	1.64 (1.64)	1.60 (1.60)	1.63 (1.63)	1.48 (1.48)
A00S	136	51.72 (137.33)	46.40 (173.00)	50.37 (145.55)	146.90 (0.81)	159.26 (3.40)	159.26 (3.40)	144.82 (0.54)
A0S0	6	51.72 (40.42)	46.40 (35.18)	50.37 (39.09)	16.91 (7.04)	18.33 (8.29)	18.33 (8.29)	16.67 (6.83)
AAS0	20	6.53 (27.74)	14.55 (2.04)	15.80 (1.12)	15.63 (1.22)	16.94 (0.55)	16.95 (0.55)	15.41 (1.37)
A0SS	1	2.46 (0.86)	2.21 (0.66)	0.37 (1.06)	0.37 (1.08)	0.40 (0.90)	0.41 (0.86)	0.37 (1.07)
AASS	0	0.16 (0.16)	0.35 (0.35)	0.06 (0.06)	0.06 (0.06)	0.06 (0.06)	0.03 (0.03)	0.03 (0.03)
0000	4431	4306.37 (3.61)	4333.91 (2.18)	4306.78 (3.58)	4260.71 (6.81)	4270.09 (6.06)	4270.05 (6.07)	4430.23 (0.00)
		337.72	236.12	211.41	34.70	32.36	32.33	12.57

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S23 Observed versus expected counts of dyads for aggression and status networks for weeks 13–17 for group B4–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	867	1132.80 (62.37)	1007.92 (19.70)	999.96 (17.68)	983.27 (13.75)	960.32 (9.07)	960.26 (9.06)	849.24 (0.37)
AA00	161	75.97 (95.17)	170.38 (0.52)	169.03 (0.38)	166.21 (0.16)	162.33 (0.01)	162.09 (0.01)	143.35 (2.17)
00S0	456	508.20 (5.36)	511.87 (6.10)	557.24 (18.39)	547.93 (15.43)	528.20 (9.87)	528.17 (9.86)	469.55 (0.39)
00SS	1	15.29 (13.36)	15.40 (13.46)	3.58 (1.86)	3.52 (1.81)	3.40 (1.69)	3.20 (1.51)	2.84 (1.19)
A00S	201	68.16 (258.88)	60.65 (324.80)	66.02 (275.94)	211.89 (0.56)	237.09 (5.49)	237.07 (5.49)	210.79 (0.45)
A0S0	9	68.16 (51.35)	60.65 (43.98)	66.02 (49.25)	19.89 (5.96)	22.26 (7.90)	22.26 (7.90)	19.79 (5.88)
AAS0	21	9.14 (15.38)	20.50 (0.01)	22.32 (0.08)	21.95 (0.04)	24.56 (0.52)	24.52 (0.51)	21.80 (0.03)
A0SS	1	4.10 (2.35)	3.65 (1.92)	0.85 (0.03)	0.83 (0.03)	0.93 (0.00)	0.88 (0.02)	0.78 (0.06)
AASS	1	0.28 (1.91)	0.62 (0.24)	0.14 (5.11)	0.14 (5.23)	0.16 (4.49)	1.07 (0.00)	0.95 (0.00)
0000	4387	4222.90 (6.38)	4253.37 (4.20)	4219.82 (6.62)	4149.36 (13.61)	4165.75 (11.75)	4165.48 (11.78)	4385.91 (0.00)
		512.49	414.93	375.34	56.57	50.79	46.12	10.55

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S24 Observed versus expected counts of dyads for aggression and status networks for weeks 16–20 for group B4–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	816	1001.69 (34.42)	904.91 (8.73)	900.83 (7.99)	891.21 (6.35)	893.94 (6.80)	893.73 (6.76)	813.14 (0.01)
AA00	132	57.20 (97.81)	131.55 (0.00)	130.96 (0.01)	129.56 (0.05)	129.96 (0.03)	129.67 (0.04)	117.98 (1.67)
00S0	418	432.93 (0.52)	435.15 (0.68)	462.75 (4.33)	457.81 (3.46)	460.18 (3.87)	460.07 (3.85)	419.84 (0.01)
00SS	1	10.69 (8.78)	10.74 (8.83)	3.00 (1.33)	2.97 (1.30)	2.98 (1.32)	2.76 (1.12)	2.52 (0.91)
A00S	131	49.44 (134.52)	44.67 (166.86)	47.50 (146.78)	142.50 (0.93)	139.71 (0.54)	139.67 (0.54)	127.47 (0.10)
A0S0	4	49.44 (41.77)	44.67 (37.03)	47.50 (39.84)	15.50 (8.53)	15.19 (8.25)	15.19 (8.24)	13.86 (7.02)
AAS0	5	5.65 (0.07)	12.99 (4.91)	13.81 (5.62)	13.66 (5.49)	13.40 (5.26)	13.37 (5.24)	12.20 (4.25)
A0SS	0	2.44 (2.44)	2.20 (2.20)	0.62 (0.62)	0.61 (0.61)	0.60 (0.60)	0.55 (0.55)	0.50 (0.50)
AASS	2	0.14 (24.84)	0.32 (8.80)	0.09 (40.78)	0.09 (41.26)	0.09 (42.16)	2.06 (0.00)	1.88 (0.01)
0000	4486	4385.37 (2.31)	4407.81 (1.39)	4387.95 (2.19)	4341.10 (4.84)	4338.96 (4.98)	4337.93 (5.05)	4485.61 (0.00)
		347.47	239.43	249.48	72.81	73.80	31.39	14.47

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S25 Observed versus expected counts of dyads for aggression and status networks for weeks 1–3 for group B3–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	457	575.07 (24.24)	527.47 (9.41)	514.67 (6.46)	495.70 (3.02)	464.25 (0.11)	464.06 (0.11)	419.85 (3.29)
AA00	85	71.27 (2.64)	99.15 (2.02)	96.75 (1.43)	93.18 (0.72)	87.27 (0.06)	87.74 (0.09)	79.38 (0.40)
00S0	249	285.35 (4.63)	290.20 (5.85)	330.95 (20.29)	318.76 (15.26)	290.38 (5.90)	290.26 (5.87)	265.01 (0.97)
00SS	4	17.55 (10.46)	17.85 (10.74)	5.73 (0.52)	5.52 (0.42)	5.02 (0.21)	5.45 (0.39)	4.97 (0.19)
A00S	188	70.73 (194.42)	64.88 (233.66)	73.99 (175.69)	201.23 (0.87)	230.58 (7.86)	230.48 (7.83)	210.57 (2.42)
A0S0	12	70.73 (48.77)	64.88 (43.10)	73.99 (51.93)	25.23 (6.94)	28.91 (9.89)	28.90 (9.88)	26.41 (7.86)
AAS0	38	17.53 (23.89)	24.39 (7.59)	27.82 (3.73)	26.79 (4.69)	30.70 (1.74)	30.86 (1.65)	28.20 (3.41)
A0SS	2	8.70 (5.16)	7.98 (4.48)	2.56 (0.12)	2.47 (0.09)	2.83 (0.24)	3.06 (0.37)	2.80 (0.23)
AASS	0	1.08 (1.08)	1.50 (1.50)	0.48 (0.48)	0.46 (0.46)	0.53 (0.53)	0.12 (0.12)	0.11 (0.11)
0000	1243	1159.99 (5.94)	1179.70 (3.40)	1151.07 (7.34)	1108.65 (16.28)	1137.52 (9.78)	1137.06 (9.87)	1240.71 (0.00)
		321.23	321.75	267.99	48.75	36.32	36.17	18.87

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S26 Observed versus expected counts of dyads for aggression and status networks for weeks 4–6 for group B3–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	414	539.95 (29.38)	499.12 (14.52)	480.84 (9.29)	459.09 (4.43)	422.33 (0.16)	422.30 (0.16)	370.58 (5.09)
AA00	75	63.68 (2.01)	87.47 (1.78)	84.27 (1.02)	80.45 (0.37)	74.01 (0.01)	74.10 (0.01)	65.03 (1.53)
00S0	242	285.26 (6.56)	289.50 (7.79)	346.28 (31.40)	330.62 (23.75)	296.54 (10.03)	296.52 (10.02)	263.02 (1.68)
00SS	1	17.77 (15.83)	18.04 (16.09)	3.80 (2.06)	3.63 (1.90)	3.25 (1.56)	3.34 (1.64)	2.96 (1.30)
A00S	204	67.29 (277.77)	62.20 (323.27)	74.40 (225.76)	219.04 (1.03)	256.18 (10.63)	256.16 (10.62)	227.36 (2.40)
A0S0	8	67.29 (52.24)	62.20 (47.23)	74.40 (59.26)	23.04 (9.81)	26.94 (13.32)	26.94 (13.32)	23.91 (10.59)
AAS0	34	15.87 (20.70)	21.80 (6.83)	26.08 (2.41)	24.90 (3.33)	29.12 (0.82)	29.15 (0.81)	25.88 (2.55)
A0SS	0	8.39 (8.39)	7.75 (7.75)	1.63 (1.63)	1.56 (1.56)	1.82 (1.82)	1.87 (1.87)	1.66 (1.66)
AASS	0	0.99 (0.99)	1.36 (1.36)	0.29 (0.29)	0.27 (0.27)	0.32 (0.32)	0.19 (0.19)	0.17 (0.17)
0000	1233	1144.51 (6.84)	1161.56 (4.39)	1119.02 (11.61)	1068.40 (25.36)	1100.49 (15.96)	1100.42 (15.97)	1230.43 (0.01)
		420.70	431.01	344.73	71.82	54.63	54.61	26.96

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions

Table S27 Observed versus expected counts of dyads for aggression and status networks for weeks 7–9 for group B3–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	512	612.39 (16.46)	572.17 (6.33)	562.06 (4.46)	543.07 (1.78)	524.01 (0.28)	523.94 (0.27)	481.11 (1.98)
AA00	108	85.10 (6.16)	107.54 (0.00)	105.64 (0.05)	102.07 (0.34)	98.49 (0.92)	98.65 (0.89)	90.59 (3.35)
00S0	172	202.45 (4.58)	205.72 (5.53)	232.64 (15.81)	224.78 (12.39)	209.74 (6.79)	209.71 (6.78)	194.28 (2.56)
00SS	1	9.30 (7.41)	9.45 (7.56)	2.31 (0.74)	2.23 (0.68)	2.08 (0.56)	2.21 (0.66)	2.05 (0.54)
A00S	157	56.27 (180.34)	52.57 (207.44)	59.45 (160.05)	167.68 (0.68)	184.03 (3.97)	184.01 (3.96)	170.52 (1.07)
A0S0	9	56.27 (39.71)	52.57 (36.11)	59.45 (42.81)	19.68 (5.80)	21.60 (7.35)	21.60 (7.35)	20.01 (6.06)
AAS0	19	15.64 (0.72)	19.76 (0.03)	22.35 (0.50)	21.59 (0.31)	23.70 (0.93)	23.74 (0.95)	22.00 (0.41)
A0SS	1	5.17 (3.36)	4.83 (3.04)	1.18 (0.03)	1.14 (0.02)	1.25 (0.05)	1.33 (0.08)	1.23 (0.04)
AASS	0	0.72 (0.72)	0.91 (0.91)	0.22 (0.22)	0.21 (0.21)	0.24 (0.24)	0.09 (0.09)	0.08 (0.08)
0000	1166	1101.70 (3.75)	1119.48 (1.93)	1099.69 (4.00)	1062.54 (10.07)	1079.87 (6.87)	1079.73 (6.89)	1163.12 (0.01)
		263.21	268.86	228.67	32.28	27.95	27.92	16.09

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S28 Observed versus expected counts of dyads for aggression and status networks for weeks 10–12 for group B3–S

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	480	593.02 (21.54)	544.35 (7.61)	532.50 (5.18)	512.67 (2.08)	490.74 (0.24)	490.71 (0.23)	443.10 (3.07)
AA00	102	78.61 (6.96)	106.74 (0.21)	104.42 (0.06)	100.53 (0.02)	96.23 (0.35)	96.31 (0.34)	86.97 (2.60)
00S0	178	211.75 (5.38)	215.64 (6.57)	248.57 (20.04)	239.32 (15.71)	221.61 (8.58)	221.60 (8.58)	202.18 (2.89)
00SS	1	10.02 (8.12)	10.21 (8.31)	2.08 (0.56)	2.00 (0.50)	1.85 (0.39)	1.92 (0.44)	1.75 (0.32)
A00S	162	56.14 (199.62)	51.53 (236.81)	59.40 (177.21)	175.62 (1.06)	195.35 (5.69)	195.34 (5.69)	178.27 (1.49)
A0S0	5	56.14 (46.58)	51.53 (42.02)	59.40 (49.82)	18.62 (9.97)	20.72 (11.92)	20.71 (11.92)	18.90 (10.23)
AAS0	24	14.88 (5.58)	20.21 (0.71)	23.30 (0.02)	22.43 (0.11)	24.95 (0.04)	24.97 (0.04)	22.79 (0.06)
A0SS	0	5.31 (5.31)	4.88 (4.88)	0.99 (0.99)	0.96 (0.96)	1.06 (1.06)	1.10 (1.10)	1.01 (1.01)
AASS	0	0.70 (0.70)	0.96 (0.96)	0.19 (0.19)	0.19 (0.19)	0.21 (0.21)	0.11 (0.11)	0.10 (0.10)
0000	1193	1118.42 (4.97)	1138.95 (2.57)	1114.14 (5.58)	1072.66 (13.50)	1092.27 (9.29)	1092.21 (9.30)	1189.92 (0.01)
		304.78	310.62	259.64	44.09	37.76	37.75	21.78

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S29 Observed versus expected counts of dyads for aggression and status networks for weeks 1–3 for group B2–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	889	1090.13 (37.11)	994.56 (11.20)	990.17 (10.34)	968.44 (6.52)	942.36 (3.02)	942.14 (3.00)	844.35 (2.36)
AA00	143	93.53 (26.16)	155.01 (0.93)	154.33 (0.83)	150.94 (0.42)	146.87 (0.10)	146.50 (0.08)	131.29 (1.04)
00S0	279	348.10 (13.72)	351.84 (15.08)	372.29 (23.38)	364.12 (19.90)	344.76 (12.54)	344.68 (12.52)	310.61 (3.22)
00SS	0	9.54 (9.54)	9.64 (9.64)	3.35 (3.35)	3.28 (3.28)	3.11 (3.11)	2.85 (2.85)	2.57 (2.57)
A00S	191	59.73 (288.46)	54.50 (341.92)	57.66 (308.31)	203.62 (0.78)	231.31 (7.03)	231.26 (7.01)	208.43 (1.46)
A0S0	3	59.73 (53.88)	54.50 (48.66)	57.66 (51.82)	15.62 (10.20)	17.75 (12.25)	17.74 (12.25)	15.99 (10.55)
AAS0	23	10.25 (15.86)	16.99 (2.13)	17.97 (1.40)	17.58 (1.67)	19.97 (0.46)	19.92 (0.48)	17.95 (1.42)
A0SS	2	3.27 (0.50)	2.99 (0.33)	1.04 (0.89)	1.02 (0.95)	1.15 (0.62)	1.06 (0.84)	0.95 (1.15)
AASS	2	0.28 (10.52)	0.47 (5.06)	0.16 (20.86)	0.16 (21.41)	0.18 (18.41)	2.07 (0.00)	1.86 (0.01)
0000	3319	3176.42 (6.40)	3210.52 (3.67)	3196.35 (4.71)	3126.22 (11.89)	3143.53 (9.79)	3142.78 (9.88)	3317.00 (0.00)
		462.15	438.60	425.88	77.01	67.33	48.89	23.77

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S29 Observed versus expected counts of dyads for aggression and status networks for weeks 4–6 for group B2–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	886	1046.75 (24.69)	963.41 (6.22)	955.51 (5.06)	940.71 (3.18)	925.10 (1.65)	925.10 (1.65)	842.83 (2.21)
AA00	128	83.51 (23.71)	136.87 (0.57)	135.75 (0.44)	133.64 (0.24)	131.42 (0.09)	131.43 (0.09)	119.74 (0.57)
00S0	277	319.83 (5.74)	322.75 (6.49)	356.81 (17.85)	351.28 (15.71)	339.13 (11.38)	339.13 (11.38)	310.23 (3.56)
00SS	0	7.80 (7.80)	7.87 (7.87)	0.94 (0.94)	0.92 (0.92)	0.89 (0.89)	0.90 (0.90)	0.82 (0.82)
A00S	150	51.03 (191.94)	46.97 (226.02)	51.92 (185.26)	161.21 (0.78)	176.88 (4.09)	176.88 (4.09)	161.82 (0.86)
A0S0	5	51.03 (41.52)	46.97 (37.50)	51.92 (42.40)	16.21 (7.75)	17.79 (9.19)	17.79 (9.19)	16.27 (7.81)
AAS0	19	8.14 (14.48)	13.34 (2.40)	14.75 (1.22)	14.52 (1.38)	15.94 (0.59)	15.94 (0.59)	14.58 (1.34)
A0SS	0	2.49 (2.49)	2.29 (2.29)	0.27 (0.27)	0.27 (0.27)	0.30 (0.30)	0.30 (0.30)	0.27 (0.27)
AASS	0	0.20 (0.20)	0.33 (0.33)	0.04 (0.04)	0.04 (0.04)	0.04 (0.04)	0.04 (0.04)	0.03 (0.03)
0000	3386	3280.22 (3.41)	3310.21 (1.74)	3283.08 (3.23)	3232.20 (7.32)	3243.52 (6.26)	3243.51 (6.26)	3384.40 (0.00)
		315.96	291.41	256.71	37.58	34.47	34.47	17.47

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S30 Observed versus expected counts of dyads for aggression and status networks for weeks 7–9 for group B2–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	946	1087.20 (18.34)	1002.20 (3.15)	997.78 (2.69)	986.67 (1.68)	979.23 (1.13)	979.23 (1.13)	914.83 (1.06)
AA00	143	93.05 (26.81)	146.28 (0.07)	145.63 (0.05)	144.01 (0.01)	142.92 (0.00)	142.92 (0.00)	133.53 (0.67)
00S0	186	215.08 (3.93)	217.23 (4.49)	234.71 (10.11)	232.10 (9.15)	227.05 (7.42)	227.05 (7.42)	212.81 (3.38)
00SS	0	3.64 (3.64)	3.68 (3.68)	0.35 (0.35)	0.35 (0.35)	0.34 (0.34)	0.34 (0.34)	0.32 (0.32)
A00S	105	36.82 (126.28)	33.94 (148.80)	36.67 (127.34)	112.67 (0.52)	119.18 (1.69)	119.18 (1.69)	111.71 (0.40)
A0S0	4	36.82 (29.25)	33.94 (26.41)	36.67 (29.10)	11.67 (5.04)	12.34 (5.64)	12.34 (5.64)	11.57 (4.95)
AAS0	10	6.30 (2.17)	9.91 (0.00)	10.70 (0.05)	10.58 (0.03)	11.20 (0.13)	11.20 (0.13)	10.49 (0.02)
A0SS	0	1.25 (1.25)	1.15 (1.15)	0.11 (0.11)	0.11 (0.11)	0.12 (0.12)	0.12 (0.12)	0.11 (0.11)
AASS	0	0.11 (0.11)	0.17 (0.17)	0.02 (0.02)	0.02 (0.02)	0.02 (0.02)	0.02 (0.02)	0.01 (0.01)
0000	3262	3175.74 (2.34)	3207.52 (0.93)	3193.36 (1.48)	3157.82 (3.44)	3163.60 (3.06)	3163.60 (3.06)	3260.62 (0.00)
		214.12	188.84	171.29	20.34	19.54	19.54	10.93

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.

Table S31 Observed versus expected counts of dyads for aggression and status networks for weeks 9–11 for group B2–U

Agg-status	Total observed dyads	Expected dyads (indep)	F1	F2	F3	F4	F5	F6
A000	873	985.32 (12.80)	912.43 (1.70)	910.05 (1.51)	903.32 (1.02)	901.29 (0.89)	901.29 (0.89)	849.65 (0.64)
AA00	114	71.90 (24.64)	118.82 (0.20)	118.51 (0.17)	117.63 (0.11)	117.37 (0.10)	117.37 (0.10)	110.64 (0.10)
00S0	149	167.92 (2.13)	169.21 (2.41)	180.00 (5.34)	178.67 (4.93)	177.34 (4.53)	177.34 (4.53)	167.53 (2.05)
00SS	0	2.09 (2.09)	2.10 (2.10)	0.17 (0.17)	0.17 (0.17)	0.17 (0.17)	0.17 (0.17)	0.16 (0.16)
A00S	68	24.51 (77.18)	22.70 (90.44)	24.14 (79.67)	74.69 (0.60)	76.44 (0.93)	76.44 (0.93)	72.22 (0.25)
A0S0	1	24.51 (22.55)	22.70 (20.74)	24.14 (22.18)	7.69 (5.82)	7.87 (6.00)	7.87 (6.00)	7.43 (5.57)
AAS0	8	3.58 (5.47)	5.91 (0.74)	6.29 (0.47)	6.24 (0.50)	6.39 (0.41)	6.39 (0.41)	6.03 (0.64)
A0SS	0	0.61 (0.61)	0.56 (0.56)	0.05 (0.05)	0.04 (0.04)	0.05 (0.05)	0.05 (0.05)	0.04 (0.04)
AASS	0	0.04 (0.04)	0.07 (0.07)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)
0000	3443	3375.52 (1.35)	3401.49 (0.51)	3392.64 (0.75)	3367.54 (1.69)	3369.09 (1.62)	3369.09 (1.62)	3442.29 (0.00)
		148.86	119.47	110.30	14.87	14.68	14.68	9.45

Columns F1–F6 represent the chi-squared values after adding each of the six constraint functions.