Supporting Information

Stochastic agent-based models

Stochastic agent-based models assume that network dynamics occur in continuous time. Thus, instead of assuming that the network "jumps" from time t to time $t+1$, these models simulate the process in which the network at time t gradually changes into the network at time $t+1$ through a series of shorter time steps.

A second assumption is that network changes are considered to be the consequence of a Markov process. That is, the current state of the network probabilistically determines its future states. This assumption appears to be realistic for modeling the behavior of non-human animals, which generally base their social decisions on their own current states and the current states of their physical and social environments.

The third assumption of these models is that individuals control their own associations. In other words, all changes are driven by individual behavior and not by any higher-level control mechanism. Here we assumed specifically that every social bond is the result of mutual "agreement" between two hyenas.

Finally, the network dynamics are simulated as a series of mini-steps in which a single social tie is altered. At any such mini-step, two randomly selected individuals are given the opportunity to form a new tie, to dissolve an existing tie, or to retain their relationship status, whether they are connected or not. An objective function depicts the value of this change, based on the short-term "preferences" of these individuals as a response to the current network state. The objective function has the general form:

$$f_i(\beta, x) = \sum_k \beta_k s_{ki}(x) \qquad [1]$$

In Equation 1, the value of the objective function depends on a linear combination of the effects $s_{ki}(x)$, weighted by the coefficients β_k. These effects represent possible causal explanations for why individuals change their network ties. For example, an individual may tend to form more ties (resulting in denser network), to form ties with individuals of the opposite sex, or to form ties with kin. A random residual adds a stochastic element to the objective function. The parameter estimation focuses on changes between observations of the network in consecutive years. Given the initial observation, this process identifies the factors that drive the network to move between states over time. The strength of this modeling approach lies in its ability to identify the underlying mechanisms affecting social network dynamics, while controlling for the effect of all other mechanisms.

The complex dependencies of these models do not allow direct calculations of likelihood. Therefore, we estimated parameter values using the method of moments (Snijders 2001). This method uses the first state of the network as a basis for estimating parameters by simulating

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subsequent changes. Simulation results are compared to the actual observed networks, updating parameter values until the simulations can produce networks with values similar to the observed ones.

We estimated the models using the R package RSiena (version 1.1.277). We used the default method of moments for estimation. Models were selected following two criteria: first, *t* ratios for all parameters estimates were smaller than 0.1 in absolute value, as is the suggested standard (Ripley *et al.* 2014); second, we employed strict goodness of fit criteria, selecting only models that could simulate networks that were similar to the observed networks. Goodness of fit was estimated by comparing the values of the degree distribution, the geodesic distribution, and triadic census, to a set of simulated networks (Figure S1). Only models for which we could not reject the null hypothesis, suggesting that the observed network belongs to the set of simulated networks, were qualified (Ripley *et al.* 2014). In all the sets of networks we modeled, although many models converged properly, we found only one model that both converged and had perfect goodness-of-fit by all network measures, and this is the model presented in this study (Fig. 2-3; Table S1-S3). To calculate *P* values for each parameter estimate we divided the parameter estimate by its SE and obtained a *t* statistic. Further details on the RSiena models are given in (Ripley *et al.* 2014) and references therein.

A **Goodness of Fit of OutdegreeDistribution**
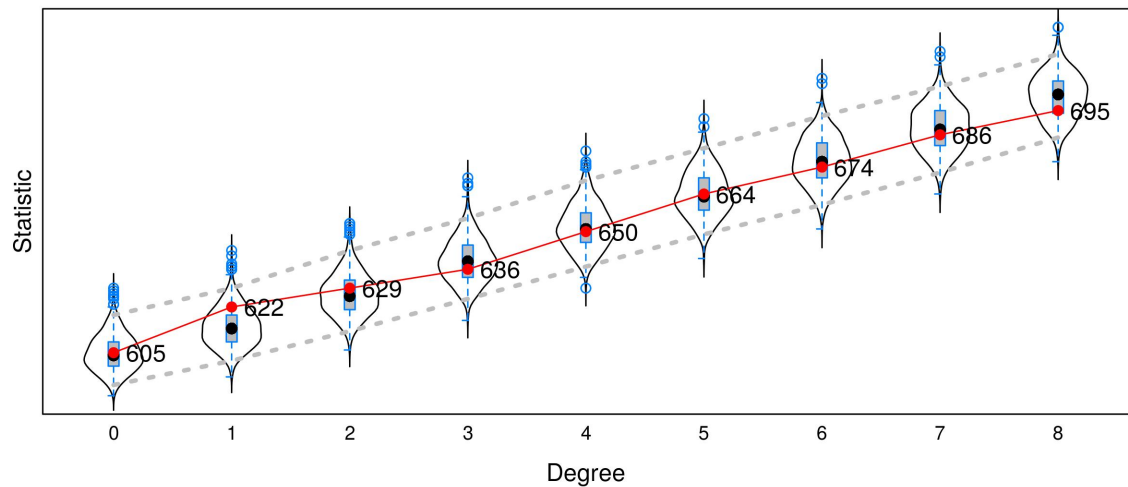
B **Goodness of Fit of GeodesicDistribution**
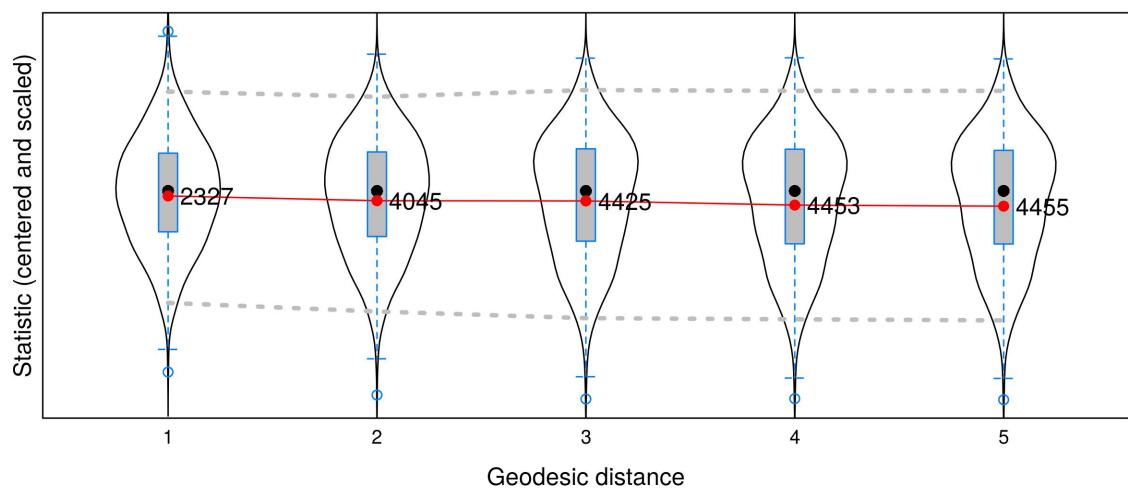
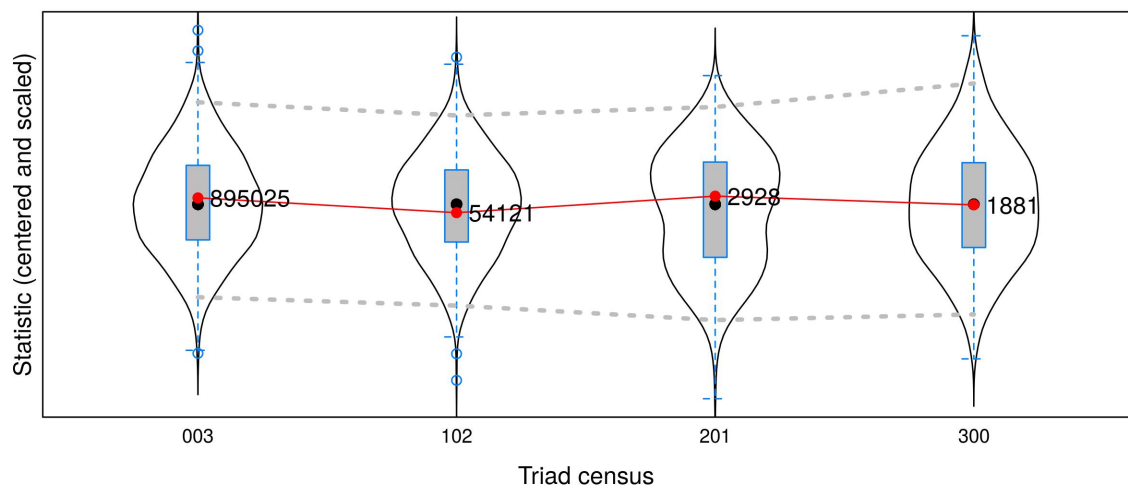**C** **Goodness of Fit of TriadCensus**

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Fig. S1: Example of goodness of fit, showing that the selected models could simulate the observed networks. (A) Violin plots depict for each number of nodes with degree lower than depicted on the x axis, the values of these statistics in simulated networks. (B) Violin plots depict the numbers of specific cumulative geodesic distance values in simulated networks. (C) Violin plots depict the numbers of triads of each type in simulated networks (003 stands for triad with no ties, 102 for one tie, 201 for two ties, and 300 for three ties). Dashed grey lines indicate 95% confidence intervals. Solid red line shows the observed values. The null hypothesis, that the observed networks belong to the simulated network "population," cannot be rejected ($P = 0.19$, $P = 0.99$, and $P = 0.93$ in A, B, and C, respectively).

Full model results

Effect	β	SE	P	Decade
Density	-1.983	0.142	<0.0001	1
Triadic closure	0.180	0.022	<0.0001	1
Degree of alter	0.106	0.024	<0.0001	1
Degree assortativity	-0.003	0.0003	<0.0001	1
Relatedness	0.390	0.153	0.11	1
Sex	-0.456	0.078	<0.0001	1
Dispersal status	-0.481	0.094	<0.0001	1
Dispersal status assortativity	0.198	0.051	0.0001	1
Social rank	0.012	0.004	0.003	1
Rainfall	-0.431	0.087	<0.0001	1
Prey	0.0008	0.0002	0.009	1
Density	-1.281	0.124	<0.0001	2
Triadic closure	0.101	0.016	<0.0001	2
Distance two	-0.063	0.012	<0.0001	2
Isolate	4.132	0.993	<0.0001	2
Degree of alter	0.093	0.026	0.0004	2
Degree assortativity	-0.002	0.0003	<0.0001	2
Relatedness	0.448	0.098	<0.0001	2
Sex	-0.139	0.065	0.032	2
Sex assortativity	0.167	0.039	<0.0001	2
Social rank	0.611	0.117	<0.0001	2
Social rank assortativity	-0.260	0.103	0.012	2

Table S1: Estimates of coefficients and standard errors in SIENA models of the full spotted hyena networks presented in Fig. 2. Full models included adults of both sexes. Decade 1 includes data from 1989-1998. Decade 2 includes data from 2002-2011. A negative estimate of the sex effect means that females were more likely to form social bonds than males. A negative estimate of the dispersal status effect means that immigrants were more likely to form social bonds than natal individuals.

Effect	β	SE	P	Decade
Density	-0.676	0.064	<0.0001	1
Triadic closure	0.147	0.010	<0.0001	1
Distance two	-0.094	0.038	0.014	1
Isolate	4.154	0.936	<0.0001	1
Social rank assortativity	1.023	0.312	0.001	1
Rainfall	-0.413	0.081	<0.0001	1
Prey	0.001	0.0002	<0.0001	1
Density	-0.846	0.165	<0.0001	2
Triadic closure	0.179	0.039	<0.0001	2
Distance two	-0.024	0.018	0.178	2
Isolate	5.249	1.203	<0.0001	2
Degree of alter	0.096	0.039	0.014	2
Degree assortativity	-0.004	0.0003	<0.0001	2
Social rank	-0.674	0.233	0.004	2

Table S2: Estimates of coefficients and standard errors in SIENA models of networks comprised of female spotted hyenas presented in Fig. 3A. Decade 1 includes data from 1989-1998. Decade 2 includes data from 2002-2011.

Effect	β	SE	P	Decade
Density	-0.196	0.280	0.484	1
Triadic closure	0.355	0.057	<0.0001	1
Distance two	-0.146	0.072	0.043	1
Isolate	4.145	1.116	0.0002	1
Degree of alter	-0.104	0.061	0.090	1
Degree assortativity	-0.004	0.002	0.064	1
Relatedness	0.390	0.336	0.246	1
Dispersal status	-0.577	0.158	0.0002	1
Dispersal status assortativity	0.239	0.100	0.017	1
Rainfall	-0.313	0.122	0.010	1
Prey	0.0008	0.0003	0.002	1
Density	-0.501	0.079	<0.0001	2
Triadic closure	0.154	0.017	<0.0001	2
Distance two	-0.121	0.056	0.031	2
Isolate	2.434	1.839	0.186	2
Relatedness	0.764	0.242	0.002	2
Dispersal status	-0.359	0.130	0.006	2
Dispersal status assortativity	0.239	0.092	0.010	2
Rainfall	-0.636	0.121	<0.0001	2

Table S3: Estimates of coefficients and standard errors in SIENA models of networks comprised of male spotted hyenas presented in Fig. 3B. Decade 1 includes data from 1989-1998. Decade 2 includes data from 2002-2011. A negative estimate of the dispersal status effect means that immigrants were more likely to form social bonds than were natal individuals.

Validation of triadic closure

Our method of social network construction used the gambit of the group approach, where each animal observed in a group during an observation session was considered to be associating with every other individual in that group (Franks *et al.* 2010). To verify that the main result of clustering (triadic closure) was not merely an artifact of our data collection methods, we conducted another analysis to remove any effects of the gambit of the group method. Here we constructed the networks by randomly choosing only two individuals from each observation session that included more than two hyenas. Thus, any effects of clustering at the observation stage were removed. We also tested simpler models, in which only structural effects were considered. These models showed similar results in terms of triadic closure, meaning this tendency is truly significantly positive (Table S4 and S5).

Effect	β	SE	P
Density	-1.042	0.066	<0.0001
Triadic closure	0.082	0.022	0.0002
Degree of alter	0.044	0.010	<0.0001

Table S4: Estimates of coefficients in a simple SIENA model. Data are from 1989-1998, but only two randomly chosen individuals were considered in observation sessions in which more than two hyenas were present. The tendency to close triads was retained here, as we also presented in the main text.

Effect	β	SE	P
Triadic closure	0.162	0.015	<0.0001
Degree of alter	-0.046	0.003	0.0002
Isolates	5.516	1.402	<0.0001

Table S5: Estimates of coefficients in a simple SIENA model. Data are from 2002-2011, but only two randomly chosen individuals were considered in observation sessions in which more than two hyenas were present. The tendency to close triads was retained here, as we also presented in the main text.

Triadic closure in weighted networks

We performed another analysis to verify that our main result regarding triadic closure is not merely a byproduct of the specific threshold used to filter the networks. Here, we tested how association indices (AIs) within triads change over time. It should be noted that triadic closure in a weighted network is undefined. For example, if we have three individuals with AIs of 0.1, 0.4, and 0.6 between them, what predictions can we make that would be similar to predictions in a binary network? To tackle this question we calculate two distances for each triad: Distance 1, defined as the difference between the median AI and the smallest AI, and Distance 2, defined as the difference between the largest AI and the median AI. Let us explore the possible configurations and predict temporal changes based on our results: 1) In triads where the hyenas are strongly associated with one another all AIs are relatively similar, and thus Distances 1 and 2 should be similar. Following our results of triadic closure we do not expect a major change in the difference between those distances, as this configuration seems to be stable. 2) A similar case is when the three hyenas are weakly associated. Again, Distances 1 and 2 should be small and similar to one another, and we do not predict a temporal change to occur. 3) Two of the hyenas are strongly connected while both are weakly connected to the third hyena (Distance 1 is small and Distance 2 is relatively large). Our results do not predict a major change in this case; hence the difference between the Distances should remain. 4) An unclosed triad, where one hyena is strongly associated with two others, but they are weakly connected. In terms of AIs, that means that the triad contains two large values and one small, i.e. Distance 1 is large and Distance 2 is

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small. Here we predict a change towards closing the triad, and Distance 1 should decrease relative to Distance 2. 5) The last case is when there is one large AI, one medium value, and one small AI. This case is undefined in binary networks because there cannot be a medium value. We do not make a prediction here.

We regressed the difference between Distance 1 and Distance 2 in the year $t+1$ on the same difference in year t (Fig. S2). Most values are around zero and can describe cases 1 and 2 above. The left side of the graph shows triads in which there is one strong association and two weak ones, and those configurations tend to be retained in the following year, as predicted. The right side shows a reverse in the trend: when there are two large AIs and one small one, there was a tendency for the triad to change in the next year towards triads that are closed or to only one strong association. This is shown by the negative correlation between (Distance 1 − Distance 2) and its future value.

Overall, this supports our main results regarding triadic closure, and shows that they hold even when considering weighted networks. The triadic configuration can thus make a non-trivial prediction about its future state.
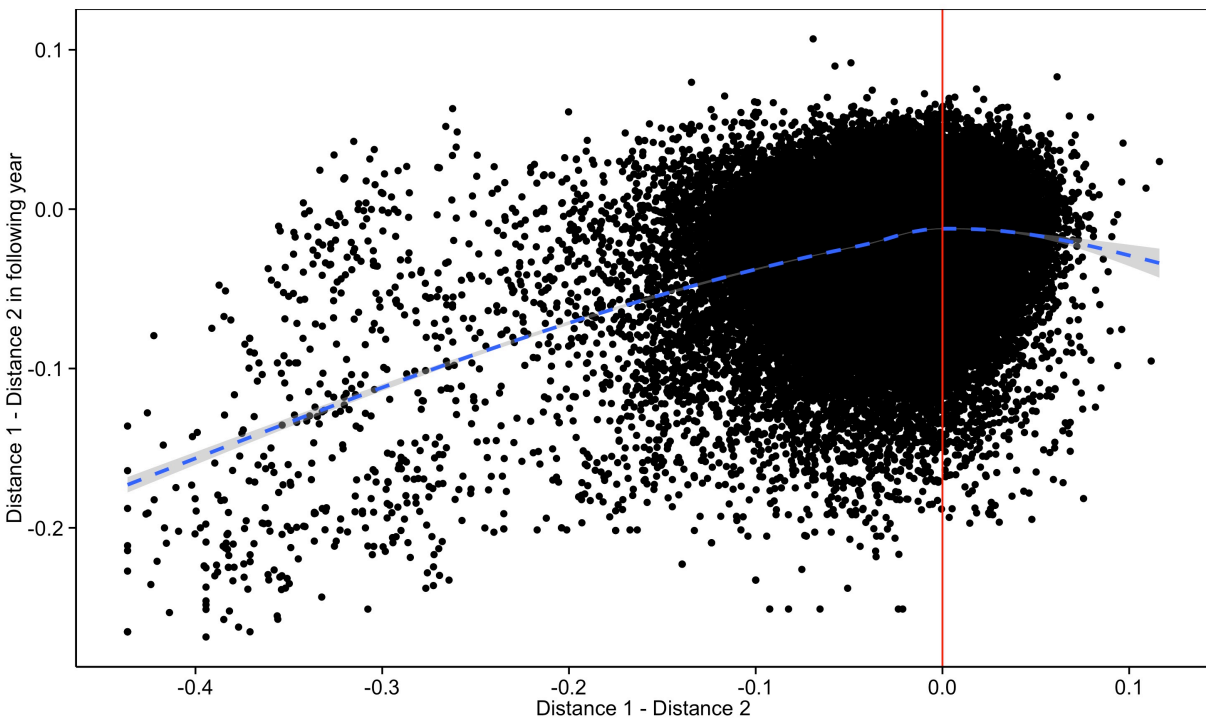

Fig. S2: The change in the distances between association index (AI) values within triads over consecutive years. Distance 1 is the difference between the median AI in a triad and the smallest AI. Distance 2 is the difference between the largest AI in a triad and the median AI. Red vertical line depicts zero distance. Dashed blue line depicts a generalized additive model fit. N = 238,168.

Filtering networks

To obtain binary networks required by the stochastic agent-based models, we tested multiple thresholds based on the twice-weight association index (AI), before settling on a threshold that defines strong social bonds as those in the upper quartile of AI values. We initially ran our models on binary networks that were constructed using various AI threshold values. Although the results were similar to those presented in the main text, it was much harder, and in some cases impossible, to achieve model convergence and proper goodness of fit. This suggests that the chosen threshold value generated useful networks that could be modelled using the parameters in which we were interested. Other networks (e.g. in which weaker association strengths were considered) featured either low variation over time (if the network was too dense) or high levels of between-year variation that could not be explained. Further development of stochastic agent-based models will enable usage of weighted networks and better model convergence. This will facilitate tests of multiple threshold values, advancing our knowledge of dynamics of multiple bond strengths.

Group size effects

As a preliminary analysis we tested the effect of group size on several features of the social networks. Group size was not significantly correlated with any of the network measures, including density (Pearson correlation: $t_{18} = -0.92$, $r = -0.21$, $P = 0.37$), mean degree ($t_{18} = 1.34$, $r = 0.30$, $P = 0.20$), and clustering coefficient ($t_{18} = -1.24$, $r = -0.28$, $P = 0.23$). Hence to reduce the number of parameters, group size was not included in the main analysis.

Movie S1: Animation of spotted hyena social network dynamics over 10 years in the Masai Mara National Reserve, Kenya. Red and blue spheres represent females and males, respectively. Lines represent strong social bonds (see Methods in main text).

References

1. Ripley RM, Snijders TAB, Boda Z, Voros A, & Preciado P (2014) *Manual for RSiena* (Department of Statistics, Nuffield College, University of Oxford).
2. Snijders TAB, van de Bunt G, & Steglich C (2010) Introduction to stochastic actor-based models for network dynamics. *Social Networks* 32(1):44-60.
3. Franks DW, Ruxton GD, & James R (2010) Sampling animal association networks with the gambit of the group. *Behavioral Ecology and Sociobiology* 64:493-503.