

ARTICLES

Policing stabilizes construction of social niches in primates

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All organisms interact with their environment, and in doing so shape it, modifying resource availability. Termed niche construction, this process has been studied primarily at the ecological level with an emphasis on the consequences of construction across generations¹. We focus on the behavioural process of construction within a single generation, identifying the role a robustness mechanism²—conflict management—has in promoting interactions that build social resource networks or social niches. Using ‘knockout’ experiments on a large, captive group of pigtailed macaques (*Macaca nemestrina*), we show that a policing function, performed infrequently by a small subset of individuals³, significantly contributes to maintaining stable resource networks in the face of chronic perturbations that arise through conflict. When policing is absent, social niches destabilize, with group members building smaller, less diverse, and less integrated grooming, play, proximity and contact-sitting networks. Instability is quantified in terms of reduced mean degree, increased clustering, reduced reach, and increased assortativity. Policing not only controls conflict^{3–5}, we find it significantly influences the structure of networks that constitute essential social resources in gregarious primate societies. The structure of such networks plays a critical role in infant survivorship⁶, emergence and spread of cooperative behaviour⁷, social learning and cultural traditions⁸.

We operationalize the social niche in graphical terms as the local connections of a node (that is, an individual) in multiple, overlapping social networks and we define social organization as the union of all social niches (Supplementary Fig. 1S). Whereas the ecological niche is composed of resource vectors⁹ (availability of wood for building dams, prey items, and so on), the social niche is composed of an individual’s vector of behavioural connections in the set of overlapping social networks in which it participates (Supplementary Fig. 1S). As with ecological niches, social niches vary in quality and affect one another: if one niche fragments, connectivity, and consequently social resource availability in other niches, is affected. The construction of stable social niches requires that individuals have time and security to engage in social interactions.

In primate societies frequent conflict threatens to destabilize social networks and robustness mechanisms have evolved to stabilize within-group behavioural interactions^{2,10}. We hypothesize that third-party policing—physically impartial intervention into conflicts, made possible by the structure of a status communication network³—stabilizes social niches (Fig. 1) (in addition to directly affecting aggression and conflict levels²), allowing group members to interact with a larger, more diverse set of well-connected partners.

Network comparisons and properties

By perturbing the status-signalling network and disabling policing, we quantify the effects of policing on the structure of four social networks: grooming, play, contact-sitting and proximity. We assess four network properties in three conditions: an observed control (OC) condition in which all individuals were present in the group; an experimental knockout condition (EK) in which all individuals except three high-status nodes (see below) were present; and a topological knockout (TK) condition, consisting of the OC condition with three high-status nodes removed from the data (Fig. 2 and Supplementary Fig. 1S).

The OC–TK–EK comparison combines two traditions that have characterized knockout studies. In cell biology, OC is typically compared to the observed network after experimental knockout (EK)¹¹. In studies of the internet and other kinds of technological networks, OC is typically compared to a virtual network (TK) in

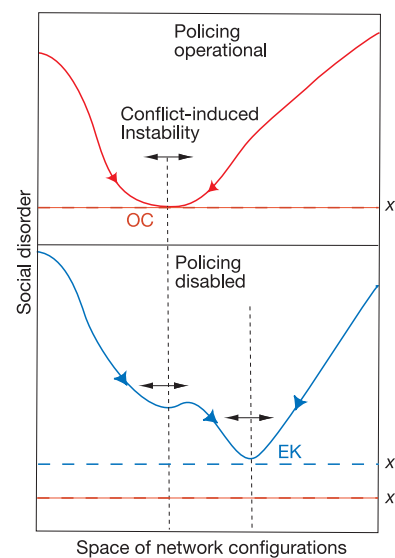


Figure 1 | Schematic showing putative basins of attraction for pigtailed macaque social networks. Policing stabilizes social networks in the OC condition by preventing chronic low-level conflict leading to network fragmentation (level of order indicated by x). When policing is disabled, conflict is no longer moderated, and the social system shifts to a new network configuration, the EK condition, associated with an elevated level of social disorder (indicated by x').

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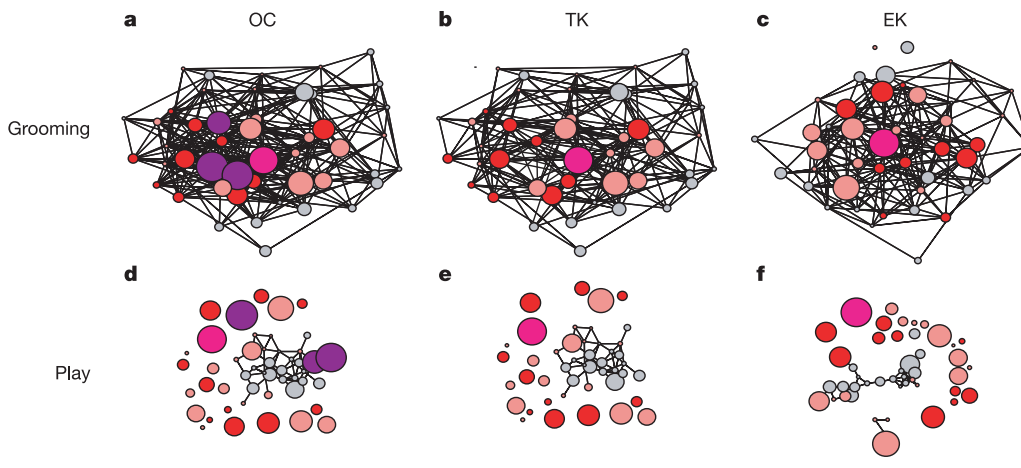


Figure 2 | Empirically derived grooming and play networks in three conditions. OC, all data included; TK, policer data were removed from OC data; EK, policers physically removed from the group. **a**, OC grooming; **b**, TK grooming; **c**, EK grooming; **d**, OC play; **e**, TK play; and **f**, EK play. Node size corresponds to frequency of signals received in the status communication network. Purple nodes: policers. Bright pink node: alpha female. Red nodes: matriarchs. Light pink nodes: other adults. Grey nodes: subadults (socially mature but not fully-grown).

which nodes have been topologically (virtually) removed¹². These comparisons are implicitly considered equivalent. The OC–TK comparison neglects consideration of reconfiguration in the experimental condition. OC–EK does not control for the structural contribution of knockout nodes to network topology. In contrast, TK–EK highlights the extent to which knockout-induced changes in interactions result from simple topological changes. Significant differences between TK and EK reflect behavioural reconfiguration and highlight the systemic role of knockout nodes in network structure.

Knockout node characteristics

The knockout nodes (Fig. 2 and Supplementary Fig. 1S) correspond to three fully grown adult males receiving a disproportionate number of subordination signals, called silent-bared teeth displays (SBT), from 45 mature (84 total) group members in peaceful contexts (for the description of the species studied and the removal procedure see Methods and Supplementary Methods). These signals are unidirectional, that is, they are always emitted by the same individual in the dyad^{13,14}. Peacefully emitted SBTs are considered an acknowledgement of power³. Because they are unidirectional and emitted relatively infrequently, power structure changes slowly.

The observed distribution of SBTs received was not significantly different from log-normal (Kolmogorov–Smirnov test, $P = 0.635$). Individuals receiving many signals were in the distribution’s tail. They performed the vast majority of policing interventions terminating conflicts, yet did so rarely compared to the total number of conflicts³. Removal of nodes with heavily weighted input edges (the three high-status nodes) in the signalling network eliminates powerful policers. We have shown elsewhere that policer removal results in organizational destabilization over short timescales as mean levels of aggression increase and mean levels of affiliation, including reconciliation, decrease². Removal, or knockout of highly connected nodes, in systems as diverse as the internet and yeast regulatory networks, has been shown to affect network functionality significantly¹⁵.

Here we investigate how knockout affects four network properties:

mean degree, reach, assortative mixing and clustering. Each of these statistics provides a different insight into the role of policing in social network construction, and differentially emphasizes local versus nonlocal interactions.

Degree results

Degree distributions of grooming, contact-sitting, and proximity networks were normally distributed in OC, TK and EK conditions. Play was right-skewed in each condition. We used repeated measures¹⁶ to analyse how mean degree (node degree is defined as the number of nodes to which it is connected) changed in the networks across the three comparisons (Table 1). TK–EK results indicate that individuals had significantly more play and grooming partners in the presence of policing. Having more partners increases partner choice and redundancy, which is important if partners vary in availability and quality, as has been suggested by work on biological markets¹⁷.

Reach results

Node reach is a measure of its indirect connectedness to other nodes in the graph¹⁸. Here we define node reach to be the number of nodes two or fewer steps away. Reach is important to primates because it affects behavioural contagion. If A grooms B, this can induce B to groom C¹⁹. In this way, positive behaviour propagates over the network. Reach in social networks will also affect contagion of aggression—as a consequence of affiliative relations²⁰, a fight erupting between X and A can cause a chain reaction in which B supports A and C supports B. We consider only two or fewer steps because A’s choice of B is more probably dependent on B’s actual partners (B’s degree) than on more socially distant individuals (B’s reach). Additionally, long contagion cascades are more likely to be interrupted by extrinsic factors.

We quantify reach in three of four networks (see Fig. 3a legend). We identify the extent of reach beyond that which would be predicted by degree alone (high degree generally implies high reach). For each network in each condition we generated an ensemble of graphs conserving the original degree distribution (Supplementary Notes

Table 1 | Degree and clustering coefficient repeated measures results

| Network | OC–TK | | OC–EK | | TK–EK | |
|---------------------------|--------------------|--------------------|--------------------|--------------------|--------------------|-------------------|
| | Degree | Clustering | Degree | Clustering | Degree | Clustering |
| Grooming, $n = 45$ | SIG D, $P < 0.001$ | SIG D, $P < 0.001$ | SIG D, $P < 0.001$ | SIG D, $P = 0.008$ | SIG D, $P = 0.009$ | D, $P = 0.36$ |
| Play, $n = 29$ | D, $P = 0.08$ | EQUAL, $P = 0.94$ | SIG D, $P = 0.016$ | D, $P = 0.87$ | SIG D, $P = 0.027$ | D, $P = 0.86$ |
| Contact-sitting, $n = 45$ | SIG D, $P < 0.001$ | I, $P = 0.028$ | D, $P = 0.16$ | D, $P = 0.99$ | D, $P = 1.0$ | D, $P = 0.70$ |
| Proximity, $n = 45$ | SIG D, $P < 0.001$ | SIG D, $P < 0.001$ | D, $P = 0.051$ | D, $P = 1.0$ | I, $P = 0.051$ | SIG I, $P = 0.03$ |

OC–TK comparison illustrates how networks change structurally following topological removal of policer data, but does not allow for reconfiguration. OC–EK comparison assesses network change following actual policer removal, thereby allowing for reconfiguration, but does not control for structural contribution of policers. TK–EK comparison allows for reconfiguration and controls for policers’ direct contribution to network structure. SIG D, significant decrease in mean; SIG I, significant increase in mean; D, mean decreases; I, mean increases; EQUAL, means are equal to two decimal places. Play was tested separately from other variables because it was based on a different sample size. We correct P values for multiple comparisons using the Sidak correction¹⁶. Full results are reported in the Supplementary Data.

and Supplementary Table 1S). We constructed a curve of reach versus degree to reflect the ensemble average. We summed the difference between the reach of each node in the empirical network and the average reach value for a node of that degree in the randomizations and then divided by the total number of nodes. This gave an estimate of average reach deviation from random for each network (Fig. 3a).

For all graphs, reach was less than random expectation given the network's degree profile. Opportunity for contagion was therefore less than expected for a random network. The networks were characterized by relatively low reach in OC, in which direct connections of all nodes, including policers, were considered. In TK (without policers' direct connections), we found policing maintained relatively high potential for contagion (compared to EK) through connections among nonpolicing individuals. The direct connections of policers therefore imparted substantial structure to the graphs. Relative reach in consequence appeared low in OC, but in actuality was high among nonpolicers. This means that policing, through its effects on network structure, maintains potential for both costly aggressive and beneficial affiliative contagion. However, policing

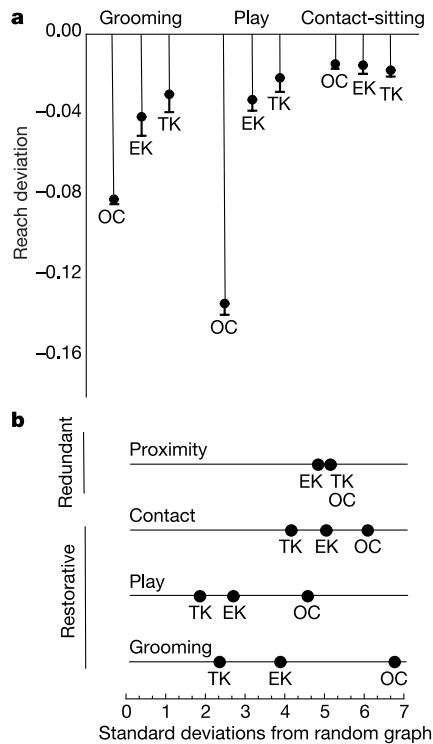


Figure 3 | Reach and assortativity results. **a**, Social network reach. Line segment length represents mean difference (over all nodes) in reach values between the empirical network and the expected reach of a node of identical degree in the randomized networks (500 randomizations). The line segment bars (heavy black lines) indicate the standard deviation of the reach deviation from the mean across all individual randomizations. (A reach deviation from the mean can be calculated for each individual randomization in the same way for the experimental data.) Relative reach in consequence appeared low in OC, but in actuality was relatively high among nonpolicers (TK) compared to EK. Proximity networks were not studied because reach saturated to one for all nodes. All reach deviations are negative because empirical networks display less reach than their randomized counterparts. **b**, Social network assortativity. An ensemble of randomized graphs is constructed for each network (play OC, play TK, play EK, grooming OC, and so on). The measured assortativity of the original graph is compared with the average observed in the ensemble, and measured in units of the standard deviation of the ensemble's assortativity values. The assortativity measures of the graphs are higher than the ensemble average in all cases. Play and grooming are most strongly perturbed by policer knockout. Contact-sitting, play and grooming restore some assortativity through a modification of behaviour by remaining group-members, suggesting a tendency towards behavioural homeostasis.

interventions directly control aggressive contagion. Consequently, when policing is operational, it makes sense for nonpolicers to build networks supporting contagion. This interpretation is further supported by low reach in EK combined with increased mean aggression and decreased mean affiliation², suggesting that when policing is absent, individuals do in fact reduce reach to prevent uncontrollable aggressive contagion.

Assortativity results

Networks display assortative mixing by degree when nodes of a given degree attach preferentially to nodes of similar degree. We calculate assortativity after Newman²¹. Assortative mixing gives insight into higher-order structural effects that cannot be gleaned from degree or reach. When individuals interact with others of like degree, they interact with others with access to similar social resources. This is thought to be important for emergence of cooperation²². However, assortativity also results in less interaction-partner diversity and therefore is not an ideal solution for promoting cooperation. As with reach, we controlled for influence of degree profile. As with reach, OC had highest assortativity for all graphs: policers' direct connections contributed structure to the graphs (Fig. 3b). Grooming, play and contact-sitting networks were relatively less assortative in TK than EK. We have shown elsewhere² that cooperation is greater in TK than EK.

Together, these results suggest that policing promotes cooperation among individuals with unequal access to social resources, and also facilitates interaction-partner diversity. When policing was absent (EK), individuals increased assortativity, modifying partner choice to interact with individuals of similar degree. This allowed recovery of some cooperation potential, but at the cost of interaction-partner diversity.

Clustering results

The local clustering coefficient²³ of a node i is the density of its open neighbourhood, where $C_i = \frac{\text{number of triangles connected to } i}{\text{number of triples centred on } i}$. The clustering coefficient for the whole network is given by: $C = \frac{1}{n} \sum_i C_i$. This measure of network transitivity expresses the likelihood that two neighbours of a node will themselves be neighbours. We used repeated measures to investigate the effect of the condition (OC, TK or EK) on clustering in each network (Table 1). Only proximity was significantly affected by policing knockout. Individuals showed more clustering when policing was absent. With policing, individuals exhibited less conservative interactions—they preferentially interacted with more socially distant individuals than with friends of their friends. Policing promotes a more open, integrated society rather than one made up mainly of cliques.

Effect of policing on social niche construction

Conflict threatens to destabilize society. Its immediate consequences include injuries and damaged relationships¹⁰. It has been demonstrated that policing can directly prevent this^{3,4}. We find that policing also has far-reaching indirect consequences, significantly altering construction of social resource networks that make group living advantageous. We demonstrated this by analysing changes to four network properties. We observe that when policing is operational, group members build larger social networks characterized by greater partner diversity and increased potential for socially positive contagion and cooperation. Without policing, high conflict frequency and severity leads to more conservative social interactions and a less integrated society. Mechanisms for buffering frequent conflicts are therefore essential for construction of stable social niches upon which individuals depend for behavioural resources.

METHODS

Pigtailed macaques are indigenous to south East Asia and live in multimale, multifemale societies characterized by female matrilineal and male group transfer upon onset of puberty²⁴. Pigtailed macaques breed all year. Females develop

swellings when in oestrus. The social systems of captive macaque species are relatively well studied²⁵.

Data were collected from a captive, breeding group of pigtailed macaques at Yerkes National Primate Research Center near Lawrenceville, Georgia. The group comprised 84 individuals, including four adult males, 25 adult females, and 19 subadults. All individuals, except eight (four males, four females), were either natal to the group or had been in the group since formation in 1985. The knockout males correspond to three of four males. The group was housed in an indoor–outdoor facility, the outdoor compound of which was 125 feet by 65 feet. During observations, the group was confined to the outdoor area, where all individuals were visible to the observer.

Observation conditions. Observations occurred for up to eight hours daily between 1,100 and 2,000 hours over a twenty-week period from June until October 1998 and were evenly distributed. Provisioning occurred before observations, and once during observations. Data were collected in two conditions: OC (156 h) and EK (78 h). During OC, all individuals were present in the group. During EK, three adult males were simultaneously removed (Supplementary Methods) for the day. OC observations were collected only on days during the twenty-week period when no manipulations to the group occurred. This ‘repeated removal’ design allowed us to control for fluctuations resulting from variation in environmental variables, such as temperature and human activity. Mean temperature was very similar in both conditions (OC, 87.9° F; EK, 89.6° F). On EK days, the group was observed for eight of ten removal hours. Observations began two hours after removal to ensure that stress induced by the benign removal procedure subsided, and did not account for observed changes to networks.

The males were partially removed (limited physical, visual, vocal access to group) on randomly chosen days every two weeks (Supplementary Methods). Removal was temporary (10 h each time) so we assessed whether social networks restructure over short timescales. The brief, partial removal made it possible to isolate effects of policing by providing insurance that observed changes to social networks did not result from an increase in competition over rank vacancies²⁶. As a precaution we evaluated elsewhere whether knockout caused social organization to reconfigure by inducing instability in the dominance hierarchy. We found no support for this hypothesis². We evaluated whether there was redundancy in the system, in that the absence of policers stimulated an increase in policing by other individuals. This was not the case². In Supplementary Data we report results of a control analysis in which a low-ranking female was removed to evaluate whether removal of any individual would negatively affect network robustness. This hypothesis was not supported.

Policers. We evaluated whether changes to social networks result from perturbing affiliation functions performed by policers in addition to their conflict-management functions. The policers were among the strongly connected nodes in three of four social networks. However, their positions in the degree distributions, which (except for play network) were normal and not marked by high variance, suggest that they were not unique. Correspondingly, they did not receive a disproportionate frequency of grooming, as they did status signals (Supplementary Data). Nor did they play ‘broker’²⁷ roles in the social networks—they were not important links connecting relatively isolated clusters of individuals. There was no Pearson correlation between node betweenness²⁸ and node SBT in degree for grooming ($P = 0.88$), contact-sitting ($P = 0.29$) or proximity ($P = 0.31$). These facts increase the likelihood that only conflict-management functionality was disrupted by removal. We note that the objective of the above analyses is to assess the likelihood that policers performed special affiliation functions in addition to conflict-management functions, not to evaluate their direct, structural contributions to the networks, which are controlled for through the three comparisons. The four networks were treated as binary undirected (symmetrical) graphs.

Data sampling methods. Instantaneous scan sampling²⁹ occurred every 15 min for ‘state’ behaviours (grooming, contact-sitting, social proximity and play). All data were collected using a digital stopwatch and voice recorder. 494 OC scans and 235 EK scans were collected. We randomly sampled scans in the OC condition until we had the same number of scans in both conditions (235). F.B.M.d.W. trained the observer (J.C.F.). α (level of significance) was set to 0.05 for repeated measures analyses.

Operational definitions of behaviours. The ‘state’ behaviours are defined as follows: grooming means passing hands or teeth through hair of another individual or plucking the hair with hands or teeth for at least five seconds. Contact-sitting means two or more individuals sitting in contact for at least 5 s. Proximity means that two or more individuals sit within arm’s reach for at least 5 s. Social play is wrestling, hitting, pinching, slapping and chasing, characterized by relaxed muscle movements and involving two or more participants.

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- Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. *Niche Construction: The Neglected Process in Evolution* (Princeton Univ. Press, Princeton, New Jersey, 2003).
- Flack, J. C., Krakauer, D. C. & de Waal, F. B. M. Robustness mechanisms in primate societies: A perturbation study. *Proc. R. Soc. Lond. B* **272**, 1091–1099 (2005).
- Flack, J. C., de Waal, F. B. M. & Krakauer, D. C. Social structure, robustness, and policing cost in a cognitively sophisticated species. *Am. Nat.* **165**, E126–E139 (2005).
- Frank, S. Repression of competition and the evolution of cooperation. *Evolution* **57**, 693–705 (2003).
- Boehm, C. in *Primate Behavior and Sociobiology* (eds Chiarelli, A. B. & Corruccini, R. S.) 161–182 (Springer, New York, 1981).
- Silk, J., Alberts, S. C. & Altmann, J. Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234 (2003).
- Watts, D. J. *Small Worlds: The Dynamics of Networks Between Order and Randomness* 199–222 (Princeton Univ. Press, Princeton, New Jersey, 1999).
- Whiten, A., Horner, V. & de Waal, F. B. M. Conformity to cultural norms of tool use in chimpanzees. *Nature* **437**, 737–740 (2005).
- Hutchinson, G. E. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22**, 415–427 (1957).
- de Waal, F. B. M. Primates—A natural heritage of conflict resolution. *Science* **289**, 586–590 (2000).
- Krakauer, D. C. Genetic redundancy. In *Encyclopedia of the Human Genome* Vol. 2, 892–897 (Nature Publishing Group/Wiley, London, 2003).
- Albert, R., Jeong, H. & Barabasi, A. L. Error and attack tolerance in complex networks. *Nature* **406**, 378 (2000).
- de Waal, F. B. M. & Luttrell, L. The formal hierarchy of rhesus monkeys: An investigation of the bared-teeth display. *Am. J. Primatol.* **9**, 73–85 (1985).
- Flack, J. C. & de Waal, F. B. M. in *Macaque Societies: A Model for the Study of Social Organization* (eds Thierry, B., Singh, M. & Kaumanns, W.) 157–181 (Cambridge Univ. Press, Cambridge, UK, 2004).
- Jeong, H., Mason, H. P., Barabasi, A. L. & Oltvai, Z. N. Lethality and centrality in protein networks. *Nature* **411**, 41–42 (2001).
- Keppel, G. *Design and Analysis: A Researcher’s Handbook* 329–415 (Prentice Hall, New Jersey, 1991).
- Noe, R. & Hammerstein, P. Biological markets. *Trends Ecol. Evol.* **10**, 336–339 (1995).
- Wasserman, S. & Faust, K. *Social Network Analysis* 107–108 (Cambridge Univ. Press, Cambridge, 1994).
- de Waal, F. B. M. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Anim. Behav.* **60**, 253–261 (2000).
- de Waal, F. B. M. & Luttrell, L. Mechanisms of social reciprocity in three primate species: symmetrical relationships characteristics or cognition? *Ethol. Sociobiol.* **9**, 101–118 (1988).
- Newman, M. E. J. Mixing patterns in networks. *Phys. Rev. E* **67**, 026126 (2003).
- Trivers, R. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57 (1971).
- Watts, D. J. & Strogatz, S. H. Collective dynamics of small-world networks. *Nature* **393**, 1302–1305 (1998).
- Caldecott, J. O. *An Ecological and Behavioral Study of the Pigtailed Macaque* (*Contributions to Primatology*, S. Karger, Basel, 1986).
- Thierry, B. in *Natural Conflict Resolution* (eds Aureli, F. & de Waal, F. B. M.) 106–128 (Univ. California, Berkeley, 2000).
- de Waal, F. B. M. The organization of agonistic social relationships within two captive groups of Java-monkeys (*Macaca fascicularis*). *Z. Tierpsychol.* **44**, 225–282 (1977).
- Lusseau, D. & Newman, M. Identifying the role that individual animals play in their social network. *Proc. R. Soc. Lond. B* **271**, S477–S481 (2004).
- Freeman, L. C. A set of measures of centrality based upon betweenness. *Sociometry* **40**, 35–41 (1977).
- Altmann, S. Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–267 (1974).

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