Knockouts of high-ranking males have limited impact on baboon social networks

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Abstract Social network structures can crucially impact complex social processes such as collective behaviour or the transmission of information and diseases. However, currently it is poorly understood how social networks change over time. Previous studies on primates suggest that 'knockouts' (due to death or dispersal) of high-ranking individuals might be important drivers for structural changes in animal social networks. Here we test this hypothesis using long-term data on a natural population of baboons, examining the effects of 29 natural knockouts of alpha or beta males on adult female social networks. We investigated whether and how knockouts affected (1) changes in grooming and association rates among adult females, and (2) changes in mean degree and global clustering coefficient in these networks. The only significant effect that we found was a decrease in mean degree in grooming networks in the first month after knockouts, but this decrease was rather small, and grooming networks rebounded to baseline levels by the second month after knockouts. Taken together our results indicate that the removal of high-ranking males has only limited or no lasting effects on social networks of adult female baboons. This finding calls into question the hypothesis that the removal of high-ranking individuals has a destabilizing effect on social network structures in social animals [*Current Zoology* 61 (1): 107–113, 2015].

Keywords Social network analysis, Social network dynamics, Knockouts, Baboons

Social network structures can crucially impact complex social processes such as collective behaviour or the transmission of information and diseases (Croft et al., 2008; Krause et al., 2009, Sueur et al., 2011; Wey et al., 2008; Whitehead, 2008). However, currently it is only poorly understood how social networks change over time and what determines the stability of social networks (Blonder et al., 2012; Pinter-Wollmanet al., in press). Studies by Flack et al. (2006) and Barrett et al. (2012) found that the removal of high-ranking individuals in primate societies was associated with changes in social network structures. Such 'knockouts', which naturally occur due to death and dispersal, therefore might be important drivers for structural changes in animal social networks.

The study of Flack et al. (2006) focussed on identifying whether a specific conflict intervention behaviour referred to as 'policing' affected the stability of social networks. For that purpose Flack et al. temporarily removed high-ranking males in a captive group of pigtailed macaques *Macaca nemestrina* and reported that these knockouts triggered changes in observed social network structures in a very short timeframe – 10 hours – after the knockouts. The study did not investigate whether such changes would have persisted on a longer timescale, and Flack et al. (2005) emphasized the need for such investigations to test whether knockouts of high-ranking individuals are important drivers of changes in social networks in pigtailed macaques and potentially other animals.

The study of Barrett et al. (2012) focussed on the question of whether a knockout-related disturbance in the dominance network could trigger compensatory changes in grooming or association networks. For that purpose Barrett et al. (2012) investigated two naturally occurring knockouts of wild adult female chacma baboons *Papio ursinus* (which were assumed to not engage in policing behaviour). In contrast to Flack and colleagues, Barrett and colleagues investigated potential changes in social networks on a timescale of months instead of hours. Their study showed that the death of the high ranking female was associated with an increase in weighted clustering coefficients of the association network during the 6 month period following the death. This result is partially consistent with results obtained by Flack et al. (2006), in that it suggests that removals

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of specific individuals can have a generally destabilizing effect on network structures.

In our study we aimed to perform a more detailed investigation of the hypothesis that the types of knockout-related changes in social network structures that were observed by Flack et al. (2006) are important drivers of change in primate social networks. To test this hypothesis we focussed on four main predictions. First, the basic effects observed by Flack et al. should occur for 'natural knockouts,' which can occur over the course of time because of deaths (from predation, conspecific conflict, or illness), and from male dispersal. Second, these effects of knockouts of high ranking males should occur across a large number of such knockouts; this prediction, that high-ranking individuals have a consistently destabilizing effect on social networks, is a natural conclusion to draw from the studies of Flack et al. (2006) and Barret et al. (2012). Third, the effects should persist for reasonably long time periods (on the order of months), because perturbations that last hours are unlikely to have strong functional consequences for the animals.

To test these predictions we used data on a well-studied population of baboons *Papio cynocephalus* in the Amboseli basin of southern Kenya (Alberts and Altmann, 2012) to examine the effects of the dispersals or deaths of high ranking males on female social networks over a period of months. Such an effect might be expected based on the study of Flack et al., because baboons are a cercopithecine primate with a behavioural repertoire similar to the macaques studied by Flack et al. To our knowledge it has not been formally investigated whether baboons engage in 'policing' behaviour (i.e., interventions in disputes that are impartial and do not favor one actor over the other). Alternatively, male knockouts might impact social relationships among females via competition among females for access to males (Cheney et al., 2012). Specifically, such competition might increase when knockouts of high-ranking males occur because females preferentially form affiliative relationships with high ranking males (Nguyen et al., 2009). In the case of knockout-related losses of such relationships, females may seek to form relationships with other males, which could trigger increased aggression among females and lead to changes in grooming and association networks.

1 Materials and Methods

We conducted social network analyses using data collected between 1984 and 2011 by the Amboseli baboon research project on five social groups of baboons (Alberts et al., 2005). A natural knockout was considered to have occurred when a given alpha or beta male was present in the group for at least three months prior to his disappearance, and then he disappeared permanently from the group. We identified 10 alpha male knockouts and 19 beta male knockouts (Appendix); 16 of the 29 knockout individuals dispersed, 2 died, and for 11 it is unknown whether they dispersed or died. In four cases of beta male knockouts the knockout male was natal to the social group, but for alpha male knockouts all of the knockout males were non-natal.

To assess knockout-related changes in social network structures we used grooming and association data collected within 30 days before and 90 days after each knockout; data after the knockout were divided into three 30-day time periods. Each of the 30-day periods before knockouts was treated as a baseline condition, and these baselines were compared to each of the three 30-day time periods after knockouts. Data on grooming between all possible pairs of adult females within each group were collected *ad libitum* and during 10-minute focal samples (Altmann, 1974); data on association (time spent in proximity) between pairs of adult females were collected only during focal samples. Specifically, focal samples involved the collection of 'point' data every minute during the sample, as well as 'all occurrences' data on grooming. At each 'point' the observer recorded the focal's activity and the identity of the nearest animal within five meters.

We constructed relationship networks of two kinds. Grooming networks were constructed based on data from focal and ad libitum sampling, which were used to determine the number of grooming events between the members of each dyad within a given time frame. Association networks were constructed based on nearest neighbour data collected during focal sampling. To avoid potential problems related to pseudo-replication of data within 10-minute focal samples, only the first point sample of each focal sample was used to determine the frequency of association between two individuals in a given time frame.

To test for changes in social behaviours, we first investigated potential changes in grooming and association rates similar to the analysis conducted by Flack et al. (2005). For each 30-day period, grooming rates were calculated as the mean number of grooming events per individual per observation hour, and association rates for each time interval were calculated as the mean number of associations per individual per focal sample.

Wilcoxon signed rank tests were used to test whether similar changes in grooming and association rates occurred across all observed knockouts.

Similar to the analysis conducted by Flack et al. (2006), we then tested for changes in mean degree and global clustering coefficients. We did not perform the same statistical analyses as Flack et al., because of differences in our study design. Flack and colleagues gathered data on short-term knockouts of a single set of individuals that were repeatedly performed in an experimental context. In contrast, our data set consists of a set of unique natural knockout events, each of which was a singular event. In our analysis we also aimed to control for the fact that observation times and rates of grooming and association were not constant across all considered 30-day periods of a knockout. For this purpose we used a randomization procedure that generates expectations of how differences in observation time or interaction rates affect network measures (in absence of any structural changes in social networks). The expected and observed differences in network measures for each knockout were then used to test whether similar changes in social networks occurred across all observed knockouts.

For a set of two networks that consist of the same individuals, the randomization procedure first generated a distribution of the expected changes in a network measure. In the execution of the test, for a single randomization, observations of single grooming events were randomized between the two sets of observed grooming or association events, o_x and o_y, at times x and y, while keeping the total number of observations in each set constant for each time period. This procedure is based on the assumption that the variation in interaction frequencies among individuals are identical in both observation periods, but that the absolute number of interactions might differ as a result of changes in observation time or grooming rate (which would result in different total numbers of observations at time y relative to time x). In all analyses we generated null distributions based on 100,000 randomizations and we used the mean of this distribution to quantify the expected change in a network measure. Wilcoxon signed rank tests were used to test whether, across all knockouts, the observed changes in network measures differed from the expected changes.

In addition, we repeated the analyses separately for alpha and beta male knockouts (see Appendix). The datasets supporting this article are available from the Dryad Digital Repository: http:// doi:10.5061/dryad.gp272.

2 Results

We found no support for the idea that knockouts of alpha or beta males resulted in changes in total grooming or association rates of adult females. Specifically, we did not find any significant effects on mean adult female grooming rates or mean association rates in the three months after knockouts (grooming rates shown in Fig. 1A, Wilcoxon signed rank tests: first month, V = 214, P = 0.949; second month, V = 219, P = 0.983; third month, V = 202, P = 0.991; association rates shown in Fig. 1B: first month, V = 191, P = 0.793; second month, V = 243, P = 0.374; third month, V = 240, P = 0.412).

We found limited support for the idea that knockouts of alpha or beta males resulted in changes in social networks. Specifically, mean degree in the grooming networks significantly decreased in the first month after knockouts (Fig. 1C, Wilcoxon signed rank test: first month, V = 113, P = 0.042); on average, adult females had slightly fewer grooming partners in the first month after a knockout than they did in the month prior to a knockout. This effect did not persist past the first month after the knockout: mean grooming degree returned to baseline levels in the second and third months after knockouts (Fig. 1C, Wilcoxon signed rank tests: second month, V = 175, P = 0.746; third month, V = 139, P = 0.361). Mean degree in the association networks experienced no significant changes as a result of knockouts (Fig. 1D, Wilcoxon signed rank tests: first month, V = 261, P = 0.358; second month, V = 269, P = 0.056; third month, V = 188, P = 0.990). Knockouts had no significant effects on global clustering coefficient in grooming networks. That is, network ties were not significantly more clustered after knockouts than before (Fig. 1E, Wilcoxon signed rank tests: first month, V = 150, P = 0.361; second month, V = 263, P = 0.077; third month, V = 126, P = 0.509). Similarly, knockouts had no significant effects on global clustering coefficient in association networks (Fig. 1F, Wilcoxon signed rank tests: first month, V = 162, P = 0.356; second month, V = 210, P = 0.628; third month, V = 112, P = 0.179).

3 Discussion

Our results provide at most limited support for the idea that knockouts of high-ranking males are important drivers of changes in social network among female baboons. We observed a decrease in mean degree in grooming networks after knockouts, which is consistent with the results of Flack et al. (2006). However, this

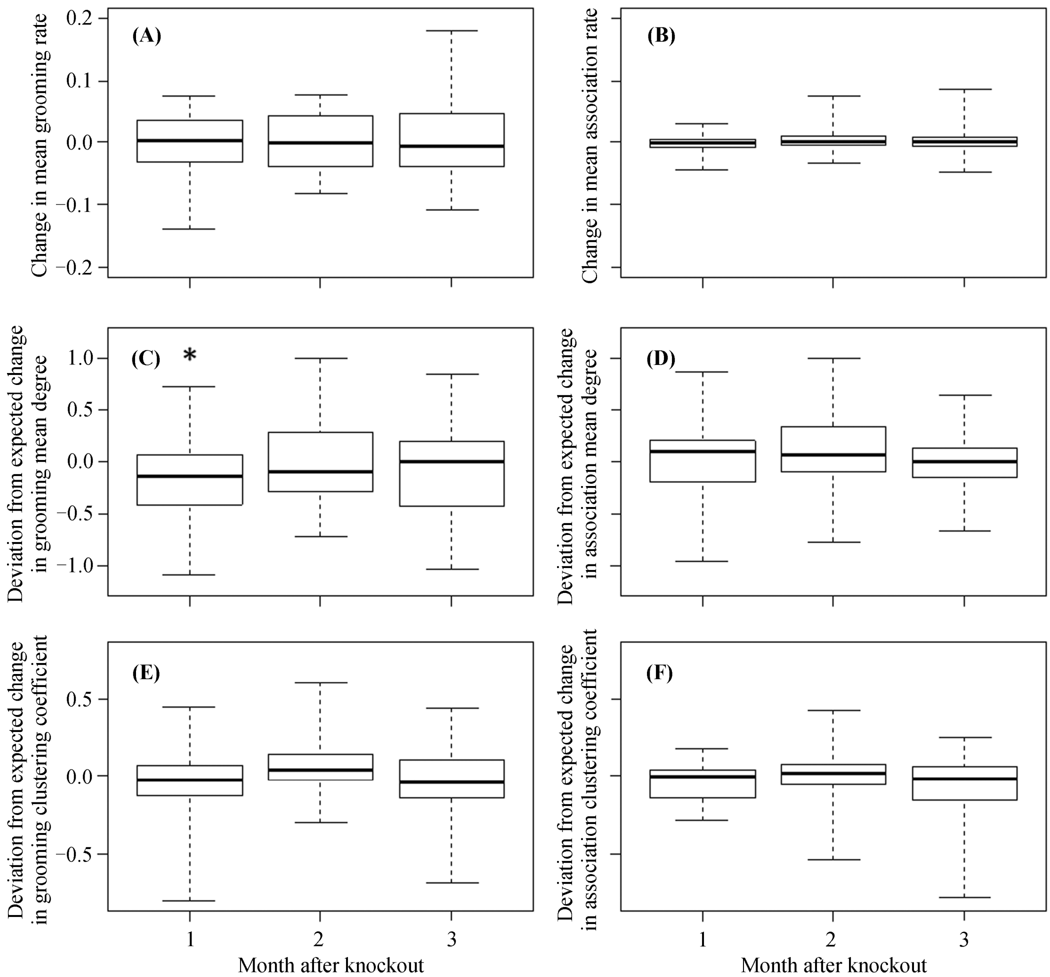

Fig. 1 Knockouts of alpha and beta males had small or no effects on adult female baboon grooming and association dynamics
Graphs A, C, and E show effects on grooming: (**A**) mean grooming rate, (**C**) network mean degree, and (**E**) global clustering coefficient. Only mean grooming degree in the first month after knockouts showed a significant decrease in a Wilcoxon test (C). Graphs B, D, and F show effects on association: (**B**) mean association rate, (**D**) network mean degree, and (**F**) global clustering coefficient. Box plots indicate maximum, 75% percentile, median, 25% percentile, and minimum of recorded values.

observed decrease in grooming mean degree was rather small, and grooming networks rebounded to baseline levels by the second month after knockouts (Fig. 1). In contrast to the results of Flack et al. (2005, 2006) we did not find significant changes in grooming and association rates or in the global clustering coefficient of association networks.

One interpretation of this result is that when high-ranking males are removed from a population, any resulting changes in social dynamics tend to be relatively short-lived, perhaps on the scale of hours or days rather than months. In other words, in natural social systems, social networks are reasonably well-buffered against the removal of any particular individual. Thus, it is possible that social networks of baboons were disrupted in a similar manner to the networks of macaques as observed by Flack et al. (2006) but that these changes were restricted to a short timeframe immediately after the knockouts. Since we did not investigate whether ‘policing’ exists in baboons and we were not able to investigate very short-term impacts of knockouts on social networks, our study does not allow us to draw any conclusion regarding the potential impact of ‘policing’ in baboon societies.

Several other reasons might explain why we failed to detect any persistent social network changes across knockouts. For instance, we investigated only knockouts of single individuals instead of simultaneous knockouts of the three highest ranking males; knocking out a whole age-sex group, or a large fraction of one (as in Flack et al.’s study (2006)), might indeed result in dramatic changes in social networks. Lack of policing is one possible cause of such a dramatic perturbation, but in general natural social networks will experience such perturbations relatively rarely. A second consideration is that knockout effects might be highly specific to the context in which the knockout occurs. Such context specific effects could be related to additional attributes of the knockout males other than dominance rank. For instance, it may be that the effects of knockouts depend on whether the departing animal died or dispersed. The limited number of observed alpha and beta male knockouts does not allow any more detailed analyses at the moment. Nevertheless, our results do not support the idea that knockouts of high-ranking males in wild baboons consistently have a long-term destabilizing effect on female social dynamics or, consequently, on female fitness. More generally, our findings call into question the idea that high-ranking individuals generally stabilize social network structures in social animals.

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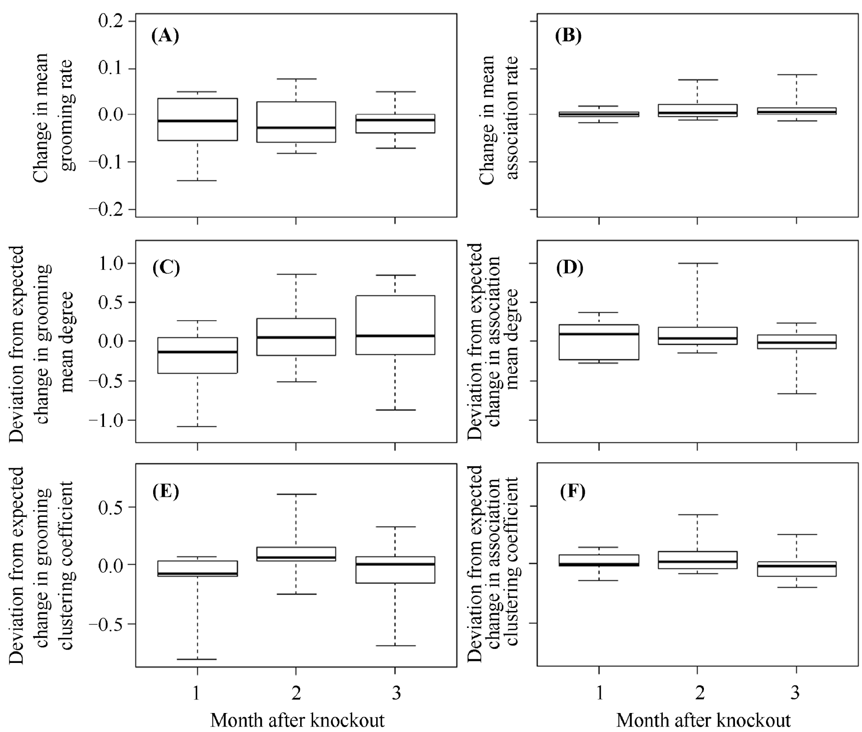
Appendix: Summary of analyzed knockouts and additional analyses

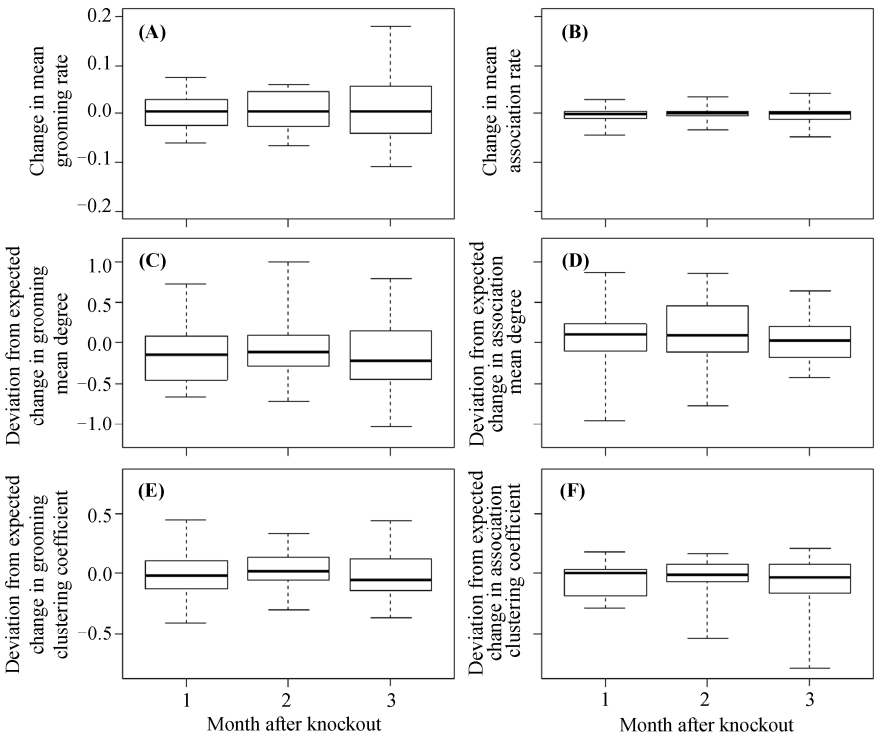
Knockout ID	Date	Group ID	Dominance rank at time of knockout	Type of dispersal	Age in years at time of knockout
28	12-Feb-1984	1	2	unknown	7.8
29	21-Oct-1984	2	2	dispersal	8.1
26	19-Apr-1986	1	1	unknown	9.0
27	6-Jun-1986	1	2	dispersal	8.5
25	31-Oct-1987	2	2	unknown	8.1
24	2-Nov-1988	2	1	dispersal	9.3
23	26-Jan-1993	2	1	dispersal	10.2
22	22-Jul-1995	2.2	2	unknown	8.2
21	6-Mar-1996	2.1	2	dispersal	9.4
20	17-Nov-1997	1.2	1	unknown	9.3
19	9-Jan-2000	2.2	2	dispersal	10.1
17	20-Apr-2000	1.22	2	dispersal	13.5
18	23-Aug-2000	1.22	1	unknown	8.2
16	2-Oct-2000	1.21	2	unknown	14.0
15	16-May-2001	1.21	2	unknown	6.0
14	5-Jan-2002	1.21	2	dispersal	12.2
12	8-May-2004	1.21	2	death	8.3
13	13-Oct-2004	1.21	2	dispersal	13.6
11	13-Aug-2005	2.1	1	unknown	10.5
10	5-Dec-2005	2.1	1	dispersal	8.0
8	13-Mar-2006	1.1	2	unknown	7.6
9	22-May-2006	2.2	2	dispersal	12.6
7	20-Apr-2008	2.1	2	dispersal	10.2
6	4-Jun-2008	1.21	2	dispersal	11.1
4	9-Apr-2009	1.21	1	unknown	9.6
5	23-Sep-2009	1.21	1	death	10.3
3	30-Jul-2010	1.1	1	dispersal	11.4
2	6-Aug-2010	1.21	2	dispersal	8.5
1	4-Mar-2011	1.21	2	dispersal	9.8

We repeated the analysis described in the main text separately for all knockouts of alpha male and all knockouts of beta males. The results of these analyses (Supplementary Fig. 1, 2) are very similar to results reported in the main text, indicating that alpha and beta males did not have different effects on grooming and association rates. However, with the reduced statistical power associated with the smaller number of data points in each analysis, we found no significant effect of knockouts.



Supplementary Fig. 1 Knockouts of alpha males alone revealed no significant effects of alpha male knockouts on adult female baboon grooming and association dynamics

Graphs A, C, and E show effects on grooming: (A) mean grooming rate, (C) network mean degree, and (E) global clustering coefficient. Graphs B, D, and F show effects on association: (B) mean association rate, (D) network mean degree, and (F) global clustering coefficient. Box plots indicate maximum, 75% percentile, median, 25% percentile, and minimum of recorded values.



Supplementary Fig. 2 Knockouts of beta males alone revealed no significant effects of beta male knockouts on adult female baboon grooming and association dynamics

Graphs A, C, and E show effects on grooming: (A) mean grooming rate, (C) network mean degree, and (E) global clustering coefficient. Graphs B, D, and F show effects on association: (B) mean association rate, (D) network mean degree, and (F) global clustering coefficient. Box plots indicate maximum, 75% percentile, median, 25% percentile, and minimum of recorded values.