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Robustness mechanisms in primate societies: a perturbation study

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Conflict management mechanisms have a direct, critical effect on system robustness because they mitigate conflict intensity and help repair damaged relationships. However, robustness mechanisms can also have indirect effects on system integrity by facilitating interactions among components. We explore the indirect role that conflict management mechanisms play in the maintenance of social system robustness, using a perturbation technique to 'knockout' components responsible for effective conflict management. We explore the effects of knockout on pigtailed macaque (*Macaca nemestrina*) social organization, using a captive group of 84 individuals. This system is ideal in addressing this question because there is heterogeneity in performance of conflict management. Consequently, conflict managers can be easily removed without disrupting other control structures. We find that powerful conflict managers are essential in maintaining social order for the benefit of all members of society. We show that knockout of components responsible for conflict management results in system destabilization by significantly increasing mean levels of conflict and aggression, decreasing socio-positive interaction and decreasing the operation of repair mechanisms.

Keywords: robustness; conflict management; policing; organization; primates; evolution

1. INTRODUCTION

The origin and maintenance of complex forms of sociality in large groups of unrelated individuals remains one of the outstanding problems in biology. Perhaps the single most important question related to sociality is how systems remain robust despite changing components that are subject to development and senescence and have only partially overlapping interests. In other words, what accounts for the persistence of complex organizational 'phenotypes'? Conflict management mechanisms are critical (Leigh 1999) to system robustness in that they serve to mitigate the negative effects of conflicts and restore damaged relationships (Boehm 1981; Ehardt & Bernstein 1992; Clutton-Brock & Parker 1995; Aureli & de Waal 2000; de Waal 2002). Apart from these immediate effects, little is known about the indirect role that conflict management mechanisms play in the maintenance of social order. Here, we use a perturbation technique to investigate whether components responsible for conflict control also indirectly affect system parameters, such as general levels of conflict, socio-positive interaction and the operation of repair mechanisms, which are essential in facilitating cooperation and cohesion. Particularly interesting is the possibility that a small number of conflict management components influence system robustness by facilitating socio-positive interactions that are, at best, indirectly related to conflict, in addition to mitigating the negative consequences resulting directly from conflict.

Investigating the indirect effects of robustness mechanisms on system integrity is methodologically challenging because control structures are often distributed or hierarchical, making focused removal of conflict management mechanisms impossible. This is a particularly difficult problem in animal and human societies, where, in addition to distributed control, individuals often have multiple roles. However, in some genetic and animal systems, robustness mechanisms are centralized and the set of component functions can be reasonably well documented. If the components responsible for conflict management can be identified, they can be disabled. This technique, often called 'knockout', enables researchers to infer the indirect effects of the mechanisms on the system by asking how the system changes when the mechanism is not operational. We borrow the 'knockout' concept from developmental genetics. Genetic knockout studies involve disabling genes assumed to serve a particular function or produce a particular phenotype. If the knockout impairs functionality or changes the phenotype, this change is attributed to the gene or gene set that was silenced. If there is no scoreable effect, this is taken as evidence of functional redundancy in the system that becomes apparent only when the primary mechanism is no longer operational (e.g. Krakauer (2003) for a review). In animal social systems, the same logic for using knockout studies applies: a social mechanism shown to have a particular local function can be disabled to determine its importance at the social system level.

Although centralized conflict management is rare in animal social systems, a few species are suited to behavioural knockout studies. For example, this method has been used by social insect researchers to study the effects of queens on aggression levels among female workers and colony productivity (West-Eberhard 1986). Little is known about the effects of conflict management components in cognitively sophisticated taxa, such as

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primates, in which complex triadic interactions (involving multiple individuals) among components are common. Preliminary results from early primate studies on the effects of animal removals on levels of aggression suggest that, in some species, removal of powerful individuals causes levels of aggression to increase (Tokuda & Jensen 1968; Sackett *et al.* 1975; Dazey *et al.* 1977; Oswald & Erwin 1977). However, these studies were not adequately controlled, only changes to aggression levels were investigated, and the function of the individuals chosen for removal was not studied. Furthermore, in other primate species, the conflict management role of so-called powerful individuals is questionable, indicating that there might be variation across populations in the importance of powerful individuals to system robustness (e.g. de Waal 1977). From a methodological standpoint, finding an appropriate species is therefore critical. A species suited to behavioural knockout is the pigtailed macaque (*Macaca nemestrina*), in which (easily removable) disproportionately powerful individuals perform the vast majority of effective conflict management by intervening in the disputes of group members (Flack *et al.* 2005).

Knockout of conflict management components from pigtailed macaque groups could have one of four effects. It could result in no change to system robustness because conflict managers affect only the outcome of conflicts in which they directly intervene, but not general levels of aggression or affiliation. As in genetic knockout studies, knockout could result in no change because of redundant functionality in the system that allows the system to compensate for removal of conflict management components. Knockout could cause the system to reconfigure into a neighbouring system in which other conflict management strategies are used (see §2). Knockout could cause the system to destabilize by leading to an increase in general levels of aggression and a decrease in socio-positive interaction. Through experimental design and statistical analyses, we control for the possibility that knockout causes the system to reconfigure or destabilize by inducing instability in the dominance hierarchy (see §2).

2. METHODS

(a) *Study species*

Pigtailed macaques are indigenous to southeast Asia. This species is reported to live in multimale–multifemale societies characterized by female matrilines and male group transfer upon onset of puberty (Fooden 1980; Fleagle 1988). Pigtailed macaques breed all year long; females develop swellings when in oestrus. In captivity, powerful individuals use interventions to effectively reduce the intensity of and terminate conflicts of group members (Flack *et al.* 2005). Effective conflict managers use low-intensity aggression or threats when intervening, often intervene impartially, and sometimes terminate conflicts through mere approaches. Detailed data on intervention of wild pigtailed macaques are unavailable. The social systems of captive macaque species are relatively well studied (e.g. Thierry 2000). Given current understanding of how social system variables are related in the macaque genus, we hypothesized that if knockout caused the pigtail system to reconfigure, such that a new conflict management strategy was adopted, reconfiguration would be towards the rhesus macaque (*Macaca mulatta*) social system, a close social neighbour (Thierry 2000). Rhesus society is characterized by higher levels of aggression, lower levels of affiliation and interventions in which either the recipient of aggression is targeted or kin are supported. If knockout causes the pigtailed system to become more rhesus like, we should observe increased aggression, decreased affiliation, and changes to the conflict management strategies and interventions variables (table 1). In contrast, if knockout causes the system to destabilize, we should observe increased aggression and decreased affiliation, but no changes to intervention and strategy variables.

(b) *Demography and housing of the study population*

Data were collected from a captive breeding group of pigtailed macaques at the Yerkes National Primate Research Center near Lawrenceville, Georgia. The group comprised 84 individuals, including four adult males and 25 adult females. All individuals, except five (one male, four females), were either natal to the group or had been in the group since formation in 1985. The group was housed in an indoor–outdoor facility that had a large outdoor compound, which was 125×65 ft.

(c) *Experimental design*

Observations occurred for up to 8 h each day between the hours of 11.00 and 20.00 from June until October 1998. Observation hours were evenly distributed over this period. Provisioning occurred before observations, and once per day during observations. The study had two conditions: CONTROL and KNOCKOUT (figure 1). We collected data for 156 CONTROL hours and 78 KNOCKOUT hours. During the CONTROL conditions, all individuals were present in the group. During the KNOCKOUT condition, three individuals (all males; see below) were simultaneously removed (see Electronic Appendix for removal procedure). Experimental removal of conflict managers was designed to emulate natural perturbations that occur when individuals succumb to disease or predation. The removals occurred on randomly chosen days once every two weeks during the 20-week study period. Control observations were collected only on days during the 20-week period when no manipulations to the group occurred. The advantage of this 'repeated' design is that it allowed us to control for fluctuations resulting from variation in environmental variables, such as temperature and human activity at the primate centre. We randomly chose removal days to prevent habituation to removal.

(d) *Choice of individuals for removal and data collection procedure*

We removed the alpha, beta and delta males (third among males but fourth-ranking overall), all of whom were fully grown. These males were introduced to the group in June 1996. Out of the removed males, two were aged approximately 13 years and one approximately 11 years. These three individuals and the alpha female were disproportionately responsible for effectively managing non-kin conflict but were not exceptional (in the tails of distributions with high variance) on other behavioural measures. Compared with the other 44 adults and sub-adults in the group, they performed the vast majority of effective conflict management interventions (mean of 34.5 compared with mean of 5.8), yet did so relatively infrequently ($<20\%$) compared with the total number of aggressive incidents (Flack *et al.* 2005). Using network analyses, we assessed the role that these

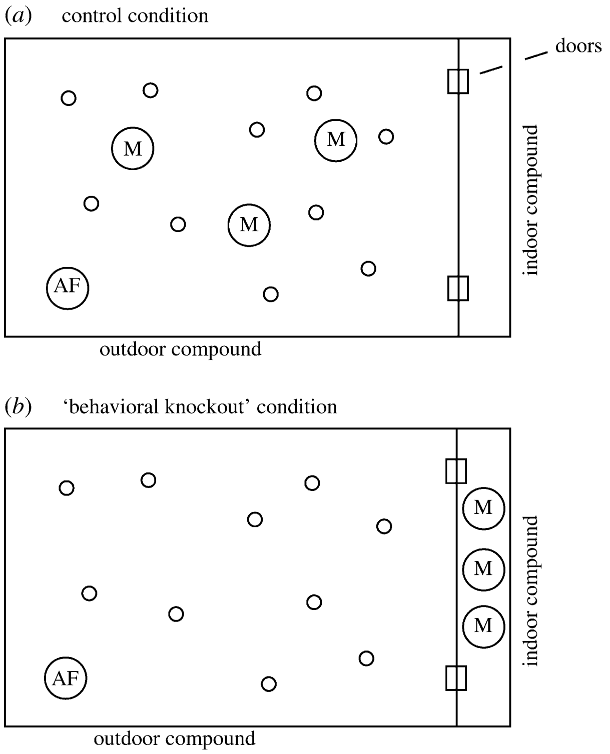

Figure 1. Schematic of (*a*) the CONTROL and (*b*) behavioural KNOCKOUT conditions. In the CONTROL condition, all 48 adults and sub-adults were present in the outdoor compound and visible to the observer. In the KNOCKOUT condition, three fully grown adult males (M), who were responsible for the large majority of effective conflict management, were confined to the indoor housing. These males had vocal and limited physical and visual contact with the group during KNOCKOUT. AF is the alpha female. She also performed conflict management but was not removed as doing so risked disrupting the female dominance hierarchy.

individuals played in other social domains and found that, except for their conflict management behaviour and the degree to which they were perceived by other group members as capable of using force successfully, they were not qualitatively different from other group members (Flack 2003). This increases the likelihood that their removal disrupted only the conflict management function since they did not appear to play any other important roles in the group. As a precaution, however, we evaluated whether the removals caused social instability by inducing changes in the dominance hierarchy (see next paragraph). Although the alpha female also performed effective conflict management, we elected not to remove her as doing so involved greater risk of disrupting the female dominance hierarchy (de Waal 1977) and confounding the results. In macaque species with strong matrilines, females alliances play an important role in dominance interactions (Thierry 2000).

The males were confined to their indoor housing for a period of 10 h, during which they had vocal and visual contact with the group but seriously constrained physical contact (see the Electronic Appendix). The brief, partial removal makes it unlikely that any observed changes to variables tested were owing to competition over rank vacancies, which might have been induced had the males been fully removed for longer periods (de Waal 1977). We assessed whether this was in fact the case by analysing changes to bidirectional aggression (when the individual receiving aggression responds with aggression) and changes to the frequency with which subordinate individuals initiated aggression. When individuals compete for dominance status, bidirectional aggression and subordinate-initiated aggression necessarily increase as subordinates challenge their dominant counterparts. Had the removals induced competition for rank vacancies because of disrupted alliances, bidirectional aggression should have increased during knockout, but did not (see §3 and table 1). Furthermore, if removal had induced instabilities in the dominance hierarchy, there should have been an increase in the knockout condition in the rate that subordinate individuals initiated aggression against dominants, which did not occur. Instead, subordinates initiated significantly less aggression against dominants during removal periods, indicating increased emphasis on hierarchy in the system when the males were not present (Wilcoxon-signed-rank test $(+30, -4, 11 \text{ ties}) = 4.28$, $p < 0.001$).

On knockout days, the group was observed for 8 h of the 10 h. Knockout observations began 2 h after removals to ensure that stress induced by the removal procedure had time to subside and did not account for any observed changes to variables. Conflict, intervention, and post-conflict data were collected using all-occurrence sampling (also called event-recording), in which sequential data on conflict-related behaviour were collected from event onset (Altmann 1974; Bakeman & Gottman 1997) continuously until the conflict was considered terminated. All-occurrence sampling was chosen over focal sampling (a) to maximize samples collected, thereby improving statistical power, and (b) because it allows for the entire conflict to be followed. Instantaneous scan sampling (Altmann 1974) occurred every 15 minutes for 'state' behaviours, including grooming, contact-sitting, play, and proximity data. Data were collected using a digital stopwatch and voice recorder. (See Electronic Appendix for data collection procedures, operational definitions of behaviour and animal removal procedure.)

During the final weeks of the study, the veterinarians permanently removed a very low-ranking adult female (LRF) owing to illness. She was absent for 41.5 out of 156 CONTROL hours, and 26 out of 78 KNOCKOUT hours. As discussed in §3, we analysed the effects of the LRF removal on the variables that significantly changed upon male removal, but because the LRF removal had no negative effect on system robustness, we pooled all CONTROL data to increase statistical power and minimize sampling error.

(e) *Analyses*

We assessed the effect of knockout on 32 social system variables using repeated measures. 'Repeated measures', which is also referred to as a within-subject design, is a statistical technique in which means for each individual are calculated for each dependent variable. The mean rate (or other measure) for each individual is then compared across conditions. The advantage of repeated measures is the control of individual differences. Further description of repeated measures techniques can be found in Keppel (1991) and Sokal & Rolf (1995). Non-parametric versions of repeated measures were used when violations of normality occurred and the variance could not be stabilized using a transform procedure (Sokal & Rolf 1995). Parametric tests were used if the distribution and residuals of the dependent variable did not significantly differ from normal according to the Kolmogorov–Smirnov one-sample test (Sokal & Rolf 1995). Statistical tests were conducted using SPSS, and the statistical computing environment, *R*. Alpha levels were

Table 1. Results of repeated measures on 32 social system variables grouped into 12 indicator categories and three broad areas. Results support destabilization hypothesis.
(*t-test instead of F test. Variables were compared across Control (C) and Knockout (K) conditions. In knockout condition, conflict management mechanism was disabled. Non-parametric tests were used when violations of normality occurred. We organized variables into three broad areas (left-most column) to test four hypotheses in order to infer the role—through knockout—of conflict management/policing in organizational robustness: (*a*) no effect of policing on organizational robustness—no change to any variables; (*b*) redundancy due to new individual performing policing function—no change to variables except increase in impartial interventions and increase in interventions terminating or reducing aggression; (*c*) knockout of policing results in organizational destabilization—increase in aggression levels and decrease in affiliation levels; and (*d*) knockout of policing causes reconfiguration to neighboring macaque (rhesus) system—increase in aggression, decrease in affiliation, and significant changes to strategy/intervention variables. For each indicator category (designated by bold lettering), one multivariate test was conducted. To control for experiment-wise error, the alpha level for each of the multivariate tests was adjusted for the number of categories within the area. For univariate-within-indicator-category tests, the alpha level was adjusted for the number of variables within the indicator category. See Electronic Appendix for operational definitions. Wilk's lambda, multivariate repeated measures statistic; F(d.f.), univariate repeated measures statistic, called F test; (d.f.), degrees of freedom; partial η^2, effect size; NA, not applicable to analysis; alpha, level of significance set for analysis based on corrections for multiple tests; p, p-value; sig, significant difference; no, no significant difference; trend, trend in direction predicted by destabilization hypothesis; notrd, no trend in predicted direction by destabilization hypothesis.)

			mean							
area	indicator categories variables	Wilk's lambda	C	K	F (d.f.)	p	partial η^2	α	sig.?	trend?
general levels of conflict and aggression	**mean rate aggression initiated**	0.72	n/a		8.25 (3,43)	<0.001	0.280	0.05/4=0.0125	sig	trend
	dyadic	n/a	0.13	0.17	5.54 (1,44)	0.02	0.110	0.05/3=0.0167	no	trend
	ln(intervention)	n/a	0.08	0.13	16.69 (1,44)	<0.001	0.270	0.05/3=0.0167	sig	trend
	redirection	Wilcoxon test (−22, +18, 5 ties)=0.27				0.98	n/a	0.05/3=0.0167	no	trend
	mean intensity aggression initiated	0.57	n/a		8.36 (3,33)	<0.001	0.430	0.05/4=0.0125	sig	trend
	dyadic	n/a	2.68	2.87	1.34 (1,35)	0.26	0.040	0.05/3=0.0167	no	trend
	intervention	n/a	3.13	3.57	13.21 (1,35)	0.001	0.270	0.05/3=0.0167	sig	trend
	redirection	n/a	2.47	3.08	8.95 (1,35)	0.005	0.200	0.05/3=0.0167	sig	trend
		Wilcoxon test (−26, +16, 3 ties)=2.53				0.01	n/a	0.05/4=0.0125	sig	trend
	mean proportion biting target of aggressive intervention	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a
	directional consistency index against recipient	n/a	0.39	0.48	$t(31)=1.53$*	0.18	n/a	0.05/2=0.025	no	trend
	ln(mean rate join interventions)	n/a	0.02	0.04	$t(44)=3.79$*	<0.001	n/a	0.05/2=0.025	sig	trend
conflict management strategies and intervention variables	**response to aggression**	0.99	n/a		0.03 (3,41)	0.93	0.002	0.05/5=0.01	no	n/a
	mean porportion bidirectional aggression given	n/a	0.28	0.29	0.70 (1,43)	0.79	0.020	0.05/3=0.0167	no	n/a
	mean proportion bidirectional+ B45al aggression received	n/a	0.24	0.24	0.02 (1,43)	0.89	<0.001	0.05/3=0.0167	no	n/a
	mean intensity of withdrawal response to aggression received	n/a	2.53	2.54	0.001 (1,43)	0.97	<0.001	0.05/3=0.0167	no	n/a
	mean proportion intervention type	0.9	n/a		1.11 (4,41)	0.36	0.1	0.05/5=0.01	no	n/a
	aggressive	n/a	0.50	0.51	0.01 (1,44)	0.92	<0.001	0.05/5=0.01	no	n/a
	affiliative	n/a	0.20	0.19	0.12 (1,44)	0.73	0.003	0.05/5=0.01	no	n/a

(*Continued.*)

Table 1 (*Continued.*)

area	indicator categories variables	Wilk's lambda	mean C	mean K	F (d.f.)	p	partial η^2	α	sig.?	trend?
	impartial	Wilcoxon test (−20, 8, 17 ties) = 1.86				0.06	n/a	0.05/5 = 0.01	no	n/a
	attend	n/a	0.17	0.18	0.16 (1,44)	0.70	0.004	0.05/5 = 0.01	no	n/a
	other	n/a	0.10	0.11	0.36 (1,44)	0.55	0.008	0.05/5 = 0.01	no	n/a
	mean proportion interventions effects	0.93	n/a		1.63 (2,43)	0.21	0.07	0.05/5 = 0.01	no	n/a
	exacerbate	n/a	0.27	0.27	0.008 (1,44)	0.93	< 0.001	0.05/3 = 0.0167	no	n/a
	reduce/terminate	n/a	0.28	0.24	2.63 (1,44)	0.11	0.06	0.05/3 = 0.0167	no	n/a
	no effect	n/a	0.45	0.49	2.02 (1,44)	0.16	0.04	0.05/3 = 0.0167	no	n/a
	mean proportion kin interventions	n/a	n/a		n/a	n/a	n/a	0.05/5 = 0.01	no	n/a
	favour kin	Wilcoxon test (−17, +12, 3 ties) = 1.55				0.12	n/a	0.05/2 = 0.025	no	n/a
	against kin	Wilcoxon test (−10, +6, 16 ties) = 0.98				0.33	n/a	0.05/2 = 0.025	no	n/a
	mean proportion support solicited	0.94	n/a		1.15 (2,38)	0.32	0.06	0.05/5 = 0.01	no	n/a
	receive requests	Wilcoxon test (−24, +21, 0 ties) = 0.68				0.50	n/a	0.05/3 = 0.0167	no	n/a
	make requests	n/a	0.08	0.07	0.81 (1,39)	0.37	0.02	0.05/3 = 0.0167	no	n/a
	provide support solicited	n/a	0.74	0.66	2.14 (1,39)	0.15	0.05	0.05/3 = 0.0167	no	n/a
general levels of socio-positive interaction	**post-conflict affiliation (PCA)**	0.59	n/a		9.70 (3,42)	< 0.001	0.41	0.05/3 = 0.0167	sig	trend
	mean proportion PCA	n/a	0.25	0.17	30.67 (1,44)	< 0.001	0.41	0.05/3 = 0.0167	sig	trend
	mean intensity PCA	n/a	3.39	3.48	0.81 (1,44)	0.37	0.02	0.05/3 = 0.0167	no	notrd
	mean proportion permanent PCA	n/a	0.89	0.89	< 0.01 (1,44)	0.99	< 0.001	0.05/3 = 0.0167	no	notrd
	mean rate active affiliation	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a
	groom-received	n/a	0.06	0.05	$t(44) = 2.99$*	0.005	n/a	0.05/2 = 0.025	sig	trend
	play	Wilcoxon test (−28, +18, 19 ties) = 2.46				0.014	n/a	0.05/2 = 0.025	sig	trend
	mean rate passive affiliation	0.84	n/a		3.96 (2,43)	0.026	0.16	0.05/3 = 0.0167	no	n/a
	proximity	n/a	0.27	0.29	7.99 (1,44)	0.007	0.15	0.05/2 = 0.025	sig	n/a
	contact sitting	n/a	0.16	0.17	0.81 (1,44)	0.37	0.02	0.05/2 = 0.025	no	n/a

Table 2. Results of removal of low-ranking female (LRF) on variables observed to change significantly during removal conflict managers (policers; see table 1).
(LRF performed no effective conflict management. LRF in: female was present in group but her data were removed from the data set (same procedure used for analyses of conflict manager removal, see text), all other individuals present. LRF out: female was not present in group, all other individuals present—note that while conflict manager removal was temporary and repeated, female removal was permanent. OPP, results significant but in opposite direction to predicted (see text) as should have been the case if LRF removal mimicked removal of conflict managers. These results suggest that removal of low-ranking individuals does not negatively affect organizational robustness. t, statistic; d.f., degrees of freedom; alpha, significance level required for analysis (after corrections for multiple tests); p, p-value.)

area	indicator categories	variable	mean LRF in	mean LRF out	t	d.f.	alpha	p	sig.?
general levels of conflict and aggression	mean rate aggression initiatied	intervention	Wilcoxon test (−30, +16, 0 ties) = 1.91				0.05/2 = 0.025	0.1	no
	target of aggressive intervention	mean rate join interventions	Wilcoxon test (−25, +16, 6 ties) = 1.48				0.05/2 = 0.025	0.15	no
	mean intensity aggression initiated	intervention	3.09	2.79	2.96	40	0.05/2 = 0.0025	0.01	yes—OPP
		redirection	2.39	2.45	0.39	28	0.05/2 = 0.025	0.70	no
	biting	mean rate biting	Wilcoxon test (−15, +27, 5 ties) = 1.44				0.05/3 = 0.0167	0.15	no
general levels of socio-positive interaction	post-conflict affiliation	mean proportion PCA	0.25	0.27	1.96	46	0.05	0.06	no
	mean rate affiliation	receive groom	0.71	0.65	0.61	46	0.05/2 = 0.025	0.55	no
		play	Wilcoxon test (−21, +20, 27 ties) = 2.1				0.05/2 = 0.025	0.84	no

adjusted from 0.05 to control for experimental error owing to multiple tests (see §3).

3. RESULTS

(a) *Analysis of removal of the primary conflict managers*

We used a multivariate repeated measures design to determine whether individual means of CONTROL and KNOCKOUT were equal, using data from all adults and sub-adults ($n = 45$), *except for the three males themselves*. We compared 32 variables ('indicators' in table 1). To simplify the analyses, we grouped the variables into three main areas (aggression, intervention strategy and socio-positive interaction) and 12 indicator categories, running a repeated measures test on the variables in each category. Choice of variables reflects effort to provide a complete picture of how the social system changes in response to knockout. These analyses are based on 2409 observed agonistic dyads and polyads gathered in the CONTROL condition, and 1324 agonistic dyads and polyads gathered in the KNOCKOUT condition. An agonistic dyad is a pair-wise interaction in which one individual aggresses or threatens another individual (see Electronic Appendix). One or several dyads can comprise a conflict. When a conflict involves multiple dyads, it is called a polyad. All conflicts are followed by a post-conflict period, during which post-conflict affiliation between conflict opponents and/or interveners can occur. We observed 1111 total conflicts in the CONTROL condition and 570 total conflicts in the KNOCKOUT condition. Grooming, contact-sitting, proximity, and play data were extracted from 494 scans (see §2d) in the CONTROL condition and 235 scans in the KNOCKOUT condition. Note that the sample size for all analyses is always based on the number of individuals used in the analysis and is denoted by n.

Table 1 shows multivariate repeated measures results. As predicted by the destabilization hypothesis, KNOCKOUT significantly increased levels of aggression, including mean (per individual) rate of aggression, intensity of aggression, rate of biting, and the mean proportion of joint interventions (when a second intervener joins a first intervener in attacking a conflict participant). It significantly decreased levels of socio-positive interaction, including mean rate of reconciliation and rates of active affiliation (play and grooming), and increased rates of passive affiliation (contact sitting and proximity). The decrease in reconciliation is important because reconciliation is thought to be a repair mechanism that restores relationships to baseline levels of affiliative interaction upon damage resulting from conflict (Aureli *et al*. 2002). The increase in joint aggression suggests that conflict spread more rapidly (higher infectivity) in the conflict managers' absence. Mean temperature during the CONTROL (87.9 F) and KNOCKOUT (89.6 F) conditions differed by 1.5 degrees, and thus is very unlikely to account for the observed changes.

(b) *Analysis of removal of a low-ranking individual*

We analysed the effects of removal of the LRF who performed no effective conflict management (Flack 2003) on variables shown in the previous analyses to be negatively affected by removal of conflict managers. Our goal was to determine whether removal of a random individual could also compromise system robustness. We used CONTROL condition data (when primary conflict managers were present) to compare data from the LRF removal period with data from the period when she was present, using all data except for the data from the female herself. Her removal did not mimic the effects of conflict manager removal, and did not negatively affect system robustness

Table 3. Summary of effects of disabling policing mechanism on organizational robustness. (Full results reported in table 1.) (To evaluate the role of policing in organizational robustness, we investigated how knocking-out, or disabling, the policing mechanism affects 32 social system variables evaluated using repeated measures at the individual level. The Knockout condition corresponds to temporary removal of three individuals who were disproportionately responsible for the majority of effective conflict management through policing interventions—impartial interventions that break up conflicts. Results indicate that knockout of policing causes social system destabilization (see table 1). We infer from these results that policing is important to maintaining relatively low levels of aggression, relatively high levels of affiliation and post-conflict repair, but has no effect on the strategies individuals use when intervening in conflicts. Policing, and conflict management more generally, appear to have both local effects on conflict outcome (Flack *et al.* 2005) and global, or systemic effects, on organizational robustness, in that they not only directly effect the outcome of conflicts that have already erupted, but also prevent conflicts from occurring in the first place, modulate the intensity of those that do occur even without direct intervention, indirectly facilitate socio-positive interactions among individuals in non-conflict contexts, and indirectly facilitate the operation of repair mechanisms to restore relationships to pre-conflict affiliation levels. The extent to which policing is important to organizational robustness is surprising considering that actual policing behavior occurs relatively rarely (Flack *et al.* 2005). This suggests that the simple presence of individuals responsible for conflict management can change the way group members are willing to interact with one another.)

	area		
	general levels of aggression	conflict management strategy and intervention variables	general levels of socio-positive interaction
observed changes to variables in each area	significantly increase	no change	significantly decrease

(table 2). The mean change for all variables, except one, was non-significant. The observed decrease in the mean intensity of aggression used during intervention that accompanied the female's removal remains unaccounted for, but could be due to fluctuations in the data resulting from the smaller sample size.

This last analysis suggests that the system is robust to perturbations in which low-status individuals are removed, but not to perturbations in which high-status conflict managers are removed. These results are supported by earlier studies investigating the effect of removing alpha males on levels of aggression, in which it was found that aggression increased only following removal of alpha males; removal of mid-ranking individuals had no effect (Dazey *et al.* 1977; Oswald & Erwin 1977).

4. DISCUSSION

Conflict management mechanisms are thought to be critical to the origins and robustness of sociality in systems composed of many unrelated individuals with only partly overlapping interests. This is because, in the absence of high relatedness, selfish behaviour limits behavioural division of labour and reduces group productivity (Michod 2000). However, little is known about the role that conflict management plays in social system robustness. We addressed this question in a captive pigtailed macaque society by using benign behavioural knockout methods, in which powerful, effective conflict managers were temporarily removed from the population, to investigate the effects of conflict management on social system robustness. Our results (summarized in table 3) suggest that in addition to terminating conflicts or reducing their intensity, conflict managers provide functional robustness, more generally, by preventing conflicts from occurring and spreading, and by facilitating active socio-positive interactions among group members. This creates the social environment necessary for the operation of conflict repair mechanisms, such as reconciliation, and therefore contributes to construction of a prosocial niche (Oldling-Smee *et al.* 2003).

To evaluate the effects of knockout on social system robustness, we tested several hypotheses. The data suggest that in the short term the social system did not reconfigure in response to knockout in that the conflict management strategies of individuals remained unchanged. It also appears that the system was not characterized by redundant functionality; other individuals did not increase their conflict management behaviour to compensate for the removal of the primary conflict managers. The data support the hypothesis that, in the short term, perturbations to conflict management cause the pigtailed macaque social system to destabilize (more conflict, less socio-positive interaction, less conflict repair). Although knockout is clearly costly in the short term, it is not clear whether the increased levels of aggression and decreased levels of affiliation would eventually result in reconfiguration, readjustment or population fission.

This study suggests that conflict management components are critical to robustness in pigtailed macaque society, and perhaps, more generally, in gregarious, multimale, multifemale societies composed of unrelated individuals. Elsewhere, we have shown that in macaques, conflict management strongly influences social network structure (Flack 2003). Taken together, the results of these studies suggest that conflict management, despite being a relatively infrequent behaviour (less than 20% of all fights received effective interventions) performed by a small subset of the group (3–4 individuals out of 84) in response to relatively rare events (conflicts occur at a rate of 0.9 h^{-1} per individual; Flack *et al.* 2005), influences large-scale social organization and facilitates levels of social cohesion and integration that might otherwise be impossible. Interestingly, in the pigtailed macaque system, effective conflict management requires power structures characterized by high variance, which emerge from status signalling interactions among individuals (Flack *et al.* 2005). This means that power structure, by making effective conflict management possible, influences social network structure and therefore feeds back down to the individual level to constrain individual behaviour. Pigtailed macaque social organization is not an epiphenomenon but a causal structure that both shapes, and is shaped by, individual interactions.

In this way the policing activities of a few key individuals confer benefits on all individuals in the group, and not just on the conflict participants with whom they interact. A single mechanism associated with a few individuals also highlights the vulnerability of the system to perturbation, as losing these individuals has systemic consequences. This rudimentary division of labour is comparable with results on scale-free network distributions in biological and engineered systems in which random perturbations tend to be benign (targeting unimportant nodes) whereas targeted perturbations are lethal (Albert *et al*. 2000). Similarly, in pigtailed macaques, knockout of conflict management functionality causes social network fragmentation, increases mean levels of aggression and decreases mean levels of affiliation, whereas knockout of individuals unimportant to conflict management has no negative effects on organizational structure (Flack 2003). This raises a question related to one frequently asked in genetic knockout studies: how can we ensure that robustness mechanisms at developmental time-scales are robust over evolutionary time-scales? For example, duplicate genes can confer short-term functional robustness on an organism following the loss of one gene copy, but the genome is not robust over generations, as the redundancy property is lost once only a single copy remains (Krakauer & Nowak 1999). Likewise, conflict management behaviour controls conflict over short time-scales, but once the police are lost over a longer time-scale, there will be a need for a means of reconstituting the policing role in the population. An interesting question for future studies is to consider the longer time-scale and assess the consequences of protracted perturbations on system reconfiguration.

The wide-ranging effects of conflict management components on social system robustness also have implications for transitions to new levels of individuality during the course of evolution (Maynard Smith & Szathmary 1995; Keller 1999; Michod 2000; Frank 2003). Although primate societies are by no means fully integrated 'individuals' at which higher levels of selection might operate, they are also not merely linear aggregates of individuals that come together for predator defence, mating opportunities or foraging. Rather, primate societies are complex organizations in which behavioural roles create opportunities for new modes of interaction, which in turn create further social opportunities. In other words, these species engage in social niche construction.

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