

Social Structure, Robustness, and Policing Cost in a Cognitively Sophisticated Species

Jessica C. Flack,^{1,2,*} Frans B. M. de Waal,^{2,3,†} and David C. Krakauer^{1,‡}

1. Santa Fe Institute, Santa Fe, New Mexico 87501;
2. Living Links, Yerkes National Primate Research Center, Emory University, Atlanta, Georgia 30322;
3. Psychology Department, Emory University, Atlanta, Georgia 30322

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ABSTRACT: Conflict management is one of the primary requirements for social complexity. Of the many forms of conflict management, one of the rarest and most interesting is third-party policing, or intervening impartially to control conflict. Third-party policing should be hard to evolve because policers personally pay a cost for intervening, while the benefits are diffused over the whole group. In this study we investigate the incidence and costs of policing in a primate society. We report quantitative evidence of non-kin policing in the nonhuman primate, the pigtailed macaque. We find that policing is effective at reducing the intensity of or terminating conflict when performed by the most powerful individuals. We define a measure, social power consensus, that predicts effective low-cost interventions by powerful individuals and ineffective, relatively costly interventions by low-power individuals. Finally, we develop a simple probabilistic model to explore whether the degree to which policing can effectively reduce the societal cost of conflict is dependent on variance in the distribution of power. Our data and simple model suggest that third-party policing effectiveness and cost are dependent on power structure and might emerge only in societies with high variance in power.

Keywords: robustness, evolution, policing, conflict intervention, primate, power.

Robustness is a fundamental property of all complex adaptive systems that persist through time despite perturbations and changing components. In evolving systems, there is the additional challenge associated with partially overlap-

ping interests, whereby individuals do not share all of the same objectives, yet they cooperate. An important robustness question in the study of animal societies is how conflict among unrelated individuals is managed (Alexander 1979; Reeve and Keller 1997; Leigh 1999). Of particular interest is whether third parties “police” (defined here as impartial monitoring and attempted control) conflicts among group members (Clutton-Brock and Parker 1995; Frank 2003). This is important because policing is assumed to be costly to the individuals performing the behavior (Frank 2003), and it remains puzzling why individuals would police in societies in which relatedness is low. Furthermore, third-party policing is interesting because it is impartial: third parties intervene in conflicts among group members without taking sides.

In the social insects where relatedness is high (Ratnieks 1988) or where worker reproduction is costly at the colony level (Foster et al. 1999), various forms of conflict control have been extensively documented (West-Eberhard 1986; Monnin and Ratnieks 2001). For example, in queenright honeybee (*Apis mellifera*) colonies, some workers can lay viable eggs and produce male drones. Although workers are more closely related to their own offspring than to offspring of the queen or other workers, they are more closely related to offspring of the queen than to offspring of other workers (Monnin and Ratnieks 2001). Consequently, it pays for them to police other workers by eating their eggs when they produce them. In social wasps (*Polistes canadensis*), queens are reported to police worker reproduction through aggression (West-Eberhard 1986).

In primates and many other large-brained, long-lived, highly social species, the evolution of policing is a more complicated issue than in the social insects. There are several reasons for this. First, despite the advantages of group living (predator detection, mutual defense, food finding, mating), individuals in primate societies have only partially overlapping interests, and selection at the individual level is strong because groups are weakly bounded. Second, because conflicts of interests in primates are expressed through dyadic (pairwise) or higher-order contests (reviewed in Aureli and de Waal 2000), primate policing re-

* Corresponding author; e-mail: jflack@santafe.edu.

† E-mail: dewaal@emory.edu.

‡ E-mail: krakauer@santafe.edu.

quires intervention by third parties into ongoing contests, which can be more costly than, for example, policing through egg eating by social insects. Third, intervention frequency and style are very likely to have learned components (Bernstein and Ehardt 1986). This suggests that some consideration of learning ability, including the effects of memory, perception, and reinforcement on behavior, in addition to evolutionary dynamics, is required to understand the evolution of primate policing. Fourth, in social insects, policers benefit through the cumulative effects that their actions have on the demographics of reproduction in the colony. In primates, conflicts are in many cases only indirectly tied to reproduction—contests erupt over valuable resources and status positions that group members learn are of value in their particular social system (e.g., de Waal 1997; Chauvin and Berman 2004). These differences between insect and primate societies suggest that in primates, questions concerned with why there is variation in the occurrence of policing across societies and heterogeneity in performance of policing across individuals should consider those proximate costs that influence learning, in addition to the reproductive costs and benefits typically present in evolutionary models.

Proximate policing costs and social power. We noted that a potentially important difference between primate third-party policing and social insect policing through egg eating is that primate policing requires the intrinsically costly act of approaching conflicts. This cost is accrued from an increased likelihood that the intervener will become a recipient of aggression. Yet, there are no quantitative data on the costs of policing, in terms of aggression received, to policers in primate or other mammalian species. Furthermore, although there are few quantitative data on the incidence of policing in primates, it appears that effective policing occurs in one-male groups, including gorillas (*Gorilla gorilla*; Watts et al. 2000) and golden monkeys (*Rhinopithecus roxellanae*; Ren et al. 1991), but, with the exception of chimpanzees (de Waal 1982), is rare in hierarchical multimale, multifemale societies (de Waal 1977; Ehardt and Bernstein 1992; Petit and Thierry 2000) like those of macaques and baboons. It is not understood why this is the case.

One possibility we explore in this article is that effective low-cost policing is related to the distribution of power, where power is quantified by measuring the degree of “consensus” among group members that an individual can successfully use force in conflicts involving many individuals (Flack 2003; see “Methods” for operational definition). A similar, lower-level concept, “individual vigor,” has been discussed by Frank (2003) as an important factor in the evolution of policing. Individual vigor takes into account the capacity of a single individual to invest resources in conflict management. In primates, consensus

about power is a useful concept as conflicts often involve several individuals, which implies that to be successful at intervening, third parties need to be perceived by all of the conflict participants as being capable of successfully using force against them. In primates, we expect power to be correlated with the cost of intervening, such that individuals perceived to be much more powerful than other group members receive little or no aggression in response to policing and are therefore more likely to engage in the behavior. The implication of this hypothesis is that policing might be sustainable only in societies in which there is high variance in power and only few exceptionally powerful individuals. Although little is known about how power is distributed in different primate societies, qualitative reports suggest that some distributions are characterized by high variance and others by low or intermediate variance (Thierry 2000).

In this study, we investigate policing in a captive, multimale, multifemale pigtailed macaque (*Macaca nemestrina*) population. Pigtailed macaques are an ideal test species for evaluating whether the distribution of power influences the cost and benefits of policing because anecdotal descriptions of the species suggest that a few individuals have disproportionately more power than others in the population (e.g., Tokuda and Jensen 1968). Furthermore, pigtailed macaques perform interventions of many types, ranging from the approach of conflicts by third parties (attendance) to attacking either the recipient of aggression, the aggressor, or both simultaneously, as well as appeasing or affiliating with one or both conflict participants, standing midway between the conflict participants (interpositions), attacking kin of conflict participants, and displaying during the conflict but directing aggression at no specific target (Flack 2003). Here we analyze the relationship between power and performance of physically impartial interventions, which include interpositions, attacking or threatening both conflict participants simultaneously, and attendance.

We address the following questions empirically: Do pigtailed macaques effectively police conflict using impartial interventions? Is there individual variation in policing effectiveness and cost? Does social power account for variation in policing frequency, effectiveness, and cost? We test social power against the alternate hypothesis that size of kin group influences frequency of policing. The logic here is that impartial interventions are a good strategy to use when breaking up conflicts among offspring or other relatives. Finally, using a simple probabilistic model, we explore the relationship between characteristics of the distribution of power, policing, and the population cost of conflict.

Methods

Data were collected from the adults and subadults of a large captive breeding group of pigtailed macaques at the Yerkes Regional Primate Center in Lawrenceville, Georgia. The group was composed of 84 individuals, including four adult males (6 years of age when the study began) and 25 adult females (4 years of age when the study began) and 19 subadults. Subadult males included those males between ages four and six, whereas subadult females included those females between ages three and four. We analyzed the intervention-related behavior of adults and subadults ($n = 48$) because the dominance relationships of juveniles are not yet established, which confounds the investigation of whether power influences conflict management effectiveness. Interactions with juveniles were included in the adult and subadult data. The demographics of our captive population were similar to those reported for natural populations (Fooden 1980; Fleagle 1988; Oi 1990), in that males are removed at puberty, females remain in their natal groups, forming matriline, and adult males are introduced and removed approximately every 4 years.

The group, which was formed in 1985, was housed in an indoor-outdoor facility, the outdoor compound of which was 125 × 65 ft. Observations occurred between 1100 and 2000 hours from June until October 1998. Provisioning occurred before observations and once per day during observations. Data were collected over 156 hours. The 150 hours preceding data collection were used for training purposes (e.g., practicing collecting complex conflict data involving several individuals). The observer, J.C.F., was trained by Frans de Waal. Conflict and postconflict data were collected using all-occurrence sampling (also called event recording), in which sequential data on conflict-related behavior (see app. A) were collected from event onset (Altmann 1974; Bakeman and Gottman 1997) continuously until the conflict was considered terminated (see app. A). All-occurrence sampling was chosen over focal sampling to maximize samples collected, thereby improving statistical power, and because it allows the entire conflict to be followed. Data were collected using a digital stopwatch and voice recorder. See appendix A for operational definitions, including criteria of “effective” interventions.

We calculated social power using an individual’s distribution of subordination signals received from group members (Flack 2003). The pigtailed macaque subordination signal is the silent bared-teeth (SBT) display (Flack 2003). In pigtailed, the SBT is nearly 100% unidirectional, meaning that it is almost always emitted by the same individual in any given pair (Flack 2003). The individual emitting the signal is typically the one to yield when conflicts arise. The SBT is thought to be the best indicator of

subordinate status in dominance relationships in certain macaque species (de Waal and Luttrell 1985; Preuschoft and van Schaik 2000).

SBT displays, as defined by van Hooff (1967), are marked by a retraction of the lips and mouth corners such that the teeth are partially bared. We collected 1,218 SBT displays under the following conditions: the display was emitted in noncontest, apparently peaceful, situations; the individual emitting the display was looking at the presumed receiver; and the individual emitting the display did not otherwise act submissively (crouch, withdraw, flee, scream).

To calculate “consensus” about social power (social power index), we took into account two factors: total number of signals of subordination an individual i receives (r_i^T) and evenness in the distribution of signals received by individual i across its population of senders, measured using Shannon’s Information Index, $H_i(R) = -\sum_{j=1}^N r_{ij} \log r_{ij}$, where r_{ij} are the normalized frequencies of signals received by individual i from j . Information content is then multiplied by the information value to produce the following index: $P_i = H_i(R)r_i^T$. The validity of this index has been shown to be highly predictive when tested against data (Flack 2003).

Analyses

Each of the four dependent variables we tested in our analyses is based on raw data that were processed into observed minus expected scores. This approach controls for variation in (in this case) the tendency to intervene; individuals policing frequently were weighted more heavily than individuals intervening less frequently but performing the same proportion of policing interventions. In appendix B, we show how we calculated the dependent variable observed minus expected scores for each individual i .

Nonparametric tests were used for analyses when violations of normality occurred and the variance could not be stabilized using a transform procedure (Sokal and Rohlf 1995). Description of regression techniques can be found in articles by Sokal and Rohlf (1995) and McCullagh and Nelder (1989). Outliers and influential data points were evaluated using a jackknife procedure and Cook’s D (Belsley et al. 1980; Cook and Weisberg 1982; Faraway 2002). Statistical tests were conducted using SPSS and the statistical computing environment, R. Significance was set to .05 for all analyses unless otherwise noted.

Empirical Results

In this study, intervention by adults, subadults, and juveniles occurred in 72.3% of 2,409 observed agonistic dy-

ads. An agonistic dyad is a pairwise interaction in which one individual aggresses or threatens another individual (see app. A). A conflict can be composed of one or several dyads. We observed 1,111 total conflicts. In this study, we report descriptive data for adults and subadults ($n = 48$) on two broad classes of intervention (1,582 interventions into the 2,409 agonistic dyads), nonpolicing interventions, which include “partial interventions” in which interveners take sides (see app. A), and policing interventions, which include physically impartial interventions (attendance, interpositions, and simultaneous attacks of both conflict participants).

Interindividual Variation in Policing Behavior

We observed adults and subadults to perform 1,135 partial interventions and 447 policing interventions. As shown in figure 1, our data indicate that there is variation in how often different individuals police. The number of policing interventions per individual varied from 0 to 102 ($n = 48$, $m = 9.31$, $SD = 15.54$), whereas the number of partial interventions ranged from five to 76 ($n = 48$, $m = 23.64$, $SD = 13.55$). We found that the distribution of policing interventions was lognormal (before log transform, K-S test, $Z = 2.15$, $P < .001$; after log transform, $Z = .75$, $P = .64$), and that the distribution of partial interventions was normal (K-S test, $Z = .85$, $P = .46$).

Policing Effectiveness

Of the 447 policing interventions we observed, 189 (42%) were successful. The number of effective interventions per individual was 0 to 85 ($n = 45$, $m = 4.2$, $SD = 13.12$). As shown in figure 2, these data do not take into account the high variance in performance of policing. To control for variation in the number of policing interventions, we calculated the observed minus expected effectiveness for each individual, given each individual’s total frequency of policing interventions (see app. B). The observed minus expected effectiveness ranged from -2.52 to 61.64 ($n = 45$, $m = 1.90$, $SD = 9.60$). The distribution of observed minus expected effectiveness was lognormal after transform (before transform, K-S test, $Z = 2.47$, $P < .001$; after transform, K-S test, $Z = 1.18$, $P = .12$).

Cost of Policing

We observed 37 aggressive responses to the 447 policing interventions ($n = 45$, $m = .15$, $SD = .25$) and 164 aggressive responses to the 1,135 partial interventions ($n = 48$, $m = .15$, $SD = .11$). The intensity of the aggressive responses varied from simple threats to severe

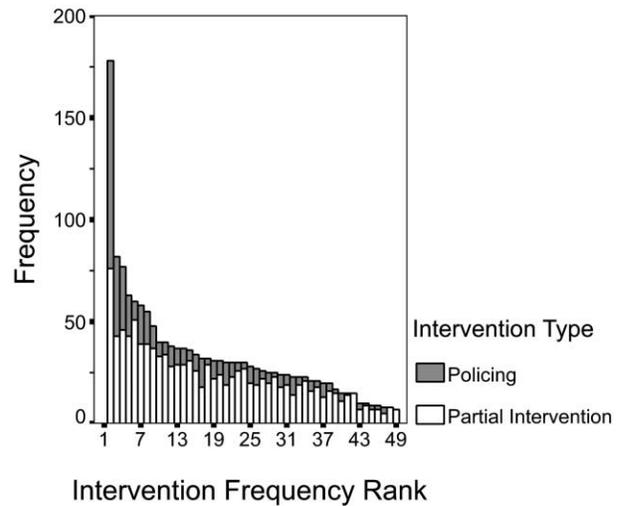


Figure 1: Frequency of policing interventions compared to the frequency of partial interventions for adults and subadults ($n = 48$). Policing interventions include interpositions, simultaneously attacking both conflict participants, and attendance (see “Methods”). Partial interventions include interventions in which the intervener attacks one conflict participant but not the other or affiliates with one conflict participant but not the other. Rank is based on the number of policing interventions performed by each individual.

biting, resulting in injury, in four of 1,582 interventions. As shown in figure 2, we found that the cost of policing per individual varied across individuals. We defined operational cost as the total frequency of aggressive responses weighted by the intensity of the response (see app. A). Intensity varied over seven aggression levels, such that the maximum possible cost was seven times the frequency of policing interventions—for example, if the intervener was bitten in response to each of its interventions. These data on aggressive responses received and cost do not take into account the high variance in performance of policing. To control for the number of interventions performed when assessing cost, we calculated the observed minus expected cost of policing to each individual (see app. B). We found that the observed minus expected cost of policing interventions varies from -30.30 to 7.73 ($n = 45$, $m = -1.36$, $SD = 5.11$). The distribution of observed minus expected cost was nonnormal and could not be log transformed because of large negative values (K-S test, $Z = 1.64$, $P = .009$).

Do Frequent, Effective Policers Pay Low Cost?

We found that the log-transformed observed minus expected values for policing frequency and effectiveness were significantly positively correlated (Pearson’s $r = .56$, $P <$

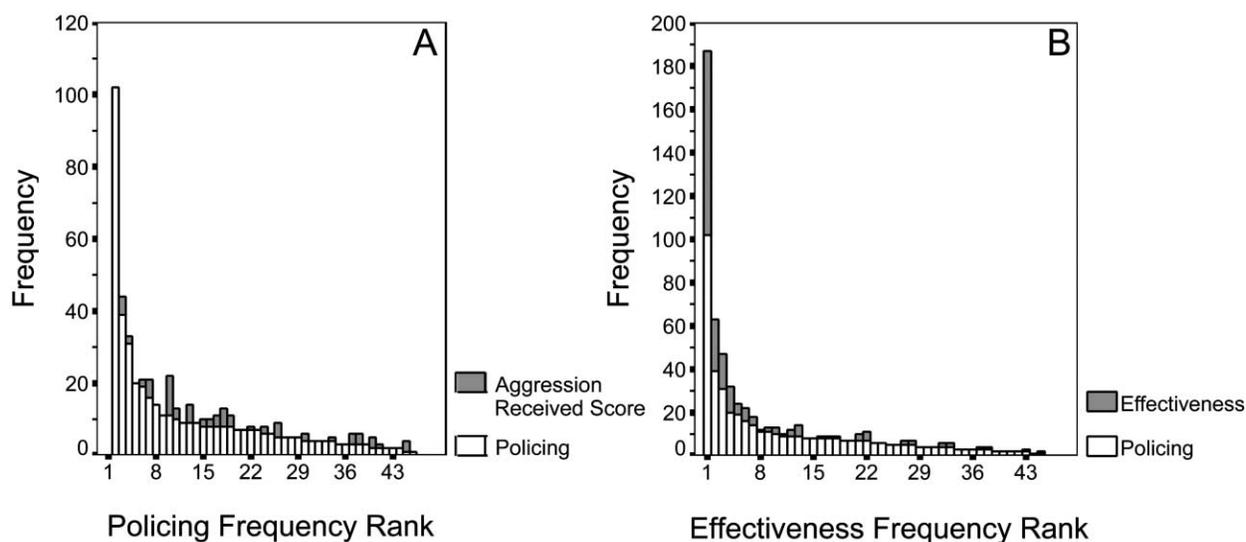


Figure 2: *A*, Total aggression (corrected for intensity) received by an individual in response to policing interventions compared with its frequency of policing interventions. Aggression is scored on a seven-point scale (see “Methods”). Rank is based on the total aggression received score. *B*, Effectiveness of policing interventions compared with policing frequency. Rank is based on policing frequency.

.001). The nontransformed, normally distributed observed minus expected values for policing frequency and cost were significantly negatively correlated (Pearson’s $r = -.45$, $P = .002$). The nontransformed observed minus expected values for policing cost and effectiveness were negatively correlated (Pearson’s $r = -.29$, $P = .05$).

Inspection of the data reveals that four individuals, the alpha, beta, and delta males, and the alpha female, account for the majority of effective, low-cost policing interventions. These four individuals performed a mean of 34.5 effective policing interventions per individual, whereas other adults and subadults ($n = 44$) performed 5.8. On average ($n = 4$), 98.5% of policing interventions by these four individuals were into dyads in which the intervener was unrelated to the conflict participants. The alpha female (age 13 years) had no relatives in the study population except for one infant. The three adult males (ages 11, 13, 13 years) were possibly related to 23 of 84, or 30.95% of the population, all of which were infants and juveniles rarely involved in conflicts (paternity data for these three males were unavailable). Following these four individuals, seven of the next nine most frequent policers were adult females belonging to large matriline.

Causes of Heterogeneities in Policing: Power and Kinship

Our data indicate that pigtailed macaques impartially control conflict but that few individuals do so effectively. Given that seven of the 13 most frequent policers in our study group were females belonging to matriline, we tested the hypothesis

that size of kin group accounts for variation in policing behavior. Size of kin group was defined as number of relatives with a shared history, where shared history means that at least one individual in a pair was born in the group during the other’s time in the group. Size of kin group ranged from 0 to 6 ($n = 48$, $m = 2.35$, $SD = 2.02$) and was normally distributed. We tested this kin-investment hypothesis against the power hypothesis, which, following theoretical models of Frank (1995, 1996, 2003), proposes that intrapopulation power differences (or some analog of power) might influence policing because more powerful individuals can afford to invest resources in intervention.

As described in “Methods,” consensus about power (hereafter referred to as “social power”) in pigtailed macaques can be calculated using the distribution of received silent bared-teeth displays, a unidirectional indicator of subordinate status (de Waal and Luttrell 1985; Flack 2003). In our study group, power was distributed lognormally (before log transform, K-S test, $Z = 2.22$, $P < .001$; after log transform, $Z = .82$, $P = .51$), such that most individuals possess similar power and a few are disproportionately powerful (Flack 2003). Social power ranged from 0 to 1,100.63 ($n = 48$, $m = 81.16$, $SD = 173.20$). Using univariate linear regression, we found that power and size of kin group together produced a good fit to the log-transformed policing frequency data ($R^2 = .48$, R^2 adjusted = .45, $F(2) = 20.46$, $P < .001$). Power accounted for the majority of this fit ($R^2 = .47$, $F(1) = 40.13$, $P <$

.001), whereas size of kin group accounted for very little of it ($R^2 = .10$, $F(1) = 1.38$, $P = .08$).

Prediction and the Lognormal Distribution of Power

The lognormal distribution of power in this population indicates that many individuals have similar power, suggesting that power will be predictive only for individuals falling toward the tails of the distribution. In the absence of a clean way to divide the population along these lines, we evaluated the predictive power of social power separately for adults and subadults above ($i_{\text{power}} > m$, $n = 12$) and below ($i_{\text{power}} < m$, $n = 33$) the mean (note that while the n is smaller for the $i_{\text{power}} > m$ sample and thus subject to larger error, high-power individuals engage in policing substantially more frequently and thus have scores that are less subject to error). We regressed four dependent variables on power for each of the two subsets of data (using observed minus expected values in each case): policing cost ("Cost"), policing effectiveness ("Effectiveness"), and two new variables, the frequency that individuals exacerbate conflicts as a result of either partial or policing interventions ("Exacerbate") and the frequency that interveners, using either partial or policing interventions, intervene into high-intensity, polyadic conflicts ("Complex"). All variables were normally distributed for both subsets of the data.

Individuals below Mean

We found that power is not a significant multivariate predictor of the variable set including Cost, Effectiveness, Complex, or Exacerbate for individuals with power scores below the mean power score (Wilks's $\lambda = .72$, $F = 2.71$, $df = 4, 28$, $P = .05$). Univariate tests indicated that power poorly fit the data (Cost, R^2 adjusted = .02, $F = 1.64$, $df = 1, 31$, $P = .21$; Effectiveness, R^2 adjusted = .12, $F = 5.33$, $df = 1, 31$, $P = .03$; Complex, R^2 adjusted = .02, $F = .51$, $df = 1, 31$, $P = .48$; Exacerbate, R^2 adjusted = .07, $F = 3.21$, $df = 1, 31$, $P = .08$). These data suggest that when variance in social power is low, power does not predict policing behavior or how frequently an intervener exacerbated conflicts or intervened into complex conflicts.

Individuals above Mean

We found that power is a significant multivariate predictor of the variable set including Cost, Effectiveness, Complex, and Exacerbate for individuals with power scores above the mean power score (Wilks's $\lambda = .03$, $F = 64.38$, $df = 4, 7$, $P < .001$). As shown in figure 3, univariate tests indicated that power fit the data very well for all variables

except Complex (Cost, R^2 adjusted = .93, $F = 149.31$, $df = 1, 10$, $P < .011$; Effectiveness, R^2 adjusted = .96, $F = 292.06$, $df = 1, 10$, $P < .001$; Exacerbate, R^2 adjusted = .82, $F = 51.41$, $df = 1, 10$, $P < .001$). Note that the relationship between power and Exacerbate is an inverse one, indicating that as individual power increases, frequency of exacerbating conflicts decreases. The fit for Complex was poor and nonsignificant (R^2 adjusted = .10, $F = .02$, $df = 1, 10$, $P < .88$). This result for Complex rules out the hypothesis that high-power individuals intervene effectively and at a lower cost simply because they intervene into less complicated conflicts, which are presumably easier to terminate.

These results suggest that power is an important explanatory variable for predicting which individuals will incur cost from policing and which will police effectively. However, as figure 3 illustrates, the relationship between the dependent variables and power is a complicated one because the power distribution is characterized by long tails and high variance. This makes interpretation of the R^2 values difficult. There are one or two points in the regressions that sit far from the other points, and these points are clearly influencing the fit of the regression. To evaluate the extent of this influence, we assessed whether these points (or others) are statistical outliers, and we quantified how much influence these points exert on the regression.

Outlier Assessment

To evaluate whether the extreme points in figure 3 are outliers, we conducted an outlier test by jackknifing the data to determine the studentized deleted residuals (Belsley et al. 1980; Cook and Weisberg 1982; Faraway 2002). The studentized deleted residual of a data point is calculated by fitting a regression to the data with that point deleted and then measuring the residual between the data point and the new regression line. It is a measure of the degree to which a residual is large versus exceptional. After calculating the studentized deleted residuals for all data points, the largest studentized deleted residual is evaluated against the Bonferroni critical value in the standardized normal distribution to determine whether it is larger than expected by chance. The Bonferroni critical value was used to assess significance because we had to control for conducting the outlier test on every data point (Faraway 2002). To calculate influence, we used Cook's D, which takes into account both leverage and the size of the studentized deleted residual in determining the degree to which removal of a point would affect the size of the fit of the regression (Belsley et al. 1980; Cook and Weisberg 1982). As shown in table 1, the extreme points in the regressions exert influence on the fit, but in no case is the point an outlier.

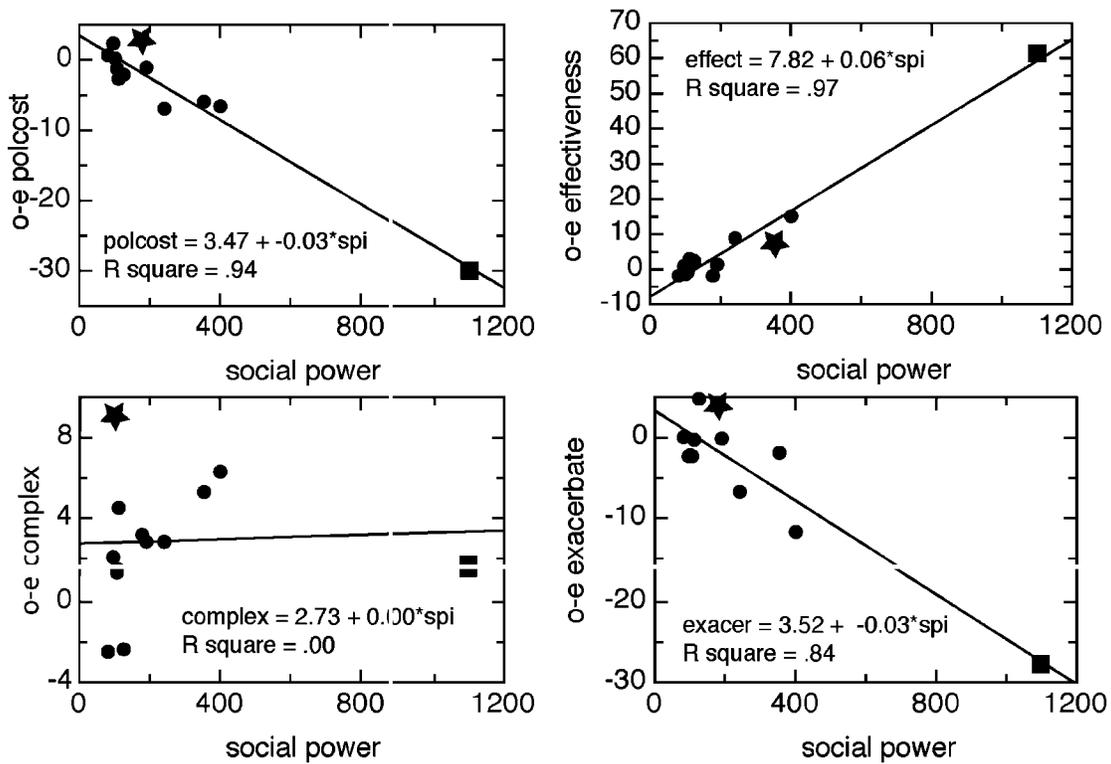


Figure 3: Regressions of four dependent policing variables (Cost [shown here as “polcost”], Effectiveness, Complex, and Exacerbate) on the independent variable, social power, for individuals with power scores greater than the mean power score. Dependent variables are corrected measures (see “Methods”). The “extreme” point in each graph is not an outlier (see table 1) but does exert substantial influence on the fit of effectiveness to social power.

In several cases, the highest studentized deleted residual belongs to visually nonextreme points.

Influence of Power Distribution: A Modeling Perspective

Unlike social insects, for which policing is directly tied to fitness, the costs of policing in gregarious multimale, multifemale primate societies appears to be mediated through societal power structure, which we capture here as a distribution. We do not observe (de Waal 1977; Ehardt and Bernstein 1992; Petit and Thierry 2000) nor do we expect policing in all multimale, multifemale primate species. In such societies, we think the likelihood of policing relates to variance in the distribution of social power. We observed a lognormal power distribution in our study group. We suggest that policing is favored in societies with this distribution for two reasons. First, the cost of policing to policers decreases as a function of power, and the cost, as we have shown, becomes negligible for values in the right tail of the distribution. These extreme values are uncharacteristic of many distributions. Second, the proximate and indirect benefits of policing (increased cooperation and

sociopositive behavior) to the population as a whole, to include interveners, might overcome the very low marginal costs of intervention generated by power distributions with high variance. In species with power distributions in which extreme values do not occur, the increased cost of conflict among individuals of disparate power comes to outweigh the reduced probability of conflict.

We explore a simple probabilistic model to demonstrate how increasing variance in the distribution of power leads to a reduction in the incidence of conflicts through policing by third parties and thereby a reduction in the population average cost of conflict (fig. 4).

Assume a probability distribution of social power with mean θ and variance σ^2 . We examine two distributions, one in which $f(x)$ is normal and another in which $f(x)$ is lognormal. In both cases we obtain two random samples X_1 and X_2 from the frequency distribution and a further value Y sampled at the ninety-ninth percentile of the distribution to capture the power of the intervener in all conflicts. We denote as MAX the maximum of X_1 and X_2 . Based on our observations, we posit that the cost of a conflict between any two randomly chosen individuals

Table 1: Statistical assessment of outliers and influence for the four regressions shown in figure 3

DV, <i>n</i>	Data point		Outlier assessment				Influence assessment		
	Symbol	SPI	SDERES	df	BCV	Significance	Cook's D	M	SD
Complex:									
12	Star	100.91	2.35	10.00	3.28	NS	.24	.59	1.84
12	Square	1,100.6	1.40	10.00	3.28	NS	6.43	.59	1.84
Exacerbate:									
12	Star	178.68	1.88	10.00	3.28	NS	.14	.07	.06
12	Square	1,100.6	.23	10.00	3.28	NS	.21	.07	.06
Polcost:									
12	Star	178.68	2.53	10.00	3.28	NS	.21	.36	1.06
12	Square	1,100.6	1.02	10.00	3.28	NS	3.71	.36	1.06
Effectiveness:									
12	Star	354.49	2.42	10.00	3.28	NS	.01	1.23	4.08
12	Square	1,100.6	2.42	10.00	3.28	NS	14.17	1.23	4.08

Note: Results reported in this table show that the “square” data point (the alpha male) is not a statistical outlier in any of the regressions (see “Methods”) even though it is far from other points. In all four cases, the data point denoted by “star,” not by “square,” has the highest studentized deleted residual score (SDERES), meaning that “star” deviates most from the pattern displayed by the majority of data. The “square” data point, however, exerts the greatest influence on the fits of the four regressions. Complex: observed minus expected proportion of interventions into fights involving two or more dyads and contact aggression; Exacerbate: observed minus expected proportion of interventions that increase the intensity of aggression used by conflict participants; Polcost (policing cost): observed minus expected intensity of aggression received by intervener from conflict participants or third parties; Effectiveness: natural log of observed minus expected proportion of policing interventions that terminated or reduced the intensity of conflict; DV = dependent variable; Symbol = data point in figure 4. BCV = Bonferroni critical value (.05/*n*). SPI = social power index.

is given by the linear function $C = k|X_1 - X_2|$, where $0 < k < 1$. The probability that two individuals engage in a conflict in the absence of a third party is a function of their respective social power values, $D = e^{-r|X_1 - X_2|}$. The probability of successful policing by an individual with high social power into a pairwise conflict is given by $P = 1 - e^{-r|Y - MAX|}$, and the cost associated with intervention when policing is given by $E = k|Y - MAX|$. The value r is a discounting parameter that determines the rate at which probability drops with differences in social power. High values of r allow for small differences in social power to correspond to large changes in the probability of conflict. The mean cost of conflict in the population is given by the expectation of the joint distribution

$$\begin{aligned} \langle F \rangle &= \int \int f(x_1)f(x_2)(1 - P(Y, MAX))D(x_1, x_2) \\ &\quad \times E(Y, MAX)C(x_1, x_2)dx_1dx_2 \\ &= \int \int f(x_1)f(x_2)e^{-r(|x_1 - x_2| + |Y - MAX|)} \\ &\quad \times k^2|x_1 - x_2||Y - MAX|dx_1dx_2, \end{aligned}$$

which we solve for the discrete case numerically (see fig. 4).

We find that increasing the variance of the power distribution first increases the expected cost of conflicts as

well as the variance in cost, and then, at higher variances in power, it leads to a reduction in the expected costs and an attendant drop in the variance in cost. Intermediate variances in power therefore give rise to the greatest expected conflict costs and variances in costs. This is because we assume (based on our empirical observations) that cost of conflict for the subordinate individual is increasing as the power difference increases, whereas the probability of conflict is decreasing with increasing power difference. At low variance in power, the rate of increase in cost is greater than the rate of decrease in conflict probability and hence expected cost increases. At high power variances, the opposite is true—the rate of decrease in conflict probabilities is greater than the increase in cost. The lognormal differs from the normal distribution (selected as a contrasting distribution) in that once past this intermediate maximum cost, the advantages to increasing variance in power in terms of reduced cost increase rapidly. The explanation for this is that increasing variance in the lognormal distribution disproportionately increases the power differentials between individuals in the population. These individuals are sufficiently rare that they engage in high-cost conflict infrequently. They are able to police very effectively, reducing conflict frequency and the variance in conflict costs. This simple model in no way attempts to explain the origin of policing. The model serves to illustrate the importance of considering distributional variation in

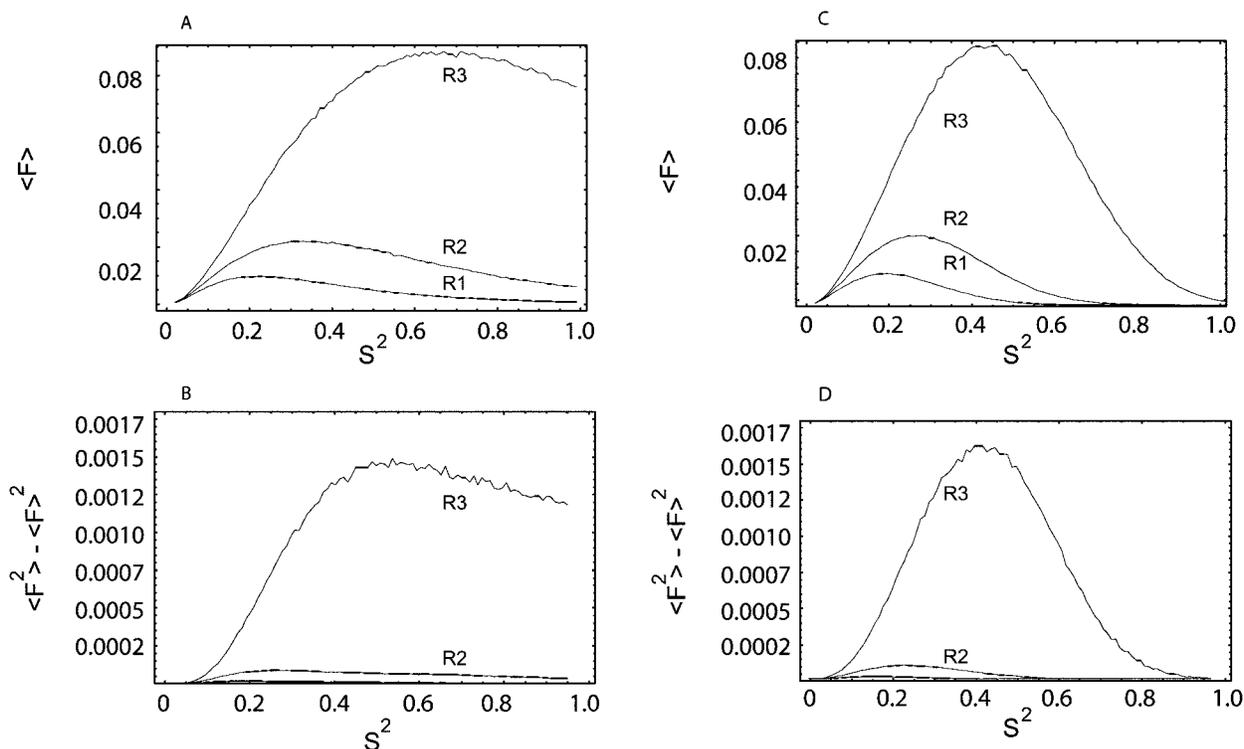


Figure 4: Expected cost $\langle F \rangle$ (A, C) and variance in cost $V(F)$ (B, D) of policing, as a function of increasing variance in the distribution of social power. We assume either an underlying normal (A, B) or lognormal (C, D) distribution. For the means (A, C), each point is an average of 5,000 paired random samples drawn from the underlying distribution. The corresponding variance in cost values are calculated from the same 5,000 paired samples. The three values of r (1, 2, 3) correspond to three different choices of r value employed in the two probability terms: $D = e^{-r|X_1 - X_2|}$ and $P = 1 - e^{-r|Y - \text{MAX}|}$ (see text) and are rank ordered $r_1 > r_2 > r_3$. These results suggest that the policing regime is not easily accessible from other regimes as a consequence of the nonlinear relationship between increasing variance and cost of conflict (intermediate variance in social power maximizes expected cost).

power on the number and intensity of fights in the population.

Discussion

A central topic over the last 25 years in evolutionary biology and animal behavior has been the origin of cooperation and conflict (Leigh 1999; Frank 2003). The origin of conflict is widely held to be heterogeneity in relatedness. At least two forms of evolutionary explanation have been used to explain cooperation: kin selection (to include extended forms of group selection; Hamilton 1964; Leigh 1999) and behavioral reciprocity (Trivers 1971). One of the motivations for this interest in cooperation and conflict is to discover how complex forms of organization such as body plans, coordinated behaviors, and animal societies are able to evolve and persist over multiple generations of time. The question of persistence relates to mechanisms of robustness. In other words, what mechanisms exist in animal societies, or at other levels of biological organi-

zation, to enable continued function despite components that are subject to conflicts of interest, development, and senescence? When considering persistence, mechanisms for managing ongoing conflicts are as important as mechanisms for preventing conflict by promoting cooperation (Leigh 1999). Secondary questions are what accounts for variation in conflict management mechanisms across different systems and what can this tell us about the evolution of robustness mechanisms.

In this study, we addressed how conflicts are managed in a multimale, multifemale macaque species, the pigtailed macaque. We asked why there is intrapopulation variability in the tendency to manage conflicts in this species and why certain forms of conflict management such as policing are rare in animal societies. Many of the published studies of policing and punishment are theoretical studies that seek to explain the evolution of behavioral forms that impose costs on the individual actors and provide benefits to the recipients (e.g., Boyd et al. 2003). Our goal here has been to develop a fuller empirical understanding of

the costs of policing in a cognitively sophisticated species and to explore how heterogeneities in cost might contribute to heterogeneities in individual interventions into conflicts. With a better understanding of the detailed mechanisms of policing, we aim to provide new material for more accurate descriptions of the evolutionary costs and benefits as well as descriptions of the social niches in which policing is maintained.

In social insect societies, where policing is well studied, policing typically involves workers eating the eggs of other workers but not of the queen, thereby controlling levels of relatedness in the colony (Monnin and Ratnieks 2001). Social insect policing largely concerns direct suppression of reproductive conflict. By contrast, it is unlikely, in the majority of cases, that primate conflicts are as closely tied to reproduction. Conflicts erupt over resources and status learned by group members to be of value in their social system. Although many primate conflicts might only indirectly impact reproductive success, they can have serious implications, both on the long-term health of the conflict participants and on social cohesion, which plays an important role in facilitating the cooperative activities that make group living worthwhile. This is because conflicts can result in injury and damage social relationships (Aureli and de Waal 2000). Conflicts also stifle sociopositive interaction among unrelated individuals, increase levels of anxiety, and spread across the population through redirection and ineffective intervention to impact many more individuals than the primary conflict participants (Flack et al., forthcoming).

Policing and Power

We sought to identify properties that might help explain intrapopulation variation in the tendency of individuals to attempt to control conflict through policing. We found that policing is strongly influenced by the distribution of power in pigtailed macaque society. Power here refers to the degree of “consensus” among group members that an individual can successfully use force during conflicts involving many individuals at once. This is important because when many individuals are involved in a conflict, to be successful at intervening, third parties need to be recognized as effective by all conflict participants. Power in primates can be related to simpler concepts in other species—concepts such as resource holding potential and individual vigor (Frank 1995, 1996). In each case, individual histories lead to state-dependent variation influencing agonistic and intervention behaviors.

Our data show that policing is an effective conflict management mechanism in pigtailed macaques when performed by powerful individuals, that policing cost is negatively correlated with power, that only a small number

of powerful individuals police, and that there is a lognormal distribution of power in the pigtail population. Our probabilistic model suggests that when variance in power is high and concentrated in the hands of a small number of individuals (such as with a lognormal distribution), policing can reduce the frequency and intensity of conflicts in the population through the interventions of a few individuals policing at negligible cost to themselves.

The Importance of Heterogeneous Cost

Mathematical models of policing and of related intervention behaviors such as punishment are able to effectively reduce their number of state variables by assuming that all individuals pay the same cost for engaging in conflict management or repressing competition. Although this is a reasonable simplifying assumption, it makes the evolution of policing appear more difficult or improbable than actually seems to be the case. There is good evidence from the study of dominance relationships in animal societies for individual variation in resource holding potential or vigor (Clutton-Brock and Parker 1995) and, from this study, for individual variation in power. By allowing for variation in state, Frank (1995, 1996) has shown that small differences in individual vigor can lead to large variations in individual contributions to policing when relatedness is low. The claim that variation in individual vigor is related to variation in investment in conflict management requires the additional assumption that the cost of conflict management varies inversely with individual state. One of the findings of this study is that cost is not only a function of the individual intervening but also of the power values of the individuals engaged in the dispute. Thus, variation in individual vigor is not sufficient. A power structure must arise in which individuals also vary in the degree to which group members perceive them capable of successfully using force. It would be interesting to extend the Frank (2003) treatment to include this assumption.

The data in this article show that the assumption of heterogeneity in state is fully justified in pigtailed macaques. Policing cost and effectiveness vary as function of state, where state is a function of power structure. The distribution of power in our pigtailed macaque population was lognormal, implying that a small number of individuals have significantly more power than the rest of the population. Only those individuals in the right tail of the power distribution were observed to engage in effective policing, and they do so at negligible cost to themselves. We were curious as to the reason why this distribution is lognormal and what consequences this might have on the frequency and incidence of conflicts and intervention in the population. Lognormal distributions are characterized

by a long right tail in which very powerful individuals are present at significant frequencies. In this respect, they resemble power law distributions. The significance of high variance in different social power distributions was illustrated by a simple probabilistic model. The model shows that even when interventions are performed by those individuals restricted to above the ninety-ninth percentile of the power distribution, policing is able to effectively reduce the population cost of conflict only when variance in the power distribution is very high.

In species with power distributions in which extreme values rarely occur (such as the normal distribution), the increased cost of conflict among individuals of slightly disparate power comes to outweigh the reduced probability of conflict. It would seem that in societies in which conflicts typically involve multiple individuals, power structure can play an important role in facilitating policing behavior. Additional support for this hypothesis is provided by data on the absence of effective policing in other multimale, multifemale primate species such as rhesus (*Macaca mulatta*) and long-tailed macaques (*Macaca fascicularis*), which appear to have power distributions characterized by lower variances than the pigtailed macaque distribution (e.g., Thierry 2000). In these species, interventions by the alpha male and other high-ranking individuals are reported to exacerbate conflict rather than terminate it (e.g., de Waal 1977).

The heterogeneity in policing cost is also suggestive of the handicap theory (Zahavi 1975; Grafen 1990), whereby powerful individuals pay a disproportionately low cost for performing a costly behavior. Unlike handicapped signals, policing is not “wasteful” in that it serves to terminate disputes, and it is not “extravagant” because the most effective policing interventions are the most low key. However, if effective policing requires heterogeneity in power, as our findings suggest, then it is possible that policers derive a net benefit from policing by being perceived by future social partners as effective at conflict resolution. Similar attempts at policing by low-power individuals lead to a higher net cost in terms of immediate retaliation by disputants.

New Directions for Research

Our data suggest that considering state dependence and the relationship between state and social structure are important parts of the puzzle in understanding the emergence of policing, but they are not the whole story. In macaques and other long-lived, large-brained mammals, complex behavior like conflict intervention is, at best, indirectly tied to reproduction and is modulated through learning. To understand how policing and other conflict management mechanisms emerge in these species, the role of learning

must be considered, and in particular, consideration must be given to how factors such as social structure, social network topology, and power structure constrain and influence learning dynamics. For example, in macaques, it is unlikely that individuals are born into the policing role. Instead, individuals assume this responsibility as a consequence of reinforcement arising during competition for status, leading to heterogeneities in power. If so, policing in macaques would be dependent on learned social rules, such as those related to status and intervention, which are conditioned on power structure. Although in this article we do not explore the role learning plays in the emergence of effective, low-cost policing in macaques, our results indicate that this is an issue critical to understanding both why, in the proximate sense, individuals engage in policing behavior and how policing emerges in the course of social evolution.

Conclusion

The primary finding of this study is that heterogeneities in power, by producing heterogeneities in the cost of conflict management for individuals, lead to heterogeneities in the tendency to police. The secondary finding is that high variance in the distribution of power seems to be required to support policing behavior. If correct, this result suggests that policing will emerge only in societies in which lognormal, or alternative high variance, power distributions can arise. This might explain why effective, low-cost third-party policing appears to be rare in primate societies. Elsewhere we have shown that in macaques temporary behavioral “knockout” of effective conflict managers results in social network fragmentation, increased aggression, and decreased affiliation (Flack 2003; Flack et al., forthcoming). These results, in conjunction with those reported here, indicate that in cognitively sophisticated species, power structure has a profound effect on the emergence of conflict management mechanisms such as policing. These mechanisms in turn modulate social cohesion by effecting social network structure. Third-party policing is therefore a critical conflict management mechanism that directly (by preventing the escalation of aggression) and indirectly (by facilitating social cohesion) benefits all group members.

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APPENDIX A

Operational Definitions

Dyadic: pairwise interaction.

Polyadic: interaction involving more than two individuals.

Affiliation: includes approach with lip smacking or puckering, brushes against the hair, genital inspection, contact sitting, gentle touches, specific touches, grooming, embracing, brief mounts (less than 5 s), and shoulder-to-shoulder walking.

Aggression: includes threats; scored on a seven-point scale: 1 = threat face or stare with head lowered and chin thrust forward; 2 = threat face or stare with vocalization or following (walking behind but within 2 m of recipient); 3 = lunge, mild slap, or push; 4 = chase <3 m; 5 = wrestle, grapple, or chase >3 m; 6 = bite <5 s; 7 = bite >5 s.

Intervention cost: total intensity score of aggressive responses received by an intervener divided by its frequency of intervention. Total intensity was calculated by summing over set of aggressive responses (see Aggression), an intervener received. For example, if intervener received one bite of less than 5 s and two threats (without vocalization or following) in response to 10 interventions, then its cost score = $(6 + 1 + 1)/10$, or 0.8. Cost can vary from 0 (no aggression in response to any intervention) to 7 (severe bites in response to every intervention).

Conflict: any interaction in which one individual aggresses a second individual. Conflict was considered terminated if no aggression or withdrawal responses (fleeing, crouching, screaming, running away, subordination signals) occurred for 2 min from the last such event. Conflict can involve multiple dyads if dyadic conflicts result in aggressive interventions by third parties or redirections by at least one conflict participant.

Complex, high-intensity conflict: two or more dyads, bidirectional, contact aggression.

Attendance: third party approaches in a directed manner to within 3–5 m of conflict but shows no other behavior.

Partial intervention: third party directs aggresses one conflict participant, or third party affiliates with one conflict

participant but not the other. Interventions performed against recipients of aggression are distinguished from those performed against aggressors.

Impartial intervention: third-party aggresses both or all conflict participants simultaneously and is equidistant to each, or stands equidistant to conflict participants but does not threaten, or approaches conflict but shows no other behavior (attendance).

Conflict termination¹: the conflict was considered terminated if, within 5 s of intervention, aggression between the conflict participants ceased for at least 2 min. Opponents must be intermittently looking at, or interacting with, intervener, or must show withdrawal related behavior in response to intervener behavior.

Reduction of intensity¹: aggression drops one intensity level within 5 s of intervention and remains at that level or lower for duration of the conflict. Opponents must be intermittently looking at, or interacting with, intervener, or must show withdrawal related behavior in response to intervener behavior.

Exacerbation of conflict¹: conflict was considered exacerbated if, within 5 s of the intervention, the level of aggression between any conflict participants increased by one intensity level, or if the response of aggression recipient increases by one intensity level.

Unclear intervention effect¹: effect of intervention on conflict was ambiguous within the first 5 s after intervention.

APPENDIX B

Calculation of Observed Minus Expected Scores for Dependent Variables

In table B1, we show how to calculate dependent variable observed minus expected scores. The state set of scores for an individual $i \in \{1, \dots, N\}$ is denoted by $X_i = \{0, 1, 2, 5\}$. In other words, the sequence of scores in the score vector \mathbf{s} assumes discrete values drawn from the state set according to the nature of the behavioral interaction. The total frequency F_i refers to the number of times individual i engaged in the larger set of behaviors from which \mathbf{s} is drawn. For example, a “policing frequency” score vec-

¹ Note regarding evaluating intervention effects. Because conflicts have multiple causes and characteristics, it was not possible to use a match-controlled procedure, as in the study of postconflict affiliation (20), to evaluate whether conflicts with interventions ended more quickly than those without. In the case of pigtailed macaques, the 5-s rule was a reasonable compromise because it was substantially shorter than the mean length of conflicts ($N = 1,111$ conflicts, $M = 39.96$ s, $SD = 81.18$ s; median = 15 s), and we only classified interventions as effective at terminating or reducing the intensity of conflicts when conflict opponents attended to the approach or behavior of intervener by at least looking in the intervener’s direction.

tor of $\mathbf{s} = \{0, 0, 1, 1, 1\}$ would describe an individual that performed two consecutive nonpolicing interventions and three consecutive policing interventions. The total frequency (F_i) would be $\{5\}$, meaning that individual i performed five interventions of all types in total. Alternatively,

if the score vector (\mathbf{s}) is an “intensity of aggression received in response to policing” vector, for example, $\{0, 1, 7, 2, 1\}$, the individual would have performed five policing interventions, receiving in response to each no aggression, a threat, a bite, a lunge, and a threat.

Table B1: Calculation of observed minus expected scores for dependent variables (see text for explanation)

Individual index	Total frequency	Observed score	Mean score	Expected mean score	Observed – expected
1	F_1	$O_1 = \sum_j^{F_1} s_j$	$m_1 = \sum_j^{F_1} s_j / F_1$	$E_1 = \langle m \rangle \times F_1$	$V_1 = O_1 - E_1$
2	F_2	$O_2 = \sum_j^{F_2} s_j$	$m_2 = \sum_j^{F_2} s_j / F_2$	$E_2 = \langle m \rangle \times F_2$	$V_2 = O_2 - E_2$
⋮					
N	F_N	$O_N = \sum_j^{F_N} s_j$	$m_N = \sum_j^{F_N} s_j / F_N$	$E_N = \langle m \rangle \times F_N$	$V_N = O_N - E_N$
Column means	$\sum_i^N F_i / N$	$\langle O \rangle = \sum_i^N O_i / N$	$\langle m \rangle = \sum_i^N m_i / N$		

Note: We have included a column cell for mean total frequency even though this is not used to calculate the observed minus expected score.

Literature Cited

- Alexander, R. 1979. Darwinism and human affairs. University of Washington Press, Seattle.
- Altmann, S. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- Aureli, F., and F. B. M. de Waal, eds. 2000. Natural conflict resolution. University of California Press, Berkeley.
- Bakeman, R., and J. M. Gottman. 1997. Observing interaction: an introduction to sequential analysis. 2nd ed. Cambridge University Press, Cambridge.
- Belsley, F. J. M., E. Kuh, and R. E. Welsch. 1980. Regression diagnostics: identifying influential data and sources of collinearity. Wiley, New York.
- Bernstein, I., and C. Ehardt, 1986. Modification and aggression and the special case of adult and adolescent male rhesus monkey (*Macaca mulatta*). *American Journal of Primatology* 10:213–227.
- Boyd, R., H. Gintis, S. Bowles, and P. Richerson. 2003. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences of the USA* 100:3531–3535.
- Chauvin, C., and C. Berman. 2004. Intergenerational transmission of behavior. Pages 209–230 in B. Thierry, M. Singh, and W. Kammann, eds. *Macaque societies: a model for the study of social organization*. Cambridge University Press, Cambridge.
- Clutton-Brock, T. H., and G. A. Parker. 1995. Punishment in animal societies. *Nature* 373:209.
- Cook, R. D., and S. Weisberg. 1982. Residuals and influence in regression. Chapman & Hall, New York.
- de Waal, F. B. M. 1977. The organization of agonistic social relationships within two captive groups of Java-monkeys (*Macaca fascicularis*). *Zeitschrift für Tierpsychologie* 44:225–282.
- . 1982. Chimpanzee politics: power and sex among apes. Harper & Row, New York.
- . 1997. The chimpanzee’s service economy: food for grooming. *Evolution and Human Behavior* 18:375–386.
- de Waal, F. B. M., and L. M. Luttrell. 1985. The formal hierarchy of rhesus monkeys: an investigation of the bared-teeth display. *American Journal of Primatology* 9:73–85.
- Ehardt, C. L., and I. S. Bernstein. 1992. Pages 83–111 in S. Harcourt and F. B. M. de Waal, eds. *Coalitions and alliances in humans and other animals*. Cambridge University Press, Cambridge.
- Faraway, J. J. 2002. Practical regression and ANOVA using R. <http://www.stat.lsa.umich.edu/~faraway/book/>
- Flack, J. C. 2003. Robustness mechanisms in primate societies. PhD thesis. Emory University, Atlanta.
- Flack, J. C., D. C. Krakauer, and F. B. M. de Waal. 2005. Robustness mechanisms in primate societies: a perturbation study. *Proceedings of the Royal Society of London B* (forthcoming).
- Fleagle, J. G. 1988. Primate adaptation and evolution. Academic Press, New York.
- Fooden, J. 1980. Classification and distribution of living macaques. Pages 1–9 in D. Lindburg, ed. *The macaques: studies in ecology, behavior, and evolution*. Van Nostrand Reinhold, New York.
- Foster, K. R., P. Seppä, F. L. W. Ratnieks, and P. A. Thorén. 1999. Low paternity in the hornet *Vespa crabro* indicates that multiple mating by queens is derived in vespine wasps. *Behavioral Ecology and Sociobiology* 46:252–257.
- Frank, S. 1995. Mutual policing and the repression of competition in the evolution of cooperative groups. *Nature* 377:520–522.
- . 1996. Policing and group cohesion when resources vary. *Animal Behaviour* 52:1163–1169.
- Frank, S. A. 2003. Repression of competition and the evolution of cooperation. *Evolution* 57:693–705.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. *Journal of Theoretical Biology* 7:1–32.
- Leigh, E. L. 1999. Levels of selection, potential conflicts, and their resolution: the role of the “common good.” Pages 15–30 in L. Keller, ed. *Levels of selection in evolution*. Princeton University Press, Princeton, NJ.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. 2nd ed. Chapman & Hall, New York.
- Monnin, T., and F. L. W. Ratnieks. 2001. Policing in queenless ponerine ants. *Behavioral Ecology and Sociobiology* 50:97–108.
- Oi, T. 1990. Population organization of wild pigtailed macaques (*Macaca nemestrina nemestrina*) in West Sumatra. *Primates* 31:15–31.
- Petit, O., and B. Thierry. 2000. Pages 267–269 in F. Aureli and F. B.

- M. de Waal, eds. Natural conflict resolution. University of California Press, Berkeley.
- Preuschoft, S., and C. P. van Schaik. 2000. Pages 77–105 in F. Aureli and F. B. M. de Waal, eds. Natural conflict resolution. University of California Press, Berkeley.
- Ratnieks, F. L. W. 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *American Naturalist* 132: 217.
- Reeve, H. K. and L. Keller. 1997. Reproductive bribing and policing as mechanisms for the suppression of within-group selfishness. *American Naturalist* 150(suppl.):S42–S58.
- Ren, R., K. Yan, Y. Su, H. Qi, B. Liang, W. Bao, and F. B. M. de Waal. 1991. The reconciliation behavior of golden monkeys (*Rhinopithecus roxellanae roxellanae*) in small breeding groups. *Primates* 32:321–327.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. 3rd ed. W. H. Freeman, New York.
- Thierry, B. 2000. Covariation of conflict management patterns across macaque species. Pages 106–128 in F. Aureli and F. B. M de Waal, eds. Natural conflict resolution. University of California Press, Berkeley.
- Tokuda, K., and G. Jensen. 1968. The leader's role in controlling aggressive behavior in a monkey group. *Primates* 9:319–322.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–37.
- van Hooff, J. A. R. A. M. 1967. The facial displays of catarrhine monkeys and apes. Pages 7–68 in D. Morris, ed. *Primate ethology*. Aldine de Gruyter, Chicago.
- Watts, D. P., F. Colmenares, and K. Arnold. 2000. Pages 281–301 in F. Aureli and F. B. M. de Waal, eds. Natural conflict resolution. University of California Press, Berkeley.
- West-Eberhard, M. J. 1986. Dominance relations in *Polistes canadensis* (L.), a tropical social wasp. *Monitore Zoologico Italiano (Nuova Serie)* 20:263–281.
- Zahavi, A. 1975. Mate selection: a selection for handicap. *Journal of Theoretical Biology* 53:205–214.

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