

Revolutionary coalitions in male rhesus macaques

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Summary

Coalitions between animals are found in a variety of taxa, but are most common among primates. Here, we present data on the relative abundance of male–male coalitions within a group of free-ranging rhesus macaques, a species in which male coalitions are reportedly rare or absent. We then report a series of revolutionary coalitions among subordinates against higher ranked individuals that transformed male dominance relationships. We use these data to test theoretical model predictions about revolutionary rank-changing coalitions among primate males. We also use data on male age, rank, group residency length, associations and relative fighting ability (morphometric variables), to test predictions about coalition members' characteristics. Contrary to model predictions, coalition sizes were large, but consistent with predictions, targets were high ranking, and members middle ranking. Coalition males were more similar to each other in rank, group residency length and body mass than other males were. Coalition members were also associates (spent more time with other members than non-members did in the preceding months), and had longer canines than other males. Our results show that males forming revolutionary coalitions were from a specific part of the male distribution and represent the first systematic analysis of male–male coalitions in free-ranging rhesus macaques.

Keywords: coalitions, co-operation, social behaviour, dominance, rank instability, primate.

Introduction

One of the most striking features of animals is their ability to co-operate with each other towards goals such as reproduction, protection of young, the building of communal nests, and hunting (Dugatkin, 1997; van Schaik

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& Kappeler, 2006). A special subset of co-operative behaviour occurs when individuals form coalitions. Though this term can be used inconsistently, we here use the ethological definition, in which members of the same or different sexes co-operate in an aggressive or competitive context (de Waal & Harcourt, 1992). Coalitions are believed to be more restricted in their taxonomic scope than other aspects of co-operation, but are still found in a variety of contexts and groups (Harcourt, 1992). These include coalitions between male bottlenose dolphins (*Tursiops* spp.) to compete with other males and to consort females (e.g., Lusseau, 2007), between male hyenas (*Crocuta crocuta*) who form coalitions against socially dominant females (Szykman et al., 2003), and between female coatis (*Nasua narica*) who combine forces against solitary males to gain access to food patches (Gompper, 1996).

Some of the most remarkable coalitions are observed among non-human primates (hereafter primates), and coalitions have been studied most extensively in this group. Coalitions occur in primates in contexts such as the acquisition and maintenance of dominance rank (Chapais, 1992), and the disruption by subordinates of consortships between higher ranked males and females (e.g., baboons, *Papio* spp.; Bercovitch, 1988; Noë & Sluiter, 1990; Tonkean macaques, *Macaca tonkeana*, Thierry, 2007; Barbary macaques, *Macaca sylvanus*, Bissonnette et al., in press). Chapais (1995) categorized coalitions in primates as three types: (1) conservative coalitions, in which coalition members are all higher ranked than the target; (2) bridging coalitions, where at least one coalition member is of higher rank, and at least one member of lower rank, than the target; and (3) revolutionary coalitions, where coalition members are all of lower rank than the target. Since then, van Schaik et al. (2006) further separated the latter two of these categories to distinguish outcomes, separating both bridging and revolutionary coalitions into 'levelling' (where ranks do not change as a result of the coalition, and where the coalition allows at least one member to obtain access to a female), and 'rank-changing' coalitions. Evolutionary models have been formulated to predict the likely determinants of coalitions (Dugatkin, 1998; Johnstone & Dugatkin, 2000; Pandit & van Schaik, 2003; van Schaik et al., 2004, 2006; Mesterton-Gibbons & Sherrat, 2007; Stamatopoulos et al., 2009). Of these, one model gives specific predictions about the factors that make coalitions among male primates more likely (Pandit & van Schaik, 2003; van Schaik et al., 2006). According to this model, the degree of despotism in a species (i.e., the extent to which the dominance hierarchy is linear and steep, and agonistic interactions between dominants and subordinates are asymmetrical and

unidirectional) predicts the degree of feasibility of revolutionary coalitions (less feasible as despotism is higher), as well as the level of reproductive skew. In turn, the level of reproductive skew predicts the relative profitability of coalitions (more profitable when skew is higher). As a consequence of the trade-off between profitability and feasibility, the model predicts that revolutionary coalitions should occur in species of medium despotism. It is also predicts that such coalitions should involve top or near top ranked targets and just below top (rather than low) ranked members, due to the higher pay-off for a rise in rank for such males when compared to the pay-off for a rise in rank for lower ranked individuals. Finally, it predicts that coalitions should be small (two or three members), as larger coalitions inevitably involve lower-ranked individuals who have a lower pay-off for rising in rank (Pandit & van Schaik, 2003; van Schaik et al., 2006).

In addition to the above models, several studies have made predictions about the features that should predispose primate males towards forming coalitions with each other (summarized in Noë & Sluiter, 1995). These include that males are more likely to form coalitions: among kin (Wrangham, 1982); among individuals of similar age and experience (Smuts, 1985); among individuals of greater familiarity and longer group residency (Collins, 1981; Smuts, 1985); among 'friends' (Smuts, 1985); and among individuals of similar fighting abilities (Bercovitch, 1988; Noë & Sluiter, 1990). Most of these predictions derive from the fact that observational studies have recorded that coalitions are more likely to occur between such males (Noë & Sluiter, 1995). Direct tests of such predictions are rare, and more data are needed to evaluate the performance of primate coalition models generally (Pandit & van Schaik, 2003; van Schaik et al., 2006). In the present study, we report, for the first time, revolutionary coalitions among free-ranging male rhesus macaques (*Macaca mulatta*), and use our data to test theoretical predictions about male–male coalition formation in primates.

The rhesus macaque is a gregarious diurnal primate that lives in highly nepotistic and despotic matriarchal societies (Maestriperi, 2007). Females obtain ranks according to the rank of their mother and the matriline as a whole. Each new daughter has a higher rank than her older sister, the result of which is an inverse relationship between rank and age within each matriline (youngest ascendancy) (Missakian, 1972). Generally, males disperse as they approach full adulthood and join a new group with unrelated individuals, and so cannot expect to receive strong family support during the course

of their lives. Once in a new group, males typically follow a 'seniority rule', whereby new immigrant males enter a group low-ranking, and rise in rank as other males emigrate or die (Manson, 1998). Given an absence of support from related females, we might expect coalitions between males, such as those seen in other macaques (*Macaca radiata*, Silk, 1992; *Macaca sylvanus*, Bissonnette et al., 2009), to occur in rhesus macaques also. However, while there is some evidence for coalitions between rhesus macaque brothers (Meikle & Vessey, 1981) coalitions among male rhesus macaques have only rarely been observed (Kaplan, 1977; Bernstein & Ehardt, 1985; Maestriperi, unpublished data). Despite early experiments showing that coalitions of subordinate rhesus macaque males against dominant males (revolutions) occur commonly when dominant animals are placed into enclosures with multiple subordinates (Maslow, 1936), it has been suggested that revolutionary coalitions are rare or entirely absent among rhesus males living in stable social groups (e.g., van Schaik et al., 2006; Maestriperi, 2007). Indeed, when discussing rhesus macaques specifically, van Schaik et al. (2006) state that "the absence of male–male coalitions now becomes an issue to be examined".

Here, we report on the occurrence and relative abundance of different types of male–male coalitions within a group of free-ranging rhesus macaques on Cayo Santiago. Although rhesus macaque societies are generally highly despotic in their social relationships, medium values of reproductive skew have been documented in groups on Cayo Santiago (e.g., Bernard et al., 1994). Further, males sometimes remain in natal groups (possibly due to large group sizes related to provisioning, which ensure large numbers of non-related group members for mating). These factors may affect the likelihood of coalitions occurring, as well as their nature. We report a collection of remarkable observations in which a series of revolutionary coalitions among subordinates against higher ranked males transformed male dominance relationships within the group, resulting in several of the top-ranked males, including the alpha (first-ranked) and beta (second-ranked) males being expelled from the group. We use these data to test theoretical predictions about male–male coalitions in primates. These are, that revolutionary rank-changing coalitions should be small (feature two or three individuals), and should have top ranked targets and just below top ranked (not low ranked) members (van Schaik et al., 2006). Having done this, we then use our data to test predictions about the characteristics of males that form coalitions.

Specifically, we predicted that coalition members would be of similar experience, age and familiarity (would be of similar ranks, age, and group residency lengths) (Collins, 1981; Smuts, 1985), would be associates (would spend more time with other coalition members in the months before revolutions started than other males did) (Smuts, 1985), and would be of similar fighting ability (would be both different from other males, and more similar to each other morphometrically) (Bercovitch, 1988; Noë & Sluijter, 1990). Collectively, the results presented represent the first systematic description and analysis of male–male coalitions in free-ranging rhesus macaques.

Materials and methods

Study site and population

This study took place on Cayo Santiago, a 15.2 ha island located 1 km off the coast of Puerto Rico. A rhesus macaque colony was established on this island in 1938 from free-ranging individuals captured in India (Rawlins & Kessler, 1986), with no new individuals introduced to the population since then except through natural births. The animals are provisioned daily with commercial monkey chow. Females in this population currently undergo a 6-month birth season from approximately September–March, followed by a 6-month breeding season that occurs from approximately March–August (Hoffman et al., 2008). Data presented in this study were collected between September 2008 and August 2009. During this time approximately 1000 animals lived on the island, in 6 social groups. Data were collected on all males in Group R, which consisted of a mean number of 268.3 individuals (range = 243–307) during the study period, with fluctuations in group size being accounted for by births, deaths, immigrations, emigrations, and by the removal of some individuals by the Caribbean Primate Research Center in Jan and Feb 2009. During June 2009 (the start of the major period of revolutionary coalitions, see Results), there were 38–41 males in Group R, of which 13 were natal to R, though only 10 of these had spent most of their lives in Group R, with the other 3 recently returning having been in other groups for a number of years. Males were aged between 5.5 (at which point males are usually considered adult; Manson, 1996) and 22.4 years old (mean age = 11.8 years). The Cayo Santiago database contains information on the dates of birth for these males, as well as on group memberships and time

spent within different social groups. All individuals in the population are tattooed and ear-notched, making it easy for observers to identify individuals.

Behavioural data collection

Coalitionary aggression was recorded ad libitum, whenever it was observed. We recorded how coalitionary aggression began whenever possible, as well as the identity of the victim, the identity of the coalition partners, and the outcome.

During the first 3 months of the breeding season (March–May 2009), we undertook 379 30-min continuous focal observations on 20 adult males. These males were of representative (from the group as a whole) age (range 5.5–22.4 years, mean = 12.9), and included males that were high, middle and low ranked, and both natal (5) and non-natal (15) individuals. We recorded the direction of any social behaviours (whether they were directed from or towards the focal), as well as the ID of the interactant partner (social behaviours) or nearest neighbour within 2 m (all other behaviours) at all times. We balanced observations for each male between from 7:00–10:00 and from 10:00–14:30, such that each male was followed at least once within each time block each week.

Dominance interactions recorded and analyzed for calculation of dominance rank were: fear grins (winner is the individual grinned at); avoidances (winner is the individual avoided); displacements (winner is the displacer); and threats, chases and lunges (winner is the aggressor in all cases). These interactions were compiled into winner–loser matrices, and Matman 1.1 (Noldus) was used to create two separate dominance hierarchies. During the first 3 months of the breeding season (March–May 2009), and before the major rank changing revolutions began in Group R, we recorded a total of 812 male–male interactions, which were used to form our first significant linear hierarchy (test of Landau's corrected linearity index, $p = 0.003$). For dominance ranks following the period of rank instability, we used male–male interactions observed in July ($N = 361$), which produced a second significant linear hierarchy (test of Landau's corrected linearity index, $p = 0.049$). We altered this second hierarchy to adjust for the alpha male's expulsion from the group on 10 August 2009, which our observations subsequently demonstrated was a permanent expulsion, with the male unable to rejoin the

group until his death. Interactions observed in June 2009 ($N = 494$), the period of most rank instability, are not included as they produced inconsistent hierarchies. In addition to considering rank as a continuous variable in analyses, we also discuss rank in broad categories of 'high', 'medium' and 'low', which we here define as being in the top third ('high', ranks 1–11), middle third ('medium', ranks 12–22) and bottom third ('low', ranks 23–33) in the 31 May 2009 hierarchy.

Collection of morphometric data

From January to March 2009, 15 males were trapped as part of the annual trapping period on Cayo Santiago (see Campbell & Gerald, 2004, for more information on a number of the measurements taken below). Trained staff members captured these males between 8:30 and 11:00 in a 100 m² feeding corral provisioned with monkey chow, netting or capturing males by hand, and then transferring them to a holding cage (0.62 × 0.42 × 0.62 m) and then to a field laboratory where they remained overnight. The following morning, veterinary technicians anaesthetized the males with ketamine (approx. 10 mg/kg via IM injection), and we weighed the anaesthetized males in a standard hanging scale. We used a 1 m ruler with 1 mm gradations to measure crown-rump length of each male in a standardized position with his back fully straight. We calculated body mass index (BMI) for each male by dividing mass (kg) by crown-rump length squared (m²). We used a caliper to measure the length of all four canines (mm) and the length of each testicle (mm), and a pincer caliper to measure body fat, about 2 cm above the umbilicus (mm). All these variables may be expected to be related to competitive ability. Body size (crown-rump length) might clearly be expected to aid in aggressive interactions with conspecifics, while measures of body condition (mass, BMI) are linked to endurance rivalry, and the ability of males to compete over time (Bercovitch, 1992). Canine length should reflect the ability of males to cause puncture wounds and gashes to rivals, while testicular size determines testicular testosterone (the endocrine parameter associated with male aggression; Wingfield et al., 1990) function directly, with male rhesus macaques exhibiting concurrent rises in testicular size and testosterone levels during the mating season (even in the absence of females; Herndon et al., 1996).

Data analysis

Description and classifications of coalitions

We present data on the number of male–male coalitions observed during our study, and categorize them according to the scheme of Chapais (1995; see above). We then describe a series of rank-changing revolutionary coalitions that occurred between 1 June 2009 and 10 August 2009, and show the changes in dominance rank that these precipitated according to the dominance rankings defined and produced above. We assess whether our data are consistent with predictions about such coalitions made by theoretical models (Pandit & van Schaik, 2003; van Schaik et al., 2006).

Characteristics of coalition partners

We use our data on these revolutionary coalitions to test hypotheses about the characteristics of coalition partners. For this, we do not treat each observation of a revolutionary coalition independently, as the majority of revolutions were against just 4 high-ranking targets (see Results). The revolutionary coalitions we observed were large, fluid and featured a number of the same individuals repeatedly (see Results). Due to difficulties in identifying every individual always involved in each coalitionary attack, and due to the repeated nature of the revolutionary attacks observed and the large and changing compositions of the perpetrators, we identified 8 individuals who we considered ‘core’ coalition members. Though this approach differs from that taken in some other studies of coalitions, we believe that the ‘gang-attack’ nature of the coalitions observed makes this the appropriate unit of analysis. Alternatives to our approach include undertaking all analyses separately for every observation of a revolutionary coalition, and its constituent males, but we are not convinced that this is appropriate given our observations. Core coalition males were confirmed as featuring in revolutionary coalitions against at least 2 of the 4 male targets. Although we cannot confirm that all these males were involved in every revolutionary event, we are more confident that over the course of all revolutionary events we observed all members. Firstly, we test the hypotheses that these core coalitionary males were of similar experience, age and familiarity (Collins, 1981; Smuts, 1985). We used a Mann–Whitney *U*-test to determine whether core coalitionary males ($N = 8$) were different in age, group residency length

(other males, $N = 33$, calculated as time since birth for natal males) or dominance rank (other males, $N = 25$, some males not ranked due to absence of recorded dominance interactions) from other group males present during June 2009. We then tested whether core coalition males, rather than just being different to other males with respect to these variables, were more similar to each other for these variables than other males were (either to core coalition males or each other). To do this, we calculated the absolute difference between two males' scores for every possible dyad across all study males for each variable. We then undertook Linear Mixed Models (LMM), in which we tested whether dyads of core coalition males had lower absolute differences between their values for each variable than other dyads did (i.e., were more similar). We controlled for multiple observations of males and male-specific variation by including the IDs of both males in each dyad as two separate random factors in models (as in, e.g., Gomes et al., 2009). Next, we tested whether males forming revolutionary coalitions were friends, or associates (Smuts, 1985). 7 of the 8 core coalition males were among our 20 focal males during the 3 months prior to the first observations of revolutions (March–May 2009). For all 20 focal males, we calculated the mean amount of time individuals spent with a focal male either as their interactant partner (in social behaviours) or as their nearest neighbour within 2 m. We then took these values and used a Mann–Whitney U -test to determine whether our 7 core coalition focals spent more time with other core coalition members in the 3 months of March–May 2009 than our other 13 focal males did. We also attempted to undertake social network analysis to investigate whether core coalition members were different from other males according to social network measures (as well as the effects that rank changes had on group structure). However the low frequency of association and interaction between rhesus males, and the absence of behavioural data for all 270 group members (or even all group males) made such analysis impossible. Finally, we tested whether core coalitionary males were of similar fighting ability (Bercovitch, 1988; Noë & Sluifster, 1990) using morphometric data, which were available for all 8 core coalitionary members, as well as for 7 non-coalition members. We tested the following variables: body length, mass, BMI, mean upper canine length, mean lower canine length, mean testicle length. We again undertook Mann–Whitney U -tests to investigate whether core coalition males and other males were different for these variables. We also undertook LMMs to

investigate whether dyads between coalition males had lower absolute differences between their values than other dyads did (i.e., were more similar), again controlling for multiple observations of males by including both male IDs from each dyad in all models.

All tests comparing whether core coalition males were different from other males for any variable were two-tailed. For tests of whether core coalition males were more similar to each other than other males were, we predicted for all variables that differences in values between males in coalition dyads would be lower (less absolute difference; hence, the two males are more similar) than differences in values between males in other dyads, and so we used one-tailed tests. Similarly, as we had a clear directional prediction that core coalition males would spend more time in association with each other than with other males, we again used a one-tailed test. Mann–Whitney U -tests were undertaken in SPSS 16.0, with exact (not asymptotic) probability values presented, while LMMs were undertaken in R 2.7.2. For all tests $p < 0.05$ was considered significant.

Results

Description and classifications of coalitions

Table 1 reports the number of different coalition types that we observed. Although we observed only one revolutionary coalition during the birth season, during the mating season we observed 15 of these coalitions. Of these, 14 represented attacks on just 4 males. On 31 May 2009, these 4 males were all high ranking males (positions 1, 2, 7 and 10). Within a little over 2 months, all four of these males had dropped in rank substantially, with the alpha male

Table 1. The number of male–male coalitions observed during the study, categorized according to the scheme of Chapais (1995).

Type of male–male coalition	No. observed (birth season)	No. observed (mating season)
Conservative	6	11
Bridging	0	1
Revolutionary	1	15*

* Although we observed revolutionary attacks on 15 occasions during the mating season, 14 of the observations that occurred actually represent repeated attacks on the same 4 individuals.

permanently expelled from the group (Table 2). Coalitionary males were the main beneficiaries of the resultant rank changes, with most (but not all) of them gaining status over this period (Table 2). As such, these coalitions can be classified as ‘all-up (revolutionary) rank changing’ (van Schaik et al.,

Table 2. Dominance ranks before and after the period of rank instability.

Rank no.	Dominance rank on 31 May 2009	Dominance rank on 10 August 2009
1	K85	* 11Z
2	83L	44T
3	* 11Z	* 50T
4	44T	03D
5	03D	**** 44H
6	* 50T	*** 50B
7	O15	** 57D
8	*** 50B	**** 21P
9	** 57D	** 91P
10	54V	** 14A
11	**** 44H	83L
12	**** 21P	54V
13	** 91P	O15
14	** 39L	** 39L
15	* 58R	**** 17K
16	** 14A	42T
17	70C	* 42F
18	61G	* 58R
19	**** 17K	46N
20	* 42F	T88
21	42T	85E
22	13N	50G
23	V83	89N
24	Z46	13I
25	99L	51J
26	85E	13N
27	X80	05I
28	T88	V83
29	46N	Z46
30	31I	01K
31	01K	X80
32	13I	70C
33	05I	61G
34		10R
35		99L

Table 2. (Continued.)

Rank no.	Dominance rank on 31 May 2009	Dominance rank on 10 August 2009
†	30Z	30Z
†	80B	80B
†	12Z	12Z
†	50G	
†	X81	
Extra group		K85

Ranks for 31 May 2009 are based on observations of male–male interactions in March, April and May ($N = 812$), while dominance ranks on 10 August 2009 are based on male–male interactions observed in July ($N = 361$), combined with observations of the attacks on the then alpha male (K85) on 10 August 2009. Target males are shown in boldface. Both sets of interactions produced statistically significant linear hierarchies. Interactions observed in June 2009, the period of most rank instability, are not included as they produced extremely inconsistent hierarchies.

† Males for whom we did not record a single interaction with other group males during the relevant periods. Although these males are formally considered part of Group R, they were extremely peripheral at the relevant times and interacted only very rarely with other group members.

* Involved in coalitions against 1 of the 4 targets.

** Involved in coalitions against 2 of the 4 targets.

*** Involved in coalitions against 3 of the 4 targets.

**** Involved in coalitions against all 4 targets. Individuals with 2 or more asterisks were classified as core coalition members.

2006). Table 3 gives a full descriptive account and timeline for these events. Contrary to theoretical predictions, coalitions were often large (five or more members; Table 3). Further, coalitions occasionally occurred with multiple targets (involving up to 3 of the 4 male targets), and also sometimes involved females.

Characteristics of coalition partners

Both non-natal and natal males took part in revolutionary coalitions against both non-natal and natal male targets. Consistent with predictions, coalition targets were high ranking, while coalition members were almost exclusively middle ranking (with one male being at the bottom of the high ranking males, most being at the top of the middle ranks, and no individuals being low ranking) (Table 2). Core coalitionary males were not different

Table 3. Chronology and description of rank-changing revolutions.

Date of first attack	Target ID	Origin of target	IDs of confirmed coalition members*	Description of revolution	Mean number of members in each observation
1 June 2009	O15	Non-natal	21P, 39L, 44H, 50B, 17K	O15 seen fear grinning at lower ranked males (21P, 39L) and being threatened by them. Further attack on 30 June when chased down cliffs along with 83L and 54V.	3
3 June 2009	54V	Natal	21P, 39L, 44H, 17K, 14A, 91P	First observed attack involved coalition of 21P, 44H, 17K; 54V was driven from the group. Sustained attacks driving 54V repeatedly from the group over the following 4 weeks with coalition members sometimes changing between each observation. Was eventually allowed to return to group periphery in a lower ranked position, probably due to natal status.	3.5
21 June 2009	83L	Natal	57D, 50B, 44H, 17K, 58R, 21P, 91P, 42F, 14A	First attack likely 21 June, first observations 22 June, involving 57D, 44H, 50B; 83L was driven from the group and into the sea. Sustained attacks over the following 2 weeks, in which 83L was chased all over both islands, and repeatedly driven into the sea. Coalition members sometimes changed between each observation. Was eventually allowed to return to group periphery in a lower ranked position, probably due to natal status.	4.8
10 August 2009	K85	Non-natal	11Z, 50B, 44H, 57D, 17K, 21P, 50T	Initiated by natal male 11Z, with many males supporting. Alpha family females were also involved in the attack directly. K85 was driven into the sea and not allowed to return, having to swim to the other side of the other island in order to come back to land. Was never allowed to rejoin group.	7**

* Note that not all of these males partook in every coalitionary incident observed, but all took part at one time or another. In each observation several individuals were involved and it was difficult always to identify all members.

** Only one observation. This should be treated as an absolute minimum, and many females were also involved.

in age (Mann–Whitney, $z = -0.190$, $p = 0.868$), rank (Mann–Whitney, $z = -1.428$, $p = 0.162$) or group residency from other males (Mann–Whitney, $z = -0.552$, $p = 0.588$). Although core coalitionary males were not more similar to each other in age than other males were (LMM, $t_{1,779} = -0.108$, $p = 0.457$), they were more similar to each other in rank (LMM, $t_{1,495} = -6.521$, $p < 0.001$; Table 2), and in length of group residency (mean difference in group residency length; core coalition male dyads, 949 ± 132 days; all other dyads, 1538 ± 51 days; LMM, $t_{1,779} = -2.041$, $p = 0.021$) than other males were. (These two variables are correlated, LMM, $t_{1,495} = 11.230$, $p < 0.001$.) In the first three months of the breeding season, before the onset of rank instability, core coalition members spent more time with other core coalition members than non-coalition members did (Mann–Whitney, $z = -1.941$, $p = 0.028$). Of the morphometric variables tested, significant differences were obtained for two; core coalition members had significantly longer lower canines than other males (core coalition males, mean = 11.7 ± 0.7 mm; other males measured, 9.2 ± 0.9 mm; $z = -2.083$, $p = 0.040$), and were more similar to each other in body mass than other males were (mean difference in body mass; core coalition male dyads, 1.6 ± 0.3 kg; other male dyads, 2.4 ± 0.2 kg; LMM, $t_{1,90} = -2.26$, $p = 0.013$). Coalitionary males were not morphometrically different from other males in other ways tested.

Discussion

This study reports the first systematic description and analysis of male–male revolutionary coalitions in free-ranging rhesus macaques. The coalitions we observed were ‘all-up (revolutionary) rank changing’ (van Schaik et al., 2006), with top ranked males expelled from the group (though all but the alpha male were able to return in lower ranked positions), and many (but not all) coalition members rising in rank. Following revolutionary coalitions, we observed individual members of the coalitions receiving fear grins and other signs of submission from individuals that were formerly higher ranked than those coalition members. Although it is always difficult to pinpoint the exact cause of a rank change, our observations suggest that the revolutionary coalitions were the cause of the observed drop in ranks of the targets. Our results support predictions that such coalitions are likely to occur against top or near-top ranked individuals (all coalition targets were in the top third

of male ranks), and consist of members just below this top rank bracket, rather than low ranking males (no males in the bottom third of ranks took part). Low ranking males did not participate in revolutionary coalitions, perhaps related to the fact that many of them were relatively recent immigrants (reflected partly in the significant differences between coalition males and other males in group residency length), and were also relatively peripheral (reflected partly in significant differences in association of coalition males with other coalition males, compared to non-coalition males). Given previous studies suggesting that coalitions are more likely among friends and associates (Smuts, 1985; supported by results in the present study), these factors may make these males less likely to form coalitions. Our results did not support theoretical predictions that revolutionary rank-changing coalitions will be of small (two or three male) size (van Schaik et al., 2006).

Although our observations demonstrate that free-ranging male rhesus macaques can form revolutionary coalitions against other males, as has been shown for other macaque species (e.g., *Macaca fascicularis*; van Schaik et al., 2006) and in some non-primates (e.g., African wild dogs, *Lycaon pictus*, de Villiers et al., 2003), it is likely that some aspects of the observed coalitionary aggression may be influenced by the characteristics of the Cayo Santiago rhesus macaque population. Medium levels of reproductive skew are commonly observed on Cayo Santiago (Berard et al., 1994; Widdig et al., 2004), whereas rhesus macaques are usually considered to be highly despotic in social structure (Maestriperi, 2007), a factor that should lead to very strong reproductive skew. The abundance of food on the provisioned island means that extremely large (up to 300) group sizes are sustainable (due to low food competition). Such large groups effectively reduce the ability of high-ranking males to monopolize females in the group, which may reduce reproductive skew (although we do not have direct measures of reproductive skew, we have no reason to believe our study group different from the medium levels of skew reported by previous studies on this and other groups on Cayo Santiago (e.g., Berard et al., 1994)). This reduced reproductive skew may be a sign of, or be associated with, reduced despotism in these large groups, which makes revolutionary coalitions more feasible (Pandit & van Schaik, 2003; van Schaik et al., 2006). In addition, in such large groups, individual males have plenty of females to mate with within their own group that they are not related to, leading to a reduced need to disperse, and consequent low dispersal. The effect of this may work in two ways. Firstly, this

could lead to natal males, who are well supported by female family members, being emboldened against non-natal males (as perhaps in the case of the revolution against the alpha male in the current study), such that there are increased incidences of natal males instigating revolutions. Secondly, and in contrast, non-natal males may find very young (not full adult size) natal males in high ranked positions, which they have achieved through the support of their family. The presence of high-ranked, small-bodied, young natal males may encourage lower-ranked fully-grown adult males to form coalitions to depose such males. In addition to an effect of large group sizes on relatedness, large group size also leads to a good number of available group males — a necessary prerequisite for male–male coalitions.

That said, there has been a very high number of observation hours on Cayo Santiago, and these observations are still highly unusual. It is difficult to highlight factors that may have led to the emergence of coalitions in this year particularly. The presence of a very old alpha male may have been a factor, as females appeared to refuse to mate with him on numerous occasions during the present study. This suggests both low levels of support for the alpha male among females, as well as, potentially, low levels of alpha male paternity in recent years. Reduced levels of despotism in social behaviour make revolutionary coalitions more feasible (van Schaik et al., 2006). However, we observed nothing else unusual about this particular year that may have led to such dramatic revolutionary coalitions at this time.

We found evidence that males forming coalitions are different from other males. Firstly, though we found no relationship between coalition membership and age (similar to results found in spotted hyenas, Zabel et al., 1992), we showed that coalitionary males were similar in rank, of similar group residency lengths (supporting previous hypotheses for baboons; Collins, 1981; Smuts, 1985; Noë, 1986), and are likely to be associates, spending longer periods of time with each other than other males do (again supporting a previous hypothesis for baboons about friendships; Smuts, 1985). It is worth noting, however, that males who were more similar in rank were also more similar in group residency length, and it was not possible to separate these effects statistically. We found some evidence to support the hypothesis that coalitionary males were of similar fighting ability (Bercovitch, 1988; Noë & Sluiter, 1990), with core coalition members being more similar to each other in mass than other males were, as well as being relatively more armoured than other males, with longer lower canine lengths. Together, these

results suggest that males forming coalitions are associates who have been in the group for a similar length of time, who are of similar overall size but who are relatively more armoured than other males. Collectively these results fit most predictions made for baboons coalitions (summarized in Noë & Sluifjer, 1995).

Despite our data meeting a number of predictions for baboon coalitions, in many ways the coalitions reported here are different both to those observed in baboons (e.g., Bercovitch, 1988; Noë & Sluifjer, 1995), and to those more commonly seen among primate males (van Schaik et al., 2006). The coalitions we observed were not like the temporary levelling coalitions seen in baboons that allow at least one coalition male access to a female (Bercovitch, 1988). Instead, they resulted in long-term changes in dominance, were large, occurred repeatedly against the same individuals, were fluid in composition, sometimes included females, and occasionally had multiple targets. In many ways, the coalitions observed were like 'gang attacks' from a group of individuals against another, smaller group of individuals, which were targeted both separately and together.

Though revolutions began in the middle of the mating season, they continued until the very end of the mating season, with the revolutionary coalition against the alpha male not occurring until after mating was almost exclusively over. As such, observed coalitions were not simply associated with very short-term mating benefits. Most (but not all) of the males participating in coalitions appeared to gain directly from them, in that they rose in rank as a result of the dominance changes they initiated. Further, they also rose in rank to positions above the targets. Given that the highest ranking males in groups on Cayo Santiago sire the most offspring (Berard et al., 1994; Widig et al., 2004), the direct benefits to males of participating in revolutionary rank-changing coalitions are obvious, and explain why such strategies are favourable. In the overthrow of the alpha male, high ranking females were involved, and their role may have been important given the reputation of the rhesus macaque as a highly matriarchal species. Despite our observations of coalition formation, there may be some truth to the notion that adult rhesus males generally have poor and uncooperative relationships with each other compared to other closely related species (Maestripieri, 2007). For example, on Cayo Santiago, low and mid ranking individuals are often found alone, and show low levels of affiliation with each other when compared with males in other closely related species, such as the Barbary macaque (Bissonnette

et al., 2009). Careful field observations and tests of evolutionary hypotheses, such as those presented here, are essential alongside models of primate male coalitions (e.g., Pandit & van Schaik, 2003; van Schaik et al., 2006; Stamatopoulos et al., 2009), in order to elucidate further one of the most complex and intriguing types of animal social behaviour.

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References

- Berard, J.D., Nürnberg, P., Epplen, J.T. & Schmidtke, J. (1994). Alternative reproductive tactics and reproductive success in male rhesus macaques. — *Behaviour* 129: 177-201.
- Bercovitch, F.B. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. — *Anim. Behav.* 36: 1198-1209.
- Bercovitch, F.B. (1992). Estradiol concentrations, fat deposits, and reproductive strategies in male rhesus macaques. — *Horm. Behav.* 26: 272-282.
- Bernstein, I.S. & Ehardt, C.L. (1985). Agonistic aiding: kinship, rank, age and sex influences. — *Am. J. Primatol.* 8: 37-52.
- Bissonnette, A., Bischofsberger, N. & van Schaik, C.P. (in press). Mating skew in Barbary macaque males: the role of female mating synchrony, female behavior and male–male coalitions. — *Behav. Ecol. Sociobiol.*
- Bissonnette, A., de Vries, H. & van Schaik, C.P. (2009). Coalitions in male Barbary macaques, *Macaca sylvanus*: strength, success and rules of thumb. — *Anim. Behav.* 78: 329-335.
- Campbell, B.C. & Gerald, M.S. (2004). Body composition, age and fertility among free-ranging female rhesus macaques (*Macaca mulatta*). — *J. Med. Primatol.* 33: 70-77.
- Chapais, B. (1992). The role of alliances in the social inheritance of rank among female primates. — In: *Coalitions and alliances in humans and other animals* (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 29-59.
- Chapais, B. (1995). Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. — *Am. J. Phys. Anthropol.* 38: 115-136.
- Collins, D.A. (1981). Social behaviour and patterns of mating among adult yellow baboons (*Papio c. cynocephalus* L. 1776). — PhD thesis, University of Edinburgh, Edinburgh.

- de Villiers, M.S., Richardson, P.R.K. & van Jaarsveld, A.S. (2003). Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*). — *J. Zool.* 260: 377-389.
- de Waal, F.B.M. & Harcourt, A.H. (1992). Coalitions and alliances: a history of ethological research. — In: *Coalitions and alliances in humans and other animals* (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 1-19.
- Dugatkin, L.A. (1997). Co-operation among animals: an evolutionary perspective. — Oxford University Press, Oxford.
- Dugatkin, L.A. (1998). A model of coalition formation in animals. — *Proc. Roy. Soc. Lond. B: Biol.* 265: 2121-2125.
- Gomes, C.M., Mundy, R. & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. — *Proc. Roy. Soc. Lond. B: Biol.* 276: 699-706.
- Gompper, M.E. (1996). Foraging costs and benefits of coati (*Nasua narica*) sociality and asociality. — *Behav. Ecol.* 7: 254-263.
- Harcourt, A.H. (1992). Coalitions and alliances: are primates more complex than non-primates? — In: *Coalitions and alliances in humans and other animals* (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 445-471.
- Herndon, J.G., Bein, M.L., Nordmeyer, D.L. & Turner, J.J. (1996). Seasonal testicular function in male rhesus monkeys. — *Horm. Behav.* 30: 266-271.
- Hoffman, C.L., Ruiz-Lambides, A.V., Davila, E., Maldonado, E., Gerald, M.S. & Maestripieri, D. (2008). Sex differences in survival costs of reproduction in a promiscuous primate. — *Behav. Ecol. Sociobiol.* 62: 1711-1718.
- Johnstone, R.A. & Dugatkin, L.A. (2000). Coalition formation in animals and the nature of winner and loser effects. — *Proc. Roy. Soc. Lond. B: Biol.* 267: 17-21.
- Kaplan, J.R. (1977). Patterns of fight interference in free-ranging rhesus monkeys. — *Am. J. Phys. Anthropol.* 47: 279-287.
- Lusseau, D. (2007). Why are male social relationships complex in the doubtful sound bottlenose dolphin population? — *PLoS One* 2: e348.
- Maestripieri, D. (2007). Macchiavellian intelligence: how rhesus macaques and humans conquered the world. — The University of Chicago Press, Chicago, IL.
- Manson, J.H. (1996). Male dominance and mount series duration in Cayo Santiago rhesus macaques. — *Anim. Behav.* 51: 1219-1231.
- Manson, J.H. (1998). Evolved psychology in a novel environment: male macaques and the "Seniority Rule". — *Hum. Nat.* 9: 97-117.
- Maslow, A.H. (1936). The role of dominance in the social and sexual behaviour of infra-human primates: IV. The determination of hierarchy in pairs and in a group. — *Pedag. Semin. J. Gen. Psychol.* 49: 161-198.
- Meikle, D.B. & Vessey, S.H. (1981). Nepotism among rhesus monkey brothers. — *Nature* 294: 160-161.
- Mesterton-Gibbons, M. & Sherrat, T.M. (2007). Coalition formation: a game-theoretic analysis. — *Behav. Ecol.* 18: 277-286.
- Missakian, E.A. (1972). Genealogical and cross-genealogical dominance relationships in a group of free ranging monkeys *Macaca mulatta* on Cayo Santiago. — *Primates* 13: 169-180.
- Noë, R. (1986). Lasting alliances among adult male savannah baboons. — In: *Primate ontogeny, cognition and social behaviour* (Else, J.G. & Lee, P.C., eds). Cambridge University Press, Cambridge, p. 445-471.

- Noë, R. & Sluijter, A.A. (1990). Reproductive tactics of male savanna baboons. — *Behaviour* 113: 117-170.
- Noë, R. & Sluijter, A.A. (1995). Which adult male savanna baboons form coalitions? — *Int. J. Primatol.* 16: 77-105.
- Pandit, S.A. & van Schaik, C.P. (2003). A model for levelling coalitions among primate males: toward a theory of egalitarianism. — *Behav. Ecol. Sociobiol.* 55: 161-168.
- Rawlins, R.G. & Kessler, M.J. (1986). *The Cayo Santiago macaques: history, behavior, and biology.* — SUNY Press, Albany, NY.
- Silk, J.B. (1992). Patterns of intervention in agonistic contests among male bonnet macaques. — In: *Coalitions and alliances in humans and other animals* (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 215-232.
- Smuts, B.B. (1985). *Sex and friendship in baboons.* — Aldine, Hawthorne, NY.
- Stamatopoulos, G., Sengupta, A., Vogel, E.R. & Janson, C.H. (2009). A game-theoretic model of within-group coalition formation in non-human primates. — *J. Bioecon.* 11: 165-183.
- Szykman, M., Engh, A.L., Van Horn, R.C., Boydston, E.E., Scribner, K.T. & Holekamp, K.E. (2003). Rare male aggression directed toward females in a female-dominated society: baiting behavior in the spotted hyena. — *Aggress. Behav.* 29: 457-474.
- Thierry, B. (2007). The macaques: a double-layered social organization. — In: *Primates in perspective* (Campbell, C., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S., eds). Oxford University Press, Oxford, p. 224-239.
- van Schaik, C.P. & Kappeler, P.M. (eds) (2006). *Co-operation in primates and humans: mechanisms and evolution.* — Springer, Berlin.
- van Schaik, C.P., Pandit, S.A. & Vogel, E.R. (2004). A model for within-group coalitionary aggression among males. — *Behav. Ecol. Sociobiol.* 57: 101-109.
- van Schaik, C.P., Pandit, S.A. & Vogel, E.R. (2006). Toward a general model for male–male coalitions in primate groups. — In: *Co-operation in primates and humans: mechanisms and evolution* (van Schaik, C.P. & Kappeler, P.M., eds). Springer, Berlin, p. 143-163.
- Widdig, A., Bercovitch, F.B., Streich, J.W., Nürnberg, P. & Krawczak, M. (2004). A longitudinal analysis of reproductive skew in male rhesus macaques. — *Proc. Roy. Soc. Lond. B: Biol.* 271: 819-826.
- Wingfield, J.C., Hegner, R.E., Dufty Jr., A.M. & Ball, G.F. (1990). The “Challenge Hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems and breeding strategies. — *Am. Nat.* 136: 829-846.
- Wrangham, R.W. (1928). Mutualism, kinship and social evolution. — In: *Current problems in sociobiology* (King’s College Sociobiology Group, eds). Cambridge University Press, Cambridge, p. 269-289.
- Zabel, C.J., Glickman, S.E., Frank, L.G., Woodmansee, K.B. & Keppel, G. (1992). Coalition formation in a colony of prepubertal spotted hyenas. — In: *Coalitions and alliances in humans and other animals* (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 113-115.
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