

Report

Dominance and Affiliation Mediate Despotism in a Social Primate

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Summary

Group-living animals routinely have to reach a consensus decision and choose between mutually exclusive actions in order to coordinate their activities and benefit from sociality [1, 2]. Theoretical models predict “democratic” rather than “despotic” decisions to be widespread in social vertebrates, because they result in lower “consensus costs”—the costs of an individual foregoing its optimal action to comply with the decision—for the group as a whole [1, 3]. Yet, quantification of consensus costs is entirely lacking, and empirical observations provide strong support for the occurrence of both democratic and despotic decisions in nature [1, 4, 5]. We conducted a foraging experiment on a wild social primate (chacma baboons, *Papio ursinus*) in order to gain new insights into despotic group decision making. The results show that group foraging decisions were consistently led by the individual who acquired the greatest benefits from those decisions, namely the dominant male. Subordinate group members followed the leader despite considerable consensus costs. Follower behavior was mediated by social ties to the leader, and where these ties were weaker, group fission was more likely to occur. Our findings highlight the importance of leader incentives and social relationships in group decision-making processes and the emergence of despotism.

Results and Discussion

The way in which group-living animals coordinate their actions is fundamental to our understanding of the evolutionary and ecological basis of sociality. The benefits of group living are largely reliant on animals remaining cohesive, which often requires consensus choices from mutually exclusive actions [3]. Thus far, empirical work on consensus decision making

has primarily concentrated on the eusocial insects [6], large insect swarms [7], fish schools [8], and bird flocks [9], in which collective behavior can emerge from simple rules of self-organization [10, 11]. Much less is known about the mechanisms underlying decision making in socially complex and heterogeneous groups, in which individuals are often related and have long-term social relationships with one another [2] (e.g., social birds, carnivores, and primates). In these groups, individual group members often differ with respect to optimal activity budgets [12], levels of information [13], and ability to monopolize resources [14]. Such differences lead to conflicts of interest that can impede the achievement of consensus decision making [15]. In the face of such conflict, two different modes of decision making might be adopted. First, consensus decisions can be reached democratically, whereby all group members contribute to the decision, independent of their individual identities or social status. At the other extreme, a decision can be despotic, taken by a single animal (“leader”) with other members (“followers”) abiding by this decision [2]. Theoretical models predict the former to be most common in nature [1, 3], and this is supported by a number of empirical examples [2]. However, despotic decisions are also widespread among group-living vertebrates [4], including humans [16]. The profusion of despotic decision making in nature therefore presents a significant challenge to our understanding of sociality.

There are conceivably several different types of animals that might emerge as a leader. In group movements, for instance, the individuals with the greatest incentives [17] or the most pertinent information [18] often lead groups, and are normally—but not always [19]—at the front of group progressions. Yet, the incentives or information required to create leaders does not necessarily generate following, and both processes are necessary for a despotic decision. New insights into group decision making may therefore be acquired by an understanding of not only what incentives may be necessary for leaders to emerge but also why followers accept a leader's decisions, especially when this compromises their own activity [2]. In the latter case, one possibility is that long-term benefits derived from social or genetic ties with the leader outweigh the short-term costs associated with accepting the leader's current decision. This explanation is supported by recent research indicating that follower roles may be primarily associated with stable vertebrate social systems [20, 21] in which kin support one another during conflicts [22] and the cultivation and exploitation of social relationships with those who are not kin can also enhance fitness [23]. In this study, we ask (1) whether the acquisition of foraging benefits by a minority of individuals creates incentives for them to lead; (2) whether group-mates are willing to follow leaders despite large consensus costs; and (3) whether such follower behavior is mediated by social and/or genetic ties to the leader.

We used an experimental approach in wild chacma baboons to estimate the benefits to leaders and costs to followers for democratic and despotic decisions. Baboon groups are an ideal model system in which to explore such questions. Previous observations of baboon movement patterns suggest that their group decisions may be largely democratic in nature but also have the potential for active leadership by both male and

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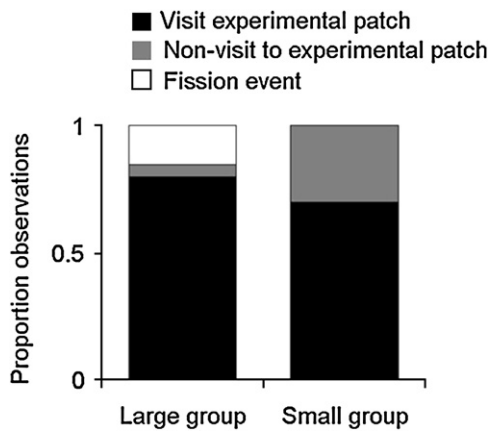


Figure 1. Group-Decision Outcomes

Two baboon groups (large, small) were presented with the opportunity to visit experimental food patches. These patches were designed to create benefits for a minority of individuals but costs for the majority. Group decisions that resulted in patch visits are shown in black, whereas nonvisits are shown in gray. Group fissions, in which groups did not reach a consensus but rather split, are shown in white.

female group members [19, 24–26]. Groups comprise a complex social system with a linear dominance hierarchy and are heterogeneous in composition. The dominance hierarchy also results in large asymmetries in resource-holding potential [14] and, thus, potentially high consensus costs from despotic foraging decisions in which dominant animals have incentives to lead. Furthermore, genetic and social ties among group members can influence individual behavior [22], providing fitness benefits [23].

Democratic or Despotic Group Decisions?

Two wild-baboon groups (one large, one small) were presented with an experimental food patch within their home range. This patch was of a size and shape predicted to create highly skewed foraging benefits among group members, relative to naturally occurring food resources. Thus, patches were expected to create consistent incentives for a minority of dominant individuals to lead and to result in consensus costs for the majority of followers. We therefore interpreted visits to experimental food patches as being the result of despotic decisions and visits to natural food patches as the result of democratic decisions.

We found that both baboon groups consistently visited the experimental food patch in preference to natural patches (Figure 1), indicating that despotic group decisions were the norm. The pattern of patch visits suggested that these decisions were made intentionally rather than opportunistically: at sunrise, the groups usually traveled directly from their sleeping sites to the patch (median travel time: 58 min). Groups then spent a large proportion of their normal foraging time at the patch location or, for those individuals who rarely entered the patch, at its periphery (mean \pm SE: 83 ± 5 min). This is comparable to >30% of the baboons' normal daily foraging time. The groups normally visited the location just once on any given day during the experimental period (median visits/day = 1) and left the patch only after it was completely empty. Additionally, examination of group daily travel routes showed that the groups passed through the experimental food patch locations significantly more often when food was present ($\chi^2_1 = 6.13$, $p = 0.01$; Figure S1, available online).

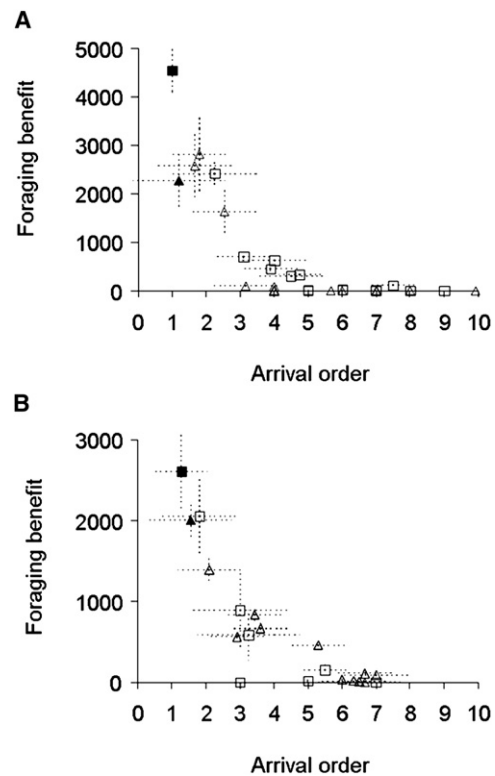


Figure 2. Leader Incentives and Identity

The mean \pm SE foraging benefit attained in experimental patches, as a function of mean \pm SE arrival order, for the large group (A) and the small group (B). Data for high-contest- and low-contest-competition treatments are shown in squares and triangles, respectively, and standard errors are depicted by dotted lines. The dominant male (filled symbols) usually arrived first and gained the highest foraging benefits, except in the large group during low-contest conditions, when his attempts to monopolize a larger area and chase off competitors resulted in a reduced intake rate. Indeed, the dominant male tended to acquire the highest foraging benefits in the high-contest-competition treatment, when food was more easily monopolized (t tests between treatments: $T_{\text{large}} = -2.25$, $df = 30$, $p = 0.04$; $T_{\text{small}} = -1.91$, $df = 25$, $p = 0.098$).

Leader Incentives and Follower Costs

During our experiments, we also varied the degree to which the experimental food patches could be monopolized. Patches were provided in two treatments: “low”- and “high”-contest competition. The low-contest treatment presented the same amount of food as the high-contest treatment but over twice the area. This design allowed us to investigate patterns of despotism in relation to different configurations of benefits to leaders and consensus costs to followers. The leader was defined as the animal that arrived first at the patch [21, 27], with others defined as followers.

In both treatment types, the dominant male was usually the first to arrive at the food patch (Figure 2). Dominant males, therefore, acted as leaders more frequently than expected by chance (Binomial tests: $p < 0.001$ for each group). Dominant males also tended to obtain more food in the high-contest patches than in the low-contest patches (Figure 2). Nevertheless, the incentives for leaders in the low-contest treatment were still sufficiently high to result in despotic decisions. Later arrivals at the patch acquired progressively less food in both treatments (Figure 2). We also found that the influence of social rank on arrival extended beyond the leader, producing a linear

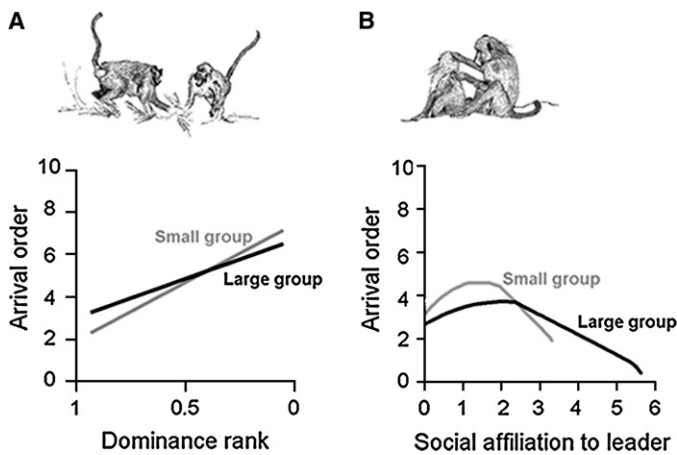


Figure 3. The Role of Dominance Rank and Social Affiliation

(A) High-ranked animals arrived earlier at experimental food patches than subordinates (GLMMs: small group, $\chi^2_1 = 32.9$, $p < 0.001$; large group, $\chi^2_1 = 2.9$, $p < 0.001$).

(B) The effect of an individual's social affiliation to the leader on that individual's arrival order (GLMMs: small group, $\chi^2_1 = 37.4$, $p < 0.001$; large group, $\chi^2_1 = 33.8$, $p < 0.001$).

The lines shown are the predicted effects from GLMMs controlling for all other significant effects and for repeated observations of individuals across days. See Table S1 for the full model results.

increase in arrival order with rank (Figure 3A). Previous research has indicated that under natural foraging conditions, leadership may be more evenly distributed across the group [28], a pattern also observed in this population (Figure S2), suggesting that the active leadership by the dominant male reported here was linked to his foraging benefits.

We then estimated the individual costs and gains of despotic decisions as the difference in consumption between natural and experimental conditions. Our analyses revealed that a minority of group members visiting the experimental patch obtained consensus gains, but the majority experienced substantial consensus costs (Figure 4). Moreover, these costs were more strongly skewed under conditions of high-contest competition than low-contest competition: the binomial skew index B [28] increased by 27%–76% between treatments in the large and small groups, respectively (Figure 4).

These findings indicate that a majority of subordinate individuals will accept despotic decisions, even where this compromises their own activity. This result is consistent for decision outcomes that differ in costs and for groups of different size and is coherent with high-ranking individuals having a particularly strong influence on the behavior of other group members [29, 30]. This influence was sufficiently strong to generate follower behavior in the absence of “herding” or any other forms of coercive behavior [31, 32].

Why Accept Despotism?

This leaves an important outstanding question: given that many followers experienced high consensus costs of following dominant-led group decisions, why follow? To answer this, we explored whether despotic group behavior could be explained by genetic and/or social ties to leaders (dominant males). We found that individuals with stronger social affiliation to the leader followed more closely. However, this was not a linear effect, since some individuals were close followers despite low affiliation (Figure 3B). These individuals were adult males who arrived closely behind the leader by virtue of their dominance rank rather than their social relationship. We found no effect of an individual's genetic relationship to the leader on follower behavior (Table S1). We also tested for a more complex “chain” effect, in which an individual's follower behavior is determined by the social or genetic relationship to the animal directly ahead of it rather than to the leader. Thus, we compared the strength of social affiliation and genetic relatedness between sequential pairs (dyads) in the arrival order with that of an average pair in the group. We found no differences

for social affiliation (Wilcoxon tests across all trials: $W_{\text{large}} = 2967$, $n = 527$, $p = 0.68$; $W_{\text{small}} = 1721$, $n = 226$, $p = 0.99$) or for genetic relatedness in the large group ($W = 3860$, $n = 527$, $p = 0.10$), whereas relatedness was lower than average in the small group ($W = 1381$, $n = 226$, $p = 0.04$).

These findings suggest that close-follower behavior is more likely when social relationships between leaders and followers are strong. Therefore, we suggest that the long-term benefits derived from social ties with the leader may outweigh the short-term costs associated with accepting the leader's current decision. Close association with these individuals may provide females and their dependent offspring with direct fitness benefits, such as increased infant survival [33] and protection from predators [34]. Taken together with the preceding results, follower behavior appears to emerge as a combination of social rank and affiliation to the leader. In the first case, high-ranking animals most likely follow out of an interest in acquiring a share of the food in the patch (Figure 2), whereas in the second case, lower-ranked animals appear to follow primarily as a consequence of social affiliation (Figure 3B). The absence of a kinship effect on follower behavior might appear puzzling. However, in this case, the leader was most often the dominant male, who is an immigrant into the group and thus unrelated to other group members.

Group Fissions and Consensus Nonvisits

Occasionally, the groups did not collectively visit the experimental patch. Rather, the groups either fissioned into two subgroups of which only one visited the patch ($n = 6/80$) or remained cohesive but failed to visit the patch entirely ($n = 14/80$) (Figure 1). In both cases, there was no clear temporal pattern to suggest that subordinates were learning to resist costly despotic decisions (Figure S3), nor was there any spatial pattern suggesting that group members were less inclined to visit on those days when travel costs were higher (t tests comparing distances between sleeping site and patch when $n \geq 6$ cases: fission, $t_{\text{large}} = 1.03$, $df = 5$, $p = 0.35$; nonvisits, $t_{\text{small}} = 0.73$, $df = 13$, $p = 0.48$). Therefore, we must seek alternative explanations for group fission and nonvisits.

Fission events occurred in accordance with the foraging benefits derived from the experimental patches, i.e., the minority subgroup was comparable in size to the number of animals acquiring a net consensus gain (Figure S4). Given the importance of social relationships in mediating follower behavior, we predicted that the distribution of fission events, which were only observed in the large group (Figure S3), reflected variation between the two groups in the strength of social relationships connecting the leader and other group members. To test this prediction, we compared the daily time spent in social activity (grooming) in the two groups, together with the size of the leader's social networks (i.e., grooming-clique size [35]). We

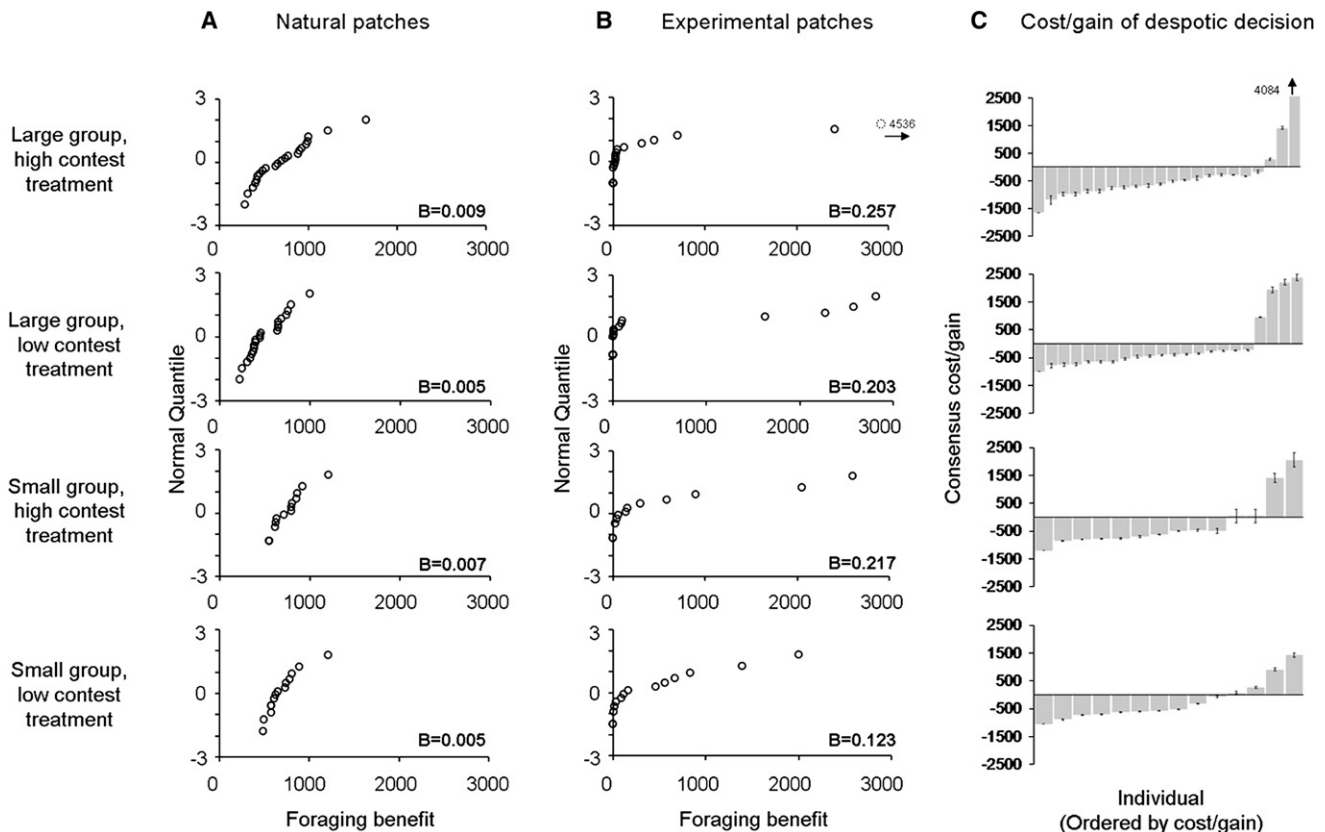


Figure 4. Foraging Benefits of Alternative Decisions and Consensus Costs of Despotism

Shown are normal quantile plots for the mean foraging benefits obtained by individual baboons belonging to the large and small group when at (A) natural and (B) experimental patches for comparable time periods, under two contest-competition treatments. Normal quantile plots are used to indicate skew from normality: where the distribution is normal, the points fall along a straight line. In addition, a binomial “B” skew index [28] is given, in which zero indicates a random distribution and higher values indicate increasing skew. The mean daily consensus cost or gain \pm SE for decisions to visit experimental patches over natural patches (i.e., foraging benefits in experimental patch minus foraging benefits in natural patch) is also shown, in panel (C).

found that not only did individuals in the larger group spend less time grooming (Mann-Whitney tests: $W = 2226049$, $n_{\text{large}} = 1644$, $n_{\text{small}} = 1096$, $p = 0.05$), but a smaller proportion of individuals interacted socially with the leader (0.50 versus 0.33 of adult females in the small and large groups, respectively). Both results support the interpretation that strong social relationships between leaders and followers are necessary for the emergence of despotic group decisions. We also considered the possibility that fission was driven by higher consensus costs, but these results did not differ between groups (Mann-Whitney tests: “high” treatment, $n_{\text{large}} = 16$, $n_{\text{small}} = 11$, $W = 266$, $p = 0.83$; “low” treatment, $n_{\text{large}} = 16$, $n_{\text{small}} = 17$, $W = 248$, $p = 0.73$) (Figure 4). Our findings are consistent with a wider pattern of time-budget stress in large groups that links reduced social time with a higher probability of fission [36].

Nonvisits are likely to reflect a different process. Specifically, in light of the preceding results, we anticipated that nonvisits might be associated with a switch in leader incentives. Consistent with our expectation, the dominant male was mate-guarding an oestrous female on the majority of nonvisiting days by the small group (9/12 cases; Figure S3), whereas he was never mate-guarding on the days that the group visited the patch (Fisher’s exact test: $p < 0.001$). No mate-guarding was recorded in the large group, and non-visits were correspondingly rare ($n = 2/40$). During mate-guarding (consortship) in baboons, males follow females closely, so it is the female

who guides and constrains her male partner’s behavior [37]. Because this particular oestrous female was only midranking (4/10 within females, and 8/14 overall) and experienced a net consensus cost from patch visits, there was no incentive for her to lead the dominant male to the patch.

Conclusions

Our field experiments on wild baboons indicate that despotic group decisions can emerge when an individual has both a strong incentive to lead and sufficient social influence to elicit follower behavior. Follower behavior occurred despite consensus costs, but where social ties were weaker, group fission was more likely. The influential role of the leader was further highlighted by the observation that groups failed to visit the food patch when the leader’s priorities changed. Our findings emphasize the importance of leader incentives and social relationships in group decision-making processes and the emergence of despotism.

Experimental Procedures

Study Site and Subjects

We conducted our study at Tsaobis Leopard Park, a wildlife reserve in the Karibib District of Namibia, Southern Africa (15° 45’ E, 22° 23’ S), with two groups of wild chacma baboons, *Papio ursinus* ($n_{\text{large}} = 60$; $n_{\text{small}} = 32$),

that were habituated to direct observation at close range and were individually recognizable. Our study focuses on adults only ($n_{\text{large}} = 22$: 4 males, 18 females; $n_{\text{small}} = 14$: 4 males, 10 females).

Foraging Experiments

Each group was offered an experimental food patch placed at a single location within its core home range (Figure S5). Patches were provided in two treatments: high-contest competition (20 days) and low-contest competition (20 days), both of which were of a size and shape that allowed access by only a minority (<50%) of baboons (although the high-contest patch excluded more individuals). The patch design was based on prior observation of the baboons' abilities to monopolize naturally occurring high-quality food patches. High-contest patches were 315 m² and 160 m² for large and small groups, respectively, equivalent to an available area of approximately 12.5 m² per adult baboon. Low-contest patches were increased by a factor of two, to 630 m² and 320 m², equivalent to approximately 25 m² per baboon. For each patch condition, the amount of food—dry maize kernels—presented remained constant per individual within groups, so that the large group received more than the small group, at approximately 80 g of maize per adult baboon in each case (each kernel was 0.39 ± 0.01 g). Low-contest patches followed high-contest patches, with an intervening period of at least 10 days during which no experiments were conducted. Consecutive experimental days started once the group had encountered the patch by chance. One experiment was run for each group, the first with the large group (6/15/06 to 8/5/06) and the second with the small group (8/24/06 to 10/15/06), during the same dry season [38] (see Figure S3).

Two observers followed the baboon groups on foot for full days throughout the study period, recording the group's daily route taken and any approach to the experimental food patches (taking group coordinates using handheld Garmin Etrex GPS units at 30 min intervals). Upon approach and entry into the patch, these observers recorded individual arrival order, bite rates, and time spent in patch for all baboons (see below). To identify any fission events and to corroborate arrival orders, a third observer was positioned at the food patches before sunrise each day.

Measuring Foraging Benefits

Foraging benefits for individuals during group visits to experimental food patches, defined as the number of kernels ingested per visit, were calculated from the time an individual spent in the experimental patch (rather than outside the patch) and his or her mean bite rate during this time (one kernel is consumed per bite). These data were obtained from patch scans and bite-rate observations, respectively. The patch scans recorded the number and identity of all individuals on the experimental patch at 5 min intervals. The bite-rate observations were 1 min focal watches, in which all hand-to-mouth consumptions of corn kernels were recorded, collected sequentially for all individuals in the patch. In total, 957 scans were completed: $n_{\text{large}} = 553$ (272, 281: scans for high-contest and low-contest patches, respectively) and $n_{\text{small}} = 404$ (138, 267). Similarly, $n_{\text{large}} = 1036$ bite-rate observations (601, 435 for high-contest and low-contest patches, respectively) and $n_{\text{small}} = 331$ (128, 203) were collected. Individually, each baboon appeared in 64 ± 1 scans and was sampled for 34 ± 1 bite-rate observations.

To measure the corresponding foraging benefits in natural food patches, one-hour focal watches on foraging adults were conducted during full-day follows. To control for any variation in foraging due to time of day, all individuals were sampled equally across both morning and afternoon observation periods. Focals were only begun once groups had been foraging for more than 20 min, to exclude periods of inactivity when resting, at waterholes, or at sleeping sites. During focals, all time spent feeding in patches (rather than traveling between patches) was recorded by continuous monitoring. Bite-rate observations were also made on individuals opportunistically during focal watches when visibility permitted. This allowed us to calculate the average food bites consumed per unit of time spent feeding in natural patches for each individual. This, in turn, allowed us to compare the number of bites obtained during feeding in the experimental patch versus the number of bites obtained over a comparable time period during feeding in natural patches: the consensus cost or gain. The natural foraging benefits corresponding to the high- and low-contest experimental patches were derived from a 20 day period preceding or following these patches, respectively (Figure S3). A mean ± SE of 15 ± 2 hr was recorded per individual, during which 25.5 ± 1.5 bite-rate observations were recorded. During these observations of natural foraging, the groups were never observed to fission.

Measures of Dominance, Social Affiliation, and Genetic Relationships

Dominance relationships were established on the basis of approach-avoid interactions (active supplants and displacements) between individuals. Dominance ranks were stable, so data were drawn from across the entire field season (May–December 2006) to provide a larger sample. These data were collected ad libitum ($n_{\text{large}} = 1485$, $n_{\text{small}} = 1698$ interactions), and their frequencies were recorded in actor-recipient matrices. Dominance hierarchies were then determined with Landau's linearity index (h) implemented in Matman [39], and linear hierarchies were found in both groups ($n_{\text{large}} = 0.65$, $p < 0.001$; $n_{\text{small}} = 0.93$, $p < 0.001$). All males outranked all females. Individual dominance ranks were then scaled by group size and assigned a value between 0 and 1, with 1 indicating the highest rank (i.e., dominant male) and 0 the lowest (i.e., most subordinate female).

Grooming is a standard measure of social affiliation in primates e.g., [40]. We used a matrix of grooming interactions collected ad libitum ($n_{\text{large}} = 2,535$, $n_{\text{small}} = 1,727$ interactions) over the course of the field season to calculate an index representing the strength of social affiliation between pairs of individuals (dyads). Because we were concerned with how evenly social contacts were distributed across dyads, our actor-recipient matrix was folded across the main diagonal and corresponding cells were summed to yield a triangular matrix. We then calculated the frequency of grooming for dyad ij divided by the mean frequency of grooming for all dyads in the group. High values of the index represent dyads that had stronger bonds than expected, and low values represent those with weaker bonds.

Variation in grooming time was calculated from scan data at 30 min intervals over the entire field season, excluding experimental periods ($n_{\text{large}} = 1645$ scans over 78 days, $n_{\text{small}} = 1097$ over 54 days). Scans began 30 min after the baboons left the sleeping site and ended at dusk at the sleeping site. Data on the proportion of baboons that were in view and engaged in five broad categories of activity were recorded: (1) traveling, (2) resting, (3) feeding, (4) grooming, and (5) drinking. Traveling was defined as brisk locomotion; feeding was defined as travel foraging (slow locomotion while searching for, manipulating, and ingesting food) and stationary foraging (searching for, manipulating, and ingesting food while remaining in one location); resting described the baboons' sedentary state in which they were not traveling or foraging and included sleeping; grooming involved affiliative allogrooming; and drinking referred to drinking from a waterhole.

Genetic relatedness between group members was derived from DNA analysis. We obtained DNA for adults in both groups from tissue ($n = 35$) and fecal ($n = 1$) samples as part of a wider investigation into relatedness in the Tsaobis baboon population (Cowlishaw et al., unpublished data). Individuals were genotyped at 17 microsatellite loci. See Table S1 for more details on the analysis of these data.

Statistical Analysis

Simple bivariate relationships were tested with standard two-tailed parametric tests (or nonparametric tests when the data could not be normalized). Arrival orders were analyzed with generalized linear mixed models (GLMMs). We conducted one model for each group and explored the effects of individual dominance rank, as well as social affiliation and genetic relatedness to the individual who arrived first. We also tested for the overall effects of treatment (high-contest patch, low-contest patch) and sex (male, female) on arrival order. All two-way interactions were tested, but none were found to be significant. We incorporated "day" and "individual ID" as random effects in our models, in order to control for nonindependence of repeated observations of individuals over experimental days. Backward elimination was used in selecting the minimal adequate model and included only those factors that contributed significantly ($p < 0.05$) to the explanatory power. The significance of fixed terms is presented as Wald statistics evaluated against the Chi-square distribution. Full model results are presented in Table S1.

Supplemental Data

Supplemental Data include five figures and one table and can be found with this paper online at [http://www.current-biology.com/supplemental/S0960-9822\(08\)01417-6](http://www.current-biology.com/supplemental/S0960-9822(08)01417-6).

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