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ORIGINAL ARTICLE

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A model for leveling coalitions among primate males: toward a theory of egalitarianism

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Abstract We present a simple model of within-group leveling coalitions among male primates. The model assumes that the value of the coalition is the sum of the payoffs of its members, that the individual's payoff is monotonically decreasing with its rank and that coalitions do not cause rank changes. It predicts that mainly mid- to low rankers engage in leveling coalitions, and that most coalition partners are of adjacent ranks. These predictions agree reasonably well with observations in nature. The model also makes the novel predictions that leveling coalitions are found where male mating competition has only a moderate contest component, and that male dominance ranks will become poorly differentiated where leveling coalitions are frequent. Both these predictions are consistent with observations on groups of macaques and baboons. The model also may account for leveling coalitions among egalitarian human foragers, without making additional assumptions about special human capabilities.

Keywords Male · Modeling · Primate · Within-group leveling coalition

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Introduction

As defined in animal behavior, coalitions are coordinated attacks by at least two individuals on one or more other individuals (targets), often preceded by signaling between the attackers (side-directed communication: Bercovitch 1988; de Waal and van Hooff 1981; de Waal and Harcourt 1992; Packer 1977). Coalitionary behavior is commonly observed among primates, but may also occur in some other mammalian lineages, such as carnivores (Zabel et al. 1992; Engh et al. 2000) and cetaceans (Connor et al. 1992, 1999), as well as in birds (Harcourt 1992).

Primate coalitions show the following general features. First, they tend to be formed by regular partners called allies (Noë 1990, 1992). Second, most coalitions have two participants, although larger ones are sometimes also observed (Noë 1990; Smuts 1985). Third, coalitions are mostly formed by members of the same sex, although intersexual coalitions may also occur (e.g. Watanabe 1979; Huffman, 1991).

However, features of primate coalitions may also vary across species. First, they may be targeted at either members of the same group or those of other groups. Coalitions targeted at other groups tend to be larger than within-group coalitions. Second, coalitions may involve either relatives or non-relatives. Those involving relatives usually take place in alliances with greater temporal stability (Pope 1990), and are more common among females (de Waal and van Hooff 1981). Third, coalitions, and the alliances they are part of, may or may not produce long term changes in dominance rank. Fourth, coalitions may either be leveling (i.e. all partners rank below the target) or not; leveling coalitions are generally thought to involve greater risks. Fifth, coalitions may be formed in response to an attack on one of the coalition partners (interventions) or they can be spontaneous (cf. militant egalitarianism: Boehm 1999). Finally, coalitions may or may not be constant-sum (van Hooff and van Schaik 1992). Coalitions among males competing over fertilization opportunities are constant sum, at least within groups, because the number of fertilizations in a given period of time is unlikely to be affected by coalition formation. On the other hand, coalitions among females competing for access to food generally are not constant sum, because individuals displaced by a coalition can find food elsewhere.

At present, we lack a general theory of coalition formation in animals that allows us to determine which of the distinctions drawn above are theoretically relevant and to comprehend their relations. As a first step, we develop a model here for one category of coalitions, inspired by Noë (1994): within-group coalitions involving unrelated males, that do not change dominance ranks, but are leveling and spontaneous and also constant-sum. Coalitions of this kind are observed in a number of primate species; the best known examples derive from savanna baboons (Bercovitch 1988; Noë 1990, 1992; Noë and Sluijter 1995; Packer 1977; Smuts 1985). These coalitions are overwhelmingly formed by past-prime, lower ranking males. They are targeted at high ranking, often top ranking, prime adult males. Coalitions generally are not thought to affect the ranks of the participants.

We are particularly interested in the coalitions over access to estrous females because they represent a constant-sum situation. Only ~25% (Noë 1989) of male-male coalitions in baboons concern access to estrous females. The other coalitions could either serve to maintain the alliance formed to improve access to estrous females, or may have a different function altogether (R. Noë, personal communication). Either way, an understanding of coalitions over estrous females is needed. We develop a one-parameter model that identifies all viable leveling coalitions among the males in a primate group and charts the degree of egalitarianism produced by them.

Methods

The model

We begin with an N -player constant-sum coalitionary game (Kahan and Rapoport 1984), where the players are arranged according to descending rank in a linear dominance hierarchy. We denote the payoffs of the players, which can be equated to *fitness* or a *fitness component*, by x_i where i is the rank of the individual. We assume that the result of coalition formation does not alter a male's rank, which allows us to identify an individual by its rank; that the ranks are unique, i.e. there are no two individuals with the same rank; and that the payoff x_i is a monotonically decreasing function of rank. These three assumptions allow us to identify an individual by its payoff. Henceforth, we will not distinguish between individual and rank.

We also assume that the value (strength) of a coalition is the sum of the payoffs of its members[1]. This assumption implies that differences in strength among players are relatively unimportant and overwhelmed by their motivations which in turn are determined by the payoffs. Analyses of fighting generally assume the importance of the benefit or value of access to a resource in decisions to escalate a contest (Maynard Smith and Parker 1976). Note that there is no immediate link between fighting ability or strength and payoff. Instead, this relationship is mediated by rank, i.e. fighting ability is assumed to determine rank, which in turn determines payoff.

The payoffs x_is of the males are the probabilities of fertilization for a given set of estrous females in the group in a particular time period, e.g. one season or one year. Rank-related payoffs are usually predicted by the priority of access model (Altmann 1962). As a result, payoff as a function of rank follows a concave, monotonically decreasing distribution, ranging from negative exponential to linear. Hence, we can assume that the difference between the payoff of the i^{th} individual and the (next higher ranking) $(i-1)^{th}$ individual is proportional to the payoff of the $(i-1)^{th}$ individual. i.e. $x_{i-1}-x_i$ proportional to x_{i-1}, or:

$$x_i - x_{i-1} = -\beta x_{i-1}, \tag{1}$$

where $0 \leq \beta \leq 1$. The value of this external parameter β reflects the environmental potential for despotism. Where the dominant male achieves all fertilizations in a group, $\beta=1$, corresponding to competition that is entirely through *contest* (sensu Łomnicki 1988). As the monopolization of sexual access by the dominant male decreases, $\beta<1$, and in the extreme case where all males in the group have approximately equal probability of siring offspring, $\beta \to 0$. Behaviorally, this situation would manifest itself as *scramble* competition. β tends to be reduced when (1) the number of females in the group increases, (2) the duration of each estrous period increases, and (3) the temporal overlap between estrous periods increases, usually because matings are seasonal (Nunn 1999). Thus, we adhere to the following terminology for the limiting cases:

β : 1 ⇔ 0
Competition : Contest ⇔ Scramble
Payoff distribution : Despotic ⇔ Egalitarian

Leveling coalitions can alter this payoff distribution and make it more egalitarian, but we assume that they always maintain the monotonic decrease of payoff with rank. This way of parameterizing the payoffs transforms our enormously complex problem into a simple one-parameter problem. We therefore model the effect of leveling coalitions through a single parameter α, and modify Eq. 1 to become $x_i-x_{i-1} = -\beta\alpha x_{i-1}$, where $0 \leq \alpha \leq 1$. The parameter α reflects the effect of coalition formation on the payoff distribution, where $\alpha=1$ corresponds to the starting point, the situation without any coalitions (of size greater than one). In a given coalition structure, the strongest coalition can alter the value of α, if doing so satisfies the condition of individual rationality (i.e. joining a coalition should not decrease the player's payoff; Kahan and Rapoport 1984). Thus, members of the strongest coalition will not agree to a change in α that would decrease their payoff.

Throughout, we assume that targeted high ranking males do not form retaliatory coalitions against the low ranking coalitionary attackers. We make this assumption because in nature it is not observed and the model actually can explain it (see Discussion). The absence of solidarity among the top rankers allows us to restrict ourselves to considering only a single multi-player coalition (if there is more than one leveling coalition then without loss of generality we need only consider the strongest among them). It is easy to see that if there is only a single successful leveling coalition in the group, then α will be reduced and hence leveling of the payoff distribution ensues. Later in this paper we will calculate the effect of successful leveling coalitions on the value of α.

The model always maintains the monotonicity of the payoff distribution. This monotonicity creates two possible artifacts. First, some higher ranking males who do not participate in the leveling coalitions will get a lower probability of paternity. In a constant-sum situation their probability should not change if successful leveling coalitions do not change the total number of potentially fertile matings. However, it is likely that the presence of leveling coalitions increases the total number of matings, which would indeed reduce their probability of paternity. Second, males ranking below those that participate in the leveling coalitions receive an increase in their probability of paternity. This creates a true discrepancy between model and reality. However, the advantage of ignoring this discrepancy is substantial because it makes the problem tractable

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[0] In this model coalitions of size one are allowed, in agreement with standard usage in game theory, but unlike usage in animal behavior.

by reducing the number of explicit parameters in the model. Moreover, this discrepancy is serious only if the successful leveling coalitions are small and involve relatively high ranking individuals only. As we show below, this situation is relatively rare.

Noë and Sluijter (1995) found that payoff distributions in groups with leveling coalitions were probably not monotonic. In particular, they suggest that the highest rankers in the leveling coalitions achieve a higher probably of paternity than those who rank immediately above them but do not participate in coalitions. This finding may reflect the true situation, although deviations from monotonicity tend to be small. However, it might also be an artifact of limited sampling. Under the model, high rankers also participate in leveling coalitions, but do so very rarely. Thus, if we could average over a vast number of coalitions monotonicity would again be approximated.

Results

For simplicity, we first consider the limiting case where coalition formation does not carry any costs, in effect equating payoff to fitness, as above. We then incorporate costs. Fitness now must become payoff minus costs (thus, costs change the relationship between payoff and fitness, not the payoff itself). This allows us to maintain the constraint that the sum of the payoffs is constant and acknowledge the absence of such a constraint on fitness.

Coalitions without cost

Consider a situation with only one coalition S_1 of size m>1. Let the lowest ranker in the coalition have rank p. For now we assume that the members of the coalition are rank neighbors. The value of this coalition is given by:

$$\begin{aligned} v(S_1) &= \sum_{i=p-m+1}^{p} x_i \\ &= \sum_{i=1}^{p} x_i - \sum_{i=1}^{p-m} x_i \\ &= x_1\left[\sum_{i=1}^{p}(1-\beta\alpha)^{i-1} - \sum_{i=1}^{p-m}(1-\beta\alpha)^{i-1}\right] \\ &= \frac{x_1}{\beta\alpha}\left[(1-\beta\alpha)^{p-m} - (1-\beta\alpha)^{p}\right]. \end{aligned}$$

Let $\sum_{i=1}^{N} x_i = 1$ (the constant-sum assumption), then the payoff of the highest ranking male is: $x_1 = \frac{\beta\alpha}{1-(1-\beta\alpha)^N}$ (Note that this payoff becomes increasingly dependent on N if the environmentally imposed contest is reduced, i.e. as $\beta \to 0$.) A coalition can change the value of α if and only if it is the strongest coalition. Since all other coalitions are of size one, we compare the value of the coalition S_1 with the value of the strongest singleton coalition $v(\{1\})=x_1$, to determine the condition for viability of S_1:

$$\begin{aligned} v(S_1) &> x_i, \forall\, 1 < p-m \leqslant p \\ ((1-\beta\alpha^{p-m} - (1-\beta\alpha)^p) &> \beta\alpha \\ 1-\beta\alpha)^p\left[\frac{1}{(1-\beta\alpha)^m} - 1\right] &> \beta\alpha \\ -m\ln(1-\beta\alpha) &> \ln\left(1+\frac{\beta\alpha}{(1-\beta\alpha)^p}\right) \\ m &> \frac{\ln\left(1+\frac{\beta\alpha}{(1-\beta\alpha)^p}\right)}{|\ln(1-\beta\alpha)|},\ \beta\alpha \neq 0 \end{aligned} \tag{2}$$

Equation 2 gives a lower bound on the size of viable coalitions (m). It also shows that the size of viable coalitions is independent of the size of the group. This is because the formation of coalitions is independent of the number of individuals ranking below the coalition partners and their payoffs. In other words, whether a group contains 10 or 50 males, the observed distribution of coalition sizes should not differ substantially.

We note that the condition derived in Eq. 2 on m is only a necessary condition. To obtain a sufficient condition we need to show that the extremum value of α for the strongest member of the coalition is less than 1, because this male would otherwise not be interested in forming a coalition. If this condition is satisfied for the strongest member, then it will also be satisfied for all other coalition members. To find the extremum value of α we calculate the first derivative with respect to α, and set it to zero. Let the extremum value of α be α_0. Hence,

$$\begin{aligned} x_i &= (1-\beta\alpha)^{i-1}x_1 = (1-\beta\alpha)^{i-1}\frac{\beta\alpha}{1-(1-\beta\alpha)^N} \\ 0 &= \left.\frac{\partial x_i}{\partial\alpha}\right|_{\alpha_0} \\ &= \frac{\beta(1-\alpha_0\beta)^{i-2}\left(1-\alpha_0\beta i + (1-\alpha_0\beta)^N(\alpha_0\beta(i-N)-1)\right)}{\left((1-\alpha_0\beta)^N - 1\right)^2} \end{aligned} \tag{3}$$

We calculate the roots of Eq. 3 using the Bisection-method for i=p–m+1 (the highest ranking male in the coalition), and we consider the coalition viable if $0 \leq \alpha_0 < 1$. This produces the upper bound on the size of viable coalitions. Fig. 1 shows the domain in which coalitions are viable as a function of β and m, for two values of p.

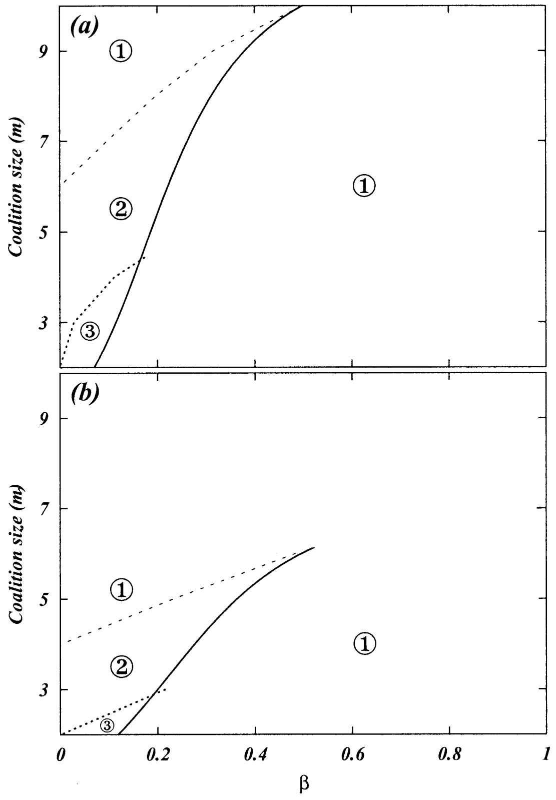

Fig. 1a, b Phase diagram of coalition formation. The *abscissa* is the environmental contest potential (β), and the *ordinate* is coalition size (m). In region ① no coalitions are predicted. In regions ② and ③ coalitions are expected in the model without cost, whereas in region ③ coalitions are expected even if coordination costs are incorporated (here with γ_3=0.004). In *panel* **a**, coalitions are built around the lowest-ranking male (rank 11 in a group of 11 males), whereas in *panel* **b**, they are built around a mid-ranking male (rank 7)

As shown in Fig. 1, coalitions are found only where the environmentally imposed degree of despotism (β) is limited. Because this value depends on several other parameters, which may be difficult to estimate in nature, it is interesting to determine the maximum value of β under which coalitions are viable. Thus, we consider the largest possible leveling coalition, p=N and m=N–1 (and α=1). Putting these values of p, m and α in Eq. 3 we write:

$$N-1 > -\frac{\ln\left(1+\frac{\beta}{(1-\beta)^{N}}\right)}{|\ln(1-\beta)|}$$

$$(1-\beta)^{-(N-1)} > 1+\frac{\beta}{(1-\beta)^{N}}$$

$$(1-\beta)-(1-\beta)^{N} > \beta$$

To determine the upper bound on β note that 1–β>β. Hence, for $\beta \geq ½$ leveling coalitions are impossible in this model, regardless of the values of the other parameters. In other words, only where the payoff curve is relatively shallow will coalitions of mid- to low rankers outperform top rankers.

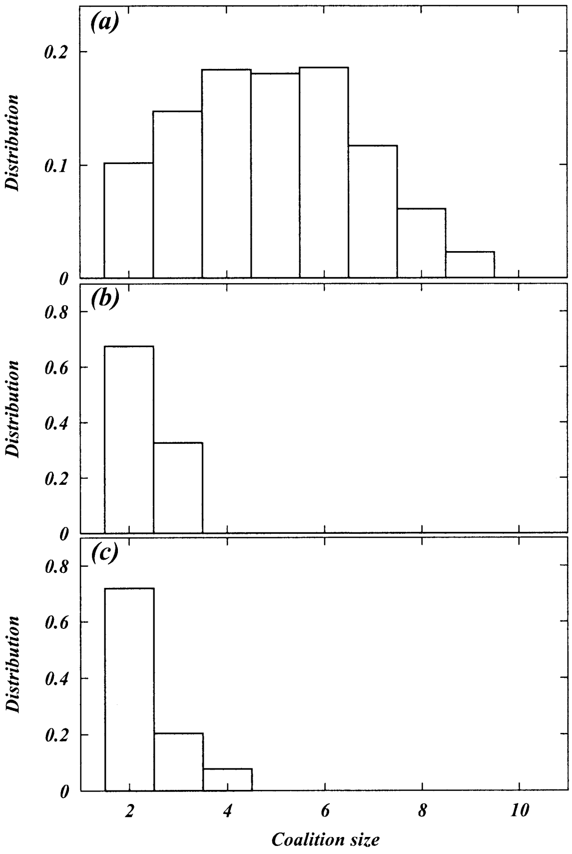

Fig. 2 The distribution of coalition sizes, averaged over all β, for all possible viable coalitions of all sizes, as predicted by the model without cost (**a**), or the model with cost (**b**), or averages of three groups observed in two field studies (**c**) (Smuts 1985; Noë and Sluijter 1995)

Figure 1 also suggests that coalitions tend to be of limited size. The lower the rank of the coalition partners, the larger the maximum size of the viable coalitions. The reason for this is straightforward: High-ranking individuals do not gain from joining coalitions. We can determine the size distribution of coalitions as follows: in a group of N=11, we systematically checked the complete range of p and β for all possible single coalitions, i.e. only one coalition of size >1 in a group. We computed the distribution of coalition size (m) over all coalitions that were viable (i.e. that satisfy individual rationality for all participants in the coalition). Figure 2a shows that m peaks at size 6, approximately half the group size.

Another important question about viable coalitions is the rank distribution of the participants. We used the same procedure as above except that instead of coalition size we studied the rank distribution for all possible viable coalitions of all sizes. Figure 3a shows that under average conditions mid- to low ranking individuals are the most likely members of leveling coalitions. The peak participation in this case is around rank 8 or relative rank ~0.75. The shape of this histogram turns out not to be sensitively dependent on the viable values of β.

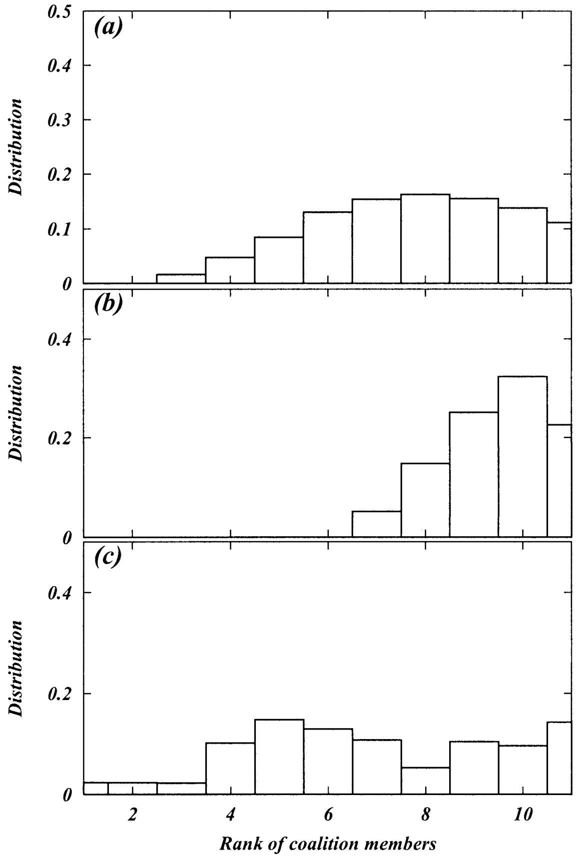

Fig. 3 The distribution of the ranks of the coalition partners, averaged over all β, for all possible viable coalitions of all sizes, as predicted by the model without cost (**a**), or the model with cost (**b**), or averages of three groups observed in two field studies (**c**) (Smuts 1985; Noë and Sluijter 1995)

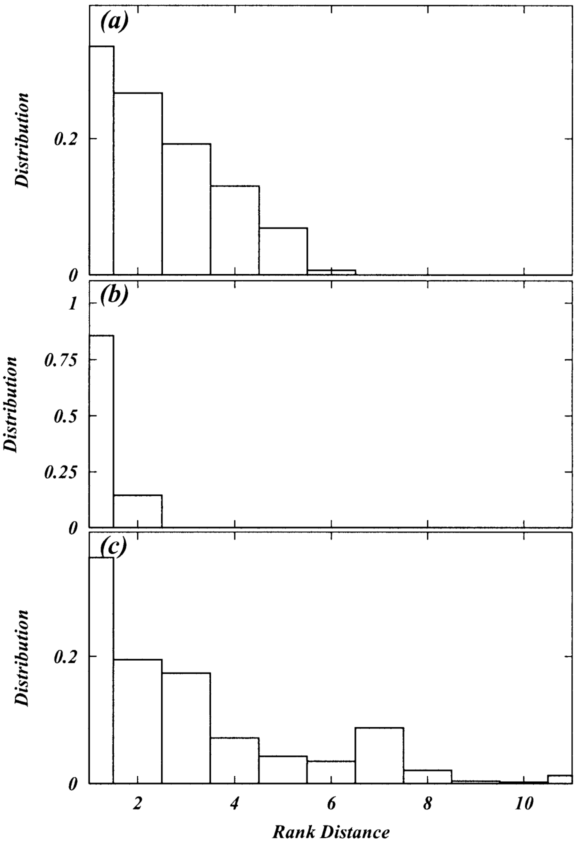

Fig. 4 The distribution of rank distance in coalitions of size 2, as predicted by the model without cost (**a**), or the model with cost (**b**), or averages of three groups observed in two field studies (**c**) (Smuts 1985; Noë and Sluijter 1995)

Finally, although our model assumes that coalition partners occupy adjacent ranks, we can also explore the viable coalitions for all possible rank distances. While it is not obvious how to define rank distances in larger coalitions, it is straightforward in coalitions of size 2. Figure 4a shows that the tendency to form coalitions of size 2 declines precipitously with rank distance. We expect that the distribution of rank distance will not change dramatically if larger coalitions were to be included.

Coalitions with costs

So far, we have equated payoff to fitness, a normal procedure in evolutionary game theory. We must now separate payoff from fitness in order to be able to incorporate costs, such that fitness will equal *net payoff*, i.e. payoff minus costs. The reason for this is as follows. Costs will affect an individual's decision whether or not to join a coalition because individual rationality is defined in terms of fitness. However, the value of the coalition, i.e. its strength, is not affected by these costs because it is determined by the ranks of its members and not by their fitness. Hence, costs must be external quantities and fitness henceforth equals payoff minus costs.

These costs can involve (1) energy and time lost to other fitness enhancing activities, (2) risk of injury, and (3) coordination costs. They are non-exclusive. These various costs can be incorporated into the model, as follows. The fitness of an individual in the coalition is reduced by these three types of costs, respectively, to become:

$$y_1 = x_1 - \gamma_1 - \gamma_2 f_2(i, N, m, p) - \gamma_3 f_3(m). \tag{4}$$

However, the value of the coalition is still unchanged, i.e. $v(S_1) = \sum_{i=1}^{m} x_i$.

First, incorporating the energy and time lost due to coalition formation will result in a constant reduction (γ_1) in fitness. These costs are not expected to appreciably affect the results presented above because all individuals are affected by the same amount.

Second, risk of injury is likely to be biased toward the lowest ranking member of the coalition, but is also likely to decrease with increased coalition size. Thus, f_2 can be written as $f_2(i, N, m, p) = \frac{r_{s_i}}{m}$ where r_{s_i} is the rank of i^{th} individual among the members of S_1. If risk of injury is appreciable, lower ranking males should be less inclined to participate in coalitions; coalitions also should become larger. Baboon males incur injuries, especially when they fight over access to estrous females or when immigrants fight with resident dominants over top rank (Drews 1996). Although none of the studies of baboon coalitions reports injuries sustained as a result of coalition formation, the risk of injury seemed substantial in one study focusing on injury in baboon males (Drews 1996). Hence, because the risk of injury while doing nothing is zero, $\gamma_2>0$. Although we do not know the value of γ_2 relative to that of the payoff, we assume that it is not negligible.

Third, the difficulty of coordinating the attack among the coalition members should increase with the number of possible dyads among them. Thus, f_3 can be written as $f_3(m)=\frac{m(m-1)}{2}$ because there is a trend for larger coalitions to be more successful in dislodging the high-ranking male from the estrous female (Noë 1990; Smuts 1985 and references therein; but see Bercovitch 1988), we would expect coalitions to be larger; yet, most coalitions are small (see below). It is possible that coordination costs, the difficulty of bringing the coalition together at the right time and place, are important. The impact of incorporating a coordination cost may be dramatic, because of the quadratic dependence of the cost function on coalition size. This leads to a narrow range of γ_3 values in which coalitions can be viable. We settled on $\gamma_3=0.004$ in our calculations to explore its effects on coalition parameters. We see a clear decline in the size of coalitions (Figs. 1 and 2b), a shift toward lower ranks in coalition members (Fig. 3b), and a sharper distribution of rank distances of coalition members (Fig. 4b).

Empirical data

Few of the empirical papers cited in the introduction present the quantitative information needed for direct comparison with the model results. However, some detailed comparisons are possible.

The model suggests that coalitions are only expected where the environmentally imposed contest potential (β) is less than ½. Although estimating β in nature is difficult, interesting contrasts between baboon populations exist. Thus, coalitions are seen in all east African baboon populations (*Papio anubis, P. cynocephalus*), but are strikingly absent in the southern African baboons (*P. ursinus*). In the latter, top ranking males tend to monopolize paternities in the group (Bulger 1993), indicating high β. In the east African baboons, male rank and siring success show a less steep relationship (Altmann et al. 1996; Alberts et al. 2003), suggesting lower β.

Coalition sizes are generally small, with mean values barely exceeding 2 (Packer, 1977): 2.11 (Bercovitch 1988), 2.12 (Noë 1990), 2.85 (Smuts 1985). Similar sizes are found for leveling coalitions among barbary macaque (*Macaca sylvanus*) males (~2.35 (Kuester and Paul 1992). Figure 2c confirms the small size of coalitions in the two studies that presented quantitative data (Smuts 1985; Noë and Sluijter 1995). This small size implies either a considerable coordination cost to coalition formation or some other constraint.

Figure 3c shows the observed participation in coalitions of males of different ranks averaged over the same two groups, from Smuts (1985)and Noë and Sluijter (1995). As expected, participants are mid- or low rankers (see also Noë 1992). This distribution suggests that coordination costs do not play a major role.

Figure 4c shows the observed rank distances among the participants for the same two groups as in Fig. 3c. These empirical data conform very closely to the prediction of the model without costs, again suggesting that coordination costs play only a minor role. Moreover, 83% of coalitions observed by Bercovitch also contained males of adjacent ranks (Bercovitch 1988).

Discussion

Overall, the model predicted aspects of baboon male coalition formation reasonably well. This suggests that it captured the essential elements of coalition formation. However, the absence of formal alternatives makes it difficult to judge the model's success.

The model without costs predicted the rank distribution and rank distance of participants reasonably well, but it failed to correctly predict the size of coalitions. In order to produce coalition sizes closer to the observed distribution, we also considered the coordination cost of forming a coalition. This modification did reduce the size of coalitions, but it also pushed the rank distribution toward the lowest rankers and created very tight rank distances among participants. Neither the predicted rank distances nor the predicted correlation between small coalitions and the predominance of lower rankers are actually found. For instance, in both Alto's and Hook's baboon groups at Amboseli (Noë 1990; Noë and Sluijter 1995), coalitions included mainly mid rankers even though they were small. We can not entirely exclude the possibility that the concentration among mid rankers is an artifact of other functions of coalitions (e.g., opportunistic attacks on shared rivals), but we conclude that coordination costs are unlikely to be major determinants of coalition size.

One possible explanation for the smaller than expected coalition sizes is the limited availability of suitable partners. Leveling coalitions in baboons and macaques are formed primarily by past-prime males. Thus, in many groups there may not be enough males available as coalition partners (Alberts et al. 2003). This of course raises the question why low ranking males that have not yet reached their prime rarely participate in coalitions. The answer to this question is not known, but could include lack of experience (i.e. high coordination costs), preoccupation with achieving high rank and thus high opportunity costs (cf. Noë and Sluijter 1995), or, most likely, risk avoidance by those whose reproductive peak lies ahead (cf. Parker 1974). The same factors could also explain the reluctance of high rankers to form retaliatory coalitions against the leveling coalitions. However, we suspect that closer analysis of the model would also show that those ranking just below the top rankers will rarely benefit from joining retaliatory coalitions.

Another possible explanation for smaller than expected coalition sizes is that the prize, i.e. access to the estrous female, can only be shared statistically because in every single instance one coalition partner ends up in consort with the female (R. Noë, personsal communication). The small number of coalitions in which particular combinations of males are involved may indeed make it a cognitive challenge for males in larger coalitions to keep track of their average payoff. Observations on males in very large groups will be able to distinguish this possibility from the previous one.

The model developed here suggests that future studies of leveling coalitions should collect systematic data on variables of currently unknown magnitude but of potential importance. These are (1) estimates of injury rates resulting from coalitionary conflicts and their impact on payoffs, (2) estimates of the impact of coalition size on the coordination costs including both selection of suitable partners (Noë and Sluijter 1995) and actual negotiation between potential partners (Smuts and Watanabe 1990), and (3) assessment of the role of demography in coalition size through comparisons of groups of different sizes and age composition.

Noë (1994) attempted to estimate physical strength from observed behavior and used those estimates (rather than payoffs as used here) to determine the "strength" of the coalition. While his model produced many of the observed features of coalitions, our model is more general, in that it allows variation in β. Perhaps the main novel insight of our model is that leveling coalitions are only found where the environmentally imposed contest component (β) is low, i.e. $\beta \leq 0.5$. A good test of its value is therefore whether the effect of β on the incidence of leveling coalitions is actually observed.

Although the presence of leveling coalitions (which reduce α) makes it almost impossible to obtain an independent estimate the value of β, a low value of β is suggested for the East African baboons. First, as we noted, the relationship of paternity with rank is not very steep (see also van Noordwijk and van Schaik 2004). Second, consortships tend to be exclusive, i.e. a higher ranking male cannot simply displace the consorting male (e.g. Noë 1992), suggesting an arbitrary convention of ownership reflective of fairly low value of exclusive access. In the more despotic long-tailed macaques (*Macaca fascicularis*), in contrast, top ranking males can easily break up mate-guarding attempts by lower ranking males (van Noordwijk 1985). Thus, the contrast in coalition formation between eastern and southern Africa, so far unexplained (Alberts et al. 2003), is almost certainly consistent with the model. Moreover, a recent review of sociosexual strategies among primate males in a large number of species with multi-male groups noted that male-male coalitions are generally found where other factors indicate low β value, e.g. seasonal breeding and large groups (van Noordwijk and van Schaik 2004). Thus, we conclude that the presence of leveling coalitions in nature is associated with low values of β, as predicted by the model.

The model further predicts that as contest competition (β) decreases, leveling coalitions become more likely, which in turn reduce α, and thus lead to further reductions in the rank dependence of payoffs. Hence, perhaps paradoxically, as leveling coalitions become more common, the payoff benefits of higher rank decrease, leading to a situation where males should be less inclined to engage in escalated fighting to improve their rank. This cascade explains why as β becomes lower (because groups get very large or mating more seasonal) leveling coalitions become increasingly frequent and dominance ranks among males become impossible to determine. Examples include the EC baboon group (Smuts 1985; Noë and Sluijter 1995), a group of Barbary macaques (Kuester and Paul 1992), and various groups of Japanese macaques (Huffman 1991; Watanabe 2001).

Leveling coalitions among human hunter-gatherers, usually by males, differ from those observed among baboon males: they are both larger and more effective in blurring ranks among male group members (Boehm 1999). Thus, these human coalitions closely resemble the predictions of the model without cost in situations of rather low β. Low β is suggested by the general pair-bonding among humans and the low incidence of polygyny among foragers, especially immediate-return foragers (Marlowe 2000). It is also possible that coordination costs in humans are lower due to language, and that risks of injury push up coalition size; there are also many available partners in the average human foraging group (participating males may actually in most cases be younger than the ones they challenge). Hence, to explain the large leveling coalitions seen among human foragers, there may be no need to invoke special human faculties, such as the presence of hunting weapons, political intelligence or moral communities, assumed to be pivotal by Boehm (1999).

Socioecological theory claims an association between contest competition and the presence of coalitions among females (van Schaik 1989; Sterck et al. 1997). That result is not at odds with the findings reported here because these female coalitions are rank changing and take place in a non constant-sum situation. In future work we will address the relationships between leveling and rank changing coalitions among males (cf de Waal 1992) and identify the critical variables needed to understand the distribution of these two kinds of male-male coalitions.

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References

Alberts S, Watts H, Altmann J (2003) Queuing and queue jumping: long term patterns of dominance rank and mating success in male savannah baboons. Anim Behav 65:821–840

Altmann J, Alberts S, Haines S, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman D, Mututua R, Saiyalel S, Wayne R, Lacy R, Bruford M (1996) Behavior predicts genetic structure in a wild primate group. Proc Natl Acad Sci USA 93:5797–5801

Altmann S (1962) A field study of the sociobiology of the rhesus monkey, *Macaca mulatta*. Ann NY Acad Sci 102:338–435

Bercovitch FB (1988) Coalitions, cooperation and reproductive tactics among adult male baboons. Anim Behav 36:1198–1209

Boehm C (1999) Hierarchy in the forest: the evolution of egalitarian behavior. Harvard University Press, Cambridge, Mass.

Bulger JB (1993) Dominance rank and access to estrous females in male savanna baboons. Behaviour 127:67–103

Connor RC, Smolker RA, Richards AF (1992) Dolphin alliances and coalitions. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 415–443

Connor RC, Heithaus RM, Barre LM (1999) Superalliance of bottlenose dolphins. Nature 371:571–572

Drews C (1996) Context and patterns of injuries in free-ranging male baboons (*Papio cynocephalus*). Behaviour 133:443–474

Engh AL, Esch K, Smale L, Holekamp KE (2000) Mechanisms of maternal rank ‘inheritance’ in the spotted hyaena (*Crocuta crocuta*). Anim Behav 60:323–332

Harcourt AH (1992) Coalitions and alliances: are primates more complex than non-primates. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals.. Oxford University Press, Oxford, pp 445–471

Hooff, J van, van Schaik C (1992) Cooperation in competition: the ecology of primate bonds. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals Oxford University Press, Oxford, pp 357–389

Huffman MA (1991) Mate selection and partner preferences in female Japanese macaques. In: Fedigan LM, Asquith PJ (eds.) The monkeys of Arashiyama: thirty-five years of research in Japan and the west. State University of New York Press, Albany, pp 101–122

Kahan JP, Rapoport A (1984) Theories of coalition formation. Erlbaum, Hillsdale, N.J.

Kuester J, Paul A (1992) Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). Behaviour 120:192–217

Łomnicki A (1988) Population ecology of individuals. Princeton University Press, Princeton, N.J.

Marlowe F (2000) Paternal investment and the human mating system. Behav Proc 51:45–61

Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Noë R (1989) Coalition formation among male baboons. PhD thesis, University of Utrecht, Netherlands

Noë R (1990) A veto game played by baboons: a challenge to the use of the prisoner’s dilemma as a paradigm for reciprocity and cooperation. Anim Behav 39:78–90

Noë R (1992) Alliance formation among male baboons: shopping for profitable partners. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 285–321

Noë R (1994) A model of coalitions formation among male baboons with fighting ability as the crucial parameter. Anim Behav 47:211–213

Noë R, Sluijter AA (1995) Which adult male savanna baboons form coalitions? Int J Primatol 16:77–105

Noordwijk M van (1985) Sexual behaviour of Sumatran long-tailed macaques (*Macaca fascicularis*). Z Tierpsychol 70:277–296

Noordwijk M van, van Schaik C (2004) Sexual selection and the careers of primate males: paternity concentration, dominance acquisition tactics and transfer decisions. In: Kappeler P, van Schaik C (eds) Sexual selection in primates. Cambridge University Press, Cambridge, (in press)

Nunn CL (1999) The number of males in primate social groups: a comparative test of the scioecological model. Behav Ecol Sociobiol 46:1–13

Packer C (1977) Reciprocal altruism in *Papio anubis*. Nature 265:441–443

Parker GA (1974) Assessment strategy and the evolution of animal conflicts. J Theor Biol 47:223–243

Pope T (1990) The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. Behav Ecol Sociobiol 27:439–446

Schaik CP van (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative socio-ecology: the behavioural ecology of humans and other mammals. Blackwell, Oxford, pp 195–218

Smuts BB (1985) Sex and friendship in baboons. Aldine, New York

Smuts BB, Watanabe JM (1990) Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). Int J Primatol 11:147–172

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Waal FBM de (1992) Coalitions as part of reciprocal relations in the Arnhem chimpanzee colony. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 233–257

Waal FBM de, van Hooff JARAM (1981) Side-directed communication and agonistic interactions in chimpanzees. Behaviour 77:164–198

Waal FBM de, Harcourt AH (1992) Coalitions and alliances: a history of ethological research. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 1–19

Watanabe K (1979) Alliance formation in a free-ranging troop of Japanese macaques. Primates 20:459–474

Watanabe K (2001) A review of 50 years of research on the Japanese monkeys of Koshima: status and dominance. In: Matsuzawa T, Matsuzawa T (eds) Primate origins of human cognition and behavior. Springer, Tokyo Berlin Heidelberg, pp 405–417

Zabel CJ, Glickman SE, Frank LG, Woodmansee KB, Keppel G (1992) Coalition formation in a colony of prepubertal spotted hyenas. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 113–135