ORIGINAL ARTICLE

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A model for within-group coalitionary aggression among males

Abstract Perhaps the most common form of cooperation among primates is the formation of coalitions. Competition among males within a group concerns a constant quantity of the limiting resource (fertilizations). Contest competition over fertilizations is known to produce payoffs that are distributed according to the priority-of-access model, and hence show an exponential decline in payoff with rank. We develop a model for rank-changing, within-group coalitions among primate males. For these coalitions to occur, they must be both profitable (i.e. improve fitness) for all coalition members and feasible (i.e. be able to beat the targets). We assume that the value of the coalition is the sum of the payoffs of the partners in their original ranks. We distinguish three basic coalition configurations, depending on the dominance ranks of the coalition partners relative to their target. We predict five basic coalition types. First, all-up, rank-changing coalitions targeting individuals ranking above all coalition partners; these are expected to involve coalition partners ranking just below their target, concern top rank, and be small, just two or three animals. Second, bridging, rank-changing coalitions, where higher-rankers support lower-rankers to rise to a rank below themselves; these are expected to be most common where a high-ranking male in a despotic system can support a low-ranking relative.

Third, bridging non-rank-changing coalitions; these are expected to be common whenever high-ranking males have low-ranking close relatives. Fourth, non-rank-changing coalitions by high-rankers against lower-ranking targets; these are expected to serve to counteract or prevent the first type. Fifth, non-rank-changing, leveling coalitions, in which all partners rank below their target and which flatten the payoff distribution; these are expected to be large and mainly involve lower-ranking males. Bridging, rank-changing coalitions are expected in situations where contest is strong, all-up rank-changing coalitions where contest is intermediate, and leveling coalitions where contest is weak. We review the empirical patterns found among primates. The strong predictions of the model are confirmed by observational data on male-male coalitions in primates.

Keywords Coalitions · Competition · Males · Primates · Rank

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Introduction

Where animals can exclude others from limiting resources, competition among them is said to be by contest (Nicholson 1954), and animals are expected to fight over access to these resources. If these animals live in groups, contest competition among group members will lead to decided dominance relationships among them and a usually linear dominance hierarchy in the group. Whenever decided dominance relations are found, there is the potential for coalitions (van Schaik 1996). Coalitions are coordinated attacks by at least two individuals on one or more targets, often preceded by signaling between the attackers (side-directed communication: de Waal and van Hooff 1981; de Waal and Harcourt 1992).

In large primate groups containing multiple adults of both sexes, males and females tend to compete over different limiting resources: food or shelter for females, fertilizations for males. Although males compete for matings, the object of competition is fertilization. In-

creased matings during a female's peri-ovulatory period improves a male's likelihood of achieving fertilization. Males competing for access to fertilizable females in a primate group face a constant-sum situation: coalition formation does not affect the total number of fertilizations in the group in a given period. This competition is described by a priority-of-access model (Altmann 1962), where the dominant male takes whatever he can monopolize, the second-ranking male takes whatever he can, and so on down. If the contested resource is mating access, the combination of a constant quantity of fertilizations over which the males compete and priority of access produces concave payoff (fitness) curves with dominance rank (see van Schaik et al, in preparation, for a general introduction). We believe that the shape of this curve has important consequences for the presence of coalitions. In this paper, we develop a general model for male-male coalitions within primate groups (coalitions among females generally are not constant-sum and the payoff curves are not universally concave; see van Hooff and van Schaik 1992).

The benefits of within-group male-male coalitions can be classified into two basic types. First, coalitions may increase access to some limiting resource, without however changing the dominance ranks of the participants (here called "leveling" coalitions). Second, a coalition may improve the dominance ranks of its members, and through that access to the limiting resource. Recently, we modeled non-rank changing leveling coalitions among primate males in a group (Pandit and van Schaik 2003). In this paper, we propose a general model for both types of coalitions in constant-sum situations (henceforth: constant-sum coalitions), with a special focus on rank-changing coalitions.

We stress that this model only concerns rank changes due to coalition formation and not the dyadic rank changes due to gradual changes in individual fighting abilities. Note, too, that we use the term coalition in its game-theoretical sense (Kahan and Rapoport 1984); from the perspective of animal behavior we can call them successful alliances, because they reflect relationship in which repeated coalitionary interactions occur rather than single interactions and assume that the goals are actually achieved. These different terms do not affect the model because costs and benefits are measured in the same units: fitness components per unit time.

Methods

The model and its predictions

The general model has the following structure. We have a group of N males. Individuals can be arranged in a linear dominance hierarchy; and each individual i's dominance rank d_i is associated with a payoff according to an inverse exponential function with exponent β, where $0<\beta\leq1$ is the environmentally determined degree of despotism. This formalism was introduced by Pandit and van Schaik (2003) and modeled after the priority of access (Altmann 1962). Thus, β approaches 1 in a situation where the dominant can monopolize access to the limiting resource (absolute contest),

whereas it approaches zero when all males gain approximately equal access (as in scramble). The value of β is determined by both demographic factors (number of females), female reproductive physiology (seasonality of breeding, duration of fertile periods, and tendency toward synchronization of fertile periods) and female behavior (preference for mating with dominant males, subordinate males, or for promiscuity). Note that the absolute values of the fighting abilities of the males involved are irrelevant: in any group, males will be ranked according to relative fighting ability and will acquire fertilizations according to the β and the number of fertile females in a given period.

Here, we are asking under which conditions these coalitions are viable, i.e. improve fitness (profitability) and are strong enough to beat the target (feasibility). Profitability requires that the benefits of improved rank exceed C, the cost of the formation and maintenance of the coalition (in terms of risk of injury, energy expenditure and stress), for at least one coalition member while at least compensating the cost for other members. This cost involves the selection of appropriate partners and the maintenance of an effective alliance through continued proximity, as well as the risk of injury associated with the actual fighting[1]. We will then examine whether these coalitions are indeed the strongest coalitions in the group (feasibility).

Both conditions of profitability and feasibility must be satisfied simultaneously for coalitions to be viable, i.e. to be expected to occur. The combined conditions determine where in β–C space coalitions are found and if so, whether they will be rank changing or not.

We will now derive the general condition for profitability for each member of the coalition. Let d_{a_i} be the dominance rank of individual i in the absence of coalitions.

Based on our previous work (Pandit and van Schaik 2003) we assume that the payoff function of this individual is

$$x_{d_{a_i}} = (1-\beta)^{d_{a_i}-1}\left(\frac{\beta}{1-(1-\beta)^N}\right). \tag{1}$$

Let d_{t_i} be the targeted rank, i.e. the rank individual i would occupy as a result of a successful coalition. We now derive the relation between β and C, starting from the basic assumption of individual rationality (Kahan and Rapoport 1984). Hence,

$$C \leqslant x_{d_{t_i}} - x_{d_{a_i}} \tag{2}$$

$$C \leqslant [(1-\beta)^{d_{t_i}-1} - (1-\beta)^{d_{a_i}-1}]\left(\frac{\beta}{1-(1-\beta)^N}\right) \tag{3}$$

and the coalition is profitable if condition 3 is satisfied for each member in the coalition.

This condition (profitability) produces rank changing coalitions if and only if the coalition is feasible (i.e. is stronger than its target). We check the feasibility of coalitions for three different configurations of coalitions, following the classification of Chapais (1995) based on the relative ranks of the participants in the coalition and their target: all-down, where targeted rank is below those of the coalition partners; bridging, where some of the coalition partners are below the targeted rank and some of them are above; and all-up, where all coalition partners rank below the targeted rank (Table 1).

All-up, rank-changing coalitions

All-up, rank-changing coalitions are potentially profitable whenever inequality (3) is satisfied for the lowest ranking member of the coalition, because under the priority of access model it is then also satisfied for every member of the coalition. To assess the feasibility of these coalitions we have to solve the problem of determining the value of the coalition. This problem has two components. First, we must decide whether the value of the coalition is the simple sum of

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[1] This cost differs from the various γ's used by Pandit and van Schaik (2003).

Table 1 Expected coalition types and their feasibility and payoff benefits

Coalition configuration	Coalition type	Feasibility	Payoff benefit
All-down	All-down, rank-changing	Always	Never profitable
	Status quo maintaining	Always	Not examined
Bridging	Bridging, rank-changing	Always	See condition (7)
	Protecting	Always	Not examined
All-up	All-up, rank-changing	See condition (5)	See condition (3)
	Leveling	See condition (5)	< Benefit of all-up, rank-changing

the values of its participants or some more complex function. We opt for the simplest assumption and use linear superposition. Second, we must determine which aspect of the individuals we need to sum: fighting ability or payoff (which is a function of both fighting ability and motivation). These two will generally be highly correlated and (in the absence of coalitions) are expected always to show a monotonic relationship. Both should be directly and monotonically related to dominance rank in the absence of coalitions. Fighting ability will generally be very difficult to estimate, even if experiments are possible. Payoff, on the other hand, can be estimated by paternity analysis. Where the benefit of higher rank is modest (i.e. β is relatively low), both payoff and fighting ability will show very similar functional forms with rank. Hence, it makes sense to use the easily estimated payoffs to evaluate the value of the coalition. This is what Pandit and van Schaik (2003) did. We will return to the possible errors introduced by this decision in the discussion.

We can now calculate the condition for feasibility. Because in this analysis we only compare payoffs of being in a particular rank position there is no need to consider the individuals occupying each rank (for inequality 3 that was necessary because we were comparing two different payoffs for the same individual). We can therefore drop the index i from the payoff. We also incorporate cost because the allies need to coordinate their attacks with great precision and need to be prepared to do so at all times, and hence at some ecological and social cost. For simplicity, we assume that the cost C we used to calculate profitability can also be used here. If this assumption is not justified, the model loses its simplicity, but in the limiting case of no cost for feasibility, we arrive at qualitatively similar results.

Let the rank of the lowest ranking member of the coalition be p and let the size of the coalition be m (Pandit and van Schaik 2003). Hence, we write

$$\sum_{r=p-m+1}^{p} x_r - mC \geqslant x_t$$

$$\sum_{r=1}^{p} x_r - \sum_{r=1}^{p-m} x_r - mC \geqslant x_t$$

$$\sum_{r=1}^{p} (1-\beta)^{r-1} - \sum_{r=1}^{p-m} (1-\beta)^{r-1} - \frac{1-(1-\beta)^N}{\beta} mC \geqslant (1-\beta)^{t-1}$$

$$\frac{1-(1-\beta)^p}{\beta} - \frac{1-(1-\beta)^{p-m}}{\beta} - \frac{1-(1-\beta)^N}{\beta} \ mC \geqslant (1-\beta)^{t-1}.$$

(4)

Therefore,

$$C \leqslant -\frac{\beta(1-\beta)^{t-1}}{m(1-(1-\beta)^N)} - \frac{(1-\beta)^p}{m(1-(1-\beta)^N)} + \frac{(1-\beta)^{p-m}}{m(1-(1-\beta)^N)}$$

(5)

Thus, condition (5) gives the relationship between C and β such that coalitions are feasible.

Figure 1a shows a family of feasibility curves for all the coalitions that target the top ranker in a group of ten and contain m participants starting from the second ranker downward. All curves
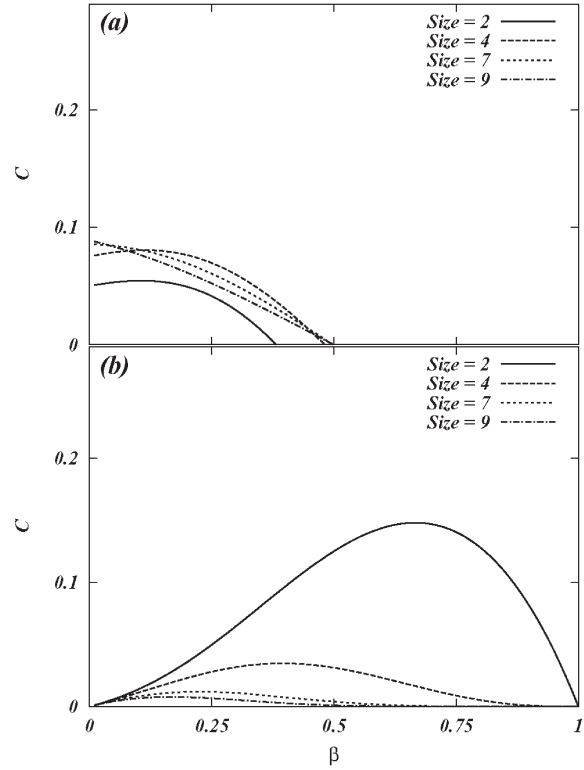

Fig. 1 a A family of feasibility curves for all-up coalitions. The curves are obtained for a group of ten individuals and for coalitions of sizes two, four, seven and nine involving the second-ranking individual. **b** The family of profitability curves for the same four coalitions

are intersecting the β axis at $\beta \leq 0.5$, as proposed earlier for the case of zero cost (Pandit and van Schaik 2003). Figure 1b shows a family of profitability curves for coalitions in which every member shifts one rank up. These curves are obtained for the lowest ranker in the coalition because every other member of the coalition is going to have higher profitability than this individual. Therefore these curves represent the profitability region boundary.

For coalitions to be viable they have to be both profitable and feasible. We are therefore looking for the area of overlap between regions below the profitability boundary and the feasibility boundary in the β–C space. Figure 2a shows the maximum admissible cost ($C_{\max}$) as a function of coalition size (m) for coalitions targeting the top ranker and starting from second ranker downward. The important result is that these all-up, rank changing coalitions are expected to be small in size. This result is independent of the size of the group (N). Figure 2b shows that as the highest-ranking member of the coalition ranks further away from the target, here always the top ranker in the group, $C_{\max}$ comes down, albeit not steeply. However, there is another, independent reason why all-up, rank-changing coalitions should attack a target ranking immedi-
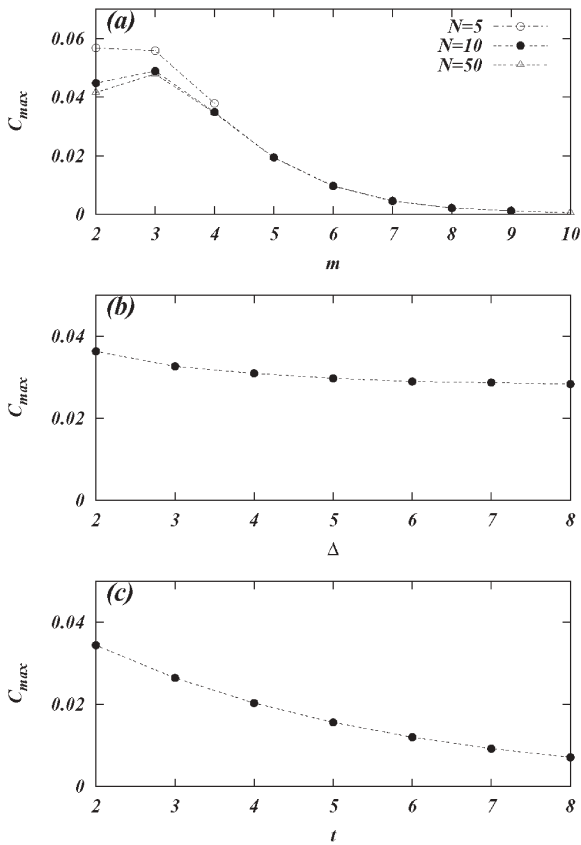
Fig. 2 a The maximum admissible cost (C_{max}) as a function of coalition size (m) for all-up coalitions targeting the top ranker and starting from the second ranker downward in groups of different sizes. **b** The maximum admissible cost (C_{max}) as a function of the rank distance (Δ) between the highest ranking member in the coalition and the target rank. **c** The maximum admissible cost (C_{max}) as a function of the target rank (t) for all coalitions of size two in which the partners occupy adjacent ranks and the target ranks directly above the top ranker in the coalition

ately above the highest-ranking member of the coalition. If the target ranks multiple rank positions above the coalition members, there will be several individuals who would be negatively affected by this coalition and with whom the target can form a retaliatory coalition and easily restore the status quo. The possibility of retaliatory coalitions also leads us to predict that cascading all-up, rank-changing coalitions that go from the lowest ranking pair of males step by step all the way to the top should never occur.

Finally, Fig. 2c shows for coalitions whose highest ranking member always ranks one step below the target that as the target becomes lower ranking C_{max} becomes smaller. In other words, most coalitions observed in a group should be about the top rank positions. To sum up, we expect all-up, rank-changing coalitions to be small (sizes 2 or 3), target the top ranker, and involve individuals ranking just below the top ranker.

All-up, leveling coalitions

In the region inside the feasibility boundary but outside the profitability boundary, we do not of course expect any all-up, rank-changing coalitions. However, in this region of lower β values, we may expect leveling coalitions because the coalitions are strong enough to beat the top ranker and thus gain temporary access to a limiting resource (a fertilizable female) but do not generate suffi-
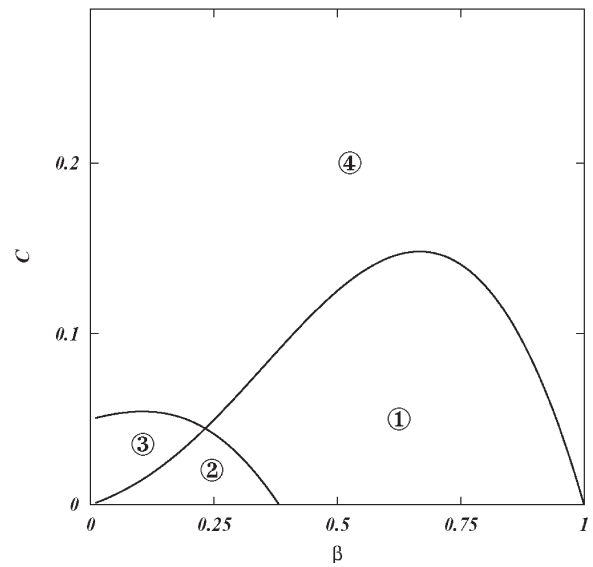

Fig. 3 Different regions of $C-\beta$ space for all-up coalitions. In region *1*, coalitions are profitable but not feasible (in this region we do expect bridging, rank-changing coalitions). In region *2*, all-up, rank-changing coalitions are both profitable and feasible. Hence, we expect these coalitions, and therefore also all-down coalitions. In region *3*, all-up rank-changing coalitions are feasible but not profitable. Hence, we expect leveling coalitions in this region (and possibly all-down coalitions). In region *4*, all-up (nor any other) coalitions are neither profitable nor feasible, and therefore not expected

cient benefits to permanently change the rank position of the coalition partners (due to low β). Leveling coalitions act to reduce the effective value of β, thus equalizing payoffs of individuals of all ranks. Thus, while these coalitions may not be profitable to change ranks, they may benefit the partners in equalizing access to the limiting resource.

Pandit and van Schaik (2003) developed a model for this kind of all-up configuration. Interestingly, that model predicts that coalitions will be large and consist of mid to lower rankers, while also targeting one of the highest-ranking males in the group. Figure 3 depicts the regions of the $\beta-C$ phase space where we expect all-up, rank-changing coalitions, where we expect leveling coalitions, and where we expect other types of rank changing coalitions. In the region where all-up coalitions are both feasible and profitable we expect all-up, rank-changing rather than leveling coalitions because the payoff benefits of rank change exceed the modest payoff increase caused by the leveling action[2].

Bridging, rank-changing coalitions

Bridging coalitions are always feasible but never profitable if decisions are based on payoff differences. However, they may be profitable if the higher ranker(s) derive(s) an indirect benefit from raising the rank(s) of other coalition member(s). Such an indirect benefit is most easily obtained through kin selection, i.e. the partners are genetic relatives (alternatively, the lower ranker could provide a highly valuable service to the higher ranker, but such a situation will be very rare in nonhuman animals). Thus, we can predict that when bridging coalitions are observed in nonhuman primates they are always between genetic relatives.

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[2] The payoff of the members of a leveling coalition increases due to the flattening of the payoff distribution, technically described in the parameter α (Pandit and van Schaik 2003)

Individual rationality (see condition [3]) can never explain the presence of bridging, rank-changing coalitions because the higher rankers never gain in payoff (in fact they pay a finite cost of coalition formation). Hence, to explain their presence we need to redefine profitability. To do so we first introduce the concept of coalitionary rationality (Kahan and Rapoport 1984). Coalitionary rationality holds when the increase in the sum of the payoffs of the coalition members is greater than the sum of the costs of coalition formation, i.e.

$$mC \leqslant \sum_i^m x_{d_{t_i}} - \sum_i^m x_{d_{a_i}}. \tag{6}$$

Hence, according to coalitionary rationality individuals will decide to form a coalition if their average net payoff increases. To incorporate the effect of kinship we modify the condition for profitability, as follows

$$D(r_{ij}) \left[\sum_i^m x_{t_i} - \sum_i^m x_{a_i} \right] \geqslant mC$$

or

$$(1 - D(r_{ij}))[x_{t_i} - x_{a_i}] \geqslant C, \tag{7}$$

where

$$D(r_{ij}) = \frac{2}{m(m-1)} \sum_{i=1}^m \sum_{j=i+1}^m r_{ij} \tag{8}$$

and r_{ij} is the genetic relatedness between the two individuals i and j. If either one or both parts of condition (7) are satisfied forming a coalition is profitable. If coalition members are non-kin, then $D(r_{ij})=0$ and the condition (7) is as before: condition (3). If in contrast the two members are identical twins (i.e. $r_{ij}=1$; the maximum possible value), then $D(r_{ij})=1$ and condition (7) becomes the condition of coalitionary rationality. In other words, individual rationality and coalitionary rationality become the same when the coalition members are identical twins.

If the coalition has only two members, then we only need to consider the profitability of the highest ranker as follows:

$$r_{ij}[x_{t_i} - x_{a_i}] \geqslant C \tag{9}$$

and the condition is equivalent to classic nepotism (Hamilton 1964). Note that in this situation the $D(r_{ij})=r_{ij}$.

We can refine our prediction if coalition formation involves some finite cost to the high-ranking relative. It is easy to show that the profitability of bridging rank-changing coalitions increases as the ranks of the coalition members increases and they attack the higher-ranker in a high β situation. Figure 4 illustrates the situation for a group with three males, where the top-ranking male help his third-ranking relative to beat the second-ranking male in the group. It shows that these coalitions produce the greatest net benefit where β is high and the coalition partners are high ranking. We therefore expect bridging, rank-changing coalitions to be most common where a top ranking male in a high β situation is aiding a relative who ranks a few rank positions below him.

Other bridging coalitions

Protection of lower-ranking relatives against attacks by other males can be seen as the non-rank-changing equivalent to the rank-changing bridging coalitions just discussed. These bridging coalitions are of course always feasible. We expect them to be profitable as well under a broad range of conditions. However, if they merely serve to protect a lower-ranking relative against damaging attacks by other males, this kind of defensive coalition would not qualify as the equivalent to all-up, leveling coalitions. If, on the other hand, this protection serves to improve this male's access to limiting resources without changing his rank, they are leveling. In practice,
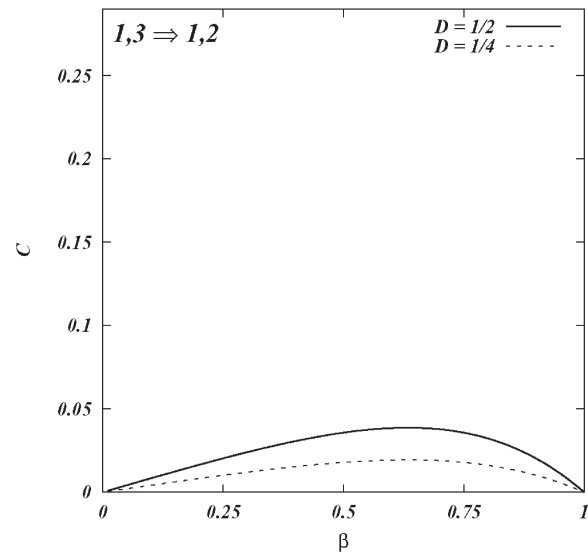

Fig. 4 Profitability of bridging, rank-changing coalition for two different values of relatedness

it may be impossible to distinguish between these situations unless the context is immediate competition for access to estrous females.

All-down coalitions

All-down, rank-changing coalitions are always feasible but never profitable because none of the coalition partners would derive a payoff benefit from changing rank. Hence, we do not expect to see such coalitions, and if they are actually observed in nature, they must serve a different function (other than changing ranks). Thus, all-down coalitions may actually serve to maintain the status quo among the males because all-up coalitions that challenge a high ranking target can easily be defeated by a coalition of the target and one or more males that rank between the target and the all-up coalition. This obvious consequence of the model leads to further predictions about the pattern in all-up, rank-changing coalitions observed in nature: all-down coalitions involving the target of an all-up, rank-changing coalition are impossible if this target ranks immediately above the highest ranking member of the all-up, rank-changing coalition (adjacent target). Any other all-up, rank-changing coalition is vulnerable to defeat by an all-down coalition. Thus, we predict that by far the most common all-up, rank-changing coalitions will be aimed at adjacent targets, because that will prevent the formation of potentially victorious all-down coalitions.

This prediction can be refined as follows. We should not see all-up, rank-changing coalitions that gradually work their way up the hierarchy by successively targeting individuals ranking immediately above them, because the obvious counter strategy to this is for higher rankers to consistently form preventive all-down coalitions against any all-up, rank-changing coalitions in their group, thus preventing cascading rank changes. This argument obviously also leads us to predict that the only all-up, rank-changing coalitions in groups should concern the group's top rank.

Results

To compare the outcome of this model with real systems, we first need to estimate the model parameters in real situations. Since the dependence on C is not very critical, we will discuss its nature and correlates elsewhere (van
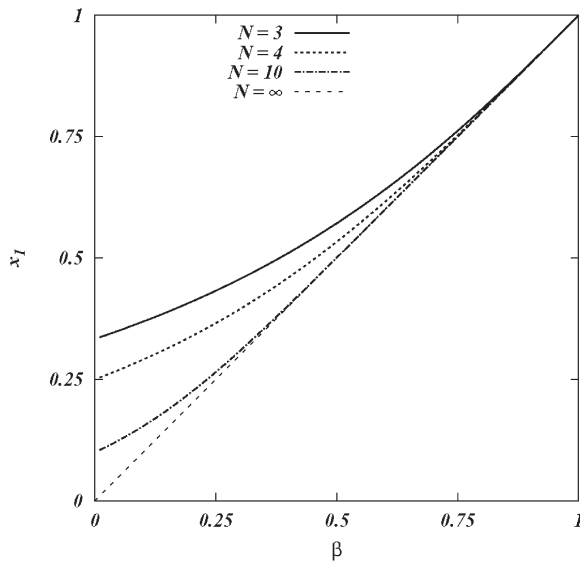
Fig. 5 Paternity percentage of top ranking male as function of β for various group sizes

Schaik et al., in preparation). Instead, we will investigate estimation of β.

There are several ways in which β can be estimated. For relatively small samples of infants, we determined through simulation that the most reliable estimate is through the proportion of infants sired by the top ranking male (paternity concentration: van Noordwijk and van Schaik 2004) rather than other possible estimates of β (see van Schaik et al., in preparation). The relation between x_1 and β is as follows:

$$x_1 = \frac{\beta}{1 - (1 - \beta)^N}. \tag{10}$$

For small N, the discrepancy between β and x_1 increases at lower values β, but those are the very situations in which N is expected to be larger (see Fig. 5 and van Schaik et al., in preparation). Thus, given the increasing availability of paternity estimates in the literature, this procedure gives a simple way to estimate β.

Many studies do not report paternity concentration for the same group at the time coalitions were studied. In those cases, we looked for estimates of β from other studies of the same population at another time (in the tables below

reported in square brackets), or studies of the same species with similar group size and composition (in the tables placed in parentheses). If no exact estimates were available, we classified β estimates in four classes: Low ($\beta \leq 0.25$), medium ($0.25 < \beta \leq 0.5$), high ($0.5 < \beta \leq 0.75$), and very high ($0.75 < \beta$).

We attempted to do an exhaustive survey of the primate behavioral literature, although we have no way of assessing the degree to which we succeeded. Several of the published studies were difficult to use because they reported coalitionary interactions without documenting the outcomes; the model concerns coalitions (alliances) that successfully reach their goal (changing dominance ranks or acquiring access to a receptive female). Moreover, they also report on coalitions not covered by the model, and sometimes they are difficult to separate (e.g. coalitions against recent immigrants that can be considered unranked). Thus, only a portion of the empirical literature can be used to test the predictions.

The main prediction for all-up, rank-changing coalitions was met among male primates (Table 2): all seven cases we found were small (involving two individuals), in all but one case targeted the top ranker, and involved males ranking immediately below the target. Values of β tend be medium to high, with data from captive populations tending to be higher than those from the wild. This range is higher than predicted. We are not yet able to evaluate negative evidence as well. However, as predicted by the model, van Noordwijk and van Schaik (2001) found that none of the males challenging for top rank in their high-β situation were members of coalitions, although various defensive coalitions (see below) were observed.

The observational data were also entirely consistent with the main prediction for bridging, rank-changing coalitions (Table 3): all four cases we found involved top-ranking males and three of the four were in high β situations. In one case, kinship among the challengers was not known with certainty, but was suspected by the observers before the actual coalition was observed (K. Jack, personal communication).

Pandit and van Schaik (2003) developed a model for the all-up, leveling coalitions. The model did account for the known features: leveling coalitions involve mid-to-low-ranking males who target a high-ranking, often top-ranking, male. The model also predicts (and this was not

Table 2 All-up, rank-changing coalitions observed among male primates (β estimates are taken from paternity studies compiled in van Noordwijk and van Schaik 2004). Estimates of β from other studies of the same population at another time shown in square brackets, and from other studies of the same species with similar group size and composition shown in parentheses

Species	Partners	Target	Number of males in group	β	Captive or wild	Source
Presbytis entellus	2+3	1	3	(High)	C	Curtin (1982)
Cebus capucinus	2+4	1	4	High	W	K. Jack, personal communication
Cebus capucinus	2+3	1	3	0.64–0.83	W	E. Vogel, unpublished
Pan troglodytes	2+3	1	3	[High]	C	de Waal (1978)
Pan t. schweinfurthii	2+3	1	4	(Medium)	W	Nishida (1983)
Pan t. schweinfurthii	3+4	2	8	[Medium]	W	Riss and Goodall (1977)
Macaca sylvanus	2+3	1	3	Very high	C	Witt and Schmidt (1981)

Table 3 Bridging, rank-changing coalitions observed among male primates (β estimates are taken from paternity studies compiled in van Noordwijk and van Schaik 2004). Estimates of β from other studies of the same population at another time shown in square brackets, and from other studies of the same species with similar group size and composition shown in parentheses

Species	Partners	Kin? (ranks)	β	Captive or wild	Number of males in group	Source
Macaca arctoides	1, 3	Y	(Very high)	C	3	Bernstein (1980)
Cebus capucinus	1, 3	Likely	0.64–0.83	W	4	Fedigan (2003) K. Jack, personal communication
Alouatta seniculus	1, 3, 4	Y	0.95	W	4	Pope (1990)
Pan troglodytes	1, 3	Y	[Medium]	W	8	Riss and Goodall (1977)

Table 4 All-up, leveling coalitions observed among male primates (β estimates are taken from paternity studies compiled in van Noordwijk and van Schaik 2004). Estimates of β from other studies of the same population at another time shown in square brackets, and from other studies of the same species with similar group size and composition shown in parentheses

Species	Partners	Target	Mean size	β	Source
Papio cynocephalus	Mid-low	Top/high	2.12	[Medium]	Bercovitch (1988); Noë (1990)
Papio anubis	Mid-low	Top/high	2.85	(Low)	Smuts (1985)
Pan troglodytes	All below top	Top	2.19	[Medium]	Goodall (1986)
Macaca sylvanus	Mid-low	Top/high	2.35	0.16	Kuester and Paul (1992)
Macaca fascicularis	Mid-low	Top/high	?	Low?	Angst (1975)
Macaca fuscata	Mid-low	Top/high	?	[Low]	Koyama (1967)

Table 5 β-range of different kinds of coalitions. The entries in the table refer to the number of studies, with the number of captive studies added in parentheses. The β estimates are taken from Tables 2, 3, 4

No. of studies	Low	Medium	High	Very high
All-up, leveling	4	2		
All-up, rank-changing		3	1 (+2)	0 (+1)
Bridging, rank-changing		1	1	1 (+1)

yet known before it was developed) that leveling coalitions occur in lower β situations. Table 4 shows these values, and documents that this prediction also holds. All observed cases were found in low- or medium-β situations.

A general prediction of the model is that the range of β values in which all-up, leveling coalitions are found is lower than that for all-up, rank-changing coalitions, which in turn is lower than that for bridging, rank-changing coalitions. Comparison of the three tables indicates that this is indeed the case (Table 5), although the numbers are as yet too small to allow statistical evaluation. It is interesting to note that within each category, the captive studies tend to have higher β values than studies in the wild. If we restrict our comparison to studies of natural populations, the fit with the model predictions is remarkably tight.

Discussion

The model presented here considers coalitions in an environment where individuals (primate males in this case) compete through priority of access in a constant-sum situation. Based on feasibility (coalition is stronger than the target) and profitability [coalition satisfies profitability conditions (3) and (7)], we identified five basic classes of coalitions (see Table 1): (1) status-quo maintaining, all-down, non-rank changing; (2) rank-changing bridging, always involving kin; (3) non-rank-changing bridging, always involving kin; (4) all-up, rank-changing; and (5) all-up, leveling, non-rank changing. This classification of types of male-male within-group coalitions extends Chapais's (1995) classification.

This embarrassingly simple model makes a variety of predictions about the features of different types of (successful) male-male coalitions within primate groups that were supported by empirical data. The only, and relatively minor, mismatch between model and data is that we found all-up, rank-changing coalitions in a broader range of β conditions than expected. We had predicted that they should not be found at $\beta > 0.5$, but we did find some. This mismatch suggests that our simple equation for the strength of the coalition (see below) is too simple. Nonetheless, the absence of all-up, rank-changing coalitions in situations with very high β indicates that the error we made was not too serious. Moreover, the predicted different ranges of β values for the different kinds of coalitions (Table 5) are actually largely sustained by the empirical data. This fit is even better if we limit the comparison to field studies only. While it is easily seen that captive studies tend to yield higher β values than field studies, the upward shift of coalitions within each type may suggest that males in captivity do not assess the captive situation entirely correctly (see below).

It is important to highlight the model's critical assumptions. The first one is that the costs in the profitability and feasibility criteria are the same. Perhaps they are not. If we omit any mention of cost for feasibility, then the feasibility curves become vertical lines in Figs. 1

and 3. This change does not qualitatively change our predictions. However, because some sort of coordination cost is bound to exist, predictions will inevitably converge on the ones we obtained. In addition, C is considered a constant, i.e. we average out all the terms in the cost as just one constant. The reasons for doing this are its simplicity and the difficulty of determining these terms separately in an experiment. The C used in this model refers to the cost of forming and maintaining a long-term alliance, unlike the γ, the ad hoc measure of interaction-level cost introduced by Pandit and van Schaik (2003) in their model of leveling coalitions.

The second critical assumption, as noted above, is that we estimate the value of a coalition as the sum of individual participants' values (payoffs) minus their cost. This convention identifies motivation (expected payoff) as the main component of coalitionary strength. It is not entirely correct, as we had anticipated. We suggest therefore that fighting abilities may still add up to feasible combinations even in high β situations where the payoff sum would no longer suggest feasibility. Unfortunately, it is not easy to improve on this assumption, because it is impossible to test experimentally the strength of a coalition. Doing so would require the ability to provoke coalitionary fights in any configuration desired by the experimenter. Nonetheless, as noted above, the order in which the different kinds of coalitions occur along the range of possible β values is as predicted by the model.

It is clear that the critical variable in the model is β. Its influence reaches beyond that of coalitions, however. Indeed, we expect to see major differences between low- and high-β situations, even within species. van Noordwijk and van Schaik (2004) note that males in low β situations tend to achieve top rank through a queuing or succession process rather than through active challenges, as at high β. They also tend to immigrate into groups with more favorable adult sex ratios, whereas young males in high-β situations tend to move to groups in which the demographic situation is such that future prospects of achieving top rank are best (although older males fall back to the low-β strategy). Male-female friendships may also differ predictably with β (van Schaik et al., in preparation). Finally, in low-β groups we expect less female-biased adult sex ratios and no solitary males or males living in all-male bands. Hence, the degree of which top males can achieve full priority of access to females is an important organizing variable for male socio-sexual strategies.

The success of the model raises a question whether males assess the local situation or whether they use some fixed rule that reflects the average β for the species. The fact that we see some variation within species in different conditions (see the Tables; Pandit and van Schaik 2003) suggest some flexibility in the decision making. The impact of β on many other aspects of male socio-sexual strategies also suggests that males use rules that serve to estimate the local β, and use the outcome to decide when to look for possible coalition partners. Future research may address the mechanisms used in this assessment. At least, intraspecific comparisons are called for that exam-

ine male-male coalitions in a variety of β situations, e.g. where group sizes and breeding seasonality vary. These intraspecific comparisons may also help to confirm the absence of coalitions, where they are predicted.

Obviously, many more coalitionary interactions take place among males within a primate group and in a constant-sum context than this model covers. As we already noted, however, some coalitions are consistent with the model; for instance, the defensive or conservative (all-down) coalitions can be regarded as serving to prevent revolutionary rank-changing coalitions. More work is needed to establish whether we should also expect counter-coalitions to prevent leveling. On the other hand, the model's success also bodes well for attempts to extend it to cover the two main remaining classes of male-male coalitions: (1) coalitions against males that are unranked (e.g. immigrants trying to take over the group) or males whose fighting abilities are changing but who still occupy the rank that corresponds to their earlier fighting ability; and (2) coalitions against other coalitions, either within the same group or in other groups (between-group coalitions).

In some species, male-male coalitions seem to be entirely absent (e.g. lemurs: Pereira and Kappeler 1997). The model ascribes the absence of male-male coalitions in multi-male groups to (1) very high β values, or (2) prohibitively high cost of coalition formation. Of course, other unknown factors could also be involved. Species with limited cognitive abilities may face a high cost of coalition formation; the absence of coalitions in multi-male groups of lemurs and many other animals might be due to such a cognitive constraint. We hope that the existence of this model inspires researchers to examine cases where coalitions are absent in large multi-male groups.

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