Toward a general model for male-male coalitions in primate groups

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9.1
Introduction

Of the many forms cooperation can take in nonhuman primates, the formation of coalitions is perhaps the most spectacular. Coalitions can be defined as coordinated attacks by at least two individuals on one or more targets, often preceded by signaling between the attackers (side-directed communication: de Waal & van Hooff 1981, de Waal 1992a; cf. Smuts & Watanabe 1990). They may serve to protect against attacks by more powerful individuals, to defend or gain access to resources or to acquire the dominance rank of the target individual. Animals forming the coalitions often are friends, as defined by Silk (2002c), although this is not true in all cases (Noë & Sluijter 1995). Friendships that involve coalitions are commonly called alliances (Harcourt & de Waal 1992a).

Mothers of many mammalian species protect immature offspring, but coalitions among adults are remarkably limited in their taxonomic distribution to carnivores, cetaceans and primates (Harcourt 1992). This pattern suggests that there are obstacles to the evolution of adult coalitions. We will briefly discuss the two major ones. First, in a functional sense, coalitions may contain altruistic acts (Packer 1977, de Waal 1982a, Noë 1990, Chapais 1995, Dugatkin 1997). Theorists often consider the presence of delays between providing the agonistic support and reaping possible rewards an important differentiating factor between the non-nepotistic categories of cooperation. In coalitionary interactions, delays are common, even when the eventual outcome is mutualistic in that all coalition partners increase their rank, perhaps after several initially unrewarded coalitions. The delays can also be quite variable, depending on the rather unpredictable outcomes of coalitions and the unpredictable time until the next opportunity. Long and variable delays may make it hard for coalitions to become established.

A second obstacle to the evolution of coalitions is that most of them at least potentially involve a high risk of injury. This is especially clear where lower-ranking animals team up to attack a higher-ranking target (but even if high-ranking individuals team up to attack a single low-ranking target, there is always some chance that others, either powerful or simply numerous, will come to the victim's aid). In general, there is a serious risk of injury when a coalition partner defects in the middle of an escalated coalitionary fight. Thus, coalitions will tend to involve some cost to the participants, unless the partners can trust each other not to defect during the fight. We believe that this trust problem may be another serious obstacle to the evolution of coalitions.

The presence of these obstacles may explain the limited taxonomic distribution of coalitions (Trivers 1971). Coalitions are common in organisms that are long-lived, live in stable associations, and form friendships (Cheney et al. 1986). Living for years in a stable group provides frequent opportunities for reciprocation, and the trust needed to form coalitions is built and maintained in friendships in which a variety of social services are exchanged.

Coalitions are common among primates, but that does not mean that all species display them. The conditions giving rise to coalitions among female primates have received much theoretical attention (Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck et al. 1997). The basic idea is that a high potential for contest competition (either within or between groups) leads related females to form nepotistic alliances and to be philopatric. It also produces predictable patterns of rank inheritance, the details of which may vary as a result of demography (Datta 1988, Chapais 1995) or the age trajectory of reproductive value (Chapais & Schulman 1980).

Coalitions among males, however, have not received similarly intensive scrutiny (but see Noë 1994), although their incidence is at least as spotty (van Schaik 1996) and within-taxon variation is also appreciable (Noë 1992, Pandit & van Schaik 2003). Although there is a trend for males to support relatives more than non-relatives (cf. Silk 1992a), nepotism does not explain much of the variation, if only because in many species the males in a group are not closely related. For instance, in male-philopatric chimpanzees, where close kin is at hand, allies are generally not close relatives (Goldberg & Wrangham 1997, Mitani et al. 2000, Vigilant et al. 2001). A different framework is therefore needed for males.

When we tally all the male-male coalitionary interactions observed in a group of primates over a given period, the emerging pattern may seem confusingly complex. Coalitions may occur in many configurations (Chapais 1995; see below for details), in various contexts (Noë 1992), in many different combinations, and not always consistently in support of the same partners or aimed at the same target (e.g. Silk 1993). They may occur spontaneously or as interventions in ongoing conflicts (de Waal et al. 1976), and some of them apparently beat their opponent(s) whereas others end in some kind of stalemate. It is not easy to identify the underlying strategic goals governing each male's decisions but it is a reasonable working hypothesis that their general goal is an increase in fitness. The most promising avenue for modeling, therefore, is to try to predict those outcomes that can be explicitly linked to fitness gains. If this approach can explain a considerable portion of the coalitions observed, we may then be able to identify the more intermediate tactical goals or as yet unknown strategic goals served by the remaining coalitions that are not immediately explained by the model. Here, we will adopt this approach, and will return to the coalitions not explained by the model in the discussion.

For the purpose of modeling, then, we are mainly concerned with outcomes. The aim of this chapter is to begin explaining the distribution of within-group male-male coalitions by developing and testing a general cost-benefit model for one class of male-male coalitions, offensive coalitions. We have so far produced

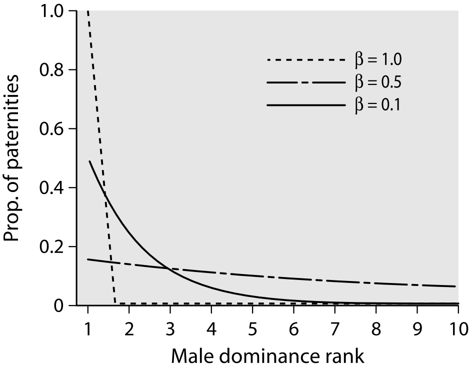

Fig. 9.1. The basic payoff curves with rank, for males competing over mating access to females: contest through priority of access in a constant-sum situation. Dotted line: β = 1.0; solid line: β = 0.5; broken line: β = 0.1

two technical papers on this subject (Pandit & van Schaik 2003, van Schaik et al. 2004). Our purpose here is to explain the basic logic underlying the models rather than the mathematical details, present the predictions and their tests, and discuss how the coalitions considered in this model fit into the overall scheme of coalitionary behavior in primates. To explain the basis for the model, we will begin with a review of the nature of male-male competition and coalitions in primates.

9.1.1
Male-male competition and coalitions in primates

Whether or not successful coalitions produce fitness benefits depends largely on the relationship between fitness and dominance rank. For males in a primate group, this curve is invariably and inevitably concave (at best approaching linearity), never convex (see Fig. 9.1). The reason for this is that males compete through contest for a set of constant-sum resources, fertilizations, which leads to a distribution of fertilizations determined by priority of access (Altmann 1962), also referred to as queuing (Alberts et al. 2003); the top-ranking male takes whatever he can monopolize of what is left, and so on down. In this model, a male's payoff is affected only by the number of males ranking above him, not by the number of males ranking below him or the total number of males in the group (as in Lomnicki's 1988 strict definition of contest). This process leads to negative exponential payoff curves with rank, except in the limiting case of complete scramble competition where males share all matings and therefore fertilizations equally.

Studies of primate males competing over females have generally confirmed the priority-of-access model (Altmann 1962, Bulger 1993, Weingrill et al. 2000, Alberts et al. 2003). We previously introduced the parameter β to describe the shape of the relationship or degree of despotism (Pandit & van Schaik 2003); β is the proportional reduction in payoff from one male to the next-lower ranking male. When β is near its upper limit of 1, virtually all fertilizations will be concentrated in the top-ranking males, whereas β approaching zero indicates pure scramble, in which all males will have approximately equal chances of fertilization regardless of their dominance rank, as a result of frequent matings by all and sperm competition.

The value of β is determined by a variety of factors: (i) demography (number of females in the group), (ii) ecology (degree of reproductive seasonality, producing more or less overlap in female mating periods), (iii) female reproductive physiology (the number of cycles per conception, the duration of the fertile window in each cycle, the presence of non-fertile mating periods, and the degree to which females actively synchronize or desynchronize their cycles), and (iv) female behavior (preferences for mating with dominant or subordinate males, or for polyandrous mating). We will postpone the discussion of how to estimate β until later.

For females in primate groups, on the other hand, the curve relating dominance to fitness will generally be near linear or even somewhat convex, but rarely concave. Females generally compete for access to food. Where food occurs in defensible patches, access to it can be contested. These patches can usually hold several females, who will all acquire approximately equal intakes. Even where the patches are smaller, however, high-ranking females will generally not systematically exclude others because that would deprive them from a major benefit of gregariousness; protection against predators (van Schaik 1983, Janson 1992). Moreover, the displaced individuals can usually find other food nearby or wait and subsequently gain access to the same food (albeit perhaps at higher risk). Thus, high-ranking females will show restraint to prevent the lower-rankers from avoiding them and forming a group on their own. Males generally have no such concerns since they tend to associate with groups of females.

We note that the resources over which the males in a group compete generally come in a fixed total amount (van Hooff & van Schaik 1992, van Schaik 1996). The number of fertilizations in a particular group during a particular period of time will be constant, and coalitions will not change this amount. As a result, the areas under each of the different curves drawn in Fig. 9.1 are all equal (an important factor in the modeling). Another implication of constant-sumness concerns leveling coalitions. Whereas these coalitions should always increase the number of matings with fertile females, they will not automatically bring increased fitness for both partners because they have to share this access. This property will therefore make it more difficult for them to gain a fitness benefit from forming coalitions; we assume approximately equal sharing of access to fertile females and hence paternity (see below; but see Noë 1990).

In sum, because of the sex difference in the shape of the curves and because nepotism is usually not a major factor among males (unlike the situation among females, we must develop an independent approach to modeling male-male coalitions within groups.

9.2
The Model

We always consider coalitions with a single target; this is also by far the most common pattern of within-group coalitions among primates. The basic approach is to identify the conditions in which coalitions are viable, i.e. expected to occur. We recognize two components of viability that have to be met simultaneously: profitability and feasibility. Coalitions are profitable when, for each coalition member, the direct benefits in terms of increase in fitness exceed the costs in terms of reduction in fitness (both relative to the situation without coalitions) through risk of injury or death and energy expenditure or stress. We will therefore employ a parameter, C, that denotes these costs, which we assume to be equal for all members (this assumption is especially reasonable for coalitions in which animals attack a higher-ranking target). Coalitions are feasible if they are strong enough to beat their target (and exceed their cost, again denoted by C), which requires that we have some way of adding up the fighting ability of the individual players.

Before proceeding to present the model, we need to insert a comment on terminology, because game theorists and behavioral biologists use coalition in a different sense. In animal behavior, the unit of analysis is the coalition, which is the actual interaction. In contrast, what in game theory (Kahan & Rapoport 1984) is called a coalition is what a behavioral biologist would call a successful alliance, i.e. the situation that arises when the alliance has achieved its goal. This difference is most acute for rank-changing coalitions, in which numerous coalitionary interactions may be needed before rank change is achieved and then may continue to be needed occasionally to maintain the new ranks. All of this is considered a single ‘coalition’ in the model. These different terms do not affect the model because costs and benefits are measured in the same units: fitness components per unit time. Incidentally, our model is not a game-theoretical model; it merely borrows useful concepts and terminology from Kahan & Rapoport (1984).

We consider three basic configurations of coalition members relative to their (single) target (Fig. 9.2): (i) all-down, (ii) bridging, and (iii) all-up. Chapais (1995) calls these conservative, bridging and revolutionary, respectively. It is obvious that all-down coalitions are always feasible; a combination of higher-rankers can always beat single lower-rankers. However, because there is no immediate fitness gain when the coalition members are already high-ranking and have priority of access to the limiting resources, they are not profitable in the sense used in the model (in the discussion, we will consider situations where they may bring indirect benefits to the participants). Bridging coalitions against a single target are always feasible as well because the highest-ranking coalition member acting alone can always beat the target. However, they are not profitable for the higher-ranking member of the coalition unless

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[1] Alternatively, the supported individual is a non-relative providing some essential support to the high ranker in return, something we only expect in humans.

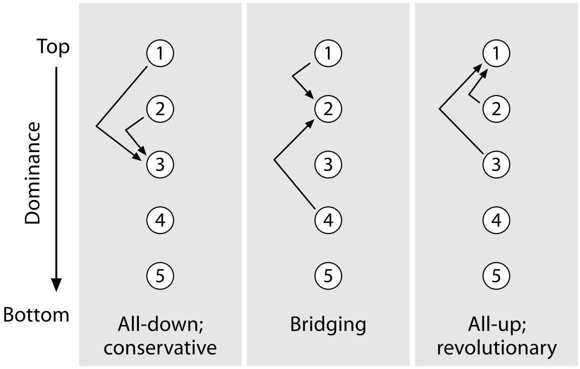

Fig. 9.2. Basic configurations of within-group coalitions (after Chapais 1995). Arrows indicate attacks.

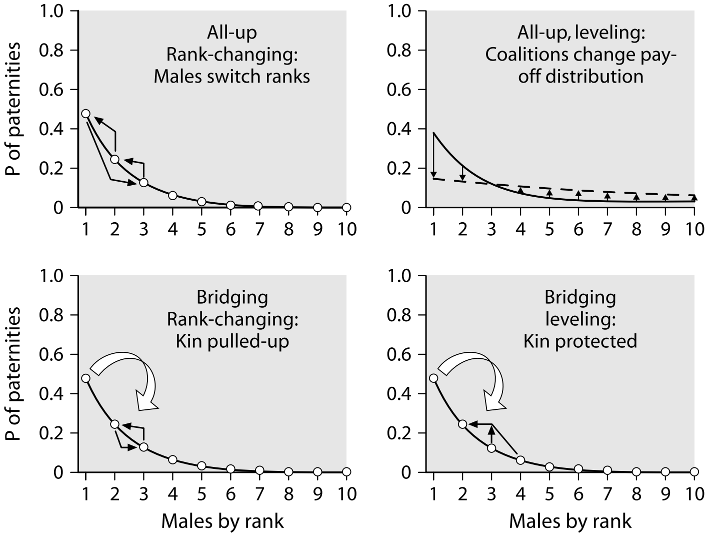

Fig. 9.3. The rank-changing and leveling varieties of both all-up and bridging coalitions.

the lower-ranking individual in the coalition is a relative, and the support can therefore improve the inclusive fitness of the supporter[1]. All-up coalitions may be feasible, when several low-rankers gang up to attack a higher-ranking target. When they succeed, they should also generally be profitable because of the improved ranks of the coalition partners, unless they are prohibitively costly due to high risk of injury or stress.

Both bridging and all-up coalitions can be profitable in two very different ways (Fig. 9.3). Coalitions can improve the ranks of the coalition members, but they can also improve the payoffs of their members by providing instantaneous (if temporary) access to the limiting resource, usually fertilizable females, without changing the ranks of the coalition members, a phenomenon we call leveling. In the case of bridging coalitions, this leveling takes the form of protection of lower-ranking relatives in contexts linked to competition. In the all-up configuration, such leveling is accomplished by coordinated attacks on a high-ranking male who is in consort with an estrous female. This context has been studied in detail in baboons (Packer 1977, Smuts 1985, Bercovitch 1988, Noë 1990, 1992), but in theory the same all-up leveling coalitions may also be found when no resource is directly at stake and then serve to induce the high-ranking male to show some restraint in mating competition. The model is really about these four kinds of situations: the rank changing and leveling varieties of bridging and all-up coalitions.

Feasibility needs to be estimated as well. To assess it, we have to solve the problem of determining the 'value' (i.e. strength) of the coalition. This problem has two components. First, we must decide how to estimate the strength of the coalition. We opted for the simplest assumption and simply added the strengths of the individuals in it, ignoring a possible effect of the number of participants. Second, we must determine which aspect of the individuals we need to sum. Here, again, we opted for the simplest solution and used the payoff before coalitions as the best estimate of a male's contribution to the alliance's strength (Pandit & van Schaik 2003, van Schaik et al. 2004). Ideally, we would like to use fighting ability, but that is very difficult to estimate, even if experiments are possible (cf. Noë 1990, 1994). Payoff, on the other hand, can be estimated by paternity analysis. Where β is modest, payoff and fighting ability are expected to show very similar functional forms with rank, allowing us to use payoff as our estimate of strength. At steep β, we expect the payoff differences to exceed those in strength, but fortunately, the model indicates no all-up coalitions (the only configuration for which feasibility is non-trivial) for $\beta > 0.5$, thus keeping the error modest.

We also incorporate a cost to feasibility because the allies need to coordinate their attacks with great precision and need to be prepared to do so at all times, and hence face some ecological and social cost. For simplicity, we have assumed that the cost C used to calculate profitability can be employed here as well. This assumption is probably not entirely correct, but the error is not likely to affect the predictions by much.

Although mathematically cumbersome, it is straightforward to calculate for each possible coalition (set of males attacking a particular target) whether it is profitable from the perspective of changing the ranks or payoffs of the allies, i.e. whether the formation of coalitions exceeds its costs, for each member. Feasibility can similarly be calculated. If for a given coalition, both conditions are satisfied for each member of the coalition, we predict the coalition to occur, although its frequency relative to other kinds of coalitions should of course depend on the net increase in payoff. We can then examine the features of these viable coalitions, such as the β range in which they are found, their sizes, the ranks of the participants, etc.

Table 9.1. Summary of predictions for within-group, male-male coalitions.

Type	Target	Members	Size	Despotism
All-up, rank-changing	Top or near-top	Just below top	Small (two or three)	Medium
All-up, leveling	Top or near-top	Mid- and low-rankers	Small-large	Low-medium
Bridging, rank-changing	Near-top	Top-ranker and relative not far below	Small (usually two)	More as despotism higher
Bridging, leveling	Anywhere	Variable	(variable)	Variable
All-down	Low-rankers threatening to form all-up coalitions	Top- and near-top-rankers	Probably small	(whenever all-up and bridging occur)

Here, we give an intuitive account of the predictions for the rank changing and leveling varieties of each of the two relevant configurations (all-up and bridging). Readers interested in the details should consult the technical papers (Pandit & van Schaik 2003[2], van Schaik et al. 2004). The predictions for each context are summarized in Table 9.1.

9.2.1
All-up, within-group coalitions: rank-changing

At constant *C*, the profitability of rank-changing coalitions increases as despotism increases, whereas their feasibility decreases. Hence, we expect them at intermediate values of β (and given our rule of calculating feasibility by comparing the sum of the coalition members' payoffs with that of the target, at $\beta < 0.5$). Because of the concave shape of the payoff curve, we expect these coalitions to be concentrated among the higher ranks; benefits are highest in that region. For the same reason, coalitions are expected to be small (larger coalitions will necessarily involve lower rankers for whom moving up in rank makes little difference in payoff). We therefore expect coalitions to concern the highest ranks, be fairly small, and involve mid- to high-ranking individuals.

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[2] We have abandoned some terms and procedures used in that paper, which was our first exploration of the problem. In particular, we now let leveling refer strictly to the process of flattening the payoff curve (rather than to all-up as done in that paper). Moreover, we no longer assign a role to motivation in estimating the strength of the coalition, because the motivations (expected payoff differentials due to coalition formation) of the target and the coalition members may tend to cancel.

We can sharpen these predictions by including another consideration. High-ranking males can form effective counter-coalitions in an all-down configuration (which are always feasible) that prevent the occurrence of successful all-up coalitions. This is especially likely for the all-up, rank-changing configuration where the fitness loss of losing rank position is likely to outweigh the moderate cost of an all-down coalition (largely in the form of opportunity costs). Because the top ranker cannot form counter-coalitions with a male that ranks even higher than him, he would be the preferred target. Thus, the sharpened prediction is that all-up, rank-changing coalitions should generally be formed by a small number of males ranking immediately below the top-ranking male.

9.2.2
All-up, within-group coalitions: leveling

We use the same rule for estimating the feasibility of all-up leveling coalitions as for all-up, rank-changing coalitions. This may not be quite correct since the maximum risk level may be slightly lower, but as with other assumptions it should be close enough for this kind of strategic model. The profitability is obviously very different from the rank-changing variety; we are now asking whether the members gain enough in fitness from improved access to mates to outweigh the costs. To calculate this profitability, we have to resort to yet another simplification. For each particular coalition that is feasible, we check whether leveling the payoff curve leads to profitability for the top-ranking member of the coalition. Because he is the most likely not to gain from forming the coalition, if the coalition is profitable for him, it will be so for each member of the coalition. If so, we accept it as a viable coalition[3].

As can be intuited from comparison of the two curves in Fig. 9.3, the predictions are that all-up, leveling coalitions are expected to be relatively large and to be formed by mid- to low-ranking males targeting very high-ranking males. Mid- to low-ranking males stand to gain the most from these leveling coalitions in terms of improved fitness. They are expected to target very high-ranking males because those are the ones with access to the estrous females. Coalitions need to be relatively large in order to be able to beat the target (see Pandit & van Schaik 2003 for details). The curves in Fig. 9.3 also suggest that at higher values of *b*, individuals derive greater fitness benefits from rank-changing coalitions,

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[3] We achieved this by introducing a new parameter α, which flattens the payoff curve, yielding a payoff function for the 1^{th} male as a function of α and β (Pandit & van Schaik 2003). We calculate the optimum value of α, which is right where the highest-ranking member of the coalition starts losing payoff compared to not forming the coalition. If this optimum value of α is less than one, the payoff curve is flattened and the coalition is accepted as profitable. In practice, we therefore assume that the coalition will systematically attempt to intimidate all members ranking above the coalition, but because intimidating the top-ranking male will effectively intimidate all males ranking below him, we expect that most harassment will be aimed at the top-ranking male. This procedure introduces a small error in that it also changes the payoffs of those not participating in the coalition (ranking below them), but we considered this error acceptable relative to the complexity of alternative ways of modeling.

and thus would prefer to form those, so the leveling coalitions are especially likely at lower values of β.

All-down counter-coalitions are still feasible, but against all-up, leveling coalitions, we expect that they are less likely to be profitable. Perhaps the most important reason for this is that the payoff of other high-ranking males is not affected because they are not targeted and their ranks are not at risk. They may also face an opportunity cost to forming the all-down coalition if at the time of the coalition they are in consort with another female or with no female at all. If counter-coalitions occur, however, they should act to suppress leveling coalitions altogether.

9.2.3
Bridging, within-group: rank-changing

These kinds of coalitions are always feasible because they involve at least one member outranking the target. Assuming that they contain only two members, it is clear that they will never be directly profitable for the higher-ranking member. When the lower-ranking member is a close relative, however, kin selection may make it profitable for the higher-ranking male (we assume that they will always be profitable for the lower-ranker) if the rank increase of the lower-ranking member, corrected for the degree of relatedness with the high-ranker, outweighs the cost. Since these benefits increase as degree of despotism increases, we expect these coalitions especially at higher β values, and among males in the higher regions of the dominance hierarchy. Chapais (in press) has developed a similar argument for females.

9.2.4
Bridging, within-group: leveling

Higher-ranking males may always be available to protect lower-ranking relatives. However, to qualify as the equivalent among the bridging coalitions to the leveling among the all-up coalitions, this protection must increase the lower-ranking relative's access to receptive females. This requires that these coalitions happen in the context of males competing directly over access to receptive females. We expect them to be viable in a broad range of conditions, but they may be difficult to distinguish from the protection of relatives against attacks by others.

9.2.5
Estimating β

There are many different ways in which one could estimate β, the degree of despotism in payoffs. Payoffs can be estimated as fertilization rates (rather than, for instance, mating success), which we assume to correlate closely with fitness (perhaps best estimated as the number of offspring sired that survive to adulthood, but obviously rarely possible in naturalistic studies). Fertilization rates can be estimated through paternity analysis, or in some obvious cases behaviorally. Studies that estimate paternity through molecular techniques (e.g. micro-

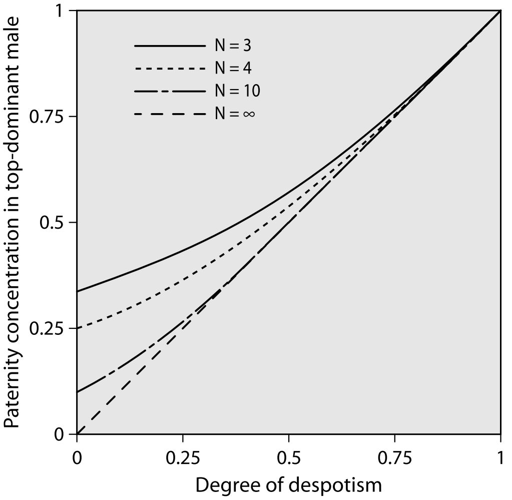

Fig. 9.4. The deviation between paternity concentration (payoff for the top-ranking male) and β. Note that the discrepancy increases as the number of males in the group (*N*) decreases.

satellites) are proliferating, and we rely on a recent compilation of these studies here (van Noordwijk & van Schaik 2004).

There are various ways of estimating β from a set of paternities across a range of male ranks: (i) the paternity of the top-ranking male (designated as paternity concentration in van Noordwijk & van Schaik 2004), (ii) the ratio of the paternity of the second-ranking male to that of the top-ranking male, and (iii) the slope of the regression of log (paternity) on rank (cf. Fig. 9.1). What is the best estimate depends on two main factors: sample size of fertilizations and the number of males (N). In smaller samples, the number of paternities going to individual lower-ranking males is likely to vary dramatically due to chance, and as a result we expect measure (iii), and even measure (ii), to be more dependent on sample size than the first one. This is indeed what we found in a simulation experiment where we had groups of 10 males compete for fertilizations and used sample sizes of 5, 10, 20 and 50 infants. Especially among smaller sample sizes, paternity concentration was both less biased and especially was more precise (i.e. it had far lower variance) than the other two measures. On the other hand, measure (i) is strictly speaking only valid for infinite N and should therefore be increasingly biased as the number of males decreases. Fortunately, however, the bias is largest at low β, where we expect N to be larger in any case (Fig. 9.4). We will, therefore, use paternity concentration (paternity of the top-ranking male) as our estimate of β.

9.3
Observations on primates

9.3.1
Model fit and discrepancies

The model attempts to explain only a subset of the many coalitions that can be seen among males in primate groups: all offensive coalitions that are strictly within a group with basically stable ranks, apart from the changes brought about by the coalitions. We have shown previously that the predictions of the model for these coalitions generally show a good fit with observations, despite the many simplifying assumptions (Pandit & van Schaik 2003, van Schaik et al., in press). Thus, the predictions listed in Table 9.1 by and large also represent the observations.

We found only four unambiguous cases in four species, in which a higher-ranking male supported a lower-ranking relative to the point that the latter moved up in rank to just below his supporter. Nonetheless, these nepotistic coalitions were observed in the very conditions where they were expected: despotic situations where the high-ranking relative is (near-) top-ranking. We did not encounter any reports of bridging, leveling coalitions in primates, in which higher-ranking males supported lower-ranking relatives in direct competition over access to females, although anecdotal accounts of support of presumed male relatives exist.

It is possible that bridging, rank-changing coalitions are so rare because close male relatives rarely find themselves together in the same group following dispersal and if they do, they may fail to recognize each other with sufficient reliability. Alternatively, the rarity of reported bridging coalitions may be an artifact. One would expect such situations to be rather common where the number of immigration targets for dispersing males is limited, if kin recognition rules are sufficiently reliable and β is high enough to produce high relatedness among male peers. New data on male relatedness will probably lead to a large increase in data on bridging coalitions and hence to further tests of the model. These data should at least show whether one form of nepotistic behavior (not modeled here) is quite common: males showing restraint to their lower-ranking relatives and thus smoothing their way to the top if the latter are pre-prime.

We identified seven cases in four species of all-up coalitions where males successfully challenged a high-ranker and switched rank, as envisioned in Fig. 9.3. The features of these coalitions were in close agreement with the model: challengers ranked near the top and challenged a top-ranker. We also identified six cases in six species of all-up, leveling coalitions. The review of empirical studies also found the predicted contrast between the rank changing and leveling varieties of the all-up coalitions, although the number of cases was small (see Table 9.1). While the targets of both tend to be top-rankers, the participants in leveling coalitions are mainly mid-rankers, whereas they tend to rank just below the top in rank-changing coalitions. However, we did not find the predicted larger mean size of leveling coalitions, although some of the leveling coalitions were indeed quite large. We will discuss leveling coalitions in more detail below.

Table 9.2. The number of reported cases for each of the three main kinds of coalitions examined here (see van Schaik et al., 2004 for details) in relation to the estimated values of β in groups of wild primates. Each β class covers a 0.25-section of the range from zero to one.

	low	medium	high	very high
All-up, leveling	4	2		
All-up, rank-changing		3	2	
Bridging, rank-changing		1	1	1

The various kinds of observed within-group coalitions also showed different ranges of β values, as expected under the model (Table 9.2; including free-ranging groups in nature only), although the observed range tended to be higher than the predicted one: rank-changing all-up coalitions were expected only at $\beta < 0.5$. We would caution, however, that estimates of β are not always from the same group or the same time period, and therefore the conclusion as to the effects of β is still preliminary. Moreover, there is a risk of circularity attached to this kind of *post hoc* testing, because successful alliances may actually produce reduced β in that males will be less likely to press their full advantage knowing that doing so may unleash all-up coalitions.

The good fit between model and observations suggests that the simplifying assumptions we have made (simple addition of the values of players to calculate the values of the coalition; use of payoff rather than some estimate of fighting ability to calculate this value; use of the α parameter in leveling coalitions) were not so far off from reality as to diminish the model's predictive value (see Pandit & van Schaik 2003 and van Schaik et al. 2004 for further details). However, the finding that coalitions are seen in a systematically higher range of β values than expected deserves comment. It indicates that simply adding up the participating players' strengths (payoff values) to arrive at the strength ('value') of their coalition is inadequate. This discrepancy may indicate some independent effect of the number of coalition members or of fighting abilities. What remains surprising, however, is not the presence of this effect but its rather modest influence. Still, there is an urgent need for field-based estimates of coalition strength based on natural variation (cf. Noë 1990, 1994).

9.3.2
More on leveling coalitions

Leveling coalitions show the only real discrepancy between model predictions and observations in that observed coalitions were smaller than expected. There may be several explanations for the model's failure. Our predictions assumed that all coalitions that moved the α parameter from one to a lower value would actually occur. In practice, many of these potential coalitions reduced α by tiny

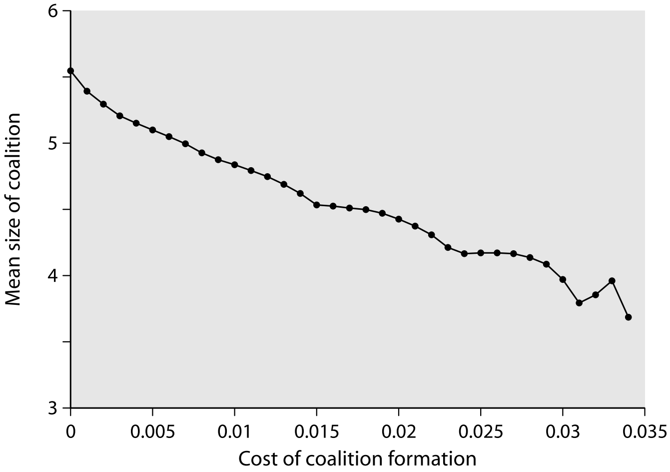

Fig. 9.5. The effect of introducing a fixed cost on the size of leveling coalitions through its effect on profitability.

amounts, and the presence of costs would almost certainly make them unprofitable in nature. Pandit & van Schaik (2003) attempted to deal with the issue of costs. Here, we re-examine this question: a fixed cost (corresponding to g_1 in our paper) does indeed reduce mean coalition size (Fig. 9.5). This cost will especially reduce the involvement of higher-ranking males.

A second problem is that we did not make N dependent on β. This issue will be discussed in more detail below, but in most cases we expect fewer males in groups with higher β. If we had made N dependent on β, the model would have generated fewer large coalitions, and hence fewer coalitions involving very low-ranking and rather high-ranking males.

Finally, we assumed that costs were constant for all males, but cost may be a function of rank distance between the coalition member and the target. If this modified assumption is used, the lowest-ranking males will be less likely to become coalition members, again reducing coalition size.

These three technical reasons contribute to explaining the discrepancy between model and predictions, but there may be biological reasons as well. In particular, it is possible that pre-prime males may avoid taking any risks that jeopardize their future rise to the top, or that males have trouble finding suitable partners for other reasons. More quantitative exploration of both model and empirical data is needed to fully resolve this problem.

Within savanna baboon groups (*Papio cynocephalus*), paternity monopolization by the top-dominant varies over time, due to demographic variation and the relative strength of the top-dominant male. Leveling coalitions vary widely in these groups. Consistent with the model, "dominance rank failed to predict mating success" (i.e. β approached zero) "when the number of adult males in the group was large, when males in the group differed greatly in age, and when the highest-ranking male maintained his rank for only short periods" (Alberts et al. 2003). It is therefore possible that, as suggested above, a demographic factor, namely the presence of many past-prime males, (even as the number of females remains constant) allows the formation of larger leveling coalitions, which the model predicts can then take place at higher β values (see Fig. 1 in Pandit & van Schaik 2003).

Because the observed paternity distribution includes the effects of effective leveling coalitions on mating access, there is some risk of circularity when testing the predictions (see Pandit & van Schaik 2003). Hence, either detailed comparisons or, if possible, experiments must be done. Pandit & van Schaik (2003) noted that the comparison between chacma (*Papio ursinus*) and savanna baboons supported the model because in chacma baboons, in which leveling coalitions are absent, top-dominant males show a strong tendency to monopolize paternity (Bulger 1993, Weingrill et al. 2000, Henzi & Barrett 2003), whereas that is usually not the case among savanna baboons (e.g. Alberts et al. 2003).

Similar coalitions involving various combinations of lower-ranking males and aimed at the top male can be seen in the absence of any direct competition over females. Such coalitions are often observed in chimpanzees (Goodall 1986). We believe they are best considered leveling coalitions as well, for the following reasons. One possible explanation for them is that they are attempts at unseating the top males. However, this interpretation lacks plausibility because they are formed in many different combinations and by (usually post-prime) males ranking well below the top rank, with little prospect of attaining that position. A second possibility is that their function is to reduce harassment by the top male, who frequently directs violent displays at subordinate males. The top-ranker may use harassment to reduce the likelihood of the formation of alliances that might later threaten to topple him. However, the involvement of past-prime males in these coalitions makes this possibility less plausible. The third interpretation is that these coalitions serve the same function as in baboons and macaques, i.e. to reduce the degree to which the top male will monopolize the matings in the community. Bettinger et al. (1993) mention that these all-up coalitions are more likely in the presence of swollen females. Thus, the mere possibility of leveling coalitions may intimidate the top male, who might therefore insist less on his priority of access.

9.4
Discussion

9.4.1
Further tests and extensions

One benefit of explicit modeling is that we can now also examine situations in which all-up, rank-changing or leveling coalitions are not expected because β is too high. We already noted the chacma baboons, but there may be other examples as well. For instance, Table 9.3 presents a summary of all male-male coalitions observed during 18 months of observation in one group of long-tailed macaques (*Macaca fascicularis*) containing between six and seven sexually mature

Table 9.3. Observed coalitions among males in group H of long-tailed macaques at Ketambe over an 18 month period during 1980-1981 (M. A. van Noordwijk & C. P. van Schaik, unpubl.)

Offensive within-group	All-up (rank-changing or leveling)	0
	Bridging, leveling	2
Defensive within-group	Challenger from within	21
	Challenging immigrant	16
	All-down, conservative	15
	Bridging, protective	17
Between-group		0
Other	(low-ranking male joins opportunistically)	3

non-natal males. Table 9.3 confirms that coalitions among males in this group occurred in a variety of contexts (see below), but not to achieve top rank (cf. van Noordwijk & van Schaik 2001). A high β value in this population has been confirmed (de Ruiter et al. 1994). More detailed work along these lines in populations with known β values will be useful in evaluating the model in greater depth.

The model also draws attention to puzzling exceptions. For example, male rhesus macaques (*Macaca mulatta*) have never been seen to form all-up coalitions, although low and medium β values are common. Dario Maestripieri (pers. com.) suggests that this absence may be due to the fact that female rhesus monkeys make good allies (see Chapais 1986, 1995), especially if they can easily recruit additional members of their matriline, thus diminishing the value of males to each other as allies. Alternative explanations might also be possible, but the important point is that the absence of male-male coalitions now becomes an issue to be examined.

9.4.2
The impacts of β

It is clear that the critical variable in the model is β. Fig. 9.6 presents the range of outcomes of male-male interactions over the full range of β values, as predicted by the model and supported by the preliminary tests conducted to date. The β values for the transitions between these outcomes are only approximately indicated because they depend on additional parameters. The appearance of clear dominance ranks depends on the cost of agonistic interactions relative to their benefit, which are a function of β. Above this β threshold, we expect all-up leveling coalitions; whether the ranks effectively disappear again as a result of the leveling coalitions is a function of both β and N, the number of males in the group (perhaps explaining why this is found only in the largest groups; Pandit &

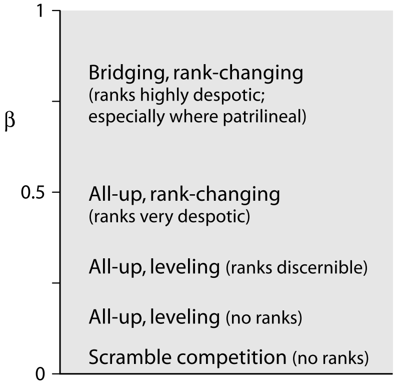

Fig. 9.6. A summary of the predicted offensive male-male coalitions in multi-male groups in relation to β. Switch points are approximate because their β value depends on additional parameters.

van Schaik 2003). The switch from leveling to rank-changing coalitions is determined by both β and the costs of coalition formation. Above $\beta = 0.5$ (or a somewhat higher value, depending on the detailed implementation of the feasibility rules), all-up coalitions should disappear, and the only coalitions expected are the bridging, rank-changing variety.

The influence of β reaches well beyond that of coalitions, however. Indeed, we expect to see major differences between low- and high- β situations, even within species. Van Noordwijk & 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. In high- β situations, the top-ranking males are therefore males in their early prime, whereas as β decreases, the age of top-rankers will gradually rise, until in the very large groups, such as those of Japanese macaques, males rise to the top by default when the old top male dies or disappears. As a result, very old and visibly aged males can occupy top rank (e.g. Watanabe 2001). In high- β situations, we not only expect escalated fights over dominance to be much more common, but also for them to be concentrated among the top ranks (see Nishida & Hosaka 1996). In low- β situations, males tend to immigrate into groups with more favorable adult sex ratios, whereas 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 understandably fall back on the low- β strategy. Male-female friendships may also differ predictably. Hence, the degree to which top males can achieve full priority of access to females is an important organizing variable for male socio-sexual strategies.

Another obvious impact of β is on N. Imagine the effect of imposing a variable cost to a male of living in a mixed-sex group, either due to the risk of injury because of attacks by other males or females (tangible even if males refrain from overtly participating in mating contests) or due to ecological costs imposed by differences in dietary preferences between males and females (van Schaik & van Noordwijk 1986). We assume that the males for whom ecological or social costs

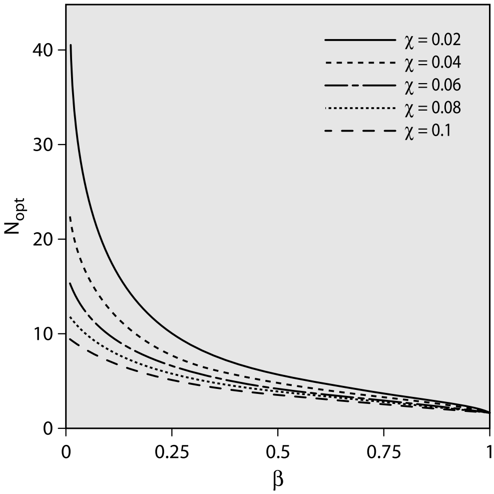

Fig. 9.7. The predicted relationship between degree of despotism (β) and the number of males in a group (*N*) of female primates when group membership entails a finite fitness cost (*C*).

outweigh the mating benefit can join all-male bands if there is also a cost to being solitary, or alternatively can join other groups in the population with lower β. Not surprisingly, such a small cost of group membership makes lower-ranking males more likely to leave the group as β increases, because lower-ranking males achieve increasingly reduced payoffs due to fertilizations. As a result, the relationship between β and N becomes concave, suggesting that the product $\beta \times N$ is approximately constant (Fig. 9.7). This expected concave shape of the relationship is actually consistent with observations (see figures in van Noordwijk & van Schaik 2004).

Within-group coalitions are only possible where there are at least three sexually active males in a group. It is therefore possible that an additional reason for the absence of coalitions at high β values is that there may not always be at least three males in the group (cf. Henzi et al. 1999)[4]. However, the most obvious relevance of the negative correlation is that it draws attention to the situation where N is unusually large despite fairly high β, which may produce leveling coalitions that would not otherwise occur. Two main conditions are expected to bring this about. First, the number of males may be largely independent of β; this could be due to male philopatry, as in chimpanzees, or the presence of (non-exclusive) pair bonds, as in humans. Second, females may reduce effective β if they benefit from the presence of additional males (e.g. van Schaik & Hörstermann 1994, Ostner & Kappeler 2004). Clearly, more work is needed to

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[4] Obviously, the other predictions of the model still hold. The number of males does not explain the contrasting features (β-range, size, ranks of members and targets) of the three main types of male-male coalitions examined here.

establish the relationship between β and the number of sexually active males per group, both within and between populations, as well as its socio-ecological correlates.

9.4.3
Other kinds of coalitions

The model has explained some of the great variety of coalitionary interactions among male primates, but obviously it does not cover many others. We focused on one class, the offensive coalitions that bring explicit fitness benefits, either because one or more of the members of the coalitions rose in rank or because they managed to increase their payoffs by taking some of the resources away from high-rankers.

The presence of offensive coalitions may also have produced several other interesting social behaviors. First, the threat of all-up offensive coalitions may have led to separating interventions by high-ranking males (de Waal 1982a, 1992a, Perry 1998). The intervening male prevents affiliative contacts between possible coalition partners that may allow the latter to build up enough mutual trust to launch coalitionary all-up attacks. The presence of preventive all-down coalitions where leveling coalitions occur needs to be confirmed. Second, we see opportunistic all-down coalitions where males who normally form high-risk, all-up coalitions attack a weak target, who is unlikely to ever attack them. These coalitions have been suggested to test the partners' willingness to engage in more risky coalitionary interactions of the offensive type modeled here or the preventive types that follow from them (e.g. de Waal 1992a, Noë 1992). Alternatively, such opportunistic coalitions could be random acts to keep subordinates stressed and therefore less likely to mount challenges to higher-ranking individuals, as suggested by Silk (2002c) for dyadic aggression, although we should then see males of all ranks, and especially the higher-ranking ones, engage in them. Under either interpretation, their function is not linked to the outcome of the interaction, but rather to the maintenance of the alliance itself.

Many defensive coalitions directly follow from the existence of the offensive coalitions we modeled. Every successful all-up, rank-changing coalition will subsequently produce persistent all-down conservative coalitions in order to prevent a reversal to the original situation. Such all-down (conservative) coalitions that serve to maintain the *status quo* are well known for females (Chapais 1995, Preuschoft & van Schaik 2000). The threat of these preventive coalitions was also thought to affect the features of the all-up and bridging coalitions considered by the model. Thus, even though they are not part of the model, such defensive coalitions directly follow from it.

We believe that there are two classes of coalitions that require separate or additional modeling: (i) defensive coalitions against unranked targets and (ii) coalitions against coalitions. This second kind of defensive coalition does not directly follow from the model, which only considers situations in which male fighting abilities are stable and where males have explicit ranks (thus excluding both immigrants and disequilibria between ranks and fighting ability). First, resident males often form coalitions against (individual) immigrant males, where these cannot be ranked yet. Where these immigrants aim at achieving top rank, the highest-ranking residents form a defensive alliance (e.g. in long-tailed macaques; van Noordwijk & van Schaik 2001; see also Table 9.3). Second, very similar coalitions aimed at defending the participants' rank positions are seen against low-ranking individuals that are improving in fighting ability, usually due to maturation, to the point that they can soon pass several others to challenge for top rank. The benefit of these successful defensive coalitions is that all members maintain their rank positions, and thus the payoff rates associated with them, for a longer time than they would without having formed the coalition. Such coalitions need further modeling to assess the possible effect of β on their presence (perhaps they are most likely where β is high but not very high) and the possibility of rank changes within the coalitions.

The other class of coalitions not elaborated in the model is when the targets of coalitions are other coalitions. For within-group coalitions against coalitions, the model can easily be generalized. All-up, rank-changing coalitions will tend not to target multiple males because the steep β will make these attacking coalitions non-feasible and make the defensive all-down coalitions generally successful (as we saw above). For leveling coalitions, coalitions against coalitions are more likely to be feasible but require large numbers of males in the group; maybe they will be seen in very large groups.

When the coalitions reside in different groups (as in lions: Packer & Pusey 1982; howler monkeys: Pope 1990; or chimpanzees: Goodall 1986), the model no longer applies mainly because the competition is no longer over a constant amount of resources. In primates, coalitionary takeovers of groups, as in brown lemurs or capuchin monkeys (Jack & Fedigan 2004, Ostner & Kappeler 2004) also fall under this rubric. A separate model is probably needed to account for these between-group coalitions.

9.5
Summary and conclusions

In this chapter, we presented a model for within-group coalitions among primate males. Coalitions occur if they are both feasible, i.e. can beat the target, and profitable, i.e. lead to a fitness benefit for all coalition members. Based on simple logic, we predict the existence of different kinds of coalitions, whose main characteristics are the relative ranks of members and targets, and whether or not they change the dominance ranks of the participants. The key predictor for the different kinds of coalitions is the value of β, the degree to which dominant males can monopolize mating access to females.

The model fits what we know about primates rather well, but its main function is to draw renewed attention to male-male coalitions, which in turn should help the development of more encompassing models. Such an empirical cycle will not only produce a better understanding of the phenomenon of male coalitions (which in general are much more opportunistic than those found among females: de Waal 1982a, 1992a, Nishida 1983), but will also allow us to identify the decision rules used by males (cf. van Noordwijk & van Schaik 2001) and the flexibility in these rules when β varies. The latter task will help us to develop a far better appreciation of the cognitive complexity associated with coalitionary behavior.

Given the importance of β, it is not surprising to see the presence of behavioral tactical decisions of males that correlate with its value. Some of the variation in male socio-sexual strategies is observed intraspecifically, especially well documented among Japanese macaques (e.g. Sprague et al. 1998). Individual male tactics also change with age, especially with respect to dispersal decisions. Males also make opportunistic decisions. Groups with rank instability at the top attract more immigrating males, probably because monopolization by top-rankers is reduced at such times, and the additional males tend to disappear again after the ranks have stabilized (van Noordwijk & van Schaik 2001). Similar intraspecific variation is seen for coalitions (see van Schaik et al. 2004).

All of this suggests some flexibility in decision-making that is linked to the value of β, although the way(s) in which males derive their implicit estimate of β is completely unknown. Despite various attempts (Matsuzawa 2001, de Waal 2003), our ability to estimate the complexity of social behavior patterns used by nonhuman primates is limited. Hence, revealing the existence of these mechanisms may help us to estimate the cognitive demands of various social decisions.

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