



## Conflict Resolution in Chimpanzees and the Valuable-relationships Hypothesis

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*Reconciliation, or peaceful postconflict interaction, can restore the usual pattern of interaction between social partners after open conflict has disrupted it—i.e., it can resolve conflicts. Researchers have documented reconciliation in >20 primate species, but the tendency to reconcile typically varies among dyads and dyad classes. The valuable-relationships hypothesis proposes that differences in the value of social relationships account for much of this variation. Value depends on how likely partners are to act in ways that benefit each other, where the benefits are ultimately direct or indirect increases in fitness. Researchers have responded to studies that have tested predictions of the hypothesis with extensive, if not universal, support. For example, kin show higher conciliatory tendencies than nonkin in many species, and conciliatory tendencies between unrelated females are high in several cercopithecines in which nonkin agonistic support is important for rank acquisition and maintenance. However, most of the support is indirect, because we lack direct evidence on the link between assays of relationship value and fitness. Also, some studies have methodological weaknesses, e.g., analyses based on pooled data and insufficient sample sizes. I review evidence in favor of the hypothesis with special attention to studies that come closest to providing evidence for predicted fitness effects. I also present new data on postconflict interactions between adult male chimpanzees at Ngogo that show how often pairs of males formed coalitions and how much time they spent grooming influenced the likelihood that they would reconcile after conflicts, and that allies were particularly likely to reconcile and to do so by grooming each other. The most important future research direction is to integrate detailed data on conflict management, analyzed at the level of dyads, with long-term data on*

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*reproductive success, such as that now available from several study sites, on the same populations.*

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## INTRODUCTION

In many gregarious primate species, individuals have ways to manage conflicts of interest among group members—to prevent them from leading to aggression—and to resolve them: to mitigate or repair damage that aggression can inflict on social relationships (Cords, 1997; Cords and Killen, 1998). They thereby reduce or eliminate incompatibility in interests and goals, and avoid costs that group living would otherwise impose (Aureli *et al.*, 2002; Cords, 1997; Cords and Aureli, 2000; Cords and Killen, 1997; de Waal, 2000; van Schaik and Aureli, 2000).

Most research on conflict management and resolution has focused on peaceful postconflict interactions (PPCIs), or reconciliation. PPCIs can stop hostility and repair disturbed relationships by restoring predictability (Aureli *et al.*, 2002; de Waal, 1986; Koyama, 2001). Researchers have documented reconciliation at group level in >20 species (Aureli *et al.*, 2002). Conciliatory tendencies typically vary across dyad types, e.g., female-female, male-male, kin, nonkin, partly owing to variation in relationship security (ability to withstand damage; Cords and Aureli, 2000) and in partner compatibility (the general tenor of relationships; Cords and Aureli, 2000). The valuable relationships hypothesis (VRH) holds that relationship value, which may be unequal for the partners, also affects tendencies to reconcile (Aureli *et al.*, 1989; Aureli *et al.*, 2002; Cords, 1997; Cords and Aureli, 2000; Kappeler and van Schaik, 1992; van Schaik and Aureli, 2000). As Preuschoft *et al.* (2002, p. 46) note, “The tendency to reconcile should be an indicator of the mutual dependence of two individuals that have to maintain each other’s inclination to cooperate against a background of competition and agonistic conflict.”

## THE VALUABLE RELATIONSHIPS HYPOTHESIS

The value of a social relationship ultimately depends on the extent to which it provides inclusive fitness benefits to partners or minimizes their losses from competition (Kummer, 1978; *cf.* Cords, 1997). Value can accrue to one or both partners for various, and sometimes multiple, reasons, and does so in the context of competition for resources such as food and

mates, for safety, or even for group membership. Partners may be mates or allies or may groom each other; they may tolerate each other's proximity while feeding on potentially monopolizable resources; or they may participate in group-level alliances against outside groups or individuals, or all of these (Aureli and van Schaik, 2002; Aureli *et al.*, 1989; Cords, 1997; Cords and Aureli, 2000; Kappeler and van Schaik, 1992; Kummer, 1978; van Schaik and Aureli, 2000). Dyad members may have asymmetrical value for each other, which can influence conflict management tactics (Aureli and van Schaik, 2002).

Genealogical relatedness increases relationship value when tolerance, affiliation, or agonistic support, or all of these, between kin can lead to indirect fitness gains. Such gains are possible for females in ecological situations in which they can benefit by forming coalitions—single acts of agonistic support—or alliances—repeated formation of coalitions between the same 2 individuals—to gain access to food patches shareable with some, but not all, group members, or to achieve and maintain dominance ranks that improve their access to food, or both. However, alliances that influence female rank acquisition and maintenance sometimes provide mutual benefits that do not depend on relatedness (Chapais, 1992, 2001; van Schaik, 1989). All females in a group may cooperatively contest access to food against other groups. Males can be valuable social partners for females because they provide benefits such as protection of offspring against infanticide, e.g., chacma baboons (*Papio ursinus*: Palombit *et al.*, 1997) and other aggression, e.g., yellow baboons (*Papio cynocephalus*: *et al.*, 2003). Males are not often valuable social partners for each other because they compete mostly over fertilizations, which are not shareable (van Hooff and van Schaik, 1994). However, male alliances are prominent in some nonhuman primates, e.g., many baboon populations (Henzi and Barrett, 2003); chimpanzees, *Pan troglodytes* (de Waal, 1982; Goodall, 1986; Nishida, 1983; Nishida and Hosaka, 1996; Watts, 1998).

The VRH was implicit in the reconciliation literature at least since de Waal and Yoshihara (1983) showed that both relatedness and the strength of affiliative ties influenced the likelihood of PPCI in rhesus macaques (*Macaca mulatta*). Kappeler and van Schaik (1992) used the term good relationships for the hypothesis that reconciliation avoids or repairs damage to relationships, and explicitly stated (p. 61) that it should occur “whenever the quality of individual relationships has important fitness consequences.” However, assessing whether relationships are good or bad usually involves measures of time in proximity, amount of grooming, or other indicators of social bond strength that may not correspond to measures of mutual dependence such as frequency of coalition formation (Cords, 1997). To formalize the distinction, de Waal and Aureli (1997) introduced the term valuable

relationships. Still, tolerance and grooming can provide benefits independently of the willingness of groupmates to give each other agonistic support, e.g., the hygienic and stress-reduction effects of grooming (Barrett and Henzi, 2001). Although valuable relationships has become the term of choice (Aureli *et al.*, 2002; Cords and Aureli, 2000; de Waal, 2000; van Schaik and Aureli, 2000), the distinction in terminology is less important than the focus on relationships as outcomes of strategic investments and on tolerance and social interactions such as grooming and coalition formation as tactics in the strategies (Aureli *et al.*, 2002).

I selectively review evidence in favor of the VRH, partly to inspire more explicit focus on what we mean by value and how we measure it. I then examine relevant research on chimpanzees and present a preliminary analysis of the relationship between variation in the occurrence of PPCIs and variation in the occurrence of coalition formation among male dyads in the chimpanzee community at Ngogo, Kibale National Park, Uganda.

## **INVESTIGATIONS OF THE VALUABLE-RELATIONSHIPS HYPOTHESIS**

### **Testing the VRH**

Tests of the VRH minimally require data on rates of PPCI in different dyad classes, e.g., kin on nonkin, adult female-adult female, on social relationships, and on the cooperative efforts of group members against threats such as other group members, extragroup conspecifics, and predators (Aureli *et al.*, 2002). Studies that pool data on all conflicts to look for reconciliation only at group level and those that pool data on all dyads in a class, e.g., all conflicts between males, cannot address the hypothesis. Analysis should at least be at the individual level: sample sizes should allow comparisons of how often individuals engage in PPCI with 1 category of opponent vs. how often they do so with another, e.g., kin vs. nonkin. If possible, it should be at the level of dyads to avoid problems with pooled data. The prediction that reconciliation should be most common between males in chimpanzees because of the importance of male alliances is a good case in point: most males are not allies in intra-community competition, and pooling data may obscure high rates of reconciliation between those that are.

Properly testing the VHR also requires showing whether the fitness benefits exist, which immediately brings up the difficulty of measuring fitness given the slow life histories of most primates and the short duration of most studies. The ideal would be, for the same population: 1) to

have a large enough sample to analyze variation in the rates at which individuals engage in PPCI with others individuals in their groups; 2) to have data on the frequencies, rates, and/or durations of potentially beneficial interactions, such as grooming, coalition formation, and interventions to protect others' infants against conspecifics or predators; 3) to show that PPCI avert or repair disturbance to relationships; and 4) to show, or at least to make a strong circumstantial case, that the benefits apply, e.g., that effective agonistic support helps recipients to acquire and maintain high ranks, and that rank and reproductive success correlate positively. Experimental manipulations of presumed value (Cords and Thurnheer, 1993) can provide strong circumstantial evidence.

Other conditions can also be relevant. For example, tolerance by powerful individuals for proximity may benefit less powerful ones; if so, close proximity should lead to better protection or increased foraging efficiency or both.

### Empirical Evidence in Species Other than Chimpanzees

Table I contains some of the studies of conflict management in nonhuman primates in which researchers have claimed support for the VRH and several others in which researchers have concluded that their data did not support it. The conclusions have rested on analysis of variation in conciliatory tendency in relation to one or more of the following factors: direct or indirect measures of social bond strength; relatedness; sex differences in behavioral ecology; impact of tolerance or cooperation on food acquisition; and frequency of coalition formation. No study has met all of the conditions.

The quality of the data and the strength of support vary. Sometimes problems arise because investigators use questionable estimates of, or assumptions about, relationship quality. For example, based on analyses at the individual level, Judge (1991) found that conciliatory tendency varied inversely with rank distance in *Macaca nemestrina*, and Castles and Whiten (1998) found a similar rank distance effect in *Papio anubis*. Judge concluded that the findings supported the VRH under the assumption that the extent of shared interests, hence relationship value, varies inversely with rank distance. However, rather than test the assumption, he merely cited Seyfarth's (1977) statement that closely ranked baboons tend to have strong social bonds. Castles and Whiten conceded that rank distance was an indirect measure of relationship quality and refrained from making strong statements about the VRH. Sommer *et al.* (2002) found a similar rank distance effect among female *Semnopithecus entellus*. They calculated ratios of rates of affiliation to

**Table 1.** Studies of selected conflict resolution in nonhuman primates that have addressed the valuable-relationships hypothesis

Species	Support?	Evidence	Comments
<i>Cebus capucinus</i> <sup>1</sup>	Yes Yes?	Conciliatory tendency higher for kin than for nonkin Importance and security of alliances apparently influences conciliatory tendency	Well-designed study, but small sample precluded statistical analysis
<i>Macaca mulatta</i> <sup>2</sup>	No	Reconciliation not more common between kin than nonkin despite despotic dominance	Conciliatory tendency between females generally low
<i>M. mulatta</i> <sup>3</sup>	Yes	Reconciliation more common among female kin than among nonkin	
<i>M. arctoides</i> <sup>2</sup>	Yes	Conciliatory tendency similar for kin and kin and nonkin female dyads	Nonkin support important for rank acquisition and maintenance
<i>M. sylvana</i> <sup>2</sup>	Yes	Conciliatory tendency similar for nonkin female dyads	Nonkin support crucial for rank acquisition and maintenance
<i>M. fascicularis</i> <sup>4,5</sup>	Yes	Conciliatory tendency higher for kin than for nonkin female dyads and for dyads with good relationships	Studies in wild and captivity give similar results
<i>M. fascicularis</i> <sup>6,7</sup>	Yes	Prevention of reconciliation reduces tolerance and prevents cofeeding; need for joint action to acquire food increases conciliatory tendency	Experimental manipulations of opportunity to repair disturbance or of partner value has expected effects
<i>M. tonkeana</i> <sup>8</sup>	Yes	Conciliatory tendencies similar for kin and nonkin female dyads	Tolerant dominance style; nonkin support important for rank acquisition and maintenance
<i>M. nemestrina</i> <sup>9</sup>	Yes (?)	Conciliatory tendency higher for kin than for nonkin female dyads and for closely ranked dyads	Assumption that value depends on rank distance not tested
<i>M. fuscata</i> <sup>4</sup>	Yes	Conciliatory tendency higher for kin than for nonkin female dyads	Despotic dominance—but non-kin support for rank acquisition and maintenance?
<i>M. fuscata</i> <sup>10</sup>	Yes	Conciliatory tendency varies positively with amount of grooming and of agonistic support for male dyads	One of few studies in which data on males support VRH
<i>M. fuscata</i> <sup>11</sup>	Yes	Absence of reconciliation leads to long-term decreases in grooming and association	Confirms that failure to reconcile disturbs relation among dyad types
<i>M. assamensis</i> <sup>12</sup>	Yes	Conciliatory tendency varies positively with amount of grooming and agonistic support for female dyads	Analysis with matrix permutation methods
<i>Papio anubis</i> <sup>13</sup>	Yes?	Conciliatory tendency higher for kin than for nonkin female dyads and for closely ranked dyads	Rank distance at best an indirect measure of value

Table 1. Continued

Species	Support?	Evidence	Comments
<i>P. ursinus</i> <sup>14</sup>	No (?)	No clear kin effects; reconciliation more common between closely ranked females, but does not lead to long-term increases in affiliation	Relationship repair just requires return to baseline, or no long-term disturbance
<i>Semnopithecus entellus</i> <sup>15</sup>	Mixed	PPCIs most common in closely ranked female dyads, but bond strength unrelated to conciliatory tendency and authors conclude that reconciliation not present	Rank distance may not assess relationship value; bond strength does not include agonistic support
<i>Gorilla beringei</i> <sup>16</sup>	Yes	Reconciliation uncommon between females, but common between males and females	Assumes male/female relationships greater fitness effects than those between females; most PPCIs involve appeasement
<i>Pan paniscus</i> <sup>17</sup>	Yes?	Conciliatory tendencies higher for dyads with close than those with weak relationships	Closeness did not include agonistic support
<i>P. troglodytes</i> <sup>18</sup>	Mixed	Conciliatory tendency higher for close friends than nonfriends, but unrelated to frequency of agonistic support	Small captive group, 1 male
<i>P. troglodytes</i> <sup>19</sup>	Yes	Reconciliation most common between males	No data on agonistic support or on variation among male dyads; captive group
<i>P. troglodytes</i> <sup>20</sup>	No	Conciliatory tendency lowest for male-male dyads	Captive group
<i>P. troglodytes</i> <sup>21</sup>	Mixed	Conciliatory tendencies not particularly high for male-male dyads, but high for dyads with high affiliation scores	Wild group; conciliatory tendencies lower than in captivity
<i>P. troglodytes</i> <sup>22</sup>	Yes	Conciliatory tendencies highest for dyads with high-benefit relationships	Wild group
<i>P. troglodytes</i> <sup>23</sup>	No	Conciliatory tendency not relatively high for male-male dyads or those with affiliative relationships	Value based just on time in proximity; no data on variation among male dyads

Note. All cited studies provided analyses at the level of individuals, i.e., researchers pooled data on all interactions that particular individuals had with members of specific dyad classes (kin, nonkin, male, female, etc.) and then compared mean values with kin vs. those with nonkin, mean values with other males vs. those with females, etc.

Sources: <sup>1</sup>Manson *et al.*, 2004; <sup>2</sup>2005; <sup>3</sup>de Waal and Yoshihara, 1983; <sup>4</sup>Aureli *et al.*, 1989; <sup>5</sup>Aureli *et al.*, 1997; <sup>6</sup>Cords, 1992; <sup>7</sup>Cords and Thurnheer, 1993; <sup>8</sup>Thierry, 1990; Demaria and Thierry, 2001; <sup>9</sup>Judge, 1991; <sup>10</sup>Majolo *et al.*, 2005; <sup>11</sup>Koyama, 2001; <sup>12</sup>Cooper *et al.*, 2005; <sup>13</sup>Castles *et al.*, 1996; <sup>14</sup>Silk *et al.*, 1996; <sup>15</sup>Sommer *et al.*, 2002; <sup>16</sup>Watts, 1995; <sup>17</sup>Palagi *et al.*, 2004; <sup>18</sup>Preuschhoff *et al.*, 2002; <sup>19</sup>de Waal and van Roosmalen, 1979; <sup>20</sup>Casperd, 1997; <sup>21</sup>Arnold and Whiten, 2001; <sup>22</sup>Wittig and Boesch, 2003; <sup>23</sup>Kutsukake and Castles, 2004.

rates of aggression in female-female dyads as estimates of bond strength. However, the ratios do not necessarily measure benefits that females provide to each other and they were actually unrelated to conciliatory tendencies.

Many studies suffer from small sample sizes. For example, Palagi *et al.* (2004) found, in a captive bonobo group, male-female and female-female dyads with close relationships reconciled more conflicts than those with distant relationships. However, their study group had only 5 members, which limited analysis at the dyad level and made any conclusions tentative. Also, they assessed closeness based on grooming and time sitting in contact, but not agonistic support. The health-related effects of grooming should influence fitness, and contact sitting may reflect tolerance and willingness to share limited food resources and consequently also influence fitness, but we know nothing about actual fitness affects.

Conciliatory tendencies are often higher among kin than among nonkin (Table I). Two arguments underlie using the result as support for the VRH. First, shared long-term (reproductive) interests between close kin can outweigh or at least partly counterbalance inevitable conflicts of interest. When kin can gain indirect fitness benefits by cooperating with, and biasing affiliative behavior toward, each other, and when either their relationships are insufficiently secure to withstand the destabilizing effects of conflicts or the conflicts are severe, they should show high conciliatory tendencies.

Second, many studies have been of species in which females form dominance hierarchies and nepotism influences female ranks. Assignment of high value to relationships between close kin follows from the assumption—not necessarily tested in the species and population in question—that rank and reproductive success correlate positively. Several macaque species showed higher conciliatory tendencies between close kin (Table I; *Macaca nemestrina*: Judge, 1991; *M. fascicularis*: Aureli, 1992; Aureli *et al.*, 1989; *M. fuscata*: Aureli *et al.*, 1993; *M. mulatta*: Demaria and Thierry, 2001; de Waal and Yoshihara, 1983; *cf.* Veenema *et al.*, 1994). In contrast, no kin vs. nonkin difference existed in *Macaca sylvana* (Aureli *et al.*, 1997), *M. arctoides* (Veenema *et al.*, 1994), or *M. tonkeana* (Demaria and Thierry, 2001; Thierry, 1990). Conciliatory tendencies were also higher between kin in *Papio anubis* Castles and Whiten, 1998) and *Cebus capucinus* (Manson *et al.*, 2005; Table I).

Nepotism influences female dominance hierarchies in all of the macaques. Variation in the extent of kin versus nonkin difference in conciliatory tendency reflects variation in dominance style and in the importance of nonkin agonistic support, but imperfectly. Pig-tailed, long-tailed, Japanese, and rhesus macaques have despotic dominance, and



kin support is more important than nonkin support for rank acquisition in at least Pig-tailed macaques (Thierry, 2000). Likewise, unrelated baboon females rarely form coalitions (Alberts and Altmann, 2004; Henzi and Barrett, 2003). Conversely, nonkin support is important for rank acquisition and maintenance in stump-tailed and Barbary macaques. Female stump-tailed macaques have relatively tolerant dominance relationships, which lessens the risk of approaching unrelated opponents in postconflict situations (Veenema *et al.*, 1994). Those of Barbary macaques are despotic, but the importance of alliances between nonkin (Aureli *et al.*, 1997; Chapais, 1992;) and the lower security of their relationships (Cords and Aureli, 2000) may make PPCI between them important. However, nonkin agonistic support is also crucially important in Japanese macaques (Chapais, 1992), while tolerance among females is high in Tonkean macaques (Demaria and Thierry, 2001; Thierry, 1990); neither shows high tendencies for nonkin to reconcile.

Data on the relationship between female dominance rank and reproductive success exist for some macaques. For example, Takahata *et al.* (1999) found that high rank led to high lifetime reproductive success in Japanese macaques in some provisioned populations, perhaps because their food often came in rich, monopolizable clumps (*cf.* Harcourt, 1987), but not others, in which food superabundance might have mitigated effects of contest competition. They found no rank effect in 3 unprovisioned populations. However, they may become evident only during periods of food shortfall or high population density or both, as Altmann and Alberts (2003) showed for *Papio cynocephalus*.

Two other macaque studies provided direct support for the VRH. Majolo *et al.* (2005) used amount of grooming as an assay of relationship quality for dyads of male Japanese macaques and found that conciliatory tendencies varied positively with the amount of grooming exchanged per dyad. Cooper *et al.* (2005) showed that the proportion of conflicts reconciled by female dyads of *Macaca assamensis* varied positively with the amount of grooming and the number of coalitions per dyad. They analyzed their data with matrix permutation methods, which control for the nonindependence of dyads.

Two long-term studies merit detailed attention. Aureli (1992) showed that conciliatory tendencies between kin were higher than those between nonkin among female long-tailed macaques at Ketambe. In the population, dominance rank has subtle but multiple effects on female foraging efficiency, survival, and lifetime reproductive success (van Noordwijk and van Schaik, 1999). High-ranking females have higher adult survival and, in large groups, higher birth rates and infant survival. Daughters of high-ranking females mature faster and start to reproduce earlier than those of

low-ranking females. High-ranking females also have higher net food intake, especially when food is scarce. Rank effects on birth rates are strongest for females that have surviving infants during years of low food availability and when groups are largest and scramble competition for food highest. Multiplying the advantages gives high-ranking females significantly higher lifetime reproductive success than low-ranking females. Maternal support helps the daughters of high-ranking females to acquire ranks immediately below their mothers' ranks, so they gain the same reproductive advantages. The data plus those on reconciliation in the same population provide the most compelling support available for the VRH.

Data on the lifetime reproductive success of female yellow baboons in Amboseli show similar advantages to high rank (Altmann and Alberts, 2003). They are strongest when food abundance is low and in large groups, in which competition for food is highest. Females also acquire dominance ranks just below their mothers' ranks. Most female-female coalitions are between close relatives, and maternal support is crucial for rank acquisition by juvenile females (Alberts and Altmann, 2004), which supports the assumption that female alliances are valuable because they influence reproductive success. Most interventions by females in contests between other females are in support of the higher-ranking opponent, which should reinforce the female dominance hierarchy. However, coalitions between adult females are uncommon and might have little importance for rank maintenance (Alberts and Altmann, 2004; cf. Henzi and Barrett, 2003, for other baboon populations). Altmann and Alberts (2003) concluded that the value of female social partners for female baboons may rest mainly on whether they are dependable grooming partners or tolerant associates at feeding sites (cf. Barrett and Henzi, 2001). Data on postconflict interactions are not available for Amboseli, but one might expect conciliatory tendencies to be higher between close kin than between distant kin and nonkin and to be positively associated with cofeeding proximity and with the amount of grooming in dyads.

However, Silk *et al.* (1996) found at best equivocal evidence for higher conciliatory tendencies between close female kin in *Papio ursinus*, and also concluded that their data did not support the VRH because reconciliation did not lead to long-term increases in rates of affiliation. Cords and Aureli (1996; cf. Aureli *et al.*, 2002) responded that the VRH merely requires that PPCI improve relationships beyond what they would have been otherwise and predicts that affiliation or tolerance decrease in the absence of reconciliation, as Koyama (2001) found for female Japanese macaques.

Several studies have examined conciliatory tendencies between potential mates (Table I). Reconciliation was more common between males

and females than between females in both *Gorilla gorilla beringei* (Watts, 1995) and *Papio hamadryas* (Colmenares and Lazaro-Perea, 1994). Male hamadryas protect females and their infants from harassment by conspecifics and from predators and often intervene in conflicts between females, and males are usually the most important adult social partners for females (Watts *et al.*, 2000). Male mountain gorillas also protect females and infants against outside threats and often intervene in contests between females, and many females spend more time close to males than to females and groom with them more. Also, female transfer is common in mountain gorillas. Consequently, researchers have interpreted high male-female conciliatory tendencies as support for the VRH, under the assumptions that PPCI maintain cooperation between males and females and, at least in mountain gorillas, help males to retain mates (Cords and Aureli, 2000; Watts, 1995; van Schaik and Aureli, 2000). However, females presumably do not need to fear loss of cooperation from males with which they have mated, because the males have no interest in failing to protect the females' infants or to protect the females against external threats. Female mountain gorillas initiate most PPCI, in response to male aggression; whether male responses influence female residence decisions is unknown.

In white-faced capuchins, alliances that can have multiple fitness effects occur within and between the sexes. Alliances between females may influence female dominance rank acquisition and maintenance (Manson *et al.*, 1999) and can increase their power in competition with males (Perry, 1997). Alliances between males and females may influence males' ability to obtain  $\alpha$  positions and their tenures as  $\alpha$  males (Perry, 1998), and females join males in cooperative attacks on strangers and on deposed  $\alpha$  males that can be fatal (Gros-Louis *et al.*, 2003). Males also form coalitions with each other in intra-group competition and in aggression between groups (Perry, 1996, 1998). Manson *et al.* (2005) reported higher conciliatory tendencies between female kin than nonkin among white-faced capuchins at Lomas Barbudal, Costa Rica. When they classified adult dyad types as high or low with respect to value and security and used individual-level analyses to test predictions about the effects of the variables on the tendency to reconcile after escalated aggression, results were in the expected directions (Table I), though the small number of individuals and of conflicts precluded statistical testing. For example, conciliatory tendencies were highest for  $\alpha$  male-female dyads (high value, low security) and low for female-female dyads (high value but also high security). The study should serve as a model for hypothesis testing in other populations, and eventual data on lifetime reproductive success should permit a more

substantial test of the VRH and of the effects of relationship security at Lomas Barbudal.

Finally, experiments with captive individuals cannot directly address questions about the relationship of conflict resolution strategies to fitness, but allow controlled manipulations of relationship value not possible in the wild and tests of some variables assumed to be important in the wild. Two exemplary studies reinforce the conclusion that PPCI help to maintain valuable relationships in long-tailed macaques. Cords (1992) provoked conflicts between juveniles and showed that allowing them to reconcile facilitated their ability to feed in close proximity, which is relevant to the argument that PPCI in the wild promote tolerance of cofeeding on clumped resources and can make contest losers safer because they might otherwise feed on group peripheries. Cords and Thurnheer (1993) established a situation in which study subjects could get food from an experimental apparatus only with the cooperation of group mates trained to work the apparatus. The frequency of PPCI between untrained individuals and their now more valuable trained partners greatly increased. Thus, the subjects recognized variation, and changes, in partner value, which can depend on behavior that influences access to food (tolerance in food patches, agonistic support that helps females to assert priority of access to food, etc.).

Most of the studies satisfy the first 2 conditions: they provide detailed data on social relationships and sample sizes adequate for analyses at least at the individual level. Results of most are consistent with the VHR in that they show PPCI to be more common between close kin, mates, or allies, or all of these, than between other dyad partners. Results of Koyama's (2001) study meet the third condition, but clearly we need more such work before we can confidently conclude that PPCI repair disturbances to relationships or at least maintain the status quo ante. Data on long-tailed macaques at Ketambe both support the VRH and meet the fourth condition: conciliatory tendencies are relatively high between social partners who cooperate in ways that bring fitness payoffs. Several other long-term studies that provide data on lifetime reproductive success have the potential to address this condition, and as more such data accumulate, studies that use a predictive framework such as that of Manson *et al.* (2005) promise to provide more robust tests of the VRH. Finally, experimental manipulations that change conciliatory tendencies in expected ways when partner value changes also address the fourth condition, albeit indirectly, and support the VRH.

### Conflict Management and Resolution in Chimpanzees

Researchers have studied postconflict behavior in chimpanzees in several captive groups (Baker and Smuts, 1994; de Waal and Aureli, 1996; de Waal and van Roosmalen, 1979; Fuentes *et al.*, 2002; Preuschoft *et al.*, 2002) and 3 wild communities (Sonso Community, Budongo: Arnold and Whiten, 2001; North Community, Tai: Wittig and Boesch, 2003; Mahale M Group: Kutsukake and Castles, 2004). De Waal and van Roosmalen (1979) argued that reconciliation should be most common between dyads of adult males because males form alliances that influence dominance ranks and thus success in intra-community mating competition, while cooperation among females or between males and females affect fitness less. Many discussions of the VRH invoke this argument (Aureli and van Schaik, 2002; Cords and Aureli, 2000; de Waal, 2000; Kappeler and van Schaik, 1992; van Schaik and Aureli, 2000). Measuring fitness in chimpanzees is extremely difficult, but alliances do influence male ranks, and  $\alpha$ -males may depend on allies to maintain their positions (de Waal, 1982; Goodall, 1986; Nishida and Hosaka, 1996). Male rank influences mating success, and alliance participation can improve mating success (de Waal, 1982; Tutin, 1979; Watts, 1998, unpublished data). Data from Gombe and Tai show that though reproductive skew among males is low, high rank, especially  $\alpha$  status, leads to relatively high reproductive success (Constable *et al.*, 2001; Vigilant *et al.*, 2002).

The importance of group-level male alliances in intercommunity aggression (Wilson and Wrangham, 2003) also implies that male-male relationships have high value and that conciliatory tendencies should be high for male dyads (Cords and Aureli, 2000; Kutsukake and Castles, 2004). In fact, the outcome of encounters between communities depends partly on the number of males present (Boesch and Boesch-Achermann, 2000; Watts and Mitani, 2001; Watts *et al.*, 2006; Wilson and Wrangham, 2003; Wrangham, 1999). Likewise, the number of males per community influences success in intercommunity competition, which in turn can influence female reproductive success through its effects on food availability and on safety (Williams *et al.*, 2004; Wilson and Wrangham, 2003).

Also, chimpanzees have a fission-fusion social system, and even allies are often apart. Separation, plus competition for allies (de Waal, 1982; Nishida and Hosaka, 1996), could lead to insecurity about the status of relationships and increase the importance of conflict resolution (Cords and Aureli, 2000).

Nevertheless, support for the VRH in chimpanzees is somewhat mixed, perhaps because its predictions differ depending on whether the focus is on group-level alliances or on alliances within communities. All males in a community are valuable partners for each other in inter-community

competition (Wilson *et al.*, 2002; *cf.* Grinnell *et al.*, 1995, for lions), though perhaps less so in large than in small communities (Watts and Mitani, 2001). If PPCI help to maintain group-level alliances, conciliatory tendencies should vary little across male dyads. If they are more important for the development and maintenance of alliances within communities, greater variation among dyads should occur, with conciliatory tendencies highest between the males that most often form coalitions. Variation in relationship security might also produce dyadic variation. Variation in other aspects of male-male relationships may also have fitness effects; for example, grooming may provide direct benefits, may influence alliance formation and maintenance, and may influence tolerance during feeding on monopolizable resources such as prey carcasses. If so, social variables besides coalition formation should also influence conciliatory tendencies.

As expected, PPCI were more common between males than between females in captive groups at the Arnhem Zoo (de Waal and van Roosmalen, 1979; de Waal, 1986) and the Yerkes Field Station (Preuschoft *et al.*, 2002). The results generally support the VRH, but they were based on data pooled either by age-sex class or by dyad type because the study groups were small, and they do not address questions about variation among male dyads. Conversely, Casperd (1997, cited in Arnold and Whiten, 2001) found lower conciliatory tendencies between male dyads in the Chester Zoo colony than between male-female dyads or female dyads.

Arnold and Whiten (2001) analyzed postconflict behavior in the Sonso community in the Budongo Forest Reserve, Uganda. When possible, they analyzed their data at the individual level, but their sample sizes were small, e.g., they based their comparison of male-male vs. male-female conciliatory tendencies on 5 individuals. They also found that conciliatory tendencies between males and between females were similar, and that, contrary to another prediction of the VRH, conciliatory tendencies between males and estrous females were not particularly high. They still concluded that their data partly support the VRH because male-male and male-female dyads that were highly compatible, i.e., whose summed scores for time spent grooming, in body contact, and in close proximity were in the top 25% of all dyadic scores, had higher conciliatory tendencies than those that were weakly compatible (bottom 25% of scores). Their sample sizes were too small for an analysis of the relationship between coalitionary support and conciliatory tendencies, but they expressed skepticism that a strong positive relationship exists and tentatively concluded that only compatibility influenced conciliatory tendencies. However, they qualified the conclusion by noting that no major rank challenges occurred during their study, and they suggested that chimpanzee conflict management and resolution behavior varies in association with ecological and demographic variation.

Kutsukake and Castles (2004) found that 29.7% of aggressive interactions between male chimpanzees in M Group at Mahale were followed by PPCI and that the conciliatory tendency was 13.7% for male dyads. They concluded that their data did not support the VRH because the values were not significantly higher than those for male-female or female-female dyads and because conciliatory tendencies were not higher for dyads with affiliative relationships than those with neutral relationships. However, their assessment of affiliation was based only on time in proximity, and their sample sizes were too small for individual-level comparisons of adult male dyads to other types and for examination of variation among male dyads in relation to variation in any measure of relationship value. Besides, association measures do not necessarily reflect aspects of male-male relationships generally considered most valuable—grooming and agonistic support.

Finally, Wittig and Boesch (2003) analyzed in detail conflict-related decision-making by members of the Northern Community in Tai National Park, Ivory Coast. They categorized dyads into those that offered low, medium, and high benefits to members based on the frequency of food sharing and agonistic support. Contrary to data from Budongo and Mahale, they found strong support for the VRH in that conciliatory tendencies varied significantly among dyad types and were highest for high benefit dyads and lowest for low benefit dyads. Because partners with high benefit relationships could repair the social costs of conflicts relatively easily, they could afford to initiate aggression against each other without undue social risks. Variation in decisions to engage in aggression also reflected relationships asymmetries; e.g., individuals were less likely to be aggressive to high benefit partners that were dominant to them when rank distances were small than when rank distances were large, because fights between closely ranked opponents lasted relatively long and presumably carried relatively high risks of relationship damage. Wittig and Boesch (2003) did not analyze data on dyads comprising different age-sex classes separately, partly because the study community had only 4 adult males. It might not have posed problems for their analysis of benefit effects, given that females at Tai sometimes form coalitions with males and with each other (Boesch and Boesch-Achermann, 2000), but it prevents any conclusion about variation among male dyads.

### **PPCI BETWEEN MALE CHIMPANZEES AT NNGOGO**

The unusually large number of males in the Ngogo chimpanzee community provides unique opportunities to examine variation in male social relationships, including variation among male dyads in postconflict

behavior. Here, I use data on male behavior to test 5 predictions derived from the VRH. The data do not come from a formal study of conflict management and resolution and the analyses are preliminary, but they can point toward future, more detailed research at Ngogo and other sites. The predictions are:

1. The proportion of aggressive conflicts followed by PPCI per male dyad varies positively with the number of coalitions per dyad.
2. The proportion of aggressive conflicts followed by PPCI per male dyad varies positively with the amount of grooming per dyad.
3. Allies more often engage in PPCI than nonallies do.
4. When they engage in PPCI, allies groom with each other more than nonallies do.
5. The dominant of 2 males is more likely to initiate a PPCI when his opponent is an ally than when his opponent is not an ally.

## METHODS

### Study Site and Subjects

I collected the data during 2 periods of fieldwork (October, 1998 through July, 1999; June through December, 2002) at the Ngogo research site in the center of the Kibale National Park. Kibale is in western Uganda between 0°13' and 0°41'N and 30°19' and 30°32'E. The Ngogo chimpanzee community uses an area about 35 km<sup>2</sup> that consists mostly of mixed mature and regenerating forest transitional between lowland and montane evergreen forest. It also includes other, more minor vegetation types, such as palm swamps and *Pennisetum purpureum* grassland (Butynski, 1990; Lwanga *et al.*, 2000; Struhsaker, 1997), some of which the chimpanzees use infrequently. The chimpanzee community is the largest on record (Watts, 1998); during the periods considered here, it contained 23–25 adult males, 14–16 adolescent males, and *ca.* 145 individuals total.

### Data Collection

I collected most data on male social interactions during focal samples on adult males (1234 h of samples in 1998–1999; 1263 h in 2002). During focal samples on males and estrous females and during breaks in sampling, I also collected data *ad libitum* on agonistic interactions (most commonly charging displays) and coalition formation between males. I designed



sampling to address questions about grooming, alliance formation, dominance, meat sharing, and other aspects of male social relationships (Watts, 2002), and I did not conduct formal postconflict and matched control samples. However, whenever possible, I recorded whether males that had been targets of charging displays had friendly interactions with the males that had charged at them  $\leq 5$  min of the display, and I did the same for opponents that had engaged in chases or fights.

### Data Analysis

Because I was not formally addressing whether Ngogo males reconcile after conflicts, I did not compare rates of PPCI to baseline affiliation rates or try to calculate conciliatory tendencies by retrospectively identifying control samples, as Wittig and Boesch (2003) did. My goal was simply to examine the relationship between the likelihood that male dyads engaged in PPCI shortly after conflicts and how often they formed coalitions or groomed with each other. I used a 5-min time window because others have found elevated rates of friendly conflict, compared to control rates, during the first few minutes of postconflict samples in chimpanzees (Arnold and Whiten, 2001; Kutsukake *et al.*, 2004; Preuschoft *et al.*, 2002).

I analyzed the relationships of social variables to the likelihood of PPCI in 2 ways. In the first, I used matrix permutation methods available in Hemelrijk's MATRIXTESTER (Cooper *et al.*, 2005; *cf.* Hemelrijk, 1990). Following Cooper *et al.* (2005), I constructed symmetrical matrices in which the entries were the number of coalitions, the time spent grooming, and the percentage of conflicts followed by PPCI for each male dyad. I treated dyads with  $< 5$  conflicts as missing values to reduce small sample size biases, and also constructed a dummy matrix for each study period in which entries were 1 for them and 0 for all other dyads to partial their values out of the analysis (*cf.* Hemelrijk, 1991). Assigning the respective individuals' mean values to cells with  $< 5$  conflicts instead (Hemelrijk, 1991) gave similar results. I performed 2000 matrix permutations to generate partial  $\tau K_r$  values between coalition frequency or grooming and the percentage of conflicts followed by PPCI. Second, following Majola *et al.* (2005), I regressed values for the percentage of conflicts followed by PPCI, after arcsin-square root transformation, against the number of coalitions or the amount of grooming time per dyad. MATRIXTESTER controls for variation among individuals, whereas the regression analyses do not, because they treat dyads as independent data points. Arguably that is not an issue, because alliances occur at the dyadic level, rather than being properties of individuals, and because, from an individual's perspective, the value of any particular

relationship varies as a function the partner's quality. In any case, both methods gave nearly identical results, and I present only those of the matrix permutation tests.

The number of coalitions per dyad vary from 0 to 22 in 1998–1999 and 0–33 in 2002; values are 0 for most dyads. In lieu of any standard, quantitative definition of alliance, I identified dyads that formed coalitions with a frequency in the top quartile among those that formed coalitions at all ( $\geq 5$  in both periods) and in which support was bidirectional as allies. I used Wilcoxon matched pairs tests for individual level tests of the prediction that males that had allies ( $n = 12$  in 1998–1999;  $n = 13$  in 2002) were more likely to engage in PPCI with their allies than with nonallies.

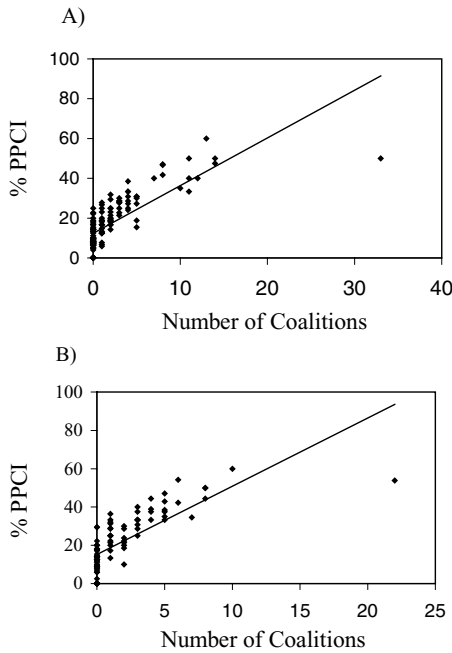
Many PPCI involved only brief physical contact, usually preceded by one opponent reaching a hand towards the other and sometimes accompanied by formal submissive signals from the lower-ranking opponent, as described for postconflict contexts at Budongo by Arnold and Whiten (2001), at Mahale by Kutsukake and Castles (2004), and at Gombe by Goodall, 1986). In others, 1 or both opponents groomed the other. Grooming has multiple functions, possibly including reduction of the immediate physiological stress of conflict, and probably helps male chimpanzees to maintain cooperative social relationships (de Waal, 1982; Goodall, 1986; Nishida and Hosaka, 1996; Watts, 2002). I also used Wilcoxon matched pairs tests for individual level tests of the prediction that grooming would account for a higher percentage of PPCI between allies than between nonallies.

## RESULTS

The results are consistent with all predictions. Frequency of peaceful contact after conflicts associate positively with frequency of coalition formation: in both study periods, the likelihood that opponents would engage in a PPCI  $\leq 5$  min of an aggressive interaction increased significantly with the number of times they formed coalitions (Fig. 1; 1998–1999: partial  $\tau K_r = 0.45$ ,  $p = 0.0005$ ; 2002: partial  $\tau K_r = 0.52$ ,  $p = 0.0005$ ).

Frequency of peaceful contact after conflicts also associates positively with the amount of grooming per dyad: in both study periods, the likelihood that opponents would engage in a PPCI  $\leq 5$  min of an aggressive interaction increased significantly with the amount of time they groomed with each other (1998–1999: partial  $\tau K_r = 0.34$ ,  $p = 0.0005$ ; 2002: partial  $\tau K_r = 0.32$ ,  $p = 0.0005$ ).

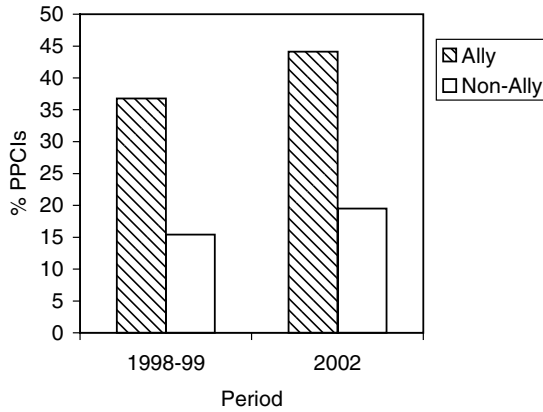
Allies were more likely to engage in PPCI with each other than with other males. The average dyad engaged in PPCI after 17% (SD = 12%) of aggressive conflicts in 1998–1999 and 21% (SD = 14%) in 2002. Allies had



**Fig. 1.** Relationship between coalition formation and the percentage of aggressive conflicts followed by peaceful postconflict interactions (PPCI) between male chimpanzees at Ngogo. Each point represents 1 dyad; values on x-axis are the number of coalitions per dyad. (A) 1998–1999; (B) 2002.

PPCI after a mean of 37% (SD = 10%) of conflicts in 1998–1999 and 43% (SD = 10%) in 2002 (Fig. 2). In contrast, the mean percentages of conflicts in non-allied dyads that were followed by PPCI are 14% (SD = 10%) in 1998–1999 and 18% (SD = 11%) in 2002 (Fig. 2). All males that formed alliances had peaceful interactions after a higher percentage of aggressive conflicts with allies (Wilcoxon matched pairs tests:  $T^+ = 78$ ,  $n = 12$ ,  $p = 0.0002$  in 1998–1999;  $T^+ = 91$ ,  $n = 13$ ,  $p = 0.0001$  in 2002).

Grooming accounted for 35% of PPCI in 1998–1999 and 36% in 2002. Grooming accounted for higher percentages of PPCI between allies than between nonallies in both periods (1998–1999: allies = 55%, nonallies = 25%; 2002: allies = 62%, nonallies = 30%; Fig. 3). In both study periods, individual males groomed with their opponents more often after aggressive conflicts with allies than after conflicts with nonallies (Wilcoxon



**Fig. 2.** For male chimpanzees at Ngogo, percentages of aggressive conflicts between allies and between nonallies that were followed by PPCI. Data analyzed at the level of individuals: for each male that had  $\geq 1$  alliances, the value for Ally was his mean percentage of conflicts followed PPCI with allies and that for Non-Ally was his mean percentage with other males. Heights of bars give means of individual means.  $N = 12$  males in 1998–1999 and 13 males in 2002.

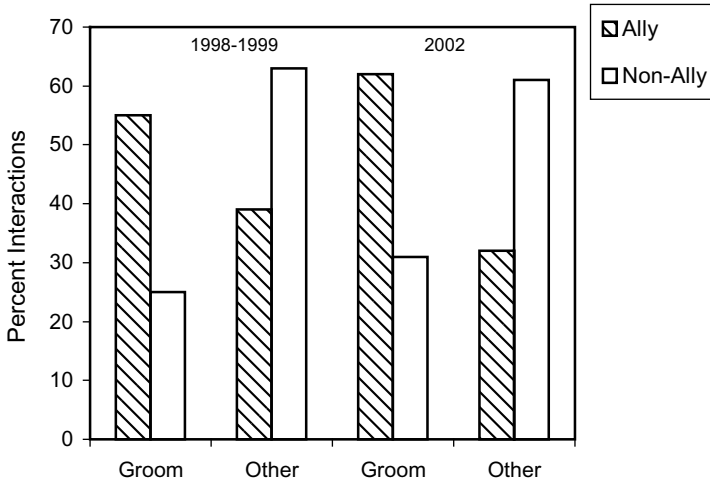
matched pairs tests:  $T^+ = 72$ ,  $n = 12$ ,  $p = 0.0034$ , in 1998–1999;  $T^+ = 84$ ,  $n = 13$ ,  $p = 0.0023$ , in 2002).

Finally, for conflicts followed by PPCI, the dominant of 2 opponents was more likely to initiate the interaction when his opponent was an ally than when not an ally. Higher-ranking opponents initiated 27% of PPCI in 1998–1999, including 45% of those with allies and 20% with nonallies. They initiated 31% in 2002, including 51% with allies and 28% with nonallies (Fig. 4). Individual males initiated more PPCI with subordinate allies than with subordinate nonallies (Wilcoxon matched pairs tests:  $T^+ = 66$ ,  $n = 12$ ,  $p = 0.0171$  in 1998–1999;  $T^+ = 81$ ,  $n = 13$ ,  $p = 0.0052$  in 2002).

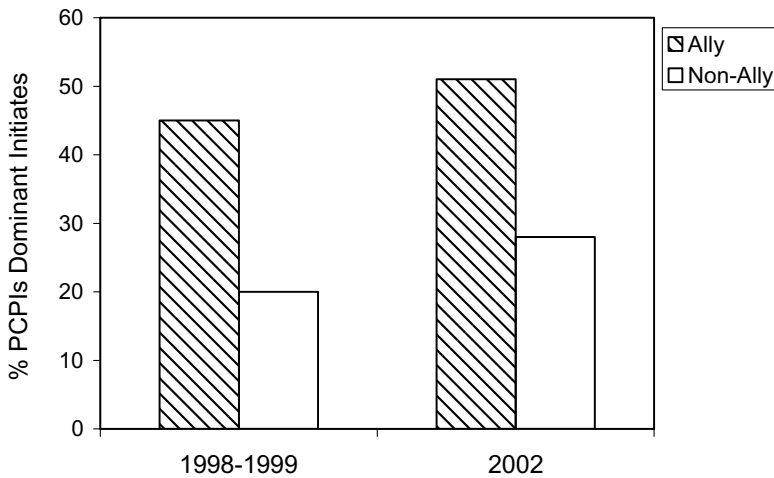
## DISCUSSION

### Postconflict Interactions Between Males at Ngogo

Male chimpanzees at Ngogo were more likely to engage in peaceful postconflict interactions when their opponents sometimes formed coalitions with them than when they did not, and were particularly likely to have PPCI with opponents with which they repeatedly exchanged coalitionary support,



**Fig. 3.** Percentages of PPCI between allies and between nonallies that involved grooming by 1 or both opponents (Groom) or only brief physical contact (Other). Data analyzed at the level of individuals; heights of bars give means of individual mean values.  $N = 12$  males in 1998–1999 and 13 males in 2002.



**Fig. 4.** Percentages of PPCI that dominant of the 2 opponents initiated, depending on whether his opponent was or was not his ally. Data analyzed at the individual level; heights of bars give means of individual mean values.  $N = 12$  males in 1998–1999 and 13 males in 2002.

i.e., their allies. The willingness of males to provide coalitionary support—along with their effectiveness as coalition partners—should be an important axis of relationship value, because alliances can influence dominance ranks and access to mates. Alliances have low security, though, and the combination of high value and low security should lead to high conciliatory tendencies (Cords and Aureli, 2000; cf. Manson *et al.*, 2005, for white-faced capuchins).

Grooming accounted for more PPCI between allies than between nonallies, while nonallies more commonly made only brief physical contact. The contrast supports arguments that grooming between male chimpanzees partly functions to develop and to maintain alliances (Watts, 2002). It also suggests that PPCI at Ngogo can reduce aggression-induced stress, as happens at Budongo (Arnold and Whiten, 2001), and reduce the risk of continued aggression, but the predictions require formal testing. The higher ranking of 2 opponents was more likely to initiate peaceful contact when the other opponent was an ally, which is consistent with the argument that males need to invest more in relationships with subordinate partners when the partners have leverage over them because they can withhold agonistic support (Lewis, 2002).

Ngogo chimpanzee results are all consistent with the VRH. However, they await further confirmation from more thorough research on aggression and conflict management in the population that should include analysis of the influence of conflict intensity and other variables on conciliatory tendencies and that should also examine the possibility that males use PPCI to signal benign intent and thereby gain short-term goals, e.g., access to food, rather than, or in addition to, repairing disturbed relationships, as Cooper *et al.* (2005) suggest helps to explain the relatively high conciliatory tendencies among male Assamese macaques. Their major immediate importance is to show that postconflict behavior, and presumably conflict management strategies generally, can vary among dyads of male chimpanzees with variation in partner value. Given such variation, we may not always find that male-male dyads as a class show a relatively high tendency to reconcile. To the extent that they do, we could take this to confirm that the importance of cooperation among all the males in a community during intergroup aggression.

### **The Future of the Valuable-relationships Hypothesis**

Since earlier reviews of the VRH (Aureli *et al.*, 2002; Cords and Aureli, 2000; van Schaik and Aureli, 2000), several more studies have added support (Cooper *et al.*, 2005; Majola *et al.*, 2005) and provided

methodological and conceptual improvements, e.g., use of matrix permutation analyses that control for individual variation; attempts to distinguish effects of relationship value from those of relationship security. Support for the VRH is strong, though not universal, but most is indirect. Even methodologically strong studies with good sample sizes assess relationship value based more on theory than on empirical evidence. This is almost inevitable, given the difficulty of measuring fitness in long-lived individuals such as most primates and of measuring the effect of agonistic support, grooming, tolerance in food patches, and other presumed indices of value on fitness. Yet much evidence from other organisms supports the theory, and considerable data on primates support the assumptions qualitatively and, sometimes, quantitatively. Not surprisingly, the best evidence comes from long-term field studies such as that on long-tailed macaques at Ketambe. Aureli (1992) confirmed that relatedness influences conciliatory tendencies in female-female dyads there as well as in captive groups. Other research showed that high-ranking females have relatively high reproductive success because of their advantages in competition for food and safety (van Noordwijk and van Schaik, 1999). Agonistic support from their mothers helps the daughters of high-ranking females also to become high-ranking, which means that they gain the same advantages (van Noordwijk and van Schaik, 1999). The picture is less complete for other macaque species, but available comparative data on how the importance of kin and nonkin support in rank acquisition and maintenance covaries with postconflict interactions between females strongly suggests that the relative openness of power networks is causally tied to the degree of kin-bias in conciliatory tendencies (Thierry, 2000; cf. Aureli *et al.*, 2002). More systematic investigation may confirm that the causal link exists and is in turn linked to variation in the fitness effects of agonistic support networks.

Progress in testing the VRH, and in research on conflict management more broadly, also requires careful statement of assumptions and examination of their validity, combined with well formulated predictions. The work of Manson *et al.* (2005) on white-faced capuchins provides a model here, despite, and even because of, the tentativeness of their conclusions: they made a strong case for restricting their analysis to escalated conflicts, but it stringently limited their sample sizes, and they reasonably stated that confirmation of predictions from the VRH depended on further research. If possible, the research should include examination of variation among dyads that belong to different classes, e.g., do  $\alpha$ -male white-faced capuchins reconcile most often with females with which they most often form coalitions against other males? Research eventually should incorporate data on lifetime reproductive success. Also, as Silk (1997) and Cooper *et al.* (2005) remind us, PPCI can serve short-term goals that may not

be tied to relationship maintenance or repair, e.g., provision of access to food.

Research on baboons provides other compelling examples. Realization that alliances between adult females are rare in some populations or subspecies, and have little influence on rank maintenance in populations in which they are more common, effectively challenges assumptions about uniformity in female dominance systems in baboons, macaques, and vervets (Alberts and Altmann, 2004; Henzi and Barrett, 2003). At the same time, long-term research at Amboseli shows that variation in the extent to which females associate closely and groom with others explains much of the variation in female lifetime reproductive success (Silk *et al.* 2003), which seems to be strong evidence that the good relationships hypothesis (or friendship hypothesis; Aureli *et al.*, 2002) can converge with the VHR: any relationship that includes a positive component—that can facilitate access to limited food resources or to safety, or that provides social partners with the health benefits of grooming, for example—can be valuable because it can influence fitness, even if it does not include direct support in contest competition with others. De Waal (2000, p. 25) noted that individuals that depend on cooperation should evolve ways to control any social damage caused by open conflict. He then defined cooperation as “. . . the dependency of social animals on group life in general.” The definition at first seems too broad, though he cited alliance formation as an outstanding example. However, the Amboseli data indeed make it look like many primates depend so strongly on group life that many aspects of their social relationships are valuable with respect to fitness.

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