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Reconciliation in Three Groups of Lion-Tailed Macaques

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*We studied postconflict behavior in three captive groups of lion-tailed macaques (*Macaca silenus*). After a conflict, we monitored the aggressee as the focal individual during a 10-min postconflict period and made control observations the following day on the same individual. Selective attraction between former opponents occurred in the first minutes of the postconflict period. The conciliatory tendency was relatively high, about 40%. Although no specific behavior was used to reconcile, postconflict contacts were especially intense and a rich repertoire of affiliative patterns was exhibited. With regard to the rate and form of reconciliation, lion-tailed macaques resemble Sulawesi macaques, which belong to the same phyletic lineage. We also discuss the possible interrelations between conciliatory patterns and other characteristics of social organization.*

KEY WORDS: *Macaca silenus*; conflict; appeasement; social organization; evolution.

INTRODUCTION

Lion-tailed macaques (*Macaca silenus*), one of the most endangered primate species, are restricted to the tropical dense evergreen forest of the western Ghats mountains of South India (Ali, 1985). They are highly arboreal and mainly frugivorous (Kumar, 1987). Most authors have reported a relatively small group size, averaging between 12 and 20 individuals, and a sex ratio strongly biased toward adult females, which is related to a low occur-

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rence of groups containing more than one adult male (Sugiyama, 1968; Green and Minkowsky, 1977; Kumar, 1987; Hohmann, 1988). Adult males have a low rate of interaction with other group members and often stand on the periphery of the group (Hohmann, 1988; Seth *et al.*, 1992; Lindburg *et al.*, 1994).

We have little information about dominance asymmetry, interindividual tolerance, rates of conciliation and degree of kin bias in affiliative interactions among lion-tailed macaque groups. Yet these are key features in current theorizing (Caldecott, 1986; van Schaik, 1989; Thierry, 1990a). Macaques species may be ordered along a scale ranging from despotic species to more egalitarian species. At one end of this scale, rhesus and Japanese macaques (*M. mulatta*, *M. fuscata*) are characterized by strong hierarchies and intolerance between unrelated individuals. On the other hand, species like the Tonkean, crested, and stump-tailed macaques (*M. tonkeana*, *M. nigra*, *M. arctoides*) display weaker differences in dominance rank associated with elaborate conciliatory patterns and high levels of tolerance, even between unrelated individuals (Thierry, 1986, 1990a; de Waal and Luttrell, 1989; Petit *et al.*, submitted). The study of reconciliation has provided indications useful in assessing social relations both qualitatively and quantitatively. Among macaques, the frequency and form of affiliative contacts that occur shortly after a conflict between former opponents appear to be related to the overall patterns of social organization. Species exhibiting intense aggression and strict hierarchies show a low reconciliation rate together with the use of few behavior patterns, while species with mild aggression and relaxed dominance have high reconciliation rates coupled with a rich repertoire of reassurance behavior patterns (Thierry, 1986; de Waal and Ren, 1988; Demaria and Thierry, 1992; Chaffin *et al.*, 1995; Petit and Thierry, 1994).

Our study is part of a broader comparative project, which aims to situate the social organization of lion-tailed macaque relatively to those of the other members of its genus and to elucidate some of the evolutive processes having produced them (Thierry, 1986, 1990a; de Waal and Luttrell, 1989). Here we focus on the patterns of reconciliation in three captive groups of lion-tailed macaques. Reconciliation is used as a standardized criterion that yields quantitative assessments about the development of appeasement and conciliatory behaviors in the groups studied.

METHODS

Subjects and Living Conditions

We observed two groups, A and B, at the Primate Center of Göttingen (Kaumanns *et al.*, 1988), and group C at the Zoological Park of Rheine

(Salzert, 1989), Germany. Group A contained eight individuals: two adult males (≥5 years), three adult females (≥4 years), one juvenile male (1–3 years), and two infants (<1 year). The older male and the older female were hand-reared, all other individuals being the oldest female's offspring. Because the older male was adopted at the age of 10 months by the older female, it was considered to be related to all group members. The group was set up in 1986 and housed in an indoor–outdoor enclosure. The outdoor part has a surface area of 1500 m^2 and contains natural vegetation; the two indoor rooms have areas of 25 and 20 m^2, respectively. Group B contained four individuals: one adult male and three adult females. It was formed in 1988: one female is unrelated, and two females are sisters, but were hand-reared. A hand-reared infant was introduced into the group in September 1994. The subjects were housed in an indoor room of 22 m^2, with an access to an outdoor tunnel. Group C contained nine individuals: one adult male, two subadult males (3–5 years), four adult females, one juvenile female, and one infant. Except for the older male, all individuals were the oldest female's offspring. This group was formed in 1969 and was kept in a three-part enclosure: one indoor section of 14 m^2, an outdoor section of 14 m^2 covered by a wire mesh, and another outdoor area of 520 m^2 with natural vegetation. All groups had vertical and horizontal wood structures in their enclosures and were provided abundant food two times a day—fruits, vegetables, seeds, commercial monkey pellets—outside the time of observation. Water was available ad libitum.

Procedure

We collected data on each group between 0930 and 1330 hr. We observed group A from July to October 1993, group B from July to October 1993 and from March to May 1994, and group C from July to October 1994. We recorded agonistic interactions involving individuals >3 years via all occurrence sampling (Altmann, 1974). An agonistic interaction is the display of an aggressive behavior by an individual—vocal or facial threat, lunge, hit, bite—and a response by the recipient of the aggression: avoidance, present, lipsmack, silent teeth-baring, gecker, scream, counteraggression, redirected aggression.

After an agonistic interaction, we monitored the aggressee as the focal individual during a 10-min postconflict period (PC), with 30-sec observation blocks, via observation procedures of de Waal and Yoshihara (1983). As the frequency of conflicts was low, we recorded all agonistic interactions, including those without a lunge >2 m. In the case of polyadic interactions, we took into account only the two first agonists. The respective percentages

of polyadic conflicts are 21, 17, and 13% for groups A, B, and C, respectively. We conducted a 10-min matched-control period (MC) on the focal individual on the next possible observation day at approximately the same time, within a range of 15 min before and 15 min after the starting time of the PC period. Before starting the matched-control period, the observer waited until the focal individual and aggressor were ≤3 m apart (York and Rowell, 1988).

RESULTS

Interopponent Contacts

To demonstrate that lion-tailed macaques reconcile, we examined the time course of first nonaggressive physical contacts between former opponents, both in the PC periods and in their corresponding MC periods. According to which minute-block the first contact was made, three outcomes were possible: the PC/MC pair was attracted when the affinitive interaction occurred earlier in the PC than in the MC, dispersed when it occurred earlier in the MC than in the PC, and neutral when it occurred during the same minute block or when it was neither in the PC nor in the MC (de Waal and Yoshihara, 1983). According to the index defined by Veenema *et al.* (1994), the conciliatory tendency pooled per group ranged between 42 and 48% in the three groups (Table I). When considering data separately for each individual for which at least three conflicts were recorded, it appears that more individuals showed attraction than dispersion or neutral results (Table I).

Among adult relatives, reconciliatory tendencies following dyadic conflicts were 44.4% (n = 27), 60.0% (n = 10), and 44.4% (n = 9) among females in groups A, B, and C, respectively, and 66.7% (n = 12) between male and females in group A. Reconciliatory tendencies between male and unrelated females were 18.2% (n = 11) and 53.3% (n = 15) in groups B and C, respectively. The only adult female without relatives in group B had a reconciliatory tendency of 42.8% (n = 14) with other females.

For comparative purposes, one should provide values for dyadic conflicts involving a lunge or a bite. However, data were sufficient only for the category of kin-related adult females in group A, whose conciliatory tendency was 38.9% (n = 18).

To test for the possibility that the nature of conflicts affected the probability of subsequent reconciliation, we calculated conciliatory tendencies for different kinds of conflicts. The comparison of conflicts involving or

Table I. Occurrence of Interopponent Contacts

	Group A	Group B	Group C
Timing of reconciliation[a]			
Greatest difference (min)	7	4	4
Kolmogorov–Smirnov (D)	0.42	0.36	0.34
P	0.001	0.01	0.001
Number of pairs	57	42	74
Categories of pairs[b]			
Number of attracted pairs	33	27	40
Number of dispersed pairs	8	7	9
Number of neutral pairs	16	8	25
Percentage of attracted pairs	57.9	64.3	54.0
Group conciliatory tendency[c]	43.8	47.6	41.9
Focal individuals[d]			
Attraction	4	2	5
Neutral	0	1	0
Dispersion	0	0	0
Sign test (P)[e]	0.062	—	0.031
Conciliatory tendency[f]			
With lunge	54.5 (n = 33)	27.3 (n = 11)	33.3 (n = 21)
Without lunge	29.2 (n = 24)	54.8 (n = 31)	45.3 (n = 53)
With contact-aggression	52.2 (n = 23)	28.6 (n = 7)	55.2 (n = 29)
Without contact-aggression	38.2 (n = 34)	51.4 (n = 35)	33.3 (n = 45)

[a]We compared PC and MC to determine during which minute the first interopponent contact was established and calculated the greatest difference between cumulative distributions via a Kolmogorov–Smirnov test (one-tailed).

[b]A pair is attracted when the first interopponent contact occurred earlier in the PC than in the MC, dispersed when the reverse happened, and neutral when the contact occurred during the same 30-sec block in both periods.

[c]The conciliatory tendency is the number of attracted pairs minus the number of dispersed pairs, divided by the total number of pairs. It includes pairs already in contact at the start of the MC period. When we excluded such pairs from the calculation, values became 45.5% (n = 55), 48.8% (n = 41), 48.6% (n = 70) for groups A, B, and C, respectively.

[d]Attraction, individuals that showed more attracted pairs than dispersed pairs; dispersion, the reverse; neutral, individuals that showed the same amount of attracted and dispersed pairs.

[e]For each group, we examined focal individual data via the sign test (one-tailed).

[f]We calculated conciliatory tendencies according to the nature of conflict (at least three occurrences for each kind of conflict are required for calculation). In parentheses, numbers of pairs.

not involving a lunge or a physical contact yielded no consistent trends among groups (Table I).

To determine the timing of reconciliation, we applied a Kolmogorov–Smirnov test on all PC and MC periods. PC and MC distributions differ

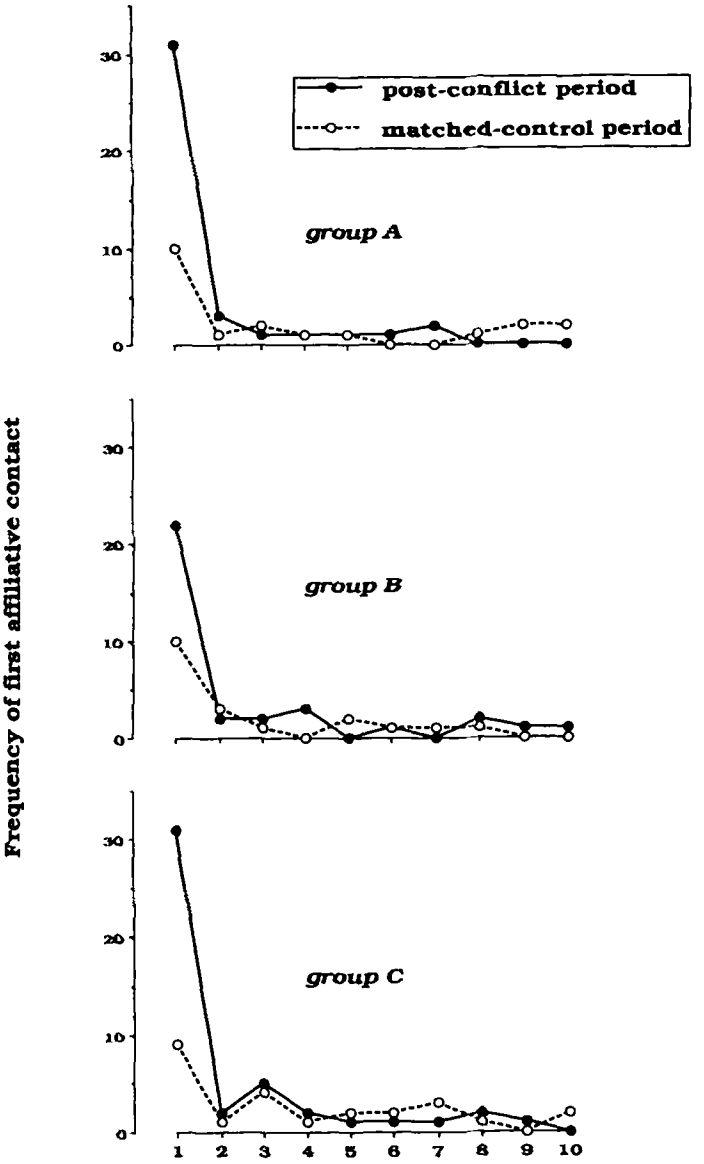

Fig. 1. The frequency of the first affiliative contact between the former opponents in 10-min periods in groups A, B, and C.

significantly for each group, demonstrating that reconciliation specifically occurred between former opponents (Table I). The greatest difference between the cumulative observations occurred at 7 min for group A and 4 min for groups B and C. However, examining the time course of interopponent contacts revealed that most contacts occurred within the first minute (Fig. 1).

Contacts Between the Focal Individual and Other Partners

In order to confirm that a selective attraction occurred between former opponents and was not merely the result of a general increase in affiliation between group members, we compared the numbers of partners other than former opponents contacted—contacts given or received—during PC and MC periods for each focal individual. This showed that fewer contacts tended to occur between the focal individual and other partners in the PC period than in the MC period (group A, contacts less frequent for four individuals, $P = 0.124$; group B, contacts more frequent for one individual and less frequent for two; group C, contacts less frequent for five individuals, $P = 0.062$; sign test, two-tailed).

Patterns of Reconciliation

We compared the proportions of first nonagonistic contacts initiated by the aggressor and the aggressee between the PC and the MC periods to examine whether the direction of contact initiative was influenced by the preceding aggression: no statistically significant trend is evident between periods. In addition, either opponent was likely to initiate reconciliation in the PC period (Table II).

To assess whether lion-tailed macaques use specific behavior patterns to reconcile, we compared the frequency of occurrence of each pattern for first PC contacts, subsequent PC contacts and MC contacts. We distinguished 13 behavioral categories. The three groups employed similar, rich repertoires of behavior (Table III). Although silent bared-teeth display, lipsmack, clasp, presentation, and mount seemed especially frequent during first postconflict contacts, there is no statistically significant difference according to contexts of interactions. In a further analysis, we compared the intensity of first contacts between former opponents in PC and MC periods. Intense contacts are groom, mount, clasp, genital inspection, mouth-to-mouth, play, and physical contact accompanied by visual or vocal expression; nonintense contacts are others contacts not accompanied by a display. Postconflict contacts were more intense than contacts in the MC

Table II. Patterns of Reconciliation[a]

	Group A	Group B	Group C
Initiation by the aggressee[b]			
Postconflict	50.0 (n = 40)	48.6 (n = 35)	52.1 (n = 48)
Matched-control	55.6 (n = 18)	72.3 (n = 18)	50.0 (n = 24)
χ^2	0.01	1.8	0.01
P	n.s.	n.s.	n.s.
Intensity of contacts[c]			
Postconflict	95.1 (n = 41)	85.7 (n = 35)	89.4 (n = 47)
Matched-control	81.0 (n = 21)	55.5 (n = 18)	50.0 (n = 24)
χ^2	1.8	4.3	11.4
P	n.s.	0.05	0.001

[a]Figures are in percentages. Numbers of pairs are within parentheses.
[b]We compared the numbers of first interopponent contacts initiated by the aggressee (percentage) in PC and MC periods with those initiated by the aggressor using a chi-square test (1 df, two-tailed).
[c]We compared the numbers of intense and nonintense contacts via a chi-square test (1 df, two-tailed).

period, the difference being statistically significant in groups B and C (Table II).

DISCUSSION

In the three groups of lion-tailed macaques, the frequency of affinitive behavior was significantly higher after an agonistic interaction than in matched-control periods not preceded by aggression. Former opponents contacted each other sooner and more often after a conflict than during the control period. In selectively contacting during the first few minutes after conflict, lion-tailed macaques follow the general pattern of reconciliation observed in other nonhuman primates (Kappeler and van Schaik, 1992; de Waal, 1993). Furthermore, the tendency to reconcile rates around 40% in the three groups, a high value relatively to other macaque species. This tendency is more than twice that recorded in Japanese and rhesus macaques (de Waal and Yoshihara, 1983; Aureli *et al.*, 1989; Thierry, 1990b; Veenema *et al.*, 1994; Chaffin *et al.*, 1995). Our matched-control observations started when previous opponents were ≤3 m apart, as in York and Rowell's study (1988), but in contrast to other studies of macaques. While the influence of such a stringent criterion is presumably low, it might have lowered the calculated tendency to reconcile during favoring contacts in the matched-control period. Note that we focused on individuals >3 years old, and juveniles generally display more frequent postconflict con-

Table III. Behavior Patterns Occurring During Contacts[a]

Behavior pattern	Group	Context of interactions: First postconflict contacts (n = 125)	Subsequent postconflict contacts (n = 63)	All matched-control contacts (n = 90)
Groom	A	32.5	30.7	41.6
	B	54.3	37.9	29.6
	C	34.0	61.9	33.3
Contact[b]	A	7.0	15.4	16.7
	B	31.4	41.4	33.3
	C	25.5	19.0	41.6
Mount	A	20.9	23.1	8.3
	B	11.4	6.9	7.4
	C	36.2	4.8	5.1
Present	A	34.9	7.7	8.3
	B	11.4	10.3	7.4
	C	40.4	4.8	5.1
Genital inspection	A	23.2	38.4	4.1
	B	2.8	3.5	7.4
	C	23.4	0	15.4
Clasp[c]	A	46.5	7.7	20.8
	B	31.5	20.6	18.5
	C	17.0	4.8	5.1
Bared-teeth[d]	A	48.8	23.1	20.8
	B	42.8	31.0	18.5
	C	42.5	9.5	12.8
Lipsmack	A	44.2	30.7	25.0
	B	42.8	34.5	26.0
	C	38.3	4.8	7.6
Toss head[e]	A	16.3	7.7	0
	B	2.8	0	3.7
	C	8.5	0	0
Mouth-to-mouth	A	4.6	0	0
	B	5.7	3.4	14.8
	C	2.1	14.3	12.8
Play	A	7.0	7.7	12.5
	B	0	6.9	3.7
	C	2.1	0	2.6
Grunt	A	2.3	0	0
	B	2.8	0	7.4
	C	6.4	4.8	5.1

Table III. Continued

Behavior pattern	Group	Context of interactions: First postconflict contacts (n = 125)	Subsequent postconflict contacts (n = 63)	All matched-control contacts (n = 90)
Redirection	A	0	0	0
	B	5.7	3.5	0
	C	2.1	0	0

[a]For each behavior pattern, numbers are expressed as percentages of the number of interactions between former opponents (within parentheses).
[b]Contact means physical contacts other than grooming, genital inspection, mount, clasping, mouth-to-mouth, or play.
[c]Clasping includes grasping, embracing, hugging and pulling head [the initiator repeatedly grips and pulls the hair of another's head or mane (Johnson, 1985)].
[d]Silent bared-teeth display with open jaws, which conveys an affiliative meaning (Johnson, 1985).
[e]A repeated and quick upward jerk of the head (Johnson, 1985).

tacts than other age classes (Thierry, 1986; Cords, 1988; de Waal and Ren, 1988).

Groups of lion-tailed macaques are usually small. The low number of individuals per group did not allow an individual treatment of the data and so we pooled them in many analyses. To counter this problem, we sampled three social groups, which provided consistent results. Another caveat of the study may be the fact that the groups studied were composed mainly of kin-related individuals and included a few hand-reared individuals. It should be asked to what extent this may have affected the results. First of all, the results obtained for groups A and B are similar to those of group C in which all individuals were mother-reared. In most studies, related opponents contacted each other more frequently than unrelated ones did (Kappeler and van Schaik, 1992), but Cords (1988) and Gust and Gordon (1993) obtained different results. However, the significance of the kin effect can also be questioned. The index of Veenema *et al.* (1994), which we used, was devised to account for the different rates of affiliative interactions occurring among various categories of individuals. Applying this index to previous studies showed that the kin effect previously found in the conciliatory tendencies of rhesus and stump-tailed groups disappeared; only long-tailed macaques still presented a kin effect (Veenema *et al.*, 1994). In the lion-tailed macaques, data from the three individuals having no relatives are consistent with other ones. Indeed, familiar nonrelatives can develop strong bonds, yielding high rates of reconciliation that are close to those

occurring between related partners (de Waal and Yoshihara, 1983; Aureli *et al.*, 1989). Our measures may be tentatively considered as representative of the species, at least for small groups kept in captive conditions.

The rates of reconciliation between adult males and females did not depart from those recorded between adult females. Such results are consistent with data from other species of macaques (de Waal and Ren, 1988; Demaria and Thierry, 1992). This reflects good relationships between both sexes in spite of the reputed peripheral situation of the lion-tailed male within the group. That suggests that the rates of reconciliation may be uncoupled from the frequency of interactions.

The occurrence of a lunge or a physical contact between opponents did not affect the probability of subsequent reconciliation in a predictable way, indicating that the intensity of the conflict was not a critical factor as in other studies (de Waal and Yoshihara, 1983; Gust and Gordon, 1993; Petit and Thierry, 1994). Neither was any postconflict effect with regard to the initiative of reconciliation; the aggressee was responsible for the first contact as often as the aggressor was in both the postconflict and the matched-control periods.

A rich repertoire of reassurance patterns is a noteworthy characteristic of lion-tailed macaques. However, we found no behavior specific to reconciliation, just as in most other groups of macaques (Cords, 1988; Aureli *et al.*, 1989, 1993; Demaria and Thierry, 1992; Petit and Thierry, 1994). On the other hand, certain behavior patterns occurred more frequently at the time of postconflict contacts in some species (de Waal and Yoshihara, 1983; de Waal and Ren, 1988). Such variation could be a mere outcome of the implementation of statistical procedures, which yielded significant differences in some cases and not in others. In most groups, it seems that postconflict contacts involved more expressive patterns than contacts that occurred in the matched-control periods. In lion-tailed macaques, reconciliatory contacts are indeed more intense than usual ones, an effect shown in other groups in which it has been tested (Demaria and Thierry, 1992; Petit and Thierry, 1994).

The association of high conciliatory rates with intense forms of reconciliation brings the lion-tailed macaque toward the more egalitarian side of the scale of macaque social organizations, together with the Tonkean (*M. tonkeana*) (Thierry, 1986; Demaria and Thierry, 1992), the crested (*M. nigra*) (Petit and Thierry, 1995; Petit *et al.*, submitted) and the stump-tailed (*M. arctoides*) macaques (de Waal and Ren, 1988; de Waal and Luttrell, 1989). Tonkean and crested macaques belong to the same phyletic lineage as lion-tailed macaques, which they resemble in many respects, behaviorally and morphologically (Delson, 1980; Fooden, 1980). They all show several behavior patterns that depart from those of other macaques, for instance, specific loud calls uttered by adult males and silent bared-teeth displays, the meaning of

which is mainly affiliative (Dixson, 1977; Hohmann and Herzog, 1985; Johnson, 1985; Thierry *et al.*, 1989, 1994; Petit and Thierry, 1992; Preuschoft, 1995). Many social characteristics appear to covary in macaque social organization. The patterns of reconciliation, in particular, seem to be correlated with the mode of aggression, the asymmetry of dominance relationships, and the function of the silent bared-teeth display (Thierry, 1986, 1990a; Thierry *et al.*, 1989, 1994; de Waal and Luttrell, 1989; Preuschoft, 1995). The pig-tailed macaque (*M. nemestrina*), another member of the silenus lineage, seems to be situated on the despotic side of the scale of macaque social organizations, not far from rhesus and Japanese macaques. Like them, the pig-tailed macaque only possesses a submissive bared-teeth display and its rate of reconciliation is quite low (Judge, 1991). If social characteristics indeed occur in clusters and lion-tailed macaques conform to such patterns, it remains to be explained why species are located at one or another point of the scale. Current socioecological theories emphasize a variety of ecological factors (Caldecott, 1986; de Waal and Luttrell, 1989; van Schaik, 1989; Preuschoft, 1995). Yet no convincing correlation has been found between macaque social organization and specific habitats (Richard *et al.*, 1989). In particular, it remains to be proved that significant ecological variations exist among the dense evergreen forest species of the silenus lineage (Fooden, 1982). We should test whether some prominent social characteristics such as dominance asymmetry and conciliatory rates are determined primarily by their interrelations or by the influence of the external environment.

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