Toward a Comparative Socioecology of the Genus *Macaca:* Different Dominance Styles in Rhesus and Stumptail Monkeys

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Captive studies can make a unique contribution to primate socioecology by documenting species-typical social dispositions under controlled conditions. Recent theories seek to connect the dominance relationships, group cohesiveness, and feeding ecology of primates. The present study explores the first two aspects by comparing the social organization of rhesus *(Macaca mulatta)* and stumptail monkeys *(M. arctoides).* Data were collected over a period of eight years, with five different methods, on three well-established captive groups in identical environments. The groups were found to share one characteristic: a clear-cut, linear formal dominance hierarchy as expressed in teeth-baring displays. The two main study groups (one of each species) differed significantly, however, with respect to nine of eleven behavioral measures. In addition to a previously reported higher frequency of reconciliation in the stumptail group, this group showed 1) more frequent but less severe aggressive behavior, 2) greater symmetry of contests, 3) greater social tolerance, 4) more nonagonistic approaches, and 5) more allogrooming. The differences can be summarized as a contrast in dominance "style," with the stumptails having a more relaxed style and placing greater emphasis on social cohesion than the rhesus monkeys. An egalitarian attitude was also reflected in approach behavior: contacts in the rhesus group were mostly initiated by dominants, whereas contacts in the stumptail group were initiated independent of rank. Comparisons with a second rhesus group, and with published reports, suggest that while some of the observed differences are probably representative of the two species, considerable intraspecific variation does exist, and a more comprehensive program of comparative studies is needed.

INTRODUCTION

In order to explain intraspecific variation in social organization, Lott [1984] has argued that natural selection does not operate on social systems per se but on

"social predispositions" [cf. Mason, 1978]. A species' dispositions can bring about multiple social system outcomes dependent on current circumstances and individual histories. Outcomes observed in captivity, we might add, are of particular interest in that they allow interspecific comparisons while taking into account immediate environmental effects. Different species can be observed under identical conditions, making it likely that behavioral differences reflect species-typical dispositions. In the field, proximate and ultimate environmental effects are confounded. Variation in the social organization of primates in different habitats may reflect their evolutionary adaptation to these habitats, flexible responses based on learning and social tradition, or both.

If captive studies can make a unique contribution to the field of primate socioecology by charting social dispositions under controlled conditions, this is facilitated by the fact that many research institutions maintain related species that, in the wild, live in totally different geographic regions. With few exceptions [e.g., Packer & Pusey, 1979; Mori, 1984; Janson, 1986], field primatologists have focused on a single species. Among students of captive primates, on the other hand, direct behavioral comparison between species has a history going back to Yerkes and Yerkes [1929].

Comparative studies of primate social behavior may assist the development of theories linking the nature of dominance relationships to group cohesiveness and ecological variables. A first outline of such a theory already exists. It explains the steepness and strictness of the hierarchy as the product of the type of intragroup food competition (scramble vs. contest), the intensity of intergroup competition, and the adaptive significance of group life in general (e.g., predation risks outside the group). The basic idea is that dominant individuals strike a balance between cooperation with and exploitation of subordinate members of their group. The balance depends on options outside the group. The higher the cost for subordinates of leaving the group, the more freedom dominants have in "despotically" appropriating resources. Conversely, if dominants are genetically related to subordinates or derive important benefits from their presence, their competitiveness will be mitigated, resulting in more "egalitarian" dominance relationships. Van Schaik [1989] presents the most detailed evolutionary model incorporating these elements, building on Wrangham [1980], Vehrencamp [1983], van Schaik and van Hooff [1983], and Hand [1986].

At the proximate level, too, competitive relationships are modified by the need to conserve the resources that other individuals represent. The typical long-term relationships of primates are best regarded as major investments [Kummer, 1979]. Because hostile behavior may jeopardize these investments, primates learn to weigh the resources that can be won in a victorious fight, not only against the risk of injury [Maynard Smith & Price, 1973], but also against the potential damage to the relationship with their competitor [de Waal, 1989a]. These constraints on competition result in variation across species as well as across relationships in what has been called "dominance quality" [Maslow, 1940] or "dominance style" [de Waal, 1989a].

Dominance hierarchies are double-layered, i.e., they have a *formal* component of "outer signs" of status and a more variable agonistic and competitive component. The issue of dominance style is not limited to status communication, but concerns the nature of the entire competitive relationship in terms of the dominant's tendency to claim or relinquish resources. Even if individual A unequivocally dominates B, as expressed in B's ritualized submission toward A (e.g., the teeth-baring display of macaques [deWaal & Luttrell, 1985]), the relationship is still considered egalitarian if A rarely excludes B from resources. In fact, there is evidence that

close and tolerant relationships among unrelated adults are hardly possible without a well-established formal hierarchy [de Waal, 1982, 1986a].

It is not difficult to recognize the continuity between the above ultimate and proximate models. Both explain dominance style as a compromise between the ability of certain individuals to claim resources and the dependency of these individuals on their competitors. Verification and further development of these models require more detailed analyses of competitive relationships than conducted thus far, including measures of subordinate liberties, peaceful means of conflict resolution, and the burden competition places on long-term relationships. This may be part of the "socioecologically referred social psychology of personal behavior and development" envisaged by Crook [1989, p. 19] as the socioecolgical paradigm of the 1990s.

Comparative studies of the nature and social context of competitive relations are most fruitfully applied to closely related species. Factors such as body size, sexual dimorphism, life span, reproductive biology, and cognitive capacity vary greatly from one primate genus to another, but relatively little within each genus. Limiting comparisons to congeners controls to some extent for these factors. Of all the primate genera, *Macaca* is particularly attractive for such comparisons. Its 19 recognized species have the widest distribution of any primate genus other than *Homo,* ranging from northern Africa to the Philippines, and occupy a great diversity of habitats [Napier & Napier, 1985]. A majority of macaque species has been extensively studied in the field.

Thierry [1985a,b] was the first to undertake a comprehensive comparison, under controlled conditions, of different macaques with respect to agonistic relationships, conflict resolution, and other dispositions relevant to the above theories. His data on tonkeana *(Macaca tonkeana),* rhesus *(M. mulatta),* and longtailed macaques *(M. fascicularis)* reveal dramatic interspecific differences in the intensity of aggression, symmetry of contests, amount of appeasement behavior, tendency to reconcile, maternal restrictiveness, and infant socialization. Recognizing causal connections between some of these variables (e.g., a low probability of violence reduces the risk of counteraggression, which may promote agonistic symmetry [cf. Popp & DeVore, 1979]), the investigator proposes coevolution of entire sets of social characteristics: "It is through appreciation of the system as a whole, without ignoring the structural constraints and the phylogenetic burden, that one can understand the role of the social system in the adaptation of a species to its environment" [Thierry, 1987, p. 99].

Documentation of social dispositions of all macaque species under both captive and natural conditions is, of course, more than a single research team can accomplish. Moreover, in view of considerable intraspecific variation even under the same conditions [e.g., Yamada, 1971; de Waal, 1977], comparisons between different species ideally should involve several groups per species per type of environment. This goal can be achieved only if the results from various sites and investigators can be combined—a long-term coordinated effort requiring that 1) investigators agree on standardized measures and 2) primatological journals accept papers that in themselves may not shed much light on macaque socioecology but contribute to the pool of comparative information. We realized the need for such a data base and decided to contribute to it, after discovering a striking behavioral contrast between captive rhesus and stumptail macaques *(M. arctoides).*

These two species are placed far apart in current macaque classifications. Fooden [1976, 1980] divides the macaques into four groups on the basis of male external genitalia, lumping rhesus macaques with three other species in the *fascicularis* group, while segregating stumptails in a group all their own. Molecular

studies do not completely agree with Fooden's classification [Lucotte et al., 1984],
but this kind of data, too, indicates considerable genetic distance between rhesus
and stumptails [Melnick & Kidd, 1985]. The reported geographic distribution of
the two species does overlap [Wolfheim, 1983], but they appear to be ecologically
separated even in areas where they may be sympatric [see Fooden, 1982]. Hybrids
between the two species have not been reported in the wild, but have been pro-
duced in the past at the Wisconsin Primate Center (Steve Eisele, personal com-
munication).

Our previous study demonstrated that stumptails reconcile a far greater pro-
portion of their agonistic conflicts than rhesus macaques and possess a richer
repertoire of reassurance gestures [de Waal & Ren, 1988]. In this respect stump-
tails resemble tonkeana macaques. If it is true that social dispositions evolved
together, one would expect these two species to share additional characteristics,
such as the reported egalitarian dominance relationships, low incidence of vio-
lence, and symmetrical contests among tonkeanas [Thierry, 1984, 1985a,b]. While
Bernstein et al.'s [1983] observation of a relatively high rate of aggression in
stumptails appears to contradict this prediction, these investigators did not find a
correspondingly high rate of biting and present indirect evidence that this species
responds relatively often to aggression with aggression.

In the present study both species were studied with the same methods in
identical environments. Several measures reflect specific interests relating to var-
ious short-term research projects. In addition, standard data on aggressive and
affiliative behavior were collected over a period of several years, initially involving
one stumptail and one rhesus group, with a second rhesus group added later on. To
facilitate comparisons with other studies, this paper provides detailed behavioral
definitions as well as two appendices with measures per individual subject.

Special attention is given to relations among unrelated adults on the assump-
tion that differences in social organization are most pronounced in this relation-
ship category. Granovetter's [1973] *strength-of-weak-ties* paradox may be applica-
ble to macaques with their well-documented kinship bias in affiliative bonding
[e.g., Sade, 1965; Kurland, 1977; de Waal & Luttrell, 1986; Ehardt & Bernstein,
1987]. Strong ties breed local cohesion and fragmentation within a social system
unless weak ties serve as bridges between cliques of tied individuals [Granovetter,
1973]. In the case of macaques, this means that social cohesion and integration at
the group level depend to a large extent on the quality of the relations between
members of different matrilineal units.

MATERIALS AND METHODS
Groups

The first group of rhesus monkeys *(Macaca mulatta)* is of feral origin. Its
original members came from a single group captured in 1972 in Uttar Pradesh,
India. During the present study 10 feral-born members still lived in the group; the
rest were born in Madison, Wisconsin. Annual removal, mainly of selected 2- to
3-year-old juveniles, was done to prevent overcrowding. Over the observation pe-
riod, group size ranged from 51 to 62 monkeys, including 4 adult males (reaching
at least 5 years of age during the study) and 20 adult females (reaching at least 4
years). There existed 11 matrilineal kinship units, ranging in size from one to
three adults per unit. Previous publications by our team concern this particular
group, which is named "Natural" group [e.g., de Waal, 1986b; de Waal & Lutrell,
1985, 1986].

A second group of rhesus monkeys, named "Delta" group, is of similar size and
composition as the first. This group was established in 1976 using adult individ-

uals from the WRPRC's laboratory colony. During the study Delta group varied in size from 51 to 60 monkeys, including 5 adult males at one time (a total of 7 males figuring in this study) and 21 adult females. Only three of the adults were of feral origin. There existed nine matrilineal kinship units, ranging in size from two to six adult individuals.

The stumptail group *(Macaca arctoides)* was about half the size of the rhesus groups. The monkeys had been living together continuously as a group since 1970. Four of the original 18 feral-born adults were still present during the study. The total group size was 21 monkeys, including 2 adult males and 12 adult females. The group included three matrilineal kinship units of between two and five adults and six unrelated adult females.

Living Conditions

The three groups are housed in the same facility in separate indoor/outdoor pens. The pens are identical except that they face in different directions from the circular building. The outdoor section of each pen is 6 m high, with a concrete floor of approximately 75 m^2 and a large, steeply sloping wall of stratified limestone blocks; the mesh floor of the inside section measures 25 m^2. For a cross section of one of the pens, see Weisbard and Goy [1976]. During the winter the inner pens are heated, and the wire mesh of the outdoor section is covered with Plexiglas, which protects against the wind and provides a greenhouse effect on sunny days. The monkeys normally have access to both sections. Each morning, before 10:30 h, the enclosures are cleaned, and Purina monkey chow is spread over the floor of the outer pen. Observations were conducted with the monkeys locked into the outdoor section.

Observation Methods

The large majority of data concern Natural rhesus group, which we have studied since 1982, and the stumptail group, on which studies began in 1983. Four different observation methods were applied to both groups: two methods were applied continuously (i.e., standard observations and water tests), and two methods for limited periods of time (i.e., focal observations and reconciliation data). As much as possible, the various behavioral measures for each group have been derived from the same or overlapping time intervals. Delta rhesus group was added to our research program in 1986, and only two of the observation methods were applied to this group (i.e., standard observations and water tests). In addition, ad libitum data on submissive facial expressions were collected on all groups.

1. Focal observations, with a duration of 15 min each, were recorded as spoken accounts on a cassette tape recorder. Sixty observations were collected on most adult subjects in Natural rhesus group (a total of 1,319 observations), and 50 observations on every adult stumptail (a total of 700 observations). The period of study was from February 1983 through December 1984 for the rhesus monkeys and from June 1984 through February 1986 for the stumptail monkeys. For each subject observations were equally divided over the seasons of the year and the time of day between 12:00 and 17:00 h. Interobserver reliability (between the authors) was determined by following the same individuals from different angles. Of the interactions recorded by either observer, 87% were recorded by both, with a kappa coefficient of agreement of 0.79 [Cohen, 1960].

2. Standard observations were collected on all three monkey groups. One observer (L.M.L.) recorded the behavior of an entire group of monkeys during sched-

uled 1 h intervals. Aggressive interactions were recorded whenever observed, provided they involved a pursuit of over 2 m or biting. For associative-"state" behaviors, on the other hand, a 10 min instantaneous sampling procedure was followed. During a sample the group was scanned from left to right for behaviors such as grooming and sitting in contact. If a major agonistic incident occurred during a sample, the sample was cancelled. Standard data on Natural rhesus group cover the period from September 1982 through August 1985 (413 h and 2,846 scan samples), on Delta rhesus group from May 1986 through August 1988 (225 h and 1,776 scan samples), and on the stumptail group from November 1983 through February 1986 (225 h and 1,149 scan samples).

3. The water test procedure has been described in detail by de Waal [1986b]. A monkey group is deprived of water for 3 h, after which water is provided in a circular, 22 cm-diameter basin large enough to allow simultaneous drinking by several adults. Tests are videotaped along with a spoken account, which serves to assist individual identification. The present analysis of social tolerance in the drinking context concerns 26 water tests recorded during the spring and summer periods of 1983–1984 on Natural rhesus troop, 20 tests on Delta rhesus group during 1987–1988, and 20 tests on the stumptail group during 1984–1985.

4. Data on reconciliation behavior have been presented for Natural rhesus group by de Waal and Yoshihara [1983] and for the stumptail group by de Waal and Ren [1988]. The two studies were conducted from September 1981 through June 1982 (Natural group) and from November 1984 through August 1985 (stumptails). The method of study has been described in detail in the above publications. It consisted of a postconflict focal observation of 10 min on an individual involved in an agonistic incident of sufficient intensity (i.e., minimally including a chase of over 2 m or biting). Each observation was compared with a control observation, collected on a subsequent day, matched to the postconflict observation with respect to duration, focal subject, and starting time. The 10 min duration of observations is justified by the fact that behavioral effects of previous aggression are limited to this interval [de Waal & Yoshihara, 1983; de Waal & Ren, 1988; Cords, 1988, York & Rowell, 1988]. This method was followed 350 times in Natural rhesus group and 400 times in the stumptail group.

5. The interindividual direction of the "silent bared-teeth face" [van Hooff, 1967] was recorded whenever observed with a one-zero sampling technique described by de Waal and Luttrell [1985]. For the stumptails, in which this expression is less common, unidirectional "teeth-chattering" was included as this occurred with very few exceptions in the same dyadic direction as silent teeth-baring. Teeth-chattering consists of baring of the teeth with rapid opening and closing jaw movements. It may be regarded as a transitional stage between silent teeth-baring and lip-smacking, and combines as such the submissive/fearful motivation of the first and the more friendly motivation of the second expression [van Hooff, 1967].

The length of the one-zero sampling intervals was 2 months. This length was selected in order to determine the long-term directional consistency of these submissive displays. The one-zero method, which gives equal weight to all dyadic directions of performance during the interval regardless of frequency of performance, maximizes unusual directions. Data were collected from November 1981 through May 1984 on Natural group (15 two-month intervals), from May 1986 through August 1988 on Delta group (14 intervals), and from November 1983 through April 1986 on the stumptail group (15 intervals). The number of ad libitum observation hours is estimated at several thousand per group.

Behavioral Measures

Directional inconsistency index (DII): The number of interactions or intervals during which a particular behavior occurred in its least frequent direction within every adult-adult dyad as a percentage of the total number of times the behavior was recorded [cf. Rowell, 1966; de Waal, 1977; Noë et al., 1980; de Waal & Luttrell, 1985]. DIIs were calculated for the distribution of 1) teeth-baring, i.e., silent bared-teeth and teeth-chattering displays recorded with the one-zero sampling technique, 2) drink exclusions, i.e., approach-avoidance interactions, both aggressive and nonaggressive, around the basin during water tests, and 3) aggression, i.e., aggressive acts of any intensity during focal observations.

Hierarchical linearity: The degree of linearity of the formal hierarchy among adults (i.e., the teeth-baring hierarchy) expressed in the transitivity index, K, adapted from Kendall by Appleby [1983]. A perfectly linear hierarchy, without triangular reversals (i.e., A dominates B, B dominates C, but C dominates A), has a K of 1.0, whereas K equals 0.0 if all individuals have equal status. Appleby [1983] also described a method to evaluate the probability of K.

Grooming duration: Performed allogrooming as a percentage of 10 min instantaneous scan samples during standard observations. This sampled measure not only best reflects duration [Suen & Ary, 1984], but was also found to correlate remarkably well with dyadic frequency [de Waal & Luttrell, 1986].

Conciliatory tendency: The percentage of attracted opponent pairs. A pair of former opponents is said to be attracted if they engage in nonagonistic body contact during the 10 min postconflict observation only, or earlier during this observation than during the matched control observation [cf. de Waal & Yoshihara, 1983; de Waal & Ren, 1988]. Conciliatory tendency was measured per focal individual regardless of whether it was this individual or its opponent that initiated the postconflict contact.

Drink tolerance: The percentage of tolerant interactions, regardless of initiative, around the water basin with subordinate adults and with juveniles of any rank. An interaction is considered tolerant if two monkeys drink simultaneously from the basin or sit together for at least 10 sec within arm's reach of the basin, usually with one of the two drinking [cf. de Waal, 1986b].

Ignored exclusions: The number of unsuccessful attempts to exclude a subordinate adult or juvenile of any rank from the water basin, expressed as a percentage of attempted plus successful exclusions. An exclusion attempt is considered unsuccessful if the approaching individual threatens, pushes, or pulls at one of the monkeys around the basin without this resulting in withdrawal by that individual.

Approach frequency: The number of nonagonistic approaches to another individual per hour of focal observation. An approach is defined as a distance decrease to within 0.5 m to the front or side of a partner or to within arm's reach behind its back. If several individuals are simultaneously approached, this counts as several approaches. Approach data concern adult-adult dyads only.

Negative approach result: The percentage of nonagonistic approaches with a negative outcome. Negative outcomes include withdrawal by the approachee (the most common type), teeth-baring by one of the two individuals, manual pushing by the approacher, and facial/vocal threats by the approachee (if the approacher itself shows such threat displays the approach is classified as agonistic).

Approach direction: The tendency to approach dominant vs. subordinate partners is expressed in the so-called *up/down index*. Let *u* be the number of approaches made by an individual to higher-ranking adults divided by the number of such adults. Let *d* be the same individual's number of approaches to lower-ranking

adults divided by the number of such adults. The up/down index is then $(u - d)/(u + d)$. This index is 0.5 if the frequency of approaches to other adults is independent of their position in the hierarchy relative to the approacher. A higher index indicates a tendency to approach dominants more, a lower index a tendency to approach subordinates more. The formal dominance hierarchy (i.e., based on teeth-baring) is used for this analysis. Note that the up/down index cannot be calculated for individuals at the top and bottom of the hierarchy.

Threat frequency: The number of initiated aggressive acts per hour of focal observation not exceeding the threat intensity. Threat is defined as staring openmouth or "pointing" facial expressions often accompanied by rough, low-pitched vocalizations [de Waal et al., 1976]. The category also includes lunges of less than 2 m, mild manual contact-aggression such as slapping and grabbing, and the species-typical mock-bite of the stumptail macaque (i.e., manual grabbing of one of the opponent's extremities with a threat face and briefly pressing an opened mouth on it [for a photograph see de Waal, 1989b, p. 158]). Classification of mild contact aggression and ritualized mock-bites in the threat category is justified by the close temporal and contextual association among these behavior patterns, but may result in differences with studies employing a dichotomy between contact and noncontact aggression.

Attack frequency: The number of initiated aggressive acts per hour of focal observation exceeding the threat intensity. This includes 1) lunge/chase over more than 2 m, 2) unritualized biting (i.e., biting unaccompanied by a threat face; the jaws are closed, but less forcefully than in fierce biting), and 3) fierce biting (i.e., sustained biting with head-shaking movements and a potential of causing skin damage). Together with the threat category, this makes for four aggression intensities; only the highest intensity observed during an aggressive action was recorded.

Fierce biting frequency: The number of fierce biting per 100 h of standard observation. This measure is included because, as will be shown, fierce biting is an extremely rare behavior not adequately covered by the focal observation technique. The standard observations provided a larger sample size, and since interactions with fierce biting are very conspicious we have confidence in the accuracy of this method.

Counter aggression: The percentage of initiated aggressive acts of any intensity during focal observations to which the recipient responds with aggression of any intensity.

Analysis

Behavioral measures concern adults only. Separate male and female data can be found in Appendices A and B, which provide behavioral profiles per subject along with information on sex and rank position. Because of the small number of adult males compared with females, however, and the similar sex ratio per group, data on both sexes have been combined in the analyses.

Each individual's behavior is expressed in an overall measure, which combines all occurrences of the behavior, and in separate measures per partner category, i.e., adult nonkin (A-NK), adult kin (A-K), juvenile nonkin (J-NK), and juvenile kin (J-K). Kinships refers to matrilineal relationships, regardless of genetic distance and paternity. The juvenile category includes individuals over 1.5 years and under adult age. Behavior aimed at individuals younger than 1.5 years has been ignored.

Individual means and standard deviations are provided per group for both the overall measure and the adult nonkin partner category separately (Table I). Most illustrations concern the latter measure, based on the assumption that relationships among unrelated adults are an important characteristic of macaque social

TABLE I. Eleven Behavioral Measures on natural Rhesus Group and the Stumptail Group and Four Measures on Delta Rhesus Group[†]

	Rhesus		Stumptails			
	N	Mean ± S. D.	N	Mean ± S.D.	z	P
With all partners						
Grooming duration	24	7.2% ± 3.2%	14	18.5% ± 10.2%	3.81	***
(Delta group)	28	9.5% ± 3.7%			3.04	**
Concilatory tendency	25	15.5% ± 12.2%	15	52.7% ± 9.3%	4.85	***
Drink tolerance	24	55.8% ± 17.2%	14	65.1% ± 12.4%	1.94	NS
(Delta group)	28	68.5% ± 16.3%			0.84	NS
Ignored exclusions	24	15.8% ± 11.3%	14	35.8% ± 22.3%	3.21	**
(Delta group)	28	28.8% ± 13.7%			0.60	NS
Approach frequency/hour	24	9.73 ± 4.87	14	18.01 ± 6.47	3.56	***
Negative approach result	24	15.6% ± 9.3%	14	5.9% ± 5.0%	3.48	***
Up/down direction	22	0.33 ± 0.14	12	0.47 ± 0.17	2.34	*
Threat frequency/hour	24	1.36 ± 0.69	14	3.47 ± 1.56	4.48	***
Attack frequency/hour	24	0.41 ± 0.23	14	0.38 ± 0.31	0.82	NS
Fierce biting/100 h	24	1.38 ± 1.54	14	0.51 ± 1.06	2.30	*
(Delta group)	28	0.88 ± 1.03			1.57	NS
Counteraggression	24	8.9% ± 11.7%	14	18.6% ± 10.8%	2.97	**
With unrelated adults only						
Grooming duration	24	4.8% ± 2.1%	14	10.9% ± 8.8%	3.00	**
(Delta group)	28	5.5% ± 2.3%			2.54	*
Conciliatory tendency	24	13.3% ± 10.9%	15	51.3% ± 14.9%	4.58	***
Drink tolerance	21	40.6% ± 15.0%	10	72.7% ± 16.4%	3.97	***
(Delta group)	24	59.9% ± 18.5%			1.49	NS
Ignored exclusions	21	9.6% ± 9.2%	7	19.4% ± 8.5%	2.50	*
(Delta group)	22	21.0% ± 16.9%			0.05	NS
Approach frequency/hour	24	8.82 ± 4.77	14	14.01 ± 7.42	1.73	NS
Negative approach result	24	16.5% ± 10.0%	14	5.7% ± 4.9%	3.69	***
Up/down direction	21	0.34 ± 0.14	12	0.55 ± 0.20	2.81	**
Threat frequency/hour	24	0.61 ± 0.50	14	0.83 ± 0.64	0.91	NS
Attack frequency/hour	24	0.22 ± 0.16	14	0.11 ± 0.15	2.44	*
Fierce biting/100 h	24	0.74 ± 1.11	14	0.32 ± 0.73	1.59	NS
(Delta group)	28	0.52 ± 0.71			1.31	NS
Counteraggression	22	5.8% ± 6.5%	12	15.7% ± 10.3%	2.90	**

[†]The table provides the number of adult subjects on which the meaure is based (N), individual means, and standard deviations. In the upper half of the table, the three aproach measures (approach frequency, negative approach result, and up/down direction) concern adult-adult interactions only; all other measures concern behavior toward individuals of 1.5 years of age or older. The lower half of the table is limited to behavior toward unrelated adults. The table also provides the outcome (z) of Mann Whitney U tests comparing the rhesus group(s) with the stumptails. Since the upper half of the table includes data of the lower half, the two sets of test results are not independent.
***$P < 0.001$, **$P < 0.01$; *$P < 0.05$, two tailed. NS, not significant.

groups (see Introduction). For the same reason, statistical evaluations of inter-group differences concern both overall behavioral measures and behavior toward unrelated adult partners separately; note that these two evaluations are not independent, i.e., the first measure includes the second. All statistical tests in this paper are two-tailed and nonparametric, and as much as possible take individual variation into account. Inasmuch as this objective makes for more conservative probability estimates than pooled data analyses, we feel justified in adopting an α of 0.05. Mann-Whitney U and Wilcoxon tests include corrections for ties, and chi-square tests include Yates' continuity correction. Proportional measures have
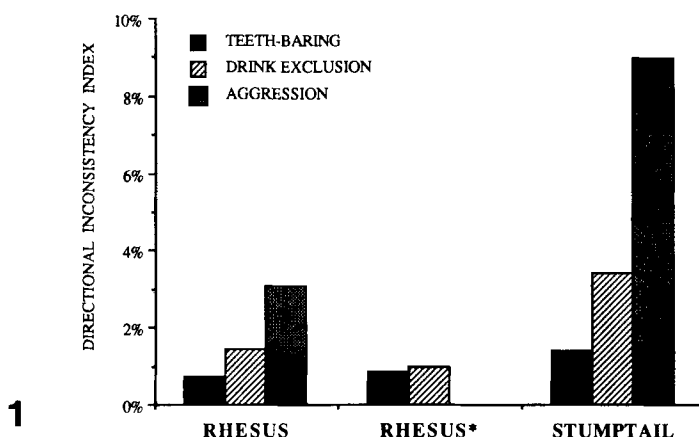
Fig. 1. The percentage directional inconsistency of three dominance indicators in adult-adult relations in Natural rhesus group (Rhesus), Delta rhesus group (Rhesus*), and the stumptail group.

been included only for individuals with five or more observations on which to base the measure.

RESULTS
Strictness of the Hierarchy

The directional inconsistency index (DII) of bared-teeth displays was 0.7% (N = 1,275) for Natural rhesus group, 0.9% (N = 1,398) for Delta rhesus group, and 1.4% (N = 560) for the stumptail group. All three DIIs are extemely low, especially in view of 1) the employed one-zero sampling technique, which maximized rare directions of performance, and 2) the extended period over which data was collected, which increased the probability of dominance reversals. Hierarchical linearity was virtually identical for the groups, i.e., K = 0.83 for Natural rhesus group, K = 0.85 for Delta rhesus group, and K = 0.83 for the stumptail group (in all cases $P < 0.001$). The proportion of decided dominance relationships among adults (i.e., dyads with at least one observation of teeth-baring) ranged between 83.5 and 88.8% in the three groups.

In spite of the difference in sampling method (i.e., no bias toward directional inconsistency), the DIIs of initiated aggression and drink exclusion exceeded those of the bared-teeth display. The differences were small in both rhesus groups, but considerable in the stumptails (Fig. 1). For example, the DII of initiated aggression reached 9.0% (N = 534) among adult stumptails. Intergroup comparisons by means of chi-square tests yielded a significant difference with respect to the DII of aggression only ($X^2 = 15.9$, $P < 0.001$). Note that this comparison was limited to Natural rhesus group and the stumptails; no focal aggression data were available for Delta rhesus group.

The predictive value of formal dominance with respect to other expressions of dominance was investigated by comparing the interindividual direction of bared-teeth displays with the main direction of drink exclusions and aggressive acts between the same individuals. The direction of drink exclusions was correctly predicted in 98.4% of the dyads in Natural rhesus group, 95.8% of Delta rhesus group, and 92.5% of the stumptail group. With respect to aggression, predictability on the basis of formal dominance was 95.1% for Natural rhesus group and 86.8%
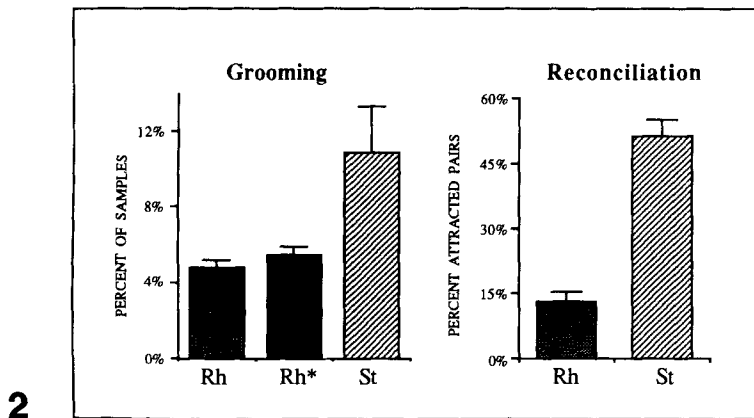
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Fig. 2. The mean (±S.E.) percentage of scan samples during which subjects groomed unrelated adults in Natural rhesus group (Rh), Delta rhesus group (Rh*), and the stumptail group (St). Reconciliation data on Natural group and the stumptails, at right, are from de Waal and Yoshihara [1983] and de Waal and Ren [1988]. The graph presents the mean (±S.E.) conciliatory tendency per focal subject with unrelated adult opponents.

for the stumptails. None of the intergroup differences was significant (chi-square tests).

Grooming and Reconciliation

As shown in Table I and Figure 2, the stumptail monkeys spent approximately twice as much time grooming than the rhesus monkeys of both the Natural and Delta groups. The differences were significant for the overall grooming duration as well as for the duration toward adult nonkin separately (Table I). While the two rhesus groups differed in overall grooming duration (Mann Whitney U test, $z = 2.22$, $P < 0.05$), they did not do so with respect to grooming of adult nonkin separately ($z = 0.88$).

The difference in grooming between the two rhesus groups predominantly concerned kin, as illustrated in Figure 3. For each subject, grooming per partner category was corrected for the number of partners in that category, resulting in the mean grooming duration per partner. All three groups showed a strong kin bias in grooming of juveniles (behavior toward kin and nonkin was compared per subject with a Wilcoxon test: $z = 4.07, P < 0.001$ for Natural rhesus group; $z = 4.01, P < 0.001$ for Delta rhesus group, and $z = 2.52, P < 0.05$ for the stumptail group). Grooming of adult partners showed the same kin bias, which was significant for both rhesus groups ($z = 3.91$ for Natural group and $z = 4.46$ for Delta group; both $P < 0.001$), but not for the stumptails ($z = 1.13$).

Reconciliation data were available for Natural rhesus group and the stumptail group (Fig. 2). Detailed comparisons, presented by de Waal and Ren [1988], demonstrated a greater conciliatory tendency in stumptails and a more varied repertoire of reassurance gestures in this species compared to rhesus monkeys. This difference was generalized to all possible partner combinations in terms of matrilineal kinship, age, and gender. The conciliatory tendencies reported in Table I differ slightly from those given by de Waal and Ren [1988], because the present analysis was limited to adult focal subjects.

Water Tests

The majority of interactions during the water tests were of a tolerant nature, i.e., individuals drank together or subordinates remained near the basin while
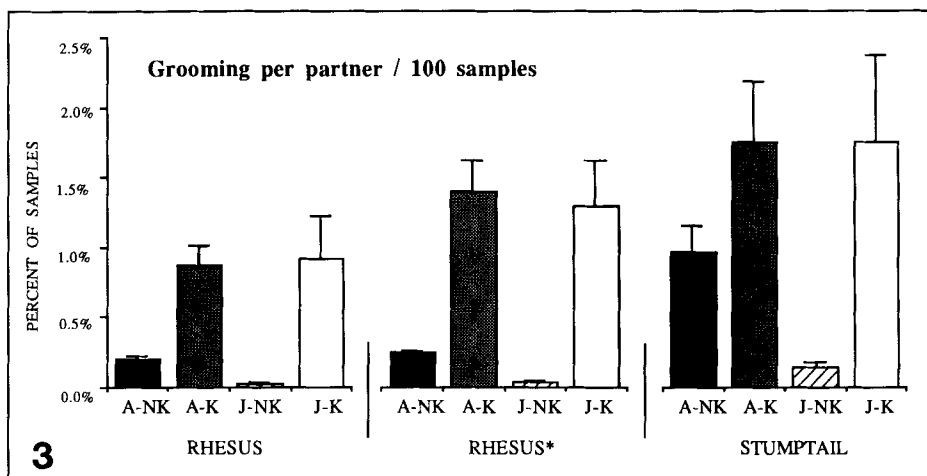
Fig. 3. The percentage of scan samples during which grooming was aimed at four partner categories, divided by the number of potential partners per category, for the three study groups. The graph provides the mean (±S.E.) per subject per category: A-NK, adult nonrelatives; A-K, adult kin; J-NK, juvenile nonrelatives; J-K, juvenile kin.

dominants drank. There existed a significant difference between the two rhesus groups in the degree of tolerance with respect to both the overall measure and the behavior toward unrelated adults separately (Mann Whitney U tests, $z = 2.55$, $P < 0.05$, and $z = 3.17$, $P < 0.01$, respectively). The drink tolerance of the stumptails did not differ significantly from Delta rhesus group, but was significantly higher than that of Natural rhesus group, particularly with respect to unrelated adult partners (Table I, Fig. 4).

Figure 5 provides a subdivision of the data according to four partner categories. A kinship bias was clearly recognizable in both rhesus groups (Wilcoxon tests for Natural and Delta group, respectively, with respect to adult partners, $z = 2.61$, $P < 0.01$, and $z = 2.31$, $P < 0.05$; juvenile partners, $z = 3.25$ and $z = 3.18$, both $P < 0.01$), but not in the stumptail group (adult partners, $z = 1.10$; juvenile partners, $z = 1.75$).

A convincing expression of social tolerance is when a dominant monkey makes an attempt to exclude a subordinate, but nonetheless accepts its presence when this attempt is unsuccessful. If such ignored exclusions are used as a measure of tolerance, Delta rhesus group and the stumptail group resembled each other even more, and the contrast with Natural rhesus group became even greater than in the previous analysis (Table I, Fig. 4). The two rhesus groups differed significantly both overall and in their behavior toward nonkin adults separately (Mann Whitney U tests, $z = 3.59$, $P < 0.001$, and $z = 2.40$, $P < 0.05$, respectively).

An interesting difference was suggested by further analysis of this material. Two types of unsuccessful exclusion attempts were distinguished: 1) ignored facial and vocal threats and 2) ignored pushing and pulling unaccompanied by the above threat displays. Figure 6 presents pooled data on these two types of ignored exclusion attempts among unrelated adults (since aggression was uncommon during drinking tests, sample sizes were too small for an analysis at the individual level). Whereas the stumptails' proportion of ignored pushing was similar to that of Delta rhesus group, their proportion of ignored aggressive exclusion attempts was higher
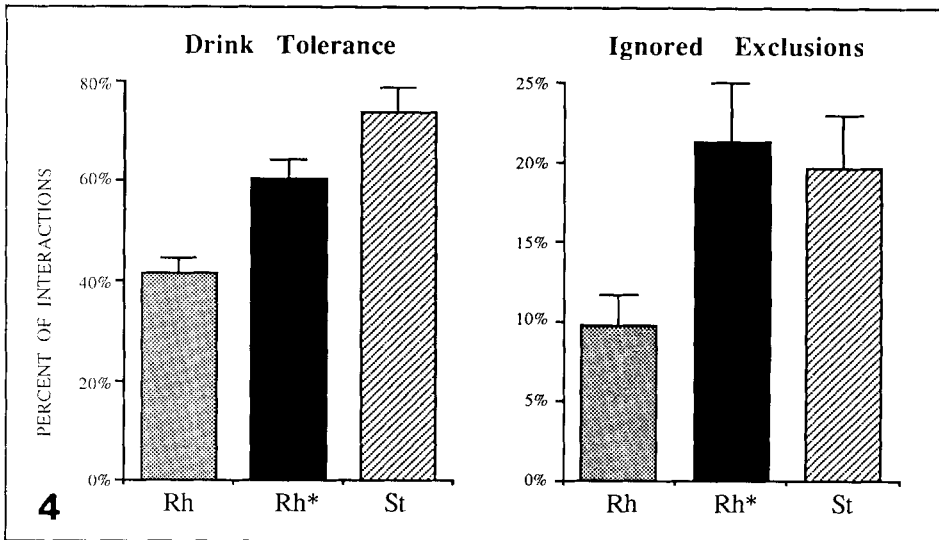
Fig. 4. The percentage of tolerant interactions during water tests (drink tolerance) and the percentage of attempts at exclusion not resulting in monopolization of the water basin (ignored exlusions). The graph presents the mean (±S.E.) per subject toward unrelated adult subordinates in the three study groups.
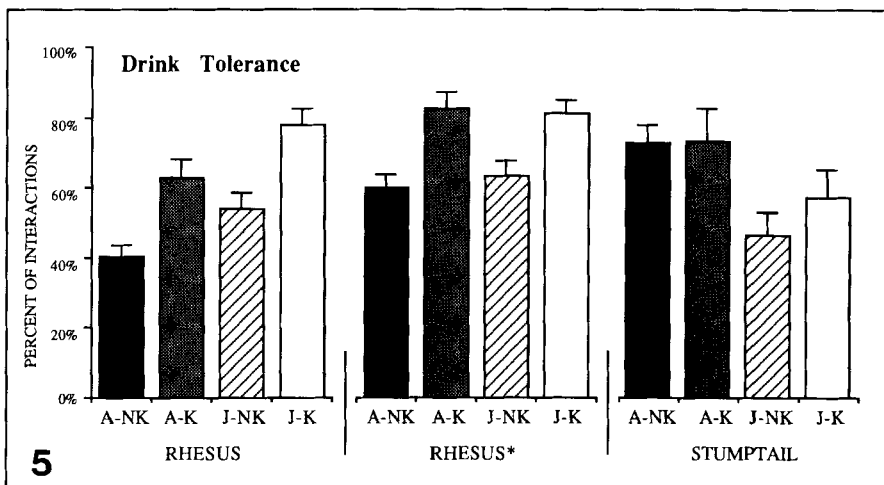

Fig. 5. The mean (±S.E.) percentage of tolerant interactions during water tests with subordinate adults or juveniles of any rank in the three study groups. See legend to Figure 3 for definitions of the four partner categories.

than that found in either rhesus group (chi-square tests, $P < 0.01$). However, since the evaluation of differences in pooled data is problematic [Machlis et al., 1985], a larger data base will be needed for a conclusive comparison.

Nonagonistic Approaches

Comparison of the control data of de Waal and Yoshihara [1983] and de Waal and Ren [1988] indicates that 1) stumptail monkeys have a higher contact rate
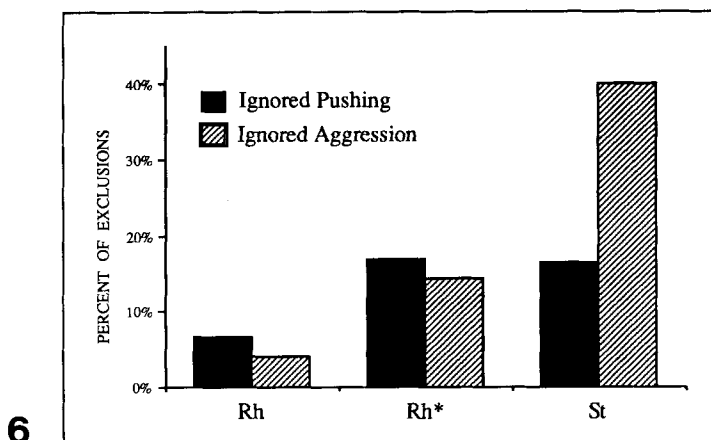
Fig. 6. The percentage of aggressive (i.e., including facial/vocal threat displays) and nonaggressive attempts at exclusion of another individual from the water basin that fail to result in monopolization. This pooled data concerns interactions of dominant adults with unrelated subordinate adults in the three study groups.

than rhesus monkeys and 2) the majority of contacts in the rhesus group, but not in the stumptail group, are initiated by the dominant party. Both differences are confirmed by the present focal data on nonagonistic approaches. In contrast to other measures, the approach data are limited to adult-adult interaction.

The hourly rate of interindividual approach was almost twice as high in the stumptail group as in natural rhesus group. Also, the stumptails approached dominant and subordinate adults approximately equally often, whereas the rhesus directed most approaches down the hierarchy (Table I, Fig. 7). The difference in the up/down index takes into account individual approach frequencies and relative positions in the hierarchy. Without these corrections, the overall result was that 57.8% of the 6,304 approaches among adult stumptails were directed by a dominant to a subordinate, compared to 70.6% of the 6,347 approaches among adult rhesus monkeys.

Approaches in the rhesus group had a negative result approximately three times more often than approaches in the stumptail group (Table I, Fig. 7). Since approaches directed down the hierarchy caused more negative results (e.g., withdrawal by the approachee) than approaches up the hierarchy, and since the rhesus monkeys showed more downward-directed approaches (see above), this might theoretically explain the intergroup difference. However, after limiting the comparison to downward-directed approaches a significant difference in the outcome of approaches remained between the two groups.

Aggressive Behavior

Focal aggression data are available for Natural rhesus group and the stumptail group. In terms of the total frequency of aggression, the stumptails scored considerably higher than the rhesus, i.e., 3.85 aggressive acts per adult stumptail per hour compared to 1.77 per adult rhesus. Most of the stumptail aggression, however, was of low intensity. The stumptails were characterized by a high overall threat rate, whereas the rhesus showed a relatively high attack rate against unrelated adults (Table I, Fig. 8).

The same data can be analyzed by calculating the contribution of each of the four aggression intensities (Materials and Methods) to the total aggression output.
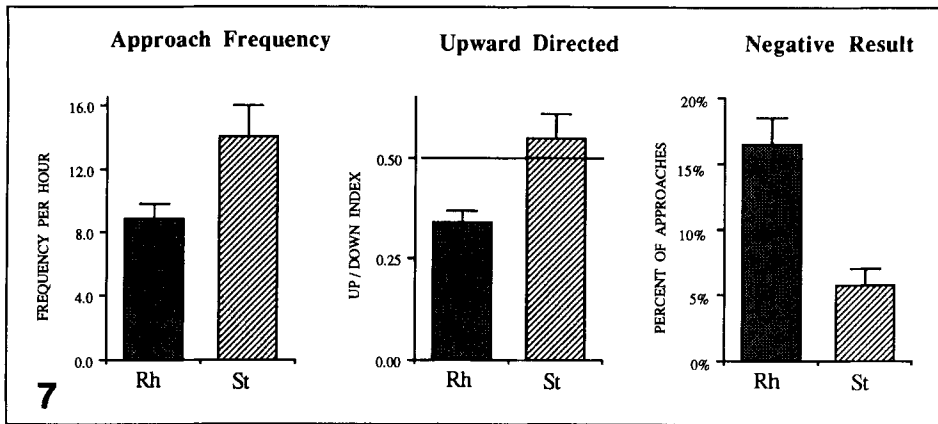
Fig. 7. Means (±S.E.) per subject for three measures of nonagonistic approach toward unrelated adults in Natural rhesus group and the stumptail group: 1) the hourly rate of approach, 2) the number of approaches directed to dominants compared to subordinates corrected for the subject's position in the hierarchy (see Materials and Methods for a definition of the up/down index), and 3) the percentage of approaches leading to a negative or agonistic interaction.

This analysis confirmed that the rhesus used aggression of higher intensity than the stumptails (Mann Whitney U test on each individual's proportion of aggression exceeding the threat intensity, $z = 3.85, P < 0.001$). Figure 9 illustrates the result for kin and nonkin opponent categories separately. Although this pooled data shows a trend toward aggression of higher intensity against unrelated opponents, Wilcoxon tests on the proportion of each individual's aggression exceeding the threat intensity revealed no significant difference between kin and nonkin opponent categories ($z = 0.11$ for the stumptails and $z = 1.01$ for Natural rhesus group).

Fierce biting, the highest aggression intensity, was rarely recorded during focal observations (i.e., once among stumptails and 17 times among rhesus). For this reason, a separate analysis was conducted on the considerably larger number of observations of this behavior during standard protocols. This also allowed inclusion of data on the second rhesus group. The overall rate of fierce biting was significantly higher in Natural rhesus group than in the stumptail group, with Delta rhesus group taking an intermediate position, not significantly different from either other group (Table I). Another way of looking at these differences, but one ignoring group size, is the rate of fierce biting by adults per entire group. This form of violence was observed once every 186 min in Natural rhesus group, once every 283 min in Delta rhesus group, and once every 844 min in the stumptail group. Fierce biting of kin was observed once in the stumptail group (6.3% of all instances), 13 times in Natural rhesus group (9.8%), and nine times in Delta rhesus group (16.7%).

With Figure 10 we return to the focal data, comparing aggression rates (of any intensity) against four opponent categories after correction for the number of potential opponents. By far the highest rate of aggression was aimed by adult stumptails against related juveniles. In Natural rhesus group this opponent category also received the most aggression, but the average number of aggressive acts per hour per juvenile kin was only 0.13 in this group compared to 0.67 in the stumptail group. In both groups the adults' rate of aggression against related juveniles was
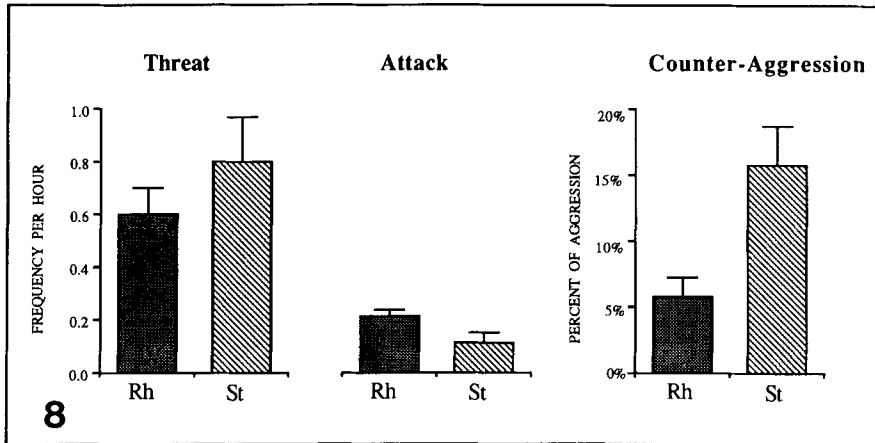
Fig. 8. The mean (±S.E.) hourly rate of threat and attack initiated against unrelated adults in Natural rhesus group and the stumptail group. At right, the mean (±S.E.) percentage of initiated aggressive acts of any intensity responded to with aggression by the recipient.
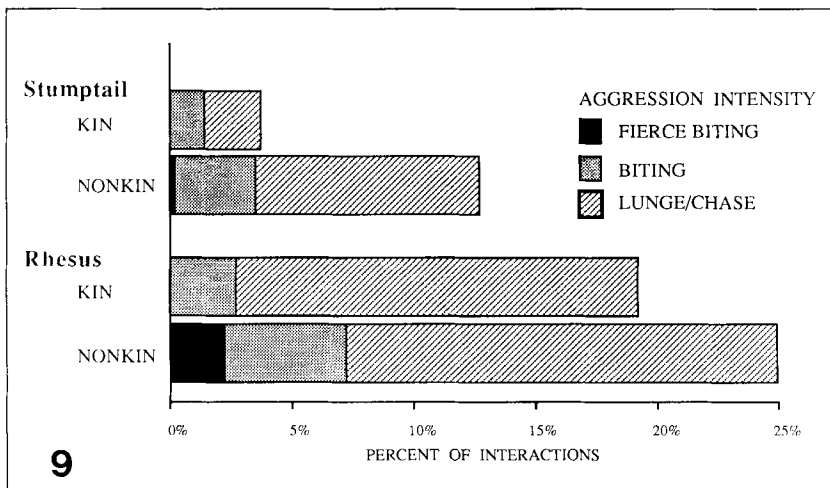
Fig. 9. Pooled percentage of aggressive acts against related or unrelated opponents (regardless of age class) involving a lunge or chase of more than 2 m, biting, or fierce biting for Natural rhesus group and the stumptail group. The remaining proportion of aggressive acts (not shown) did not exceed the threat intensity.

significantly higher than against unrelated juveniles (Wilcoxon tests, $z = 2.49$ for Natural rhesus group and $z = 2.20$ for the stumptails, both $P < 0.05$). A nonsignificant kin bias in the same direction existed with respect to adult-adult aggression ($z = 1.46$ for the rhesus and $z = 0.77$ for the stumptails).

Finally, the probability of received counteraggression was investigated. It was found that significantly more aggression was returned by stumptails than by the rhesus monkeys of Natural group (Fig. 8, Table I). The large majority of instances of mutual aggression consisted of two individuals threatening or slapping at one another. Aggression of higher intensity was rarely countered.

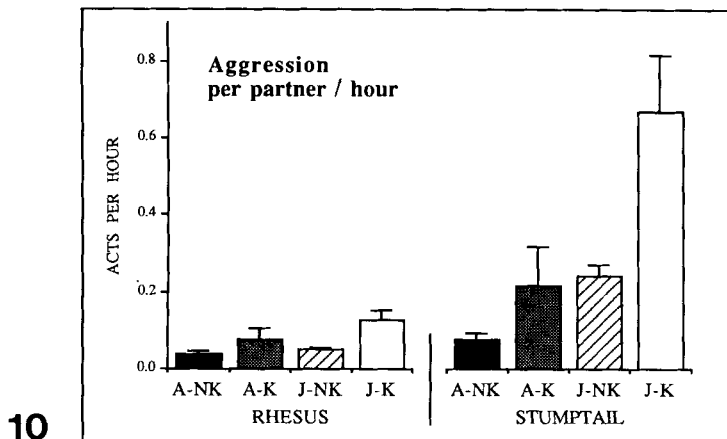Fig. 10. Hourly rate of initiated aggression against four opponent categories, divided by the number of potential opponents per category for Natural rhesus group and the stumptail group. The graph provides the mean (±S.E.) per subject per opponent category (as defined in legend to Fig. 3).

DISCUSSION
Dominance Styles in the Two Main Study Groups

Dominance style is defined here as the nature of the entire competitive relationship in terms of 1) the frequency and intensity of the dominant's aggression and the subordinate's fear responses and 2) the dominant's tendency to claim or relinquish resources. Dominance relationships are viewed as double layered, that is, formal dominance, which is expressed in ritualized status communication, does not necessarily vary with dominance style; the formal component may be quite pronounced in otherwise egalitarian relationships (cf. de Waal, 1986a, 1989a).

Formal dominance. The one fundamental characteristic shared by Natural rhesus group and the stumptail group was the presence of a clear-cut formal hierarchy among adults. Consistency in the interindividual direction of ritualized status communication (i.e., silent bared-teeth and teeth-chattering displays) approached 100%, and dominance relations were transitively arranged. The K value of 0.83 found in both groups is the same as the average linearity reported by Jackson and Winnegrad (1988) for a variety of species, both primate and nonprimate.

Aggression level and tolerance. Although the overall frequency of aggressive interaction was more than twice as high among the stumptails compared to the rhesus monkeys, the probability of violence among stumptails was considerably lower both relatively (i.e., the proportion of aggressive acts escalating beyond the threat level) and absolutely (i.e., the rate of fierce biting). The stumptails were also more inclined to reconcile following fights and were more tolerant in the drinking tests, at least toward unrelated adults. The stumptails might be characterized, therefore, as easily aroused aggressively yet conciliatory, tolerant, and nonviolent compared to the rhesus group. Aggression in the rhesus group was more serious with respect to both the potential of physical damage and the disruption of future relationships (i.e., the chances of subsequent reunion).

Symmetry of contests. Reduced risk associated with aggressive confrontation allows subordinates to resist coercion, protest against aggression, and engage dominants in confrontation. It is not surprising, therefore, that the stumptails, the

group with the lower incidence of violence, further differed from the rhesus group in the following three areas: 1) the direction of initiated aggression was less predictable, 2) aggression was countered with aggression more often, and 3) subordinates more often ignored exclusion attempts by dominants during water tests. Hence, contests among the stumptails were more flexible and symmetrical than among the rhesus monkeys.

Social cohesiveness. Socially positive activities were more common in the stumptail group. First, the stumptails spent more than twice as much time grooming than the rhesus monkeys. Second, the frequency of nonagonistic approaches among the stumptails was higher, and their approaches less often led to negative results, such as withdrawal or threat, than in the rhesus group. Perhaps as a consequence of the reduced risk of rejection, subordinate stumptails made approximately as many approaches to dominants as the reverse, whereas approaches in the rhesus group tended to be directed down the hierarchy. Third, the stumptails' greater conciliatory tendency also contributed to social cohesiveness by reducing interindividual distances following fights.

In summary, the stumptails exhibited a looser, more relaxed dominance style than the rhesus monkeys. Frequent retaliation, resistance to priority claims, and unhesitant approach behavior made subordinate stumptails seem relatively "disobedient" and lacking of fear. Affiliative relations were closer, and aggressive incidents were resolved in a nondispersive manner among the stumptails. The entire set of intergroup differences is perhaps most elegantly explained as a shift in the balance between basic social values. One of the rhesus monkeys' priorities seemed to be enforcement of the hierarchy and associated privileges; one of the stumptails' priorities seemed to be group cohesiveness.

First of all, these differences confirm the double-layered nature of the hierarchy; the contrast in dominance style coexists with formal hierarchies of equal rigidity in both species. Second, if it is true that dominant stumptails sacrifice certain competitive advantages for the sake of amicable relations, we must assume that dominant stumptails depend more on the presence and cooperation of subordinates than do dominant rhesus monkeys. In other words, group cohesion and close ties with subordinates are expected to carry benefits for stumptails that offset the reduction in privileges associated with their lenient dominance style [cf. Vehrencamp, 1983; van Schaik, 1989]. Unfortunately, very little is known about the ecology of this species. De Waal [1989b] has speculated that stumptail monkeys, which appear anatomically adapted to a terrestrial life, may rely on communal defense against predators in the same way as they reportedly mob people [Bertrand, 1969].

As predicted, stumptail monkeys resemble tonkeana monkeys in more respects than their high conciliatory tendency [Thierry, 1985a,b]. This supports the notion of coevolution of a number of social characteristics in response to environmental demands. Thus, we may assume that tonkeana monkeys, too, depend heavily on group cohesion, although the socioecological factors involved may be different from those applying to stumptail monkeys.

Intergroup or Interspecific Differences?

The difference between the study groups, with the monkeys of one group emphasizing the hierarchy and those in another group the social fabric, may be caused by a great many factors. Because different species are involved, however, it is logical to speculate that the behavioral contrast is due to species-typical "temperaments" or social dispositions.

The problem with this interpretation is that, at this stage, we do not know to

what extent our measures are representative of rhesus and stumptail macaques. Inclusion of a second rhesus group in the study seriously complicated the picture. Delta rhesus group did resemble the other rhesus group in terms of grooming activity, but resembled the stumptail group in measures of social tolerance (except for ignored aggressive exclusion attempts) and yielded an intermediate result regarding the rate of fierce biting. This outcome confirms the need for a more comprehensive research program involving multiple social groups per species per environment.

A comparison with grooming and aggression data in the literature suggests the generalization potential of some of the interspecific differences in the present study. Assuming that several reports of "time spent grooming" have lumped given and received grooming, we have halved these results for comparison with our measure of *performed* grooming. For 24 groups of macaques and baboons covered by our literature review, the average (± S.D.) grooming rate was 7.2 ± 4.9% [Rhine, 1973; Bernstein, 1980; Maruhashi, 1981; Dunbar & Sharman, 1984; Malik, 1986; Seth & Seth, 1986; Kurup, 1988; Mahlman & Chapais, 1988). It is noteworthy that the highest rate reported concerns a captive stumptail group (i.e., 25% [Rhine, 1973]). This suggests that this species' high grooming activity in the present study may not be atypical. The grooming rate in our two rhesus groups was only slightly higher than the (corrected) rates reported by Seth and Seth [1986] and Malik [1986] for free-ranging urban and temple groups of this species.

Aggression rates as well may be similar across conditions. De Waal [1988] demonstrates remarkable agreement between the present aggression data on Natural rhesus group and data on corral-living rhesus monkeys [Ruehlmann et al., 1988] and temple groups in Nepal [Teas et al., 1982]. For stumptails, however, there exists no such agreement. In the present study, the aggression rate per adult male was 2.5, and per adult female 4.1 (Appendix A), which differs from rates reported by Whitten and Smith [1984] and Ruehlmann et al. [1988] for corral-living stumptails. Despite this variation, the stumptail studies share the finding that aggression rates were as high or higher than in rhesus monkeys and that escalation of aggression was uncommon, i.e., high aggression rates were not reflected in correspondingly high rates of biting.

We fully realize that the conclusions that can be drawn on the basis of a comparison between three captive monkey groups are limited, but the above evidence from other studies suggests that at least some of the differences reported here may be representative of the two macaque species. Inasmuch as the high rate of aggression among stumptails in our study concerned the least crowded monkey group, it seems unlikely that this difference can be explained by differences in population density. Moreover, Bernstein et al. [1983] specifically noted for the stumptail macaque that its frequent aggressive behavior did not lead to a scattered group of individuals, thus indicating the same social closeness as observed in the present study.

Effects of Kinship

Previous research has indicated a strong matrilineal kinship bias in macaque social relationships, including preferential alliance formation [e.g., de Waal, 1977; Massey, 1977; Kaplan, 1977] and close affiliative ties among kin [e.g., Sade, 1965; Kurland, 1977; Ehardt & Bernstein, 1987]. The grooming and tolerance data on our two rhesus groups confirm this bias, with significantly more grooming and tolerance toward both adult and immature kin. The stumptails showed the same preferential treatment of kin as far as grooming of immatures was concerned, but no other significant differences.

In addition to intimate and supportive relationships, disproportionally high levels of aggression among kin have been reported in one field study and one captive study of macaques [Kurland, 1977; Bernstein & Ehardt, 1986]. This result may seem paradoxical, but not if one knows that reconciliation is also more common among kin than nonkin; frequent aggression is not incompatible with social bonding [de Waal & Yoshihara, 1983; de Waal & Ren, 1988]. Our analysis of aggression replicates the one by Bernstein and Ehardt [1986] on rhesus monkeys, with the difference that we took individual variation into account, whereas theirs was a pooled analysis.

The present results support Bernstein and Edhardt's [1986] conclusions. Matrilineal kin, particularly juveniles, received more aggression than nonkin. The amount of aggression aimed at juvenile kin by stumptails was particularly high. A possible explanation of this high level can be derived from Bernstein and Edhardt's [1986] suggestion that physical punishment is used by older kin to "train" youngsters to become responsive to noncontact aggression. Because rhesus monkeys tend to show severe aggression, the disciplinary process may be more rapid in this species. The stumptails' more ambiguous expressions of aggression and easy subsequent reconciliation may be less effective in modifying unacceptable behavior in youngsters. In other words, during the socialization of immature kin, rhesus monkeys may make their point more clearly, and stumptails, of necessity, more frequently. If so, experience with relaxed dominance relationships starts early in life for stumptails, beginning with their relationship with their mother and other adult kin.

CONCLUSIONS

1. Two captive groups of rhesus macaques and one group of stumptail macaques shared the characteristic of a clear-cut, linear formal dominance hierarchy, as expressed in teeth-baring displays.

2. Compared to the main study group of rhesus monkeys, the stumptail group was characterized by 1) frequent mild aggression, but rare violence, 2) greater symmetry of agonistic encounters, 3) greater social tolerance, 4) more reconciliations, 5) more time spent grooming, 6) a higher rate of nonagonistic approaches, and 7) no effect of rank on approach direction.

3. These differences can be summarized in terms of dominance style, with stumptails having a more relaxed style than rhesus monkeys. The stumptails appeared to emphasize social cohesiveness, whereas the rhesus appeared to emphasize a strict hierarchy.

4. A comparison with data on a second rhesus group, and with published reports, suggests that while some of the above differences are probably representative of the two species, considerable intraspecific variation does exist. A comprehensive program of comparative studies on the genus *Macaca*, both in captivity and in the field, is proposed to verify and further develop theories linking species-typical social dispositions to ecological factors.

5. The distribution of grooming, social tolerance, and aggression was affected by matrilineal kinship relations. For the first two measures, the kinship effect was stronger in the rhesus monkeys than in the stumptails, and for all three measures it was stronger toward immatures than toward adults.

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APPENDIX A. Overall Behavioral Measures per Adult Individual*

	Sex	Formal rank	Threat (per hour)	Attack (per hour)	Fierce biting (per 100 h)	Counter-Aggression (% received)	Grooming (% samples)	Approach (per hour)	Negative result (% approach)	Up/down direction index	Conciliatory tendency (% attraction)	Drink tolerance (% interaction)
Stumptails												
Mx	M	1	2.24	0.84	4.00	0.0	17.2	28.96	20.3		56.5	44.0
Gx	F	2	4.08	0.68	0.89	3.6	4.4	15.72	10.7	0.37	76.9	60.3
Wx	F	3	4.00	1.12	0.00	14.0	12.4	27.60	7.0	0.50	50.0	52.6
Ma	F	4	2.96	0.40	0.44	17.9	19.9	20.20	7.1	0.46	57.6	60.0
Wa	M	5	1.52	0.40	0.89	26.7	8.0	17.08	6.8	0.52	53.1	66.7
Cx	F	6	1.88	0.28	0.00	7.9	39.2	22.60	8.3	0.44	47.6	57.8
Dx	F	7	2.84	0.32	0.00	11.5	7.5	7.56	2.1	0.31	42.9	58.9
Sx	F	8	3.40	0.20	0.00	16.9	19.3	12.84	1.6	0.42	61.5	89.3
Su	F	9	7.36	0.28	0.00	20.7	18.5	24.32	2.8	0.41	57.9	63.4
Sp	F	10	5.48	0.16	0.00	21.8	25.5	21.32	3.9	0.46	51.9	58.3
Sl	F	11	1.76	0.00	0.00	30.8	34.8	13.64	2.9	0.63	37.3	85.0
St	F	12	3.84	0.08	0.44	21.6	26.4	17.16	4.0	0.93	50.0	80.0
Yx	F	13	3.64	0.32	0.00	27.9	11.1	9.28	1.3	0.24	54.6	68.4
Ho	F	14	3.60	0.20	0.44	39.7	14.9	13.88	4.3		50.7	66.7
Rhesus (Natural group)												
Sx	M	1	3.13	0.55	1.45	2.5	3.6	13.46	20.4		33.3	30.7
Ox	F	2	3.10	0.99	5.57	1.9	11.0	13.46	31.5	0.57	22.2	47.1
Hu	M	3	1.05	0.78	2.67	2.6	1.9	8.83	39.0	0.27	15.4	22.8

Mo	M	4	2.06	0.77	0.74	5.7	3.1	10.50	9.9	0.35	31.8	53.2
Ro	F	5	1.47	0.72	2.66	5.8	3.7	17.57	22.2	0.37		46.3
Be	F	6	1.43	0.55	2.42	2.2	7.9	17.01	19.6	0.50		32.8
Bo	F	7	1.98	0.55	2.42	1.6	10.5	21.08	27.4	0.45	6.7	43.6
Hx	F	8	0.75	0.41	5.08	0.0	10.4	13.18	21.6	0.60	7.7	53.2
Ho	F	9	1.29	0.41	1.21	5.3	12.8	9.15	25.9	0.43	0.0	35.6
Mx	F	10	1.75	0.53	1.24	3.8	11.3	6.83	10.4	0.25	0.0	52.9
Mi	M	11	0.56	0.24	0.00	7.1	5.6	9.28	6.0	0.43		77.2
Gl	F	12	1.09	0.38	1.94	12.5	8.0	8.49	13.9	0.28	35.7	47.6
Gx	F	13	1.42	0.25	0.00	11.1	1.8	12.00	18.1	0.17	12.0	52.4
Ti	F	14	0.96	0.27	1.94	3.4	9.1	9.70	16.1	0.31	21.2	56.3
Go	F	15	1.36	0.32	1.90	4.0	6.7	9.91	20.2	0.15		62.0
Tx	F	16	1.47	0.45	0.48	2.3	5.5	3.83	9.1	0.13	21.4	63.2
Ta	F	17	1.16	0.34	0.25	11.1	7.6	11.54	13.7	0.18	12.5	59.9
Nx	F	18	1.12	0.14	0.00	14.8	7.4	10.92	8.3	0.23	12.5	80.8
Fx	F	19	1.22	0.14	0.48	11.1	12.2	1.63	6.4	0.28	11.1	54.5
Cx	F	20	0.94	0.34	0.49	27.3	3.2	4.70	2.2	0.30	21.1	77.4
Ch	F	21	0.85	0.24	0.00	13.6	7.2	4.38	4.8	0.39	7.1	69.6
Nu	F	22	1.65	0.24	0.24	8.3	8.4	9.57	11.3	0.48	5.9	77.6
Kx	F	23	0.40	0.20	0.00	0.0	5.8	2.30	8.7	0.14	0.0	50.0
Kl	F	24	0.48	0.12	0.00	55.6	7.2	4.24	6.6			91.7

APPENDIX B. Behavioral Measures per Adult Individual Concerning Interaction With or Against Other Adults Not Matrilineally Related to the Subject.*

	Sex	Formal rank	Threat (per hour)	Attack (per hour)	Fierce biting (per 100 h)	Counter-aggression (% received)	Grooming (% samples)	Approach (per hour)	Negative result (% approach)	Up/down direction index	Conciliatory tendency (% attraction)	Drink tolerance (% interaction)
Stumptails												
Mx	M	1	1.17	0.54	2.67	0.0	14.6	27.16	19.1	0.37	55.6	68.6
Gx	F	2	1.84	0.12	0.00	6.1	3.9	15.72	10.7	0.48	71.4	64.0
Wx	F	3	2.11	0.24	0.00	15.5	6.4	26.76	7.0	0.52	42.9	58.9
Ma	F	4	1.17	0.00	0.44	21.4	16.9	19.48	7.4	0.52	57.1	48.6
Wa	M	5	0.32	0.16	0.89	16.7	4.6	15.68	7.4	0.52	51.7	66.7
Cx	F	6	0.76	0.12	0.00	4.5	36.6	22.60	8.3	0.44	69.2	70.0
Dx	F	7	0.92	0.08	0.00	16.0	7.0	7.56	2.1	0.31	77.8	73.6
Sx	F	8	0.43	0.05	0.00	10.0	5.6	6.96	2.9	0.61	71.4	
Su	F	9	0.29	0.00	0.00	16.7	2.7	7.92	2.5	0.76	33.3	100.0
Sp	F	10	0.29	0.00	0.00	16.7	6.8	7.36	4.3	0.60	42.1	76.5
Sl	F	11	0.05	0.00	0.00		17.5	7.36	0.5	0.82	42.1	
St	F	12	0.10	0.00	0.00		8.2	8.36	1.9	0.91	28.6	
Yx	F	13	1.32	0.16	0.00	27.0	9.1	9.28	1.3	0.24	46.2	
Ho	F	14	0.80	0.04	0.44	38.1	12.6	13.88	4.3		62.5	100.0
Rhesus (Natural group)												
Sx	M	1	1.40	0.33	0.97	1.9	3.5	13.46	20.4	0.57	44.7	
Ox	F	2	2.24	0.64	3.63	2.3	9.4	13.46	31.5		27.3	69.1

		No.									
Hu	M	3	0.17	0.24	1.70	8.3	1.5	7.27	44.0	0.29	14.3	37.5
Mo	M	4	0.62	0.10	0.00	14.3	2.5	9.57	9.8	0.35	33.3	18.3
Ro	F	5	0.90	0.43	1.94	5.0	3.0	17.57	22.2	0.37		33.8
Be	F	6	0.79	0.31	1.45	3.1	6.0	14.89	20.3	0.53		40.2
Bo	F	7	1.10	0.48	0.97	0.0	5.5	20.35	28.4	0.46	23.1	41.1
Hx	F	8	0.35	0.28	3.87	0.0	6.2	10.75	24.6	0.60	0.0	35.6
Ho	F	9	0.52	0.35	0.48	4.0	5.7	7.97	29.3	0.36	12.5	6.4
Mx	F	10	1.05	0.28	0.25	5.3	8.8	6.26	11.3	0.25	0.0	17.0
Mi	M	11	0.16	0.16	0.00	12.5	2.9	8.04	6.5	0.38		49.2
Gl	F	12	0.48	0.24	0.24	4.8	5.2	7.76	12.6	0.28	11.1	45.8
Gx	F	13	1.10	0.25	0.00	12.5	1.1	9.83	18.6	0.10	0.0	28.3
Ti	F	14	0.49	0.14	0.97	0.0	7.8	8.10	16.7	0.32	12.5	30.8
Go	F	15	0.50	0.15	0.95	7.7	4.3	9.32	21.0	0.13		46.3
Tx	F	16	0.73	0.28	0.00	0.0	4.6	3.30	10.5	0.12	16.7	51.0
Ta	F	17	0.28	0.07	0.00	0.0	5.6	10.91	14.5	0.18	30.0	46.7
Nx	F	18	0.44	0.14	0.00	23.5	5.6	9.95	9.1	0.23	14.3	45.6
Fx	F	19	0.37	0.07	0.24	0.0	5.9	1.63	6.4	0.28	0.0	40.0
Cx	F	20	0.14	0.07	0.00	16.7	2.7	3.86	2.7	0.42	0.0	
Ch	F	21	0.31	0.10	0.00	0.0	5.3	3.93	5.3	0.37	25.0	62.5
Nu	F	22	0.44	0.10	0.00	6.3	4.7	8.42	12.8	0.46	26.7	50.0
Kx	F	23	0.00	0.00	0.00		2.9	1.80	11.1		11.1	57.1
Kl	F	24	0.04	0.04	0.00		4.2	3.24	6.2			

Definitions of the measures are provided in the text. Reconciliation data on the rhesus group concern a different time period with a partially different population of adult subjects.