Evolutionary Anthropology 16:224–238 (2007)

Unity in Diversity: Lessons From Macaque Societies

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The macaque radiation is as old as the hominin radiation, approximately 7 million years. After *Homo, Macaca* has the widest geographical range among primates, and both of these genera are present in tropical and temperate regions as well. Whereas the single extant representative of the genus *Homo* diverged through processes of cultural diversification, extant species of macaques emerged through processes of evolutionary diversification. Macaque societies are characterized by profound unity and great diversity, and can best be described as variations on the same theme. To understand macaque variation and adaptation, we must take into account the processes that insure the persistence of their societies across generations and environments.

We presently recognize 22 species in the macaque genus distributed into several lineages (Box 1). On one hand, macaques share the same basic patterns of grouping and dispersal. They are semiterrestrial primates that form multimale, multifemale groups that permanently contain both adult males and females with offspring. The adult sex ratio is biased toward females. Neighboring groups have overlapping home ranges. Most males disperse and periodically transfer from one group to another. Most females stay in their natal group and maintain enduring relationships with their relatives, constituting matrilines that lead to the coexistence of several generations in the same group. Whereas the dominance status of males varies through their lifetimes, following shifts in their competitive abilities, the positions of females in hierarchies remain quite stable owing to kin-based alliances.

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Key words: social style; correlated variation; robustness; constraint; epigenesis; phylogeny; *Macaca*

DOI 10.1002/evan.20147

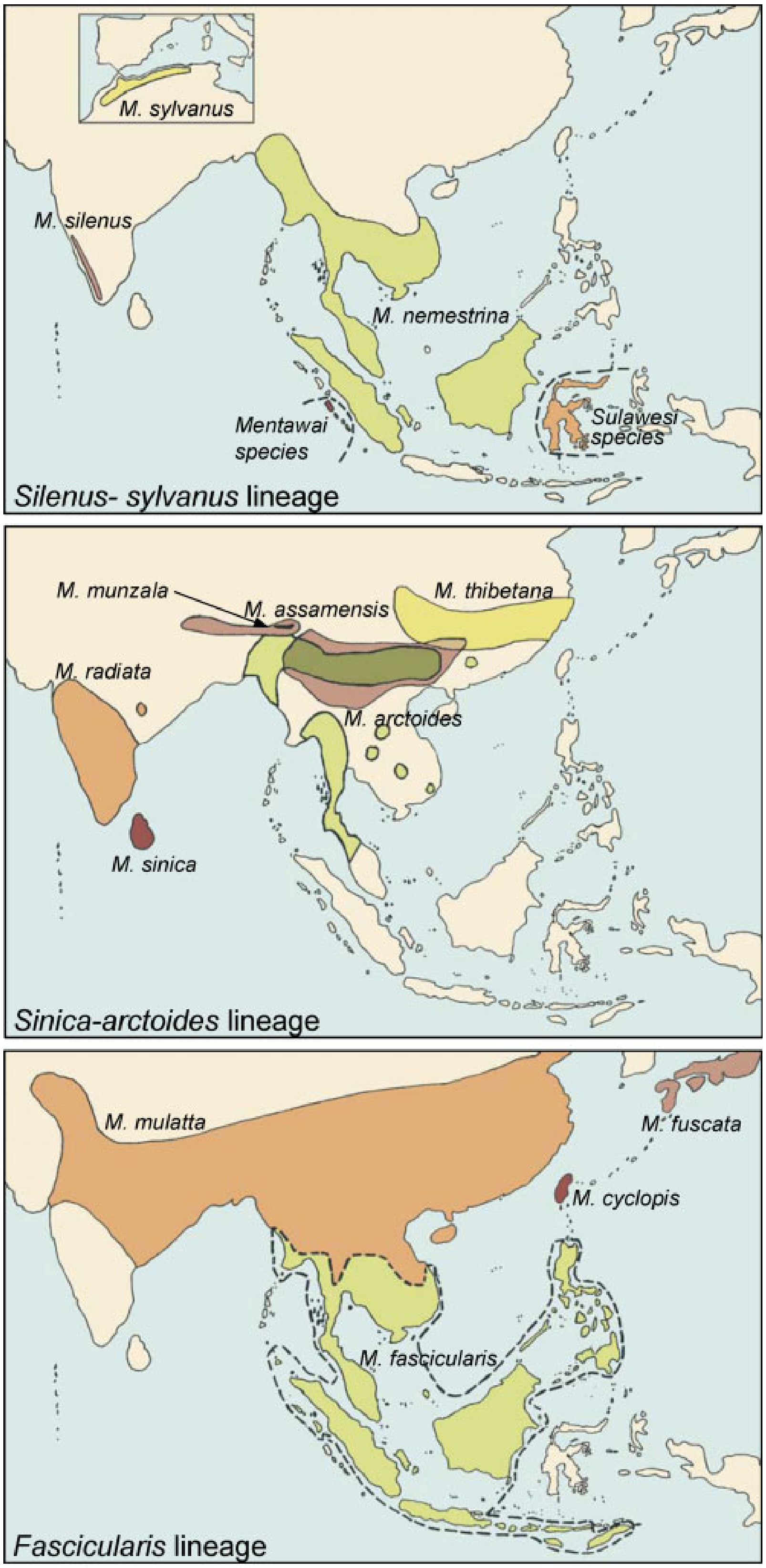
On the other hand, the diversity reported in the relationships of individual macaques appears to be unmatched among nonhuman primates. Macaques display varying degrees of dominance asymmetry and preference for kin. Affiliative behaviors are developed in some species and limited in others. There are striking disparities in maternal control over offspring across species. Mating patterns range from regular changes in sexual partners to prolonged female guarding by males.

A commonly unstated assumption is that the components of a social organization can be modified separately to fulfill fitness requirements. An organization is an integrated whole, a change in one component is liable to induce changes in others.[1,2] We may take advantage of the diversity of macaque societies to investigate correlations between behavioral traits. To explain diversity, mainstream evolutionary thinking focuses on natural selection as the preeminent driving force behind adaptative processes. It deals with the *mutability* of livings beings to explain how they cope with the requirements of an ever-changing environment.[3] This approach shaped the study of primate social organization during the last three decades, allowing us to formulate and test specific hypotheses about the adaptive function of behaviors. Nowadays, there is growing interest in the stability or, more exactly, the *robustness* of living beings. They preserve their state of adaptation by protecting the dynamics of developmental and functional systems against potentially disruptive factors.[3–5] To make sense of variations, we must be able to specify the constraints that shape an organization and exert strong stabilizing selection on its components.

From the start of modern primatology, the study of behavioral variation in macaques has produced a number of scientific discoveries. We learned that early mother-infant separation induces irreversible psychological damages in the developing individual, that kinship has overwhelming structural effects on social relationships, and that acquired changes may be socially transmitted from one generation to the next, giving rise to traditions. The following decades delivered further lessons, the most remarkable of which have emphasized the robustness of primate societies and their underpinnings: (1) Social relations remain

Box 1. Species, Phyletic Lineages and Geographical Distribution of the Genus *Macaca*

Macaques constitute a monophyletic group of the cercopithecine subfamily. The fossil record indicates that they colonized Eurasia 5 to 6 million years ago via the Near East. They then branched into several phyletic lineages that have been identified from morphological and molecular evidence.[6–11] We distinguish three main lineages of extant macaques, corresponding to three dispersal waves in Asia. The *silenus* lineage has the most disjunct geographical distribution, indicating an early dispersal. Only the pigtailed macaque has a large distribution range. The liontailed macaque is found in the evergreen forests of southern India. The other species of the lineage inhabit the Sulawesi and Mentawai Islands. The *sinica* lineage has a moderately fragmented distribution in southern Asia and is thought to be the second lineage to have dispersed. Four of its species are found in tropical and subtropical continental areas, while the fifth species, the toque macaque, lives on Sri Lanka. The most broadly and continuously distributed lineage is *fascicularis,* which is likely to be the third lineage to have dispersed. The longtailed macaque is present in equatorial and tropical regions; the other three species are found in subtropical and temperate Asia. The taxonomic position of two further species remains debated. The Barbary macaque, which lives in the montane forests of North Africa, is the most ancient taxon of the genus. It is alternatively classified as either being the only member of its own species group or one belonging to the *silenus-sylvanus* lineage. The stumptailed macaque inhabits broadleaf evergreen forests of southern Asia. It is either ascribed to its own species group or included in the *sinica-arctoides* lineage.[6,7,9]



Silenus- sylvanus lineage

Sinica-arctoides lineage

Fascicularis lineage

(modified from Fooden[8])

Silenus-sylvanus **lineage**


Barbary
Macaque,
M. sylvanus

(Algeria,
Morocco)


Liontailed
macaque,
M. silenus

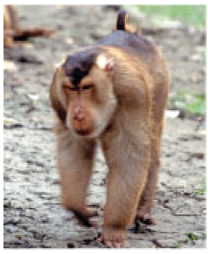
(Southwest
India)


Siberut
macaque,
M. siberu

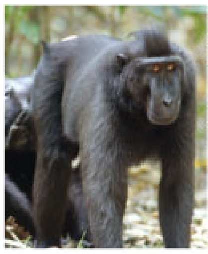
(Mentawai:
Siberut
Island)


Pagai
macaque,
M. pagensis

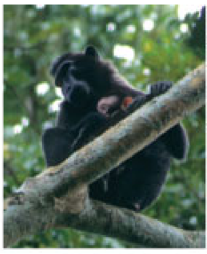
(Mentawai:
Pagai and
Sipora islands)


Pigtailed
macaque,
M. nemestrina

(Indochinese
peninsula,
Sumatra,
Borneo)


Crested
macaque,
M. nigra

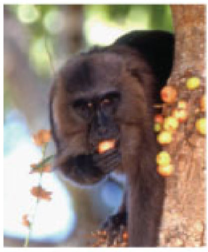
(North
Sulawesi)


Gorontalo
macaque,
M. nigrescens

(North
Sulawesi)


Heck's
macaque,
M. hecki

(North
Sulawesi)


Moor
macaque,
M. maurus

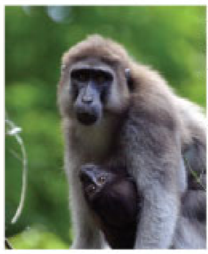
(Southwest
Sulawesi)


Tonkean
macaque,
M. tonkeana

(Central
Sulawesi)

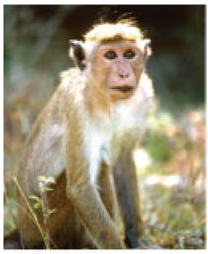

Booted
macaque,
M. ochreata

(Southeast
Sulawesi)


Muna-Butung
macaque,
M. brunnescens

(Southeast
Sulawesi)

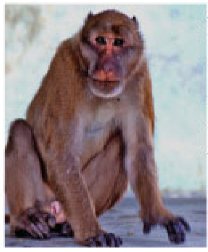
Sinica-arctoides **lineage**


Toque
macaque,
M. sinica

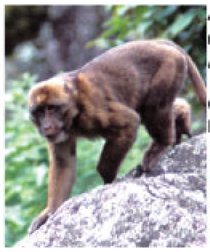
(Sri Lanka)


Bonnet
macaque,
M. radiata

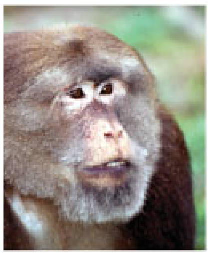
(South and
West India)


Assamese
macaque,
M. assamensis

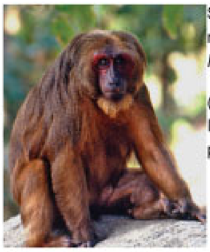
(Continental
Southeast
Asia)


Arunachal
macaque,
M. munzala

(Northeast
India)


Tibetan
macaque,
M. thibetana

(East and
Central China)


Stumptailed
macaque,
M. arctoides

(South China,
Indochinese
peninsula)

Photo credits: B. Thierry (*sylvanus, nigra, tonkeana, thibetana, fascicularis, mulatta, fuscata*), R. Seitre (*nemestrina, hecki, maurus, sinica, assamensis, arctoides*), C. Abegg (*silenus, siberu, pagensis, radiata*), N. Herrenschmidt (*ochreata*), M.J. Hsu (*cyclopis*), M.D. Madhusudan (*munzala*), N. Rowe (*nigrescens*), N. Priston (*brunnescens*).

Fascicularis **lineage**


Longtailed
macaque,
M. fascicularis

(Indochinese
peninsula,
Indonesia,
Philippines)


Rhesus
macaque,
M. mulatta

(Continental
South and
East Asia)


Japanese
macaque,
M. fuscata

(Japan)


Taiwan
macaque,
M. cyclopis

(Taiwan)

consistent despite individual plasticity; (2) variation is circumscribed to a limited number of social styles; (3) linkages between behavioral traits arise at any level of organization; (4) cross-species contrasts are better explained by phylogeny than by ecology; (5) evolutionary transformation depends on a balance between external and internal determinants; (6) mating patterns are largely independent from social styles. I will review them in turn to examine how adaptation trades off against robustness in primate societies.

CONSISTENCY OF SOCIAL RELATIONS: THE CASE OF THE RHESUS MACAQUE

The social organization of each species of nonhuman primates seems to gravitate to some norm.[12,13] Two alternative viewpoints have long since been suggested for the extent to which societies are variable. Observed regularities led some to believe that "the genetic potential of some nonhuman species may indeed be restricted to one type of society which environmental change would hardly alter."[1] The fluctuations observed in demographic patterns and behavior rates led others to wonder whether there exists "such thing as a 'normal social structure' for a given species."[14]

There is no better example than the rhesus macaque for use in examining the possible extent of variation in social behaviors of nonhuman primates. This is the most extensively studied monkey and also the most adaptable. In the laboratory, rhesus macaques are able to cope with multiple experimental conditions, including outer space. In the wild, they are found from 70°E longitude in Afghanistan to 120°E longitude in China. They live in diverse habitats: tropical, temperate, and subalpine forests, tidal areas, arid lands, regions of human settlement, and even urban zones (Fig. 1).[15,16] Their diet is exceptionally flexible. They are mainly folivorous in the deciduous forests of the Himalayan foothills, but appear to be largely frugivorous in other habitats. Rhesus macaques are well adapted to ecologically disturbed zones. As humans clear forests they adjust their diet to include cultivated crop plants.[16] Group size usually ranges between 20 and 40 individuals, but can be as large as 100–200 individuals. Home-range areas also vary widely, fluctuating between some hectares and 20 km^2 according to ecological resources.[15]

Experimental changes in the availability of social partners may affect the quality of individuals' social interactions and development. Among group-living rhesus macaques, adult males show little interest in infants and rarely affiliate with them. Nonetheless, when a wild-born male is pair-housed with an infant, he develops a strong bond with that infant and will groom and play with it.[17] In the absence of mothers, there is potential for males and infants to form affiliative relationships. In experiments where young rhesus macaques were co-housed with slightly older stumptailed macaques, the conciliatory tendencies of the former were multiplied threefold, stabilizing at levels comparable to those of the latter.[18]

The study of free-ranging groups of rhesus macaques introduced on the Caribbean island of Cayo Santiago has shown that the rates of offspring rejection of females are similar to those of their own mother.[19] There is intergenerational transmission of mothers' rearing style. Cross-fostering experiments have demonstrated that abusive behaviors toward offspring may be transmitted from mothers to daughters through experience.[20,21] Maternal behavior additionally depends on demographic factors. The number of nonrelatives in proximity to infants increases with the size of groups. In smaller groups, mothers spend less time monitoring their infants and are less restrictive regarding their moves and social contacts.[22] These effects have an impact on the developmental trajectory of individuals by influencing the degree of exclusivity of the mother-offspring bond and the extent of immatures' social networks.

Variation may also originate from genetic diversity. A fair amount of heritability has been documented in the temperament of individuals. Temperament is trait-like; that is, individuals display stable behavioral dispositions across different situations throughout their lives.[23] Genetic analyses in infant rhesus macaques have revealed high heritabilities of anxiety-related behaviors like inhibition and distress responses.[24,25] Temperament characteristics have biological correlates; a wealth of data demonstrate that high impulsivity and aggressiveness are related to reduced serotonin activity. Serotonin is a neurotransmitter involved in control of the neurohormonal stress axis. Studies of rhesus macaques have shown that low levels of serotonin are associated with a consistent suite of behavioral tendencies that includes impulsive risk-taking, unrestrained aggression, and lack of submission. Low-level males additionally have tendencies toward social isolation, early dispersal, frequent wounding, and heightened mortality rates, whereas low-level females, though the most protective mothers, nevertheless experience higher rates of infant loss.[26–28]

Interindividual differences in central serotonin turnover are under genetic influence. There is polymorphism at the promoter region of a gene encoding the serotonin transporter protein. Two main alleles of the gene, *S* and *L*, have been identified. The *S* allele is associated with less efficient serotonin promotion, meaning that, in rhesus macaques, as in humans,[20] different genotypes produce individuals with different levels of impulsivity. Interestingly, the rearing environment modulates the phenotypic expression of the gene. In peer-reared subjects, individuals carrying the *S* allele consistently present lower serotonin concentrations. However, mother-reared subjects display normal concentration levels regardless of whether or not they possess the *S* allele. The rearing environment seems to buffer the infant from the potentially negative effects of the allele on serotonin metabolism.[29]

The buffering effect of the social milieu may explain a paradoxical lesson learned from the study of rhesus macaques. Despite the extensive plasticity reported for individuals, their social relations follow consistent patterns. In any of the places where they have been studied, we see the intractable and aggressive temperament that drives rhesus macaques to threaten others at the slightest provocation, using the stare open-mouth facial display; subordinates perform a silent bared-teeth response that specifically expresses submission and reveals strong dominance asymmetry in social relationships. Most contests are unidirectional; that is, the attacked individuals flee or submit without any attempt to counter their aggressor.[30,31] Measuring the proportion of reconciliations between mature females and unrelated partners regularly yields values below 10%.[32,33] Mothers exert close control over the social interactions of their infant. Adult females and immatures exhibit strong preference for maternal kin. The degree of relatedness is a main predictor of affiliation, dominance, and support.[34,35] Whenever matrilines are large enough, the support of relatives in contests produces strict rules of rank inheritance among adult females:[36–38] (1) Females inherit their mother's rank relative to others; (2) they hold rank just below their mothers; (3) younger daughters dominate their elder sisters. Dominance ranks correspond inversely with age within matrilines because mothers and sisters choose to help their youngest relatives. These traits form what may be called the "social style" of rhesus macaques, something like a behavioral archetype.

With regard to mating patterns, Carpenter[39] described the "norm of sexual activities for *Macaca mulatta*" as early as 1942. He pinpointed the communicative signals associated with copulation, the increase in aggression during the mating season, and the relationship between male dominance and consortship. He also identified more peculiar patterns, such as that receptive females mate with a succession of males and that dominant males disrupt the consorts of lower-ranking males by threatening the females rather than their rivals. Subsequent reports repeatedly corroborated the accuracy of Carpenter's first account.[40,41]

By experimentally modifying social density, we can significantly alter the frequencies or durations of behaviors like aggression and social grooming.[32,42,43] In contrast to this, the quality of social interactions shows little range in variation. The form of the interactions in which an individual is involved is, by nature, heavily dependent on the behavior of partners. When comparing rhesus macaques living in different environments, variables such as the proportion of reconciled conflicts, as well as patterns of support and contact regulation between mother and infant, show relatively limited fluctuations.[19,32,42–45] As once noted by Richard,[38] similarities in the social organization of the provisioned groups of Cayo Santiago and the wild populations of the Pakistan forests are more striking than their differences.

Figure 1. A subgroup of rhesus macaques sitting on the rooftop of a building in the sacred city of Vrindavan, India. The species is present in a wide variety of environments, including towns and cities, where it lives commensally with humans (photo by R. Seitre).

Social style has a learned component. Some behavior patterns may be transmitted to the next generation, as illustrated by the social inheritance of dominance rank and maternal behavior. In light of these facts, we might expect to find cultural effects in social styles, that is, social patterns, would continuously change through time and consistently differ between groups. We do not actually know of any examples of such an effect. If cultural evolution is identified by the irreversible drift it produces, we have no evidence for cultural evolution among macaques. Socially acquired behaviors represent fluctuations in the system, which periodically returns to initial conditions.[46] Indeed, without what is called the ratchet effect, socially transmitted changes cannot accumulate over time.[47] Moreover, there are no hints that macaques would become abnormal if they failed to learn the social knowledge acquired by previous generations. A natural experiment made by Stephen Suomi (personal communication) nicely illustrates this point. In 1973 he established a breeding colony by gathering eight 6-month-old peer-reared rhesus macaques. Each of them had been removed from its mother at birth and was hand-reared in a nursery for the first month of life. The infants were then allowed to interact with peers for two hours a day until six months of age. Thereafter, they were put together to form a breeding group. In less than three decades, the group expanded to more than one hundred individuals. The outcome is, today, a multigenerational troop maintained in semi-free ranging conditions at the NIH Animal Center in Poolesville, Maryland. The group

Box 2. Contrasts in Patterns of Conflict Resolution

The study of reconciliation provides a standardized tool for comparing social relations in macaques. Reconciliation is defined as a positive contact occurring after conflict between former opponents. To quantify reconciliations, one opponent is followed during a 10-minute postconflict period (PC). Then a 10-minute matched-control period (MC) is conducted on the same individual on the next possible observation day.[48] By matching PC and MC, each pair of former opponents is classified as "attracted" if contact between individuals occurs earlier or only in the PC, "dispersed" if contact occurs earlier or only in the MC, or "neutral" if contact occurs at the same time or did not occur in the PC and MC. The *conciliatory tendency* is calculated as the number of attracted minus the number of dispersed pairs, divided by the total number of PC-MC pairs. The data collected by three research teams during the last twenty years show that conciliatory tendencies were consistently below 20% in some species, and rated around 50% or more in other species (Fig. A).[33]

Statistical analyses first showed that several traits related to the resolution of conflicts display correlated variation. Species cannot be considered as independent units, however, since they may share traits through common ancestry. Therefore, the method of independent contrasts[49] was used in a second step to control for phylogenetic relatedness. It showed that associations between traits were still consistent. In particular, rates of explicit physical contacts (for example, mounts and clasps) were more elevated in species characterized by higher conciliatory tendencies (Fig. B), supporting the view that such contacts are instrumental in promoting reconciliation. Another significant association was found between the percentage of counter-aggression and kin-bias in reconciliation; preference for kin was greater in species characterized by a lower number of protests and counter-attacks in conflicts (Fig. B). This result is consistent with the hypothesis that the occurrence of coalitions creates a causal link between levels of dominance asymmetry and kin bias in female macaques. When most coalitions involve relatives, the dominance status of individuals depends primarily on the power of the kin subgroup to which they belong. This increases rank differences between nonrelatives and further develops kin coalitions, generating group networks based on strong hierarchies. In contrast, when kin-bias is less pronounced, coalitions involving nonrelatives are more common. Dominance appears to be more a question of individual attributes and the individual retains some degree of freedom with regard to power networks. Dominance relationships remain balanced among group members and close ties exist even between nonrelatives. A consequence of the connection between dominance asymmetry and degree of kin preference is that environmental factors cannot separately act on either of these two traits.

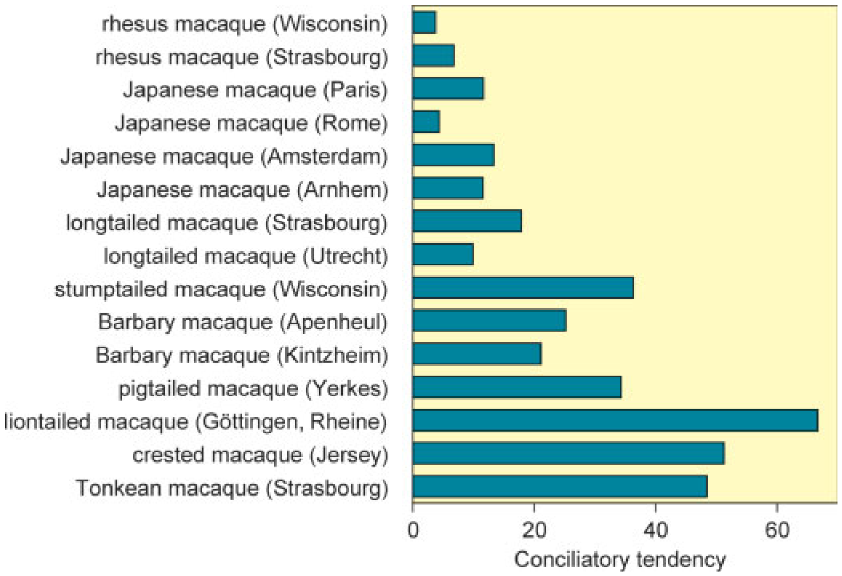


Figure A. Mean conciliatory tendencies in fifteen captive populations of macaques representing nine species of macaques.[33] To standardize data, only dyadic conflicts occurring between pairs of unrelated females (older than 3.5 years) and between pairs of females and unrelated juveniles (between 1.5 and 3.5 years of age) were taken into account.

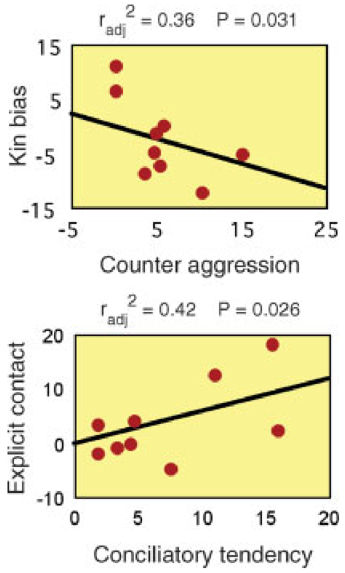


Figure B. Associations between counter-aggression and kin bias (above), and between conciliatory tendency and explicit contact (below).[33] Regression analyses used independent contrasts computed from the phylogeny provided in Purvis.[50]

TABLE 1. Tentative Scaling of Macaque Social Styles (modified from Thierry[61])[a].

Grade 1	Grade 2	Grade 3	Grade 4
Rhesus macaque	Longtailed macaque	Stumptailed macaque	Tonkean macaque
Japanese macaque	Pigtailed macaque	Barbary macaque	Moor macaque
(Taiwan macaque)	(Assamese macaque)	Liontailed macaque	Crested macaque
	(Tibetan macaque)	Bonnet macaque	(Muna-Butung macaque)
		(Toque macaque)	(Booted macaque)
			(Heck's macaque)
			(Gorontalo macaque)
			(Siberut macaque)

[a] Social tolerance increases from left (grade 1) to right (grade 4). The least known species are indicated in brackets.

exhibits the normal social organization of rhesus macaques, including all of the species-typical behavior patterns regarding communication, aggression, affiliation, dominance, kinship and socialization. Even if their relationships were not normal at the start, individuals deprived of the experience of previous generations succeeded in creating a social organization that converged toward the archetypal style of their species.

SOCIAL STYLES AS COVARIANT SETS OF TRAITS

Strong nepotism and dominance hierarchies were once believed to be typical of the entire macaque genus, if not other primate families.[51,52] Subsequent studies showed that these features were, in fact, those characterizing the two better-known representatives of the genus, the rhesus macaque and its sister species, the Japanese macaque. Other macaques actually depart, to varying degrees, from the *mulatta/fuscata* archetype. In the latter two species, conflicts are unidirectional, high-intensity aggression is common, and reconciliations are not frequent.[32,53–58] Quantitative analyses have shown quite different patterns of aggression and response to aggression in Sulawesi macaques (Tonkean, crested, and moor macaques). A majority of their conflicts are bidirectional, and most aggressive acts induce protest or retaliation. Aggression is generally of low intensity. Measuring conciliatory tendencies yields high values, around 50% among unrelated partners (Box 2).[31,54,57,59,60]

Other macaques are located intermediately between previous species regarding patterns of aggression and reconciliation. Longtailed and pigtailed macaques are most similar to rhesus and Japanese macaques, whereas stumptailed, Barbary, liontailed, and bonnet macaques are most comparable to the Sulawesi macaques.[61] When measuring different populations of the same species, conciliatory tendencies fall within a narrow range of variation, indicating that they reflect species-typical social styles (Box 2).[32,33,42,56,58,61–63] I have proposed to arrange macaque species along a 4-grade scale mainly based on patterns of aggression and reconciliation (Table 1).[61] Species from grades 3 and 4 display higher rates of tension-reducing contacts than do others. The meaning of the silent bared-teeth display consistently varies along the scale. In macaques from grades 1 and 2, subordinates use it to express submission, formally acknowledging their lower status relative to higher-ranking conspecifics. In grade-3 species like Barbary and liontailed macaques, the same display may either have a positive meaning or express submission according to contexts. In species from grade 4, formal indicators of subordination are absent; the bared-teeth display signals the sender's peaceful intentions like a smile (Fig. 2).[61,64]

The degree of kin-bias in social relationships covaries with patterns of aggression and dominance. The degree to which females prefer maternal relatives for contact, social grooming, and coalition is less pronounced in the third than in the first two grades[34,53,55,65,66] and kin-bias is still weaker in Sulawesi macaques (grade 4).[52,67,68] The socialization process also contributes to the species social style. Except for the high-

Figure 2. Silent bared-teeth displays among males in semi-free ranging Tonkean macaques, Strasbourg Primate Center, France. Baring the teeth serves to initiate affiliative interactions in all Sulawesi macaques (photo by B. Thierry).

est-ranking females, mothers in the first two grades are protective of their infants, frequently retrieving them, restricting their interactions mostly to relatives. The amount of care provided by females other than the mother is limited. By contrast, mothers belonging to species from the other two grades are permissive; many females in the group may handle infants from an early age.[61] Although we lack quantitative data about female rank acquisition in most macaque species, we know that in longtailed macaques (grade 2) rank acquisition follows the inheritance rules described in rhesus and Japanese macaques. However, rank reversals between mothers and daughters are not uncommon.[69] In Barbary macaques (grade 3), daughters often outrank older mothers and females are usually subordinate to their older sisters.[66,70] In Tonkean macaques (grade 4), rank reversal of mothers and daughters is not rare and the rule of youngest ascendancy does not apply (Thierry, unpublished data).

The 4-grade scale may be used as a periodic table that allows for falsifiable predictions to be made (Table 1). A few traits may be used to predict others. Several expectations of the covariation hypothesis have already been verified, including the permissive mother style of stumptailed macaques,[71] the moderate female kin-bias of Barbary macaques,[65] the high proportion of retaliation of Muna-Butung macaques,[72] and the elevated conciliatory tendency of bonnet macaques.[73] Direct interspecific comparisons have been carried out for only a limited sample of species, groups, and traits, however, and intraspecific variability calls for caution.[61] While it is easy to group those species that fit into either the first or the fourth grade, it is more difficult to group intermediate species. Recent studies indicate that Assamese and Tibetan macaques belong to grade 2. They confirm that their patterns of aggression, reconciliation, and dominance consistently covary, with the caveat that they display tension-reducing behaviors alike to species from grades 3 and 4.[74,75] Although each species is assigned to one grade, a more accurate picture would represent the various study populations of each species as a cluster of points centered on one modal location.

Stating that the components of macaque societies are arranged in a limited subset of social styles amounts to saying that large parts of the macaque sociospace remain unoccupied. This is the second lesson to be drawn from the study of macaques. Sociospace may be defined as the set of forms that a particular kind of social organization may take. It is described by all possible combinations in the values of the parameters characterizing the social organization. By acknowledging a family of established styles, it is possible to identify an empirical sociospace defined by the variation of behavioral traits. The question then arises why some social styles do *not* exist in macaques, such as those characterized by strong dominance asymmetry *and* weak preference for kin, or low conciliatory tendency *and* regular infant handling by group members. To answer this question, we have to look at the processes responsible for the coupling of traits.

SOURCES OF LINKAGES BETWEEN BEHAVIORAL TRAITS

Identifying the connections among constituent parts of a biological system is a notoriously tricky task. It may involve genetic and acquired components. For example, several processes may account for the association found between levels of aggression and maternal protectiveness among macaques.[2] Reduced serotonin activity may yield both heightened aggression and low rates of infant rejection by the mother. Alternatively, elevated risks of aggression may lower rejection rates through an increase in maternal anxiety. Mothers from the first two grades live in a social milieu characterized by intense aggression and marked hierarchies, and they restrict their infant's interactions. A third process may also take place. Anxiety is a trait of temperament. If its variation range differs between species, this may result in interspecific disparities in infant rejection rates.

Regular interspecific variation has been shown in the temperament of macaques. They differ in response to stress and novelty as measured by arousal, alarm, and exploration behavior, corticosteroids or heart rate.[61,76] Species from grades 3 and 4 are less easily aroused than are species from grades 1 and 2. Such variations in behavioral responses have meaningful biological correlates. Higher aggression intensity is associated with lower serotoninergic activity in rhesus compared with pigtailed macaques.[77] Also, tolerant macaques (stumptailed, Barbary, and Tonkean macaques) are mostly monomorphic for serotoninergic genes, while more intolerant macaques (pigtailed, longtailed, and rhesus macaques) appear to be polymorphic. Moreover, polymorphism regarding the serotonin gene transporter includes the *S* allele only in rhesus macaques. Naturally, we cannot expect that a limited number of alleles accounts for the full spectrum of behavioral variations reported in macaques, but these results do point out a genetic influence on interspecific variation.[78] We have evidence of the neurochemical and genetic basis of further cross-species differences in anxiety-related behaviors.[78,79] Such findings should be considered the first steps toward unraveling the genetic underpinnings of macaque temperament.

Links between traits may originate from two main mechanisms, common source or interaction between constituent parts of the system. Such mechanisms may arise at different levels: genome, individual phenotype, and social phenotype.[2] An example of a common source is gene pleiotropy; a single gene locus affects a variety of traits, producing multiple correlated effects. For instance, low rates of serotonin are responsible for a broad behavioral syndrome as reported in rhesus macaques. Some correlations may be an outcome of the systemic variation of a single hormone or neurotransmitter acting on several targets, but variations may also affect the distribution and responsiveness of targets. At the level of individual temperament, impulsivity, aggressivity, and lack of submission are likely to be different facets of one and the same dimension,[23] meaning that they cannot be separated. At the social level, a single temperament dimension may produce a range of various outputs depending on the context. Those associated with lower serotoninergic activity may engage in social isolation, early dispersal, and heightened maternal protectiveness.

Slight differences in the temperament of individuals may yield significant variations in individual behaviors and social relationships.[13,23] By acting on behavioral propensities and response thresholds, selective processes can shift social styles from one part of the macaque sociospace to another. Hemelrijk[80] was able to generate self-organized patterns that resemble those found in macaques by implementing simple rules of attraction and competition in a multiagent model. She demonstrated that a quantitative shift in aggression intensity leads to correlated changes in spatial cohesion and conflict asymmetry.

Various linkages stem from social interactions. Individuals' behaviors may complement or reinforce one another, or oppose and even exclude one another. Tactical considerations indicate that competitors' readiness to struggle for a resource depends on the risk they incur. If the risk of being wounded in a conflict is elevated, the better tactic for the weaker individual is to submit or flee rather than to counterattack the opponent. Conversely, when the dominance gradient is low, the threatened individual can easily retaliate, forcing the adversary to avoid potentially dangerous attacks. In animals able to use graded threats, if a high proportion of retaliations in conflicts resulted in frequent biting and wounding, it would represent poor tactics. This explains why intensity in aggression, asymmetry of conflict, and submission patterns are covarying traits in macaques.[2] On one hand, asymmetric conflicts and high risk of injury inhibit the occurrence of affiliative contacts between opponents. On the other hand, uncertainty about outcomes creates room for negotiation. Appeasement behaviors reduce the probability of conflict escalation by allowing information exchange,[81] which may account for the correlation found between rates of explicit contacts and proportions of reconciliations (Box 2).

A third lesson from macaques is that linkages underpinning societies may arise at any level of organization. An important consequence of this is that some traits represent byproducts of others. The matrilineal structuring of dominance relationships in rhesus and Japanese macaques (that is, females ranking below their mothers and age-reversed rank order among sisters) may be regarded as an incidental side effect of the support given to relatives, which is quite exclusive compared with that reported in more tolerant species. Similarly, cross-species differences in rates of infant handling by group members appear to be derived from variations in mothering style. Regardless of the motives of individuals trying to interact with infants, their access to infants is a function of the mother's protectiveness. She shapes her offsprings' social network by selectively allowing or preventing others from approaching (Fig. 3). From this perspective, there is no need to provide a particular adaptive explanation for the occurrence of low or high rates of infant handling.[2]

ECOLOGICAL AND PHYLOGENETIC CORRELATES

In order to unravel the origins of cross-species differences in the social styles of macaques, we must examine their evolutionary past. There is a consensus that social organization patterns in primates are linked to the characteristics of the environment in which they have evolved. But how deterministic the influence of the environment is remains an open question. The predominant socioecological model assumes that predation pressures compel female primates to live in groups, while the distribution of resources subsequently determines the strength of feeding competition within and between groups, thus shaping the nature of social relationships.[82–84] Does this model account for the interspecific variation observed in macaque social styles? In a recent review, Ménard[85] examined the fit between theoretical

Figure 3. A mother lets another female handle her infant in semi-free ranging Barbary macaques, Kintzheim, France. Infant handling and caretaking by individuals other than the mother is especially frequent in the species (photo by B. Thierry).

expectations and what we know about the ecology of wild populations of macaques. She concluded that available data on habitats and modes of exploitation by macaques "do not indicate any consistent features of known ecological conditions for each species that appear to be correlated with their characteristic dominance styles." In the tropics, for instance, macaques mainly depend on clumped foods like fruits, whereas in more temperate areas Barbary, rhesus, and Japanese macaques heavily rely on more evenly distributed seeds, buds, leaves, and herbs. From the assumption that levels of within-group contest competition are weak when high-ranking females cannot monopolize food, the model predicts that the latter three species should display tolerant relationships.[85] Quite to the contrary, rhesus and Japanese macaques share the same "despotic" social style; only Barbary macaques exhibit relaxed dominance relationships (Table 1). The socio-ecological model additionally states that species undergoing strong between-group competition should display more tolerant social relationships than do those not facing such competition. High-ranking females should accept a more equal exploitation of resources in exchange of the help of low-ranking females in communal defense against other groups.[83,84] Here again, the model is not supported by the results of field research.[85] The rates of aggressive between-group encounters do not differ between tolerant and intolerant macaques, and low levels of between-group competition are reported in females from tolerant species such as bonnet and moor macaques.[86,87]

Whereas related primate taxa often cluster together based on ecological variables,[88] the ecological preferences of macaques appears weakly connected with their phylogenetic relations.[8,16] The development of statistical comparative methods[49] has made it possible to test the occurrence of historical effects on social organization patterns. It was found that Cercopithecine monkeys typically share traits like female philopatry and kin-relations.[89] Study of the macaque genus further showed that its three main phyletic lineages have a different distribution on the 4-grade scale and that variations in social style correlate with phylogeny.[2,87,90] By tracing each of the traits on the phylogenetic tree of macaques, it is possible to recognize the most ancient states and reconstruct the typical ancestral organization of macaques. The resulting set of traits closely matches grade 3 on the scale, which may be tentatively considered as the ancestral state.[90] The fact that Barbary and liontailed macaques are located in grade 3 reinforces the previous finding since these two species come closest to the root of the phylogenetic trees established from morphological and molecular data. The other species of the first lineage have diverged, moving either to grade 4 (Sulawesi macaques) or grade 2 (pigtailed macaques). Members of the second lineage have remained on grade 3 or drifted to grade 2. The third lineage evolved toward grades 1 and 2. The location of every lineage is mostly restricted to two grades in the scale. This means that the core of the species-typical system of social relationships underwent limited changes during several hundreds of thousands of years and even millions of years in some species.

The importance of linkages between traits challenge equilibrium models based on direct associations between traits and the environment. Another lesson from macaques is that social organization is underdetermined by environmental factors.

In a recent study we used data from several species to test correlations between the proportion of counter-aggression and traits related to reconciliation, conciliatory tendency, degree of preference for kin, and proportion of explicit physical contacts leading to the reunion of previous opponents.[33] The analysis showed that several traits additionally displayed correlated evolutionary changes even after controlling for phylogeny (Box 2). This confirms the occurrence of internal connections responsible for the clustering of behavioral traits. The importance of linkages between traits challenge equilibrium models based on direct associations between traits and the environment. Another lesson from macaques is that social organization is underdetermined by environmental factors.

BALANCE BETWEEN EXTERNAL AND INTERNAL DETERMINANTS

We cannot explain macaque diversity by considering environmental pressures and linkages between traits separately. Any evolutionary explanation must account for the fact that macaque social styles are quite stable packages of integrated behavioral traits. To account for phyletic stasis (that is, the absence of evolutionary changes), one classically resorts to phylogenetic inertia. Present traits would have been selected for in the past under conditions different from those of today and would persist across environmental changes because of the time lag in adaptations.[66,85] Phylogenetic inertia is the black hole of socioecological theory; it spares functional hypotheses at the expense of reasons lost in the past.[91] Moreover, calling on species lag says nothing about the forces at work. We still have to specify whether the absence of changes is produced by a lack of effective selection or because of stabilizing selection.[92]

Linkages between traits are not just slave proximate mechanisms under the command of ultimate factors. They act as constraints that reduce the probability of trade-offs for evolutionary changes.[3,4,93] Employing the word "constraint" conveys the message that structural and functional linkages channel the adaptive pathways open to biological systems by "constraining" their mutability. This view advocates a transformational approach, which investigates how organizational properties may shape the transformation of biological systems throughout history.[94] We may alternatively describe optimization models as "models under constraints" that aim to unravel trade-offs endowed with a higher fitness. This second view promotes an equilibrium approach by focusing on the counterbalancing actions of factors liable to drive changes. For the last two decades, misunderstandings about the definition of constraints was a primary cause of controversy between the proponents of the equilibrium ("functionalist") and the transformational ("structuralist") paradigms.[94,95]

It should be apparent that both approaches complement each other. A game-theory model developed by Matsumura and Kobayashi[96] helps to clarify this point. To account for the outcomes of contests over resources, they proposed three possible tactics for opponents with unequal fighting abilities: (1) *hawk,* escalate fighting until injury or opponent retreats; (2) *dove,* display but retreat if opponent escalates; (3) *retaliator,* start by displaying but escalate if opponent escalates. The main parameters of the model are the resource value (V), the cost of injury (D), and the probability of winning the contests (x). The implementation of this model reveals that several strategies are evolutionarily stable: hawk against dove, dove against dove, hawk against hawk, and retaliator against retaliator. Moreover, different strategies may co-exist for the same values of V, D, and x, which signifies that strategies are not merely determined by ecological conditions.[96] The use of an optimality model thus indicates that aggression intensity and conflict asymmetry are functionally related traits and that they are partly disconnected from the environment as seen in macaques. Alternative strategies may be regarded as different fitness peaks in an adaptive landscape. A classical explanation is that evolutionary pathways lead species to occupy different peaks. It is difficult for them to reach a peak of higher fitness because of the low-fitness valleys surrounding the peaks. Linkages between traits have arisen throughout history and they are not easily broken by selection.

The same device may be functional at one organization level and act as a constraint at another. This is a fifth lesson from macaques, applicable to the study of other societies. Note that this was already known to be applicable to the biology of organisms. "Constraint" is a relative concept.[3] It remains meaningless if we do not specify a null model of evolution regarding the trait considered. The null model states how traits would evolve in the absence of constraint; we commonly define it as the adaptation to external pressures.[3,4,93] From this viewpoint, a constraint is a mechanism that limits the evolutionary response of traits to external selective pressures acting at a given organizational level.[3] A correlate is that selection has an internal component that results from the fitness consequences of trait variation as determined by the dynamics of biological systems. It maintains the robustness of systems by eliminating the disrupting variations that would correspond to low payoffs for individuals. The concept of constraint captures those causal mechanisms that produce stabilizing selection and are less dependent on the external environment.

The crucial point is that the wheels of the social machinery exert strong stabilizing selection that opposes the adaptative changes possibly required by the ecological milieu. Evolutionary transformation depends on a balance between the respective strength of external pressures and stabilizing processes.

Like organisms, societies result from a balance between organizational and environmental pressures. Each individual in a society submits to the consequences of these two components of selection. Organizational pressures arise from social dynamics. We may resort to game models to explore frequency-dependent strategies and understand why some behaviors are favored or discarded. We may also employ the language of constraints or trade-offs to explain that a change in one trait induces a change in another. The crucial point is that the wheels of the social machinery exert strong stabilizing selection that opposes the adaptative changes possibly required by the ecological milieu. Evolutionary transformation depends on a balance between the respective strength of external pressures and stabilizing processes. Theory predicts that the more numerous the interconnections between the components of a system, the more limited the optima open to the system and the greater their number,[97] which may account for the various social styles observed in macaques.

A difficulty that arises when considering behavioral phenotypes is that we may choose to consider either the ecological milieu (abiotic and biotic, excluding conspecifics) or both the ecological and the social milieu as the external environment, which influences the scope of potential constraints. Aware that the requirements of sexual selection may conflict with ecological pressures, behavioral ecologists included sexual selection among the external forces liable to shape primate social organization.[84,98,99] By recognizing the different outcomes of selection components, we may be close to reconciling the transformational and equilibrium approaches for studying primate societies.

Figure 4. Female mate guarding in wild crested macaques, Tangkoko Dua Saudara Nature Reserve, Sulawesi, Indonesia. The female presents her hindquarters to the male. Her anogenital swelling has not yet reached its maximal size. The male closely follows the female during days. His high rank allows him to keep rivals away until the end of the female's fertile period (photo by A. Engelhardt).

QUASI-INDEPENDENCE OF MATING PATTERNS

A main assumption in socioecology is that the exploitation of environmental resources by females determines grouping patterns, whereas males follow this distribution to compete for mating access.[82,100] Patterns of mating competition fluctuate between two extremes in macaques.[101] In *mate guarding,* an adult male closely follows and mates with a fertile female over a period of several days, excluding other males from reproduction. This tactic is based on contest competition and only dominant males can use it. The pressure exerted by males leaves little room for female mate choice. The second pattern is *opportunistic mating,* in which associations between males and females do not last for more than hours or even minutes. Competition is typically scramble, but it also involves some contest component; males regularly shift from one fertile female to another, and may also supplant a lower-ranking male from the proximity of a female. Conversely, a female may express mate preferences, refusing to copulate with a male and accepting another, even a lower-ranking one.[41,102] A major variable determining mating competition is the operational sex ratio, or the number of fertilizable females relative to the number of sexually active males.[100] For males, reproductive success depends on their ability to monopolize access to females. When only a few females are ovulating at the same time, high-ranking males tend to mate guard and dominance rank functions as a queue for mating opportunities; if there is a single peri-ovulatory female, only the first-ranking male is able to mate. When many females cycle synchronously, however, no male can monopolize reproduction and opportunistic mating becomes the primary tactic.

In multimale groups, the operational sex ratio may change according to the number of perio-ovulatory females. A primary source of variation is the more or less periodic nature of reproduction in macaques, which entails broad interspecific differences in the mating system. In tropical species where reproduction occurs year round, there is usually no more than one fertilizable female in a group at any given time. This promotes long-lasting periods of mate guarding by top-ranking males in, for example, liontailed, Tonkean, and crested macaques (Fig. 4).[101] In contrast, there is an annual breeding season for species living in temperate regions. Strong environmental seasonality entrains the synchrony of reproductive cycles. This way, females secure adequate resources during the good season, when their nutritional needs are highest. Most reproductive females cycle during the fall within a two- to three-month period, which favors opportunistic mating.[41,101,102] Lengthy guarding can coexist with opportunistic mating depending on the operational sex ratio. Not surprisingly, this is especially common in species experiencing limited seasonality, such as long-tailed and pigtailed macaques. Since there can be one or several peri-ovulatory females at any given time, female defendability is quite changeable. The duration and exclusivity of associations between sexes is variable too. It is worth adding that exclusive mate guarding by top-ranking males prevails in any species each time that the number of available mates decreases to two peri-ovulatory females or just one, which frequently occurs in small groups. In Japanese macaques, when the number of simultaneously cycling females decreases, the time spent by subordinate males in proximity to them decreases[103] and dominant males sire more offspring.[104]

Paternity analyses show that tropical macaques are characterized by a high male reproductive skew; that is, top-ranking males father a disproportionate number of progeny.[102,105] This has far-reaching consequences for the life history of males who cannot reproduce unless they acquire a high dominance status. This favors high-risk tactics for rank acquisition.[101,106] At some point in their lifetime, adult males face a go or no-go decision. They must aggressively challenge top-ranking males and defeat them to gain access to females. In comparison, the reproductive skew remains low among male seasonal breeders.[102,105] Because no male has complete control over mating access, the door is open to alternative mating tactics. Being dominant is just one of them. Subordinates may practice "sneak copulations"; they go out of the view of high-ranking males to surreptitiously mount females. Males also compete by "endurance rivalry"; some may forego reproductive opportunities because of the high energetic expenditures incurred by long periods of mating competition.[41,103] Furthermore, females have room to counter male coercion and pursue their own interests. The point of interest here is that seasonally breeding males can produce a fair amount of progeny without necessarily acquiring a top-rank position. Except in small groups, severe fighting between adult males is rare. Most of them increase in dominance rank with age and tenure in a group.[101,106]

Contrary to what may be expected, the correlation between male dominance rank and the number of progeny is not weaker in more tolerant species.[61,102] For instance, the reproductive skew is significantly higher in stumptailed macaques (grade 3) and Tonkean macaques (grade 4) than in rhesus and Japanese macaques (grade 1). This is a further lesson learned from the study of macaques. Patterns of mating competition appear to be quasi-independent from social style. Dominance relationships have more influence on reproductive sorting in year-round breeders with limited dominance asymmetry than in seasonal breeders with strong dominance asymmetry. When a single fertile female is available at a time, males directly reach the go or no-go decision point regardless of the nature of their social bonds. Social styles and mating system serve as two different modules in macaque social organization.

Phylogenetic analyses have revealed that species-typical social styles underwent limited changes over long periods of time.[2,90] The plasticity of reproductive patterns contrasts with such stability. Macaque populations have more than once experienced a change between warm and temperate climate during recent geological time. Not only does switching between seasonal and aseasonal reproduction probably represent a simple adaptation regarding hormonal processes, it also suggests that individuals may shift from one tactic to another depending on circumstances. The selective pressures responsible for the maintenance of social styles appears largely independent from those expressed in mating competition.

The overwhelming effects of reproductive periodicity on reproductive skew raises questions about the meaning of cross-species differences in social style and particularly for dominance asymmetry. It seems that only males able to outrank rivals have progeny under the tropics while variability in reproductive success remains limited in temperate regions. Environmental seasonality is a contingent factor on the evolutionary path of macaques; individuals cannot help but cope with variable sorting rules. It may be asked in which relative proportions the viability conditions attached to social styles and the conditions of reproductive competition affect the representation of individuals in the next generations. If the periodicity of reproduction modulates the strength of sexual selection, it would influence the genetic structure of social groups. While offspring have different fathers in temperate regions, a strong age-cohort effect should be found in the tropics, with all members of the same generation being paternal half-siblings. We do not know what could be the evolutionary consequences of such disparities in sibship.

PROSPECT

Over time, primatology has gone through stages similar to those in other fields of research. It began with descriptive explanations and then evolved to testing theoretical explanations.[51,107] A pending question is to what extent we may progress to a final, synthetic stage where the models proposed to explain different phenomena would become special cases of a general theory. Although primatologists cannot hope to reach unification levels similar to those achieved by the so-called exact sciences, the embedding of their study subjects in biological evolution allows them to foster a more deterministic project than their social anthropologist fellows.[51] The very historical dimension of the evolutionary process puts some limits on this project, however. Macaques teach us that the evolutionary pathways of primate societies are more complex than was previously thought. Their behavioral patterns cannot be reduced exclusively to the action of ecological and sexual selection pressures. We must introduce explanations for stability to the picture. Aware that primate societies are co-determined by internal and external factors, we have to investigate the strength of the linkages holding them up and the ability of adaptive processes to break them up.

ACKNOWLEDGMENTS

I thank S. Suomi and A. Engelhardt for valuable inputs, C. Abegg for drawing the maps, and M. Dindo for language advice. I am grateful to R. Seitre, C. Abegg, A. Engelhardt, M. J. Hsu, A. Sinha, N. Herrenschmidt, N. Priston, Operation Wallacea and N. Rowe (Pictorial guide to the living primates) for providing photographs.

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