PRIMATES, 40(1): 23–31, January 1999
Special Edition: Primate Socioecology

The Evolution of "Egalitarian" and "Despotic" Social Systems Among Macaques

SHUICHI MATSUMURA
Kyoto University

ABSTRACT. Recent studies of captive macaques have revealed considerable inter-species differences in dominance styles among females. In "egalitarian" species such as stumptail (*Macaca arctoides*) or tonkean macaques (*M. tonkeana*), social interactions are more symmetrical and less kin-biased than in "despotic" species such as Japanese (*M. fuscata*) or rhesus macaques (*M. mulatta*). Field observations of moor macaques (*M. maurus*), close relatives of tonkean macaques, suggest that tolerance during feeding characterizes their egalitarian dominance style in the natural habitat. Although it has been proposed that communal defense against other groups may be the main selective force in the evolution of egalitarian dominance style among females, few field data support this prediction. A game theory analysis showed that both an "egalitarian" strategy and a "despotic" strategy are possible evolutionarily stable strategies (ESS) under certain conditions. The difference in dominance styles might reflect the difference in ESS. This means that an egalitarian dominance style can emerge without strong between-group contest competition. A phylogenetic comparison among macaques suggests that despotic dominance styles very likely evolved from egalitarian dominance styles. In the future, primate socioecological studies should pay more attention to the evolutionary history of each species.

Key Words: Moor macaques; *Macaca maurus*; Macaques; Dominance styles; Game theory; Phylogeny.

INTRODUCTION

Since the pioneering studies on Japanese macaques (*Macaca fuscata*) in the 1950s (e.g. KAWAI, 1958; KAWAMURA, 1958), it has been believed that social interactions in macaque groups are strongly influenced by dominance and kinship. Recent studies of captive macaques have revealed considerable inter-species differences in the effects dominance and kinship have on social interactions. These differences are summarized as a contrast in dominance style (DE WAAL & LUTTRELL, 1989). "Egalitarian" species such as stumptail (*M. arctoides*) or tonkean macaques (*M. tonkeana*) exhibit (1) less severe (but sometimes more frequent) aggression, (2) greater symmetry in contests (more-counter attacks), (3) higher rate of affiliation such as grooming, (4) higher rate of peaceful post-conflict contacts or "reconciliation," and (5) less effect of kinship on social interactions than "despotic" species such as Japanese (*M. fuscata*) or rhesus macaques (*M. mulatta*) (DE WAAL & LUTTRELL, 1989; THIERRY et al., 1994). Barbary macaques (*M. sylvanus*), bonnet macaques (*M. radiata*), lion-tailed macaques (*M. silenus*), and macaques living in Sulawesi Island have been classified as egalitarian species (DE WAAL & LUTTRELL, 1989; MOORE, 1992; THIERRY et al., 1994; PREUSCHOFT, 1995).

In contrast to captive studies, few field studies have been conducted on the ecology and social behavior of egalitarian macaque species. Moor macaques in the Karaenta Nature Reserve, South Sulawesi, Indonesia, have been observed intermittently by Japanese researchers since 1981 (WATANABE & MATSUMURA, 1996). Intensive observation of their ecology and social behavior started in 1988 on the basis of individual identification. Results of these studies on wild moor macaques suggested that tolerance during feeding among non-related individuals characterizes their egalitarian dominance style in the natural habitat. Encounters within 1m among adult females during feeding were frequent and symmetrical (MATSUMURA, in press), and kinship had little effect on spatial proximity among group members during feeding (MATSUMURA & OKAMOTO, 1997).

Several authors have tried to explain the reason why dominance styles differ between macaque species. VAN SCHAIK (1989) argued that strong contest competition between groups would make female relationships more egalitarian, with special reference to macaques living in Sulawesi. In this paper, I examine whether strong between-group competition is found in egalitarian species before presenting an alternative explanation for the evolution for dominance styles by using two methods common in evolutionary ecology: game theory approaches (MAYNARD SMITH, 1982; DUGATKIN & REEVE, 1998) and the phylogenetic method for comparison (HARVEY & PAGEL, 1991). Recently, MATSUMURA and KOBAYASHI (1998) proposed a general model for dominance relations among group-living animals on the basis of an asymmetric Hawk-Dove model (MAYNARD SMITH, 1982). They examined how differences in fighting ability and relative resource value influence dominance relations. I apply their results to the evolution of macaque dominance style.

In the present paper, I use the term egalitarian as it is used by VAN SCHAIK (1989), that is, weakly linear or shallow dominance relations. In a recent review by STERCK et al. (1997), this type of dominance was called "tolerant," while "egalitarian" was fuzzy, non-linear, or lacked formalized dominance.

IS STRONG BETWEEN-GROUP CONTEST COMPETITION COMMON IN EGALITARIAN SPECIES?

VAN SCHAIK (1989) argued that Strong Between-Group Contest competition (BGC) would make female relationships more egalitarian. He assumed that communal defense against other groups may be the main selective force in the evolution of egalitarian dominance style among females. That is, subordinate females can force dominant females not to exert their full power to suppress the subordinates' food intake. The BGC hypothesis originated from a paper which mathematically examined a single dominant's behavior toward the other individuals in a social group (VEHRENCAMP, 1983). CALDECOTT (1986) proposed another ecological model for behavioral differences among macaque species. His argument, however, concentrated on the mating strategies of both sexes rather than dominance styles among females. Since the BGC hypothesis is the only one which tries to explain dominance styles from the viewpoint of adaptive significance, many authors have used this hypothesis in their papers (PREUSCHOFT, 1995; AURELI et al., 1997; STERCK et al., 1997).

The BGC hypothesis, however, does not appear to fit moor macaques. Although the population density at Karaenta is high (WATANABE & MATSUMURA, 1996; MATSUMURA, in press), no aggressive behavior of females during 16 intergroup encounters was observed during four months of observation in 1990—1991 (MATSUMURA, in press). Therefore, egalitarian relationships would not be expected to emerge. This conclusion was not altered by our successive observation. Few aggressive behaviors by females were seen during 30 months of observation between 1990 and 1997 (OKAMOTO & MATSUMURA, unpubl. data).

Moreover, from the available literature I can find no clear evidence to support that BGC in egalitarian macaques is stronger than that in despotic macaques. A study of Sulawesi crested macaques (KINNAIRD & O'BRIEN, 1994) suggested that the degree of BGC changed in relation to the abundance and distribution of fruiting trees. This was later referred to as the only evidence of strong BGC in egalitarian macaques (STERCK et al., 1997). Although intergroup encounters in wild Barbary macaques have been studied (DEAG, 1973; MEHLMAN & PARKHILL, 1988), the frequency appears to be "well within the range reported for other wild and free-ranging macaque species" (Mehlman & Parkhill, 1988). Barbary macaques were sometimes considered to have more peaceful intergroup relationships than most other species (Wrangham, 1980, p.287). For stumptail macaques, only anecdotal episodes of communal defense by *adult males* have been reported (Bertrand, 1969; de Waal, 1989). In contrast, many field studies of despotic species reported severe aggressive behavior of adult females during intergroup encounters (Lindburg, 1971; Maruhashi, 1982; Cheney, 1987).

DOMINANCE STYLES AND A GAME THEORY APPROACH

Dominance relations between two individuals in a social group are characterized by a consistent outcome of agonistic interactions (Drews, 1993). It has been pointed out that dominance relations within social groups are characterized by the subordinate's behavior rather than by the dominant's (Rowell, 1974; Bernstein, 1981). Contest over resources appears to be avoided by the subordinate's avoidance or retreat from resources occupied by more dominant individuals (Furuichi, 1983). Escalated fights are infrequently seen after the dominance relation between two individuals is settled. These characteristics are reminiscent of a conditional strategy in the Hawk-Dove game (Maynard Smith, 1982): they appeared to play 'Hawk, if dominant' and 'Dove, if subordinate.' Since the optimal strategy for a given individual to compete for resources depends on behavioral strategies of other group members, we should consider an evolutionarily stable strategy (ESS) (Maynard Smith & Price, 1973; Maynard Smith, 1982). Once all animals in a population adopt an ESS, an animal cannot achieve greater success by adopting any other strategy. If a behavioral strategy is not an ESS under the given condition, the strategy cannot evolve.

The players of a typical Hawk-Dove game have two choices at an encounter over a resource, i.e. Hawk or Dove (Table 1a). Hawks always fight over a resource in an escalated manner, while

Table 1. Payoff matrixes of Hawk-Dove games.

(a) Simple Hawk-Dove game

		Opponent's choice	
		Hawk	Dove
Own choice	Hawk	0.5V-0.5C	V
	Dove	0	0.5V

(b) Hawk-Dove-Bourgeois game

		Opponent's choice		
		Hawk	Dove	Bourgeois
Own choice	Hawk	0.5V-0.5C	V	0.75V-0.25C
	Dove	0	0.5V	0.25V
	Bourgeois	0.25V-0.25C	0.75V	0.5V

(c) Original Hawk-Dove-Retaliator game

		Opponent's choice		
		Hawk	Dove	Retaliator
Own choice	Hawk	0.5V-0.5C	V	0.5V-0.5C
	Dove	0	0.5V	0.5V
	Retaliator	0.5V-0.5C	0.5V	0.5V

For detailed assumptions, see Maynard Smith (1982). V: Resource value; C: cost of injury. Hawk: escalate and continue until injured or until opponent retreats. When Hawk meets another Hawk, it wins on half of the occasions. If it loses, it suffers injury. Dove: display; retreat at once if opponent escalates. When Dove encounters another Dove, it shares the resource with the opponent. Bourgeois: behave like Hawk if owner; behave like Dove if intruder. Retaliator: behave like Dove, but behave like Hawk if opponents escalate.

Doves retreat without an escalated fight if the opponent escalates. If the value of a resource (V) exceeds the cost of injury (C), mutant strategists cannot enter a population wherein all individuals adopt the Hawk strategy. Thus, the Hawk is an ESS if $V>C$. Hawk cannot, however, be an ESS if $V<C$. Under this condition, a mixed strategy which plays Hawk with a probability V/C and Dove with a probability of $1-V/C$ is an ESS. If an asymmetry in ownership of territories is introduced (MAYNARD SMITH, 1982), the Bourgeois strategy, with which the individual behaves like 'a Hawk, if it is owner' and 'a Dove, if it is intruder' can be an ESS (Table 1b).

MATSUMURA and KOBAYASHI (1998) showed that if an asymmetry between group members is considered instead of ownership asymmetry, a Bourgeois-like strategy based on the asymmetry can be an ESS. When all group members adopt a Bourgeois-like strategy, in a certain dyad one individual consistently acquires resources while the other retreats. The observer sees the Hawk as dominant and the Dove as subordinate. In this paper, I call this type of Bourgeois-like strategy the *Despotic strategy*, since it has been reported that subordinate adult female Japanese macaques tend to avoid unrelated dominants during feeding (FURUICHI, 1983; SAITO, 1996).

A high level of tolerance during feeding in egalitarian species (PETIT et al., 1992; MATSUMURA, in press) suggests that animals may not adopt the Despotic strategy. A high possibility of counter-attack during agonistic interactions (THIERRY, 1985; DE WAAL & LUTTRELL, 1989) is reminiscent of the 'Retaliator strategy' (MAYNARD SMITH, 1982). The Retaliator behaves like a Dove against a Dove or another Retaliator, but if its opponent escalates, the Retaliator also escalates and acts like a Hawk (Table 1c). MATSUMURA and KOBAYASHI (1998) also showed that the Retaliator strategy can be an ESS irrespective of the asymmetries between group members. When all group members adopt the Retaliator strategy, the observer sees it as if they usually play Dove and share resources. However, the Retaliator would respond with escalation against the opponents' accidental escalation. I call the Retaliator strategy here the *Egalitarian strategy*.

Once all animals in a population adopt either of the ESSs, an animal cannot achieve any more success by adopting any other strategy than the ESS. When the Despotic strategy is an ESS and all members adopt it, animals in the "subordinate role" should choose avoidance rather than escalation because the expected benefits of escalation are outweighed by the risk of injury. When the Egalitarian strategy is an ESS and all members adopt it, animals in the "dominant role" should share the resource with the opponents. If they escalate, the opponents also escalate. The risk of injury exceeds the expected benefits of winning.

Thus, the difference in dominance style may reflect the difference in strategy of contest over food. Namely, in despotic species all animals adopt the Despotic strategy, while in egalitarian species all animals adopt the Egalitarian strategy. Each dominance style can be observed in species under conditions where the respective strategy is an ESS. The important point is that under broad conditions both the Despotic strategy and the Egalitarian strategy can be ESSs simultaneously (MATSUMURA & KOBAYASHI, 1998). This implies that the characteristics of dominance relations in a population can not be determined simply by ecological conditions.

DOMINANCE STYLES AND PHYLOGENETIC RELATIONSHIPS

When comparing certain characteristics between species, their phylogenetic relationships should be taken into consideration (PAGEL & HARVEY, 1989; HARVEY & PAGEL, 1991). CHAN (1996) carried out a pioneer study on reproductive and social features in macaque species by using the phylogenetic method, although he did not consider the dominance styles among females. THIERRY et al. (1994) noted the importance of a phylogenetic perspective for discussion of dominance styles.

Macaque species were divided into four species groups by FOODEN (1976) on the basis of

Table 2. Female dominance styles of each macaque species.

Species	E or D	References
Silenus-sylvanus group		
M. sylvanus	E	Preuschoft, 1995; Aureli et al., 1997
M. silenus	E	Preuschoft, 1995; Abegg et al., 1996
M. nemestrina	D?	Thierry et al., 1994
M. nigra	E	Petit & Thierry, 1994; Petit et al., 1997
M. nigrescens		
M. hecki		
M. tonkeana	E	Thierry, 1985, 1994; Preuschoft, 1995
M. ochreata		
M. brunnescens		
M. maurus	E	Matsumura, 1996, in press
Sinica group		
M. sinica		
M. radiata	E?	Moore, 1992; Thierry et al., 1994
M. assamensis		
M. thibetana	E?	Ogawa, pers. comm.
Arctoides group		
M. arctoides	E	de Waal & Luttrell, 1989; Butovskaya, 1993
Fascicularis group		
M. fascicularis	D	Thierry, 1985; Butovskaya, 1993; Aureli et al., 1997
M. mulatta	D	Thierry, 1985; de Waal & Luttrell, 1989; Butovskaya, 1993
M. cyclopis		
M. fuscata	D	Chaffin et al., 1995; Petit et al., 1997; Aureli et al., 1997

E: Egalitarian; D: despotic.

morphology of the sexual organs. Fooden (1976) suggested that the widely disjointed pattern of distribution of the *silenus-sylvanus* group implies an early spread, followed later by the moderately disjointed *sinica* group, with the final dispersal of the contiguously ranging *fascicularis* group. These species groups are largely compatible with the phylogenetic tree obtained from morphological and molecular genetic studies, although many authors consider that the *arctoides* group is a sister group of the *sinica* group and that *M. sylvanus* separated from other species at a very early stage (Delson, 1980; Fooden & Lanyon, 1989; Fa, 1989).

Table 2 summarizes dominance styles exhibited by various macaques species. Although *M. radiata* has been treated as an egalitarian species (Moore, 1992; Thierry et al., 1994), systematic comparisons have not been carried out yet. Thierry et al. (1994) further suggested that *M. nemestrina* are despotic, but sufficient data are not available. Most species of the early spread *silenus-sylvanus* group exhibit an egalitarian dominance style, while species of the *fascicularis* group are despotic in dominance style (Table 2).

A phylogenetic analysis was carried out using *MacClade 3.0.5* (Maddison & Maddison, 1992). The phylogenetic tree in Chan (1996), which was based on Fooden (1980), Delson (1980), Melnick and Kidd (1985), and Fooden and Lanyon (1989), was used in the present analysis. The two values, Consistency Index (*CI*) and Retention Index (*RI*), were calculated by the program. In short, a high *CI* means a strong phylogenetic influence and the likelihood of similarities due to common descent, and a high *RI* means a strong likelihood that character state would be retained once it had evolved (Chan, 1996; Wimberger & Queiroz, 1996). Both indices range from zero to one. The present analysis suggested that dominance styles are influenced by phylogeny (CI=0.50; RI=0.67). We can postulate that ancient types of macaques might have exhibited an egalitarian dominance style, with a later shift to a despotic dominance style (Fig. 1). Moreover, despotic dominance styles may have evolved twice independently.

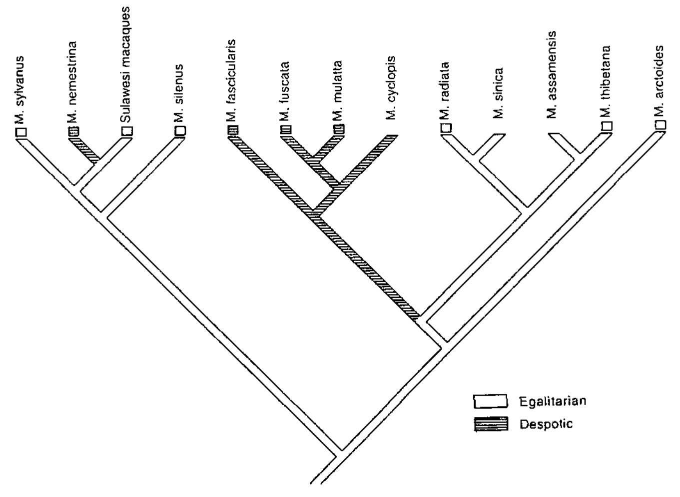

Fig. 1. Female dominance styles and the phylogenetic relationship among macaque species (CI=0.50; RI=0.67).

The possible shift from egalitarian to despotic agrees with results of the game theory approach. An accidental shift from the state wherein all individuals adopt the Egalitarian strategy to the state wherein all adopt the Despotic strategy should occur more easily than vice versa (Matsumura & Kobayashi, 1998).

DISCUSSION

The socioecological model of van Schaik (1989) has attained general success in explaining variations of female relationships in primates. The predictions of the model were generally supported by recent studies (e.g. Mitchell et al., 1991; Borries, 1993; Barton et al., 1996; Sterck & Steenbeek, 1997), and the model was extended by Sterck et al. (1997). However, the model does not explain the difference in dominance styles of female macaques. There is no clear evidence of strong BGC (between-group contest competition) in egalitarian macaque species as the model predicted. Since macaques have been studied intensively, behavioral variations in the genus are known in more detail than those in other genera. Similar unexplained differences may be found in other genera when more detailed studies are made.

The present paper suggests that the difference in dominance styles among macaque females might be explained without strong BGC if the results of the game theory analysis of dominance relations (Matsumura & Kobayashi, 1998) are considered. The different dominance styles may reflect different behavioral strategies of contest over food, i.e. the egalitarian strategy and the despotic strategy. Each strategy can be an ESS under certain conditions. Animals should change their behavior in response to social environments as well as natural environments. The "best" behavioral strategies for one animal would depend on the behavior of its other group members. The ESS approache is needed when we discuss social behavior or social systems.

Several factors could influence which strategies can be ESSs and how stable these ESSs are. Ecological factors such as the distribution and abundance of food are important because they affect the value of the resource under competition. Relatedness between group members also influences ESSs because the payoff in contests changes according to the relatedness between the two individuals. MOORE (1992) has already pointed out possible influences of relatedness on dominance styles.

It seems important that both the egalitarian strategy and the despotic strategy can be ESSs simultaneously under broad conditions (MATSUMURA & KOBAYASHI, 1998). Although STERCK et al. (1997, p.296) suggested that the shift from one type of female social relationship to another would be seen at the critical point of ecological conditions, ecological factors need not determine social systems linearly. Different types of social systems can be observed in the same environment. A macaque example would be helpful. This non-linear relationship makes it possible for epigenetic social processes to play a role in determining social systems (THIERRY, 1990). The present study, however, does not provide an ecologically neutral hypothesis, since ecological conditions influence which strategies can be ESSs and how stable the ESSs are.

As CHAN (1996) noted, the adaptive nature of socioecological features has been overemphasized in the primatological literature (WRANGHAM, 1980; DUNBAR, 1988; VAN SCHAIK, 1989). On the other hand, Japanese primatologists have traditionally emphasized phylogeny in the discussion of primate social structure (e.g. ITANI, 1977). Primatologists need to pay greater attention to the evolutionary history of the species being compared. Current evolutionary biologists now agree upon the use phylogenetic trees for comparative analysis (HARVEY & PAGEL, 1991). The phylogenetic method has been used implicitly in comparison of both behavior and vocalizations (e.g. WASER, 1980; MORI, 1983). If a social system is recognized as a product of the social behavior of individuals (HINDE, 1983), phylogenetic influences on social systems would be expected. The present study also suggests that the evolutionary equilibrium of social systems works as a kind of phylogenetic constraint.

The variations between populations or the differences between dyads should be examined, if we can obtain enough data to analyze. The present study considered female dominance styles as the general nature of each species. If some differences between populations within a species are found, similar phylogenetic analysis can be done within the species. The distribution of types of male-male relationships in the macaque phylogeny may differ from that of female-female relationships, because the behavioral strategies can differ between classes.

Acknowledgements. The author is very grateful to the organizing committee of the symposium "Recent Trends in Primate Socioecology," in particular, Dr. Y. SUGIYAMA, Dr. J. YAMAGIWA, and Dr. M. A. HUFFMAN. Sincere thanks to Dr. T. KANO, Dr. K. WATANABE, Mr. T. KOBAYASHI, Dr. K. OKAMOTO, Mr. T. MIYAMOTO of Primate Research Institute, Kyoto University, Dr. H. OGAWA of Chukyo University, and three anonymous referees for their helpful comments and useful information.

REFERENCES

ABEGG, C.; THIERRY, B.; KAUMANNS, W. 1996. Reconciliation in two groups of lion-tailed macaques (*Macaca silenus*). *Int. J. Primatol.*, 17: 803–816.

AURELI, F.; DAS, M.; VEENEMA, H. C. 1997. Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis, M. fuscata*, and *M. sylvanus*). *J. Comp. Psychol.*, 111: 91–99.

BARTON, R. A.; BYRNE, R. W.; WHITEN, A. 1996. Ecology, feeding competition and social structure in baboons. *Behav. Ecol. Sociobiol.*, 38: 321–329.

BERNSTEIN, I. S. 1981. Dominance: the baby and the bathwater. *Behav. Brain Sci.*, 4: 419–457.

BERTRAND, M. 1969. *The Behavioral Repertoire of the Stumptail Macaque*. S. Karger, Basel.

BORRIES, C. 1993. Ecology of female social relationships: hanuman langurs (*Presbytis entellus*) and the VAN SCHAIK model. *Folia Primatol.*, 61: 21–30.

BUTOVSKAYA, M. 1993. Kinship and different dominance styles in groups of three species of the genus *Macaca* (*M. arctoides, M. mulatta*, and *M. fascicularis*). *Folia Primatol.*, 60: 210–224.

CALDECOTT, J. O. 1986. Mating patterns, societies and the ecogeography of macaques. *Anim. Behav.*, 34: 208–220.

Chaffin, C. L.; Friedlen, K.; DE WAAL, F. B. M. 1995. Dominance style of Japanese macaques compared with rhesus and stumptail macaques. *Amer. J. Primatol.*, 35: 103–116.

CHAN, L. K. W. 1996. Phylogenetic interpretations of primate socioecology: with special reference to social and ecological diversity in *Macaca*. In: *Phylogenies and the Comparative Method in Animal Behavior*, MARTIN, E. (ed.), Oxford Univ. Press, New York, pp. 324–360.

CHENEY, D. L. 1987. Interactions and relationships between groups. In: *Primate Societies*, SMUTS, B. B.; CHENEY, D. L.; SEYFARTH, R. M.; WRANGHAM, R. W.; STRUHSAKER, T. T. (eds.), The Univ. of Chicago Press, Chicago, pp. 267–281.

DEAG, J. M. 1973. Intergroup encounters in the wild Barbary macaques *Macaca sylvanus* L. In: *Comparative Ecology and Behaviour of Primates*, MICHAEL, R. P.; CROOK, J. H. (eds.), Academic Press, New York, pp. 315–373.

DELSON, E. 1980. Fossil macaques, fhyletic relationships and a scenario of development. In: *The Macaques: Studies in Ecology, Behavior and Evolution*, LINDBURG, D. G. (ed.), Van Nostrand Reinhold, New York, pp. 10–30.

DREWS, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour*, 125: 283–313.

DUGATKIN, L. A.; REEVE, H. K. 1998. *Game Theory and Animal Behavior*, Oxford Univ. Press, Oxford.

DUNBAR, R. I. M. 1988. *Primate Social Systems*. Groom Helm, London.

FA, J. E. 1989. The genus *Macaca*: a review of taxonomy and evolution. *Mammal Rev.*, 19: 45–81.

FOODEN, J. 1976. Provisional classification and key to the living species of macaques (Primates: *Macaca*). *Folia Primatol.*, 25: 225–236.

FOODEN, J. 1980. Classification and distribution of living macaques (*Macaca Lacepede*, 1799). In: *The Macaques: Studies in Ecology, Behavior and Evolution*, LINDBURG, D. G. (ed.), Van Nostrand Reinhold, New York, pp. 1–9.

FOODEN, J.; LANYON, S. M. 1989. Blood-protein allele frequencies and phylogenetic relationships in *Macaca*: a review. *Amer. J. Primatol.*, 17: 209–241.

FURUICHI, T. 1983. Interindividual distance and influence of dominance on feeding in a natural Japanese macaque troop. *Primates*, 24: 445–455.

HARVEY, P. H.; PAGEL, M. D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford Univ. Press, Oxford.

HINDE, R. A. 1983. *Primate Social Relationships: An Integrated Approach*. Blackwell Scientific Publ., Oxford.

ITANI, J. 1977. Evolution of primate social structure. *J. Human Evol.*, 6: 235–243.

KAWAI, M. 1958. On the rank system in a natural group of Japanese monkey (I) (II). *Primates*, 1: 111–148. (in Japanese with English summary)

KAWAMURA, S. 1958. The matriarchal social order in the Minoo-B group: a study on the rank system of Japanese macaque. *Primates*, 1: 149–156. (in Japanese with English summary)

KINNAIRD, M. F.; O'BRIEN, T. G. 1994. Intergroup interactions in *Macaca nigra*: a random walk or resource defense? In: *Handbook and Abstracts of XVth IPS Congress*, p. 301.

LINDBURG, D. G. 1971. The rhesus monkey in North India: an ecological and behavioral study. In: *Primate Behavior: Developments in Field and Laboratory Research, Vol. 2*, ROSENBLUM, L. A. (ed.), Academic Press, New York, pp. 1–106.

MADDISON, W. P.; MADDISON, D. R. 1992. *MacClade: Analysis of Phylogeny and Character Evolution, Version 3*. Sinauer & Associates, Massachusetts.

MARUHASHI, T. 1982. An ecological study of troop fissions of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 23: 317–337.

MATSUMURA, S. 1996. Post-conflict affiliative contacts between former opponents among wild moor macaques (*Macaca maurus*). *Amer. J. Primatol.*, 38: 211–219.

MATSUMURA, S. in press. Relaxed dominance relations among female moor macaques (*Macaca maurus*) in their natural habitat, South Sulawesi, Indonesia. *Folia Primatologica.*

MATSUMURA, S.; KOBAYASHI, T. 1998. A game model for dominance relations among group-living animals. *Behav. Ecol. Sociobiol.*, 42: 77–84.

MATSUMURA, S.; OKAMOTO, K. 1997. Factors affecting proximity among members of a wild group of moor macaques during feeding, moving, and resting. *Int. J. Primatol.*, 18: 929–940.

MAYNARD SMITH, J. 1982. *Evolution and the Theory of Games*. Cambridge Univ. Press, Cambridge.

MAYNARD SMITH, J.; PRICE, G. R. 1973. The logic of animal conflict. *Nature*, 246: 15–18.

MEHLMAN, P. T.; PARKHILL, R. S. 1988. Intergroup interactions in wild Barbary macaques (*Macaca sylvanus*), Ghomaran Rif Mountains, Morocco. *Amer. J. Primatol.*, 15: 31–44.

MELNICK, D. J.; KIDD, K. K. 1985. Genetic and evolutionary relationships among Asian macaques. *Int. J. Primatol.*, 6: 123–160.

MITCHELL, C. L.; BOINSKI, S.; VAN SCHAIK, C. P. 1991. Competitive resimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). *Behav. Ecol. Sociobiol.*, 28: 55–60.

MOORE, J. 1992. Dispersal, nepotism, and primate social behavior. *Int. J. Primatol.*, 13: 361–378.

MORI, A. 1983. Comparison of the communicative vocalizations and behaviors of group ranging in eastern gorillas, chimpanzees and pygmy chimpanzees. *Primates*, 24: 486–500.

PAGEL, M. D.; HARVEY, P. H. 1989. Comparative methods for examining adaptation depend on evolutionary models. *Folia Primatol.*, 53: 203–330.

PETIT, O.; ABEGG, C.; THIERRY, B. 1997. A comparative study of aggression and conciliation in three Cercopithecine monkeys (*Macaca fuscata, Macaca nigra,* and *Papio papio*). *Behaviour*, 134: 415–432.

PETIT, O.; DESPORTES, C.; THIERRY, B. 1992. Differential probability of "coproduction" in two species of macaques (*Macaca tonkeana* and *M. mulatta*). *Ethology*, 90: 107–120.

PETIT, O.; THIERRY, B. 1994. Reconciliation in a group of black macaques (*Macaca nigra*). *Dodo J. Wildl. Pres. Trusts*, 30: 89–95.

PREUSCHOFT, S. 1995. *"Laughter" and "Smiling" in Macaques: An Evolutionary Perspective.* Faculteit Biologie, Univ. Utrecht, Utrecht.

ROWELL, T. E. 1974. The concept of social dominance. *Behav. Biol.*, 11: 131–154.

SAITO, C. 1996. Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. *Anim. Behav.*, 51: 967–980.

VAN SCHAIK, C. P. 1989. The ecology of social relationships amongst female primates. In: *Comparative Socioecology: the Behavioural Ecology of Humans and Other Mammals*, STANDEN, V.; FOLEY, R. (eds.), Blackwell Scientific Publ., Oxford, pp. 195–218.

STERCK, E. H. M.; STEENBEEK, R. 1997. Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour*, 134: 749–774.

STERCK, E. H. M.; WATTS, D. P.; VAN SCHAIK, C. P. 1997. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.*, 41: 291–309.

THIERRY, B. 1985. Patterns of agonistic interactions in three species of macaques (*Macaca mulatta, M. fascicularis,* and *M. tonkeana*). *Aggr. Behav.*, 11: 223–233.

THIERRY, B. 1990. Feedback loop between kinship and dominance: the macaque model. *J. Theor. Biol.*, 145: 511–521.

THIERRY, B.; ANDERSON, J. R.; DEMARIA, C.; DESPORTES, C.; PETIT, O. 1994. Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In: *Current Primatology, Vol. 2*, ROEDER, J. J.; THIERRY, B.; ANDERSON, J. R.; HERRENSCHMIDT, N. (eds.), Louis Pasteur Univ. Press, Strasbourg, pp. 103–117.

VEHRENCAMP, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.*, 31: 667–682.

DE WAAL, F. B. M. 1989. *Peacemaking Among Primates.* Harvard Univ. Press, Cambridge, Massachusetts.

DE WAAL, F. B. M.; LUTTRELL, L. M. 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stumptail monkeys. *Amer. J. Primatol.*, 19: 83–109.

WASER, P. M. 1982. The evolution of male loud calls among mangabeys and baboons. In: *Primate Communication*, SNOWDON, C. T.; BROWN, C. H.; PETERSEN, M. R. (eds.), Cambridge Univ. Press, Cambridge, pp. 117–143.

WATANABE, K.; MATSUMURA, S. 1996. Social organization of moor macaques, *Macaca maurus*, in the Karaenta Nature Reserve, South Sulawesi, Indonesia. In: *Variations in the Asian Macaques*, SHOTAKE, T.; WADA, K. (eds.), Tokai Univ. Press, Tokyo, pp. 147–162.

WIMBERGER, P. H.; DE QUEIROZ, A. 1996. Comparing behavioral and morphological characters as indicators of phylogeny. In: *Phylogenies and the Comparative Method in Animal Behavior*, MARTIN, E. (ed.), Oxford Univ. Press, New York, pp. 206–233.

WRANGHAM, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, 75: 262–300.

—— Received: *April 28, 1998*; Accepted: *August 31, 1998*

Author's Name and Address: SHUICHI MATSUMURA, *Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan.* e-mail: matsumur@smtp.pri.kyoto-u.ac.jp