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Emergence of Social Organizations  
in Non-Human Primates

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## EMERGENCE OF SOCIAL ORGANIZATIONS IN NON-HUMAN PRIMATES

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### Abstract

The paper describes how the iterative action of similarly built individuals may create morphogenetic effects into the social organization of non-human primates. The consequences of subjects' abilities to perceive and abstract any part of their own sociodemographic forms is emphasized. In particular, any knowledge about social relationships or networks is liable to induce feedback shaping effects on the social organization itself. Additionally, as the sociodemographic forms that are recognized depend on who is observing them, we cannot merely equate what human observers perceive from the social organization with essential patterns on which natural selection may act.

### Résumé

Dans cet article, on décrit comment l'action itérative d'individus de constitution semblable peut créer des effets morphogénétiques au niveau de l'organisation sociale des primates non humains. On souligne les conséquences de l'existence chez les individus de facultés permettant de percevoir ou d'abstraire tout ou partie de leurs propres formes sociodémographiques. Tout savoir concernant les relations sociales et les réseaux, en particulier, est susceptible de modeler en retour l'organisation sociale elle-même. En outre, comme les formes sociodémographiques qui sont reconnues dépendent de celui qui les observe, nous ne pouvons assimiler *ipso facto* ce que l'observateur humain perçoit de l'organisation sociale à des caractères essentiels sur lesquels s'exercerait la sélection naturelle.

In the field of distributed artificial intelligence, it is common to roughly distinguish between systems of "reactive" agents and those composed of "cognitive" agents (Bond and Gasser, 1988). Reactive agents have no mental state, they respond to stimuli from the environment following simple rules, but complex organizational

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patterns may be generated from the interactions of numerous such units. On the other hand, cognitive agents are often endowed with intentionality. The decision rules and communication of cognitive agents are complex by nature, modeling their organization is limited to a small number of interacting units; moreover, the number of assumptions required is so high that there is a risk of ending with unworkable systems. In this context, the social organizations of non-human primates offer the opportunity to contemplate sophisticated non-verbal social worlds, affording insight into possible realms. As observers of group living, sociodemographic forms are already present, we usually have to consider individuals as black boxes and social organizations as sets of black boxes in interaction. We have little information on the animal mind, we are just beginning to see how elaborated are the representations of primates about conspecifics. One of our main tasks is to understand how physical attributes, responsiveness to conspecifics and cognitive abilities operate in the emergence of social organizations.

## I. INDIVIDUAL ATTRIBUTES

"Social organizations are emergent phenomena resulting from interactions between individuals"; such a proposition implies that an individual's contribution to any social outcome cannot be fully described: as the outcome depends on a particular combination of individuals, its properties cannot be found in the attributes of either individual alone (Hinde, 1974; Mendoza and Mason, 1989). One main consequence is that an ontology of social organizations based exclusively upon knowledge of the individual is impossible; even a perfect acquaintance with the individual's moods, motives, cognitive abilities or life history traits would not allow us to predict the shape of the resulting social organization. However, this does not mean that no insight on how organizations are built can be gained by examining the attributes brought by the individual to the social situation.

In laboratory settings, it is possible to assess what Mason and collaborators have called the "profile of social dispositions" or "temperament", by studying individual patterns of behavioural and physiological responsiveness (Mason, 1978; Mendoza and Mason, 1989). A number of studies have shown that specific sociodemographic forms are related to specific individual propensities. The most thorough evidence comes from a series of comparative studies carried out in squirrel (*Saimiri sciureus*) and titi monkeys (*Callicebus moloch*) (Mason, 1971; Visalberghi and Mason, 1983; Anzenberger *et al.*, 1986; Mendoza and Mason, 1989). These two New World primates belong to the same taxonomic family, they are of similar body size, often inhabit the same forests and possess comparable

cognitive capacities. Squirrel monkeys form large mixed parties of some tens of individuals ranging over broad undefended areas: they are organized around subgroups of adult females followed by offspring; males have a peripheral position and interact infrequently with females outside the mating season. In contrast, titi monkeys live in monogamous family units typically composed of a mated pair and one or two offspring; they occupy a territory of several hectares, the borders of which are vocally advertized and defended against neighbours. When separated from their pairmate in laboratory experiments, titi monkeys display intense emotional arousal as measured by locomotor activity, emission of high-pitched vocalizations, heart rate and levels of plasma cortisol; in the same circumstances, squirrel monkeys do not exhibit marked physiological and behavioural manifestations. In experimental confrontations using various combinations of conspecifics, titi monkeys are strongly and specifically attracted to the pairmate, they behave in a coordinated manner and are aggressive toward strangers. This is in contrast to the squirrel monkeys, in which there is no mutual attraction between male and female cage-mates, but a conspicuous behavioural sexual divergence in response to strangers: while females are attracted by other females, males do not show reliable preferences for familiar or unfamiliar individuals of either sex and readily display agonistically toward males. The ability to cope with environmental change differs among species; squirrel monkeys are more adaptable than titi monkeys, which is associated with consistent interspecific variations in baseline activity and responsiveness of pituitary-adrenal and autonomic nervous systems (Mendoza, 1991). Differences in individual responsiveness and bonding thus appear responsible for the generation of the contrasting social organizations of these two species in the wild.

Life history traits also impose limits on the range of interactions open to individuals. Variables such as life span, age at first birth, and interbirth interval influence the size of families and the age-sex distribution of populations: by channelling demographic processes, they determine the number, age, sex and relatedness of partners with whom an individual can interact (Altmann and Altmann, 1979; Dunbar, 1988). For instance, when reproductive rate is low relative to life span, there is little overlap between generations and no room for many extant close relatives; when it is high, females may possess adult offspring: the individual grows up among kin, this makes possible the occurrence of such interactions as play among siblings, mating with a son, or helping by a grandmother. When pairs of female hamadryas baboons (*Papio hamadryas*) are separated from their group, subjects do not show the same partner preferences as when they are in the group (Stammbach and Kummer, 1982). When adult females are removed from a group of squirrel

monkeys, the rates of affiliative interactions between males and infants increase dramatically, demonstrating that the usual lack of infant-male interactions is mainly due to females' presence preventing males' access to infants (Vaitl, 1978). This raises the question of the levels of organization whereby influences are mediated.

## II. LEVELS OF ORGANIZATION

Three levels have been delineated by Hinde (1976) in the social organizations of non-human primates: interactions, defined by current behaviour of participants, relationships, which involve a succession of social interactions between participants known to each other, and structures, which result from the patterning of relationships. While "surface structure" is used to describe social networks, the term "deep structure" refers to models which abstract the form and functioning of social organizations through the operation of principles of organization (Lévi-Strauss, 1958; Hinde, 1976). Here, surface and deep structures will be referred to respectively as networks and structures.

While social interactions consist of events describable in physical terms, other levels of organization are inferred rather than observed (Altmann, 1981). When two individuals, for instance, display some degree of consistency and predictability in the outcomes of their competitive encounters across contexts, we may postulate the existence of an intervening variable that we call a dominance relationship – or, strictly speaking, a relationship involving an asymmetry in power, labelled dominance; this makes sense for us and we may then look for determinants of dominance such as size, experience or presence of allies (Hinde, 1974; Hinde and Datta, 1981). There is no need to assume that partners are aware of their relationship or abstract properties such as intensity, reciprocity or dominance. By using dominance as an explanatory concept, we consider relationships exclusively in terms of human representation, *i.e.* meaningless for animals and with no influence on behaviour in most species (Altmann, 1981). However, individuals learn and remember. Each interaction is influenced by the history of past interactions between the individuals concerned (Hinde, 1976). Whatever the affective or cognitive supports underlying their knowledge, and even if there is no effect of the relationship *per se*, knowledge held by the subjects creates emergent properties influencing their behaviour and that of others. Both participants are liable to act and react in relation to each other, even in response to the external world. As an example, if an individual has learnt to avoid a stronger partner to avoid conflicts, it may respond to the presence of an incentive by moving off and leave access to the other. According to past interactions, individuals react differently to partners,

associate according to affinities, hostilities and so on. This shapes the spatiotemporal distribution of individuals within populations, and influences the composition and cohesiveness of social groups, giving rise to sociodemographic forms. As a consequence, social groups may have boundaries, take collective decisions and behave as ecological units that transcend lower organizational levels (*e.g.*, Sigg and Stolba, 1981; Abegglen, 1984).

In so far as relationships are considered in terms of human representation, they cannot represent causal agents. As remarked by Hinde (1974), they arise from behavioural interactions, they are not entities superimposed on individuals. However, we may ask to what extent relationships belong to the animal world and are not just concepts abstracted by the observer's mind. A number of facts support the belief that monkeys and apes possess sophisticated knowledge about their social environment and make inferences about it (Cheney and Seyfarth, 1990). If we accept that they behave in compliance with representations built from series of interactions involving particular conspecifics, we are compelled to accept the existence of an entity that we humans call a social relationship and consider as such. Such a view may account, for instance, for the discrepancy found between results of conflicts and direction of submission. Whereas the social context and motivational states of opponents usually produce inconsistencies in the outcomes of contests (Bernstein, 1981), the ritualized signals addressed by subordinates toward dominants are characterized by reliable directionality, both inside and outside the context of aggression; this is true in particular for chimpanzees (*Pan troglodytes*) and many macaques (*Macaca* sp.) (de Waal, 1982; de Waal and Luttrell, 1985; Demaria and Thierry, 1990). Hypothesizing that individuals are aware of their relative status appears the best way to explain such unidirectionality: in displaying submissively, the subordinate communicates its perception of the relationship to the other, which formalizes their relation for a time and buffer against transient fluctuations (de Waal, 1982). However, if individuals come to differ about their respective status, overt conflicts arise and submissive signals no longer occur. It is only when the question is settled that formal acknowledgment of dominance reappears, in one or the other direction. A reasonable interpretation is that the participants have reached agreement about their respective status and that both then form consistent representations about the state of their relationship.

Abstract representation may not be limited to awareness about one's own social relationships. In some monkeys and apes, there is growing evidence that an individual can recognize the kind of relationships that exist among other group members (Bachmann and Kummer, 1980; Cheney and Seyfarth, 1990). An experimental study carried out in longtailed macaques (*Macaca fascicularis*) has shown

that a subject discriminates between slides featuring different pairs of group members: it distinguishes mother-offspring or siblings from pairs of unrelated or less closely related individuals (Dasser, 1988a, b). This suggests that monkeys can classify others' relations according to some unknown abstract properties—*e.g.*, closeness of bond, alliance, affiliation, hostility, difference in assertiveness. The recognition of relational properties and use of such knowledge by individuals introduce a further degree of complexity into social organization. This awareness may influence behaviour: individuals may compete for access to the highest-ranking individuals (Seyfarth, 1977), and threaten or appease the relatives of an opponent (Cheney and Seyfarth, 1989; Judge, 1991); bonds and alliances existing between group members may make it difficult for newcomers, immigrants having first to establish relationships before being accepted (Smuts, 1985).

Like relationships, networks can be used as intervening variables accounting for patterns of social grouping. We can recognize hierarchies, clans, matriline and even social classes (de Waal, 1986). However, the reality of networks as a level of organization has been questioned (Strum and Latour, 1987; Rowell, 1991). Do they coincide with emergent properties and have consequences, or are they merely shorthand terms for certain aspects of sociodemographic forms? The point is that networks exist only if relationships can interact to produce them. Relationships do not interact in the physical world, it is the individuals who interact, according to their knowledge about partners. As a consequence, the emergent properties of subgroups and groups may be analyzed exclusively in terms of interactions and relationships. In most animal species, we must consider network as a description of social organizations, *i.e.* a creation of human observers.

On the other hand, social networks may become a reality providing that social relationships can interact: if such an interaction occurs, it will take place in the animal's mind. For such an outcome, a first requirement is that individuals be aware of relationships between others and able to compare them; a second one is the ability to conceive relations between relationships and have an overview of sets of relationships. Individuals could then recognize classes of conspecifics tied by some type of relationship or construct a rank order of the members of their group. There is no proof that monkeys identify families or dominance hierarchies but some authors have advocated this (Walters, 1980; Seyfarth, 1981; de Waal, 1986). There is no firmer evidence for group or subgroup awareness in apes. However, we know that parties of male chimpanzees may perform aggressive raids in the core area of neighbouring communities, they also make regular visits to peripheral parts of their range: when engaged in "boundary patrols", chimpanzees tend to travel in compact groups, moving silently and stealthily, stopping frequently

to gaze around and listen, while any sudden sound induces mutual reassurance contacts (Nishida, 1979; Goodall, 1986). Ascribing to chimpanzees an overview of their community membership and discrimination of neighbouring groups parsimoniously accounts for this set of behaviours. The representation of social networks in the chimpanzee mind would then play the role of a causal agent, a view consistent with the assumption that male chimpanzees intentionally strive for the top of the dominance hierarchy (de Waal, 1982; Nishida, 1983; Goodall, 1986).

### III. MORPHOGENETIC MECHANISMS

As soon as individuals are together in a group, structural patterns appear in their spatial distribution, and their interaction sequences already obey recognizable rules (Kummer, 1975). A main approach to uncovering the *principia* that govern the emergence of social organizations is to build models (see Lévi-Strauss, 1958; Hinde, 1976) that start from basic patterns, then deduce the self-structuring consequences of their combinations. In this respect, the model of grooming distribution proposed by Seyfarth (1977) represents a cornerstone. The task was to explain why, in female macaques and baboons, the amount of grooming received is correlated with individual social rank, and why the majority of grooming interactions occurs between females occupying adjacent positions in the hierarchy. It was hypothesized that the main function of social grooming is to establish and maintain alliances with valuable partners; the model assumes that individuals compete for access to the highest-ranking individuals. As there is limit to the availability of highest-ranking partners, the most successful individuals are those ranking next to the object of competition. This results in most grooming occurring between individuals close in rank, from the subordinate toward the dominant. The model was originally proposed to account for dominance effects on grooming distribution and, in spite of criticisms (*e.g.*, de Waal and Luttrell, 1986), it has proved to be robust providing that preferences for related partners are incorporated into the assumptions (Seyfarth, 1983), and that dominance asymmetry is marked in the species considered (Thierry *et al.*, 1990).

The occurrence of interactions connecting individuals above the dyadic level is particularly liable to shape social organization. According to Thierry (1990), the existence of coalitions may create a link between degree of nepotism and dominance asymmetry in macaque societies. When most coalitions involve relatives, individual dominance depends primarily on the power of the kin subgroup; this increases rank differences between non-relatives and further develops kin-alliances. This positive feedback loop generates a highly structured organization with strict



rules of rank inheritance (see below). Conversely, when help to non-relatives is frequent, dominance appears more dependent on fighting ability and the individual retains a certain degree of freedom with regard to power networks; as an output, dominance relationships remain balanced among group members, close ties exist even between non-relatives, and no strong morphogenetic effect develops (see also Das and van Hooff, 1993; Thierry, 1993).

Other models have assessed the effect of demographic constraints upon the structures generated by the existence of coalitions. In rhesus and Japanese macaques (*Macaca mulatta*, *M. fuscata*, species governed by high dominance asymmetries), rank acquisition among females follows three empirical rules:

1) females inherit their mother's rank, 2) mothers dominate daughters, 3) younger sisters dominate older ones (*e.g.*, Datta, 1989). These rules stem from alliances among relatives, in particular from the help given by mothers to daughters, the youngest being supported against the oldest. From these rules, Hausfater *et al.* (1987) produced a computerized simulation showing that the degree of nepotism varies as a function of group composition. Datta (1989) went further in examining how the availability of partners determines the ranks of females by acting on the formation of alliances. Such life history traits as life span, age at sexual maturity, interbirth interval and mortality rates affect the number of suitable allies together with the fighting abilities of competitors. By simulation analyses, she demonstrated that the demography produced by an environment enhancing reproduction and survival may favour the dominance of mother over daughters and the outrank of older sisters by younger ones; in a harsher environment, the lack of allies shifts the balance in favour of older sisters, and daughters may outrank mothers more often. It may be noted that in species where coalitions do not occur frequently, or when daughters and sisters may call for the help of non-relatives against their family members, kin-alliances are not very powerful, and behavioural effects similar to those produced by a harsh environment are expected (Thierry, 1990, 1993). The structures of rank acquisition observed in female rhesus and Japanese macaques might be regarded as morphogenetic consequences of species-specific dispositions expressed in a given demographic context.

A recent model has used a computer methodology similar to those developed in distributed artificial intelligence. The goal was to account for the patterns of social grouping in chimpanzees by exclusively resorting to maintenance rules (te Boekhorst and Hogeweg, 1991). An artificial world inhabited by male and female entities, and paralleling the real habitat of chimpanzees, was created. The authors assumed that the entities' behaviour is triggered by nothing more than local information about the environment: females forage for fruits and protein sources; males

seek fruits and females: in precedence to foraging, they move towards visible conspecifics to inspect them, ready to follow if this a female in oestrus. From these simple rules, the authors were able to generate patterns of traveling and grouping similar to those of chimpanzees, including in particular the formation of the all-male parties typical of the species. They concluded that these sociodemographic patterns might represent mere side-effects of responses to the availability of food and potential mates; consequently, there would be no need to search for evolutionary reasons for their existence (te Boekhorst and Hogeweg, 1991).

Morphogenetic models allow to reproduce part of the sociodemographic forms that we observe. In doing so, they question common functional explanations that try to account for every recognized pattern by *ad hoc* adaptive hypotheses (see Gould and Lewontin, 1979). However, as stressed by their authors, it would be an oversimplification to reduce primate social organizations to the development of algorithms. The structuring consequences of lower levels generate higher levels but, as a feedback, emergent properties springing at higher levels act upon lower ones (Feibleman, 1954; Hinde, 1976). A correlate is that social influence may be mediated from any level to any other. For example, individuals may react not only in terms of social relationships but also directly to attributes like sex and reproductive status (Mendoza and Mason, 1989). In fact, in many animal species, social organizations are shaped exclusively at the interaction level. Moreover, the number of sociodemographic patterns that animals recognize is probably underestimated. The possibility of awareness of relationships or networks has been previously discussed. However, primates may perceive forms without resorting to such awareness. For instance, they could abstract units from the spatiotemporal distribution and movements of individuals – either including or omitting awareness about relationships. Groups would be then conceived of as global units, *e.g.* strange vs. familiar groups, or say, "the brown troop" or "the troop from the cliffs". There are many reports of interactions between groups and subgroups in the wild, but we have no information as to whether the animals react to sets of individuals or exclusively to individual members (see *e.g.*, Kummer, 1968; Abegglen, 1984).

#### IV. CONCLUSION

Throughout the paper, the expression "sociodemographic forms" was used to mean sets of individuals that are distributed and behave in a structured manner. Sociodemographic forms represent the visible aspect of social organizations. Of

course, what is seen depends on who is watching. Nothing indicates which forms are relevant with respect to individuals' adaptation to the environment. A widespread belief in sociobiology is that sociodemographic forms have evolved to maximise fitness, and that social interactions and relationships represent the proximate means by which ultimate sociodemographic forms are achieved (see van Schaik and van Hooff, 1983; Wrangham, 1987; Dunbar, 1988). This is an essentialist perspective in which forms are considered as types retained by natural selection. But nowhere are social organizations "programmed" (see Oyama, 1985), they are "performed" by individuals (Strum and Latour, 1987). No organization level can be considered as more significant than another *a priori*. Sociodemographic units, for example, may not reflect mating systems: in many species, being resident or the highest-ranking male does not ensure being the main progenitor of the social unit (Rowell, 1988). The influence of ecological factors such as food availability, climatic conditions, pathological agents or predation may be channelled through any level of organization. Neither does the genotype operate exclusively at the individual level; as life-history traits and social dispositions are in part determined genetically, the variance in the resulting social environment is partly heritable (Altmann and Altmann, 1979). The iterative action of similarly built individuals has structuring power, and modest changes in individual attributes may have far-reaching consequences at upper organization levels. Closedness of groups towards strangers might be an output of the existence of intragroup coalitions. The extermination of one chimpanzee community by another (Nishida, 1979; Goodall, 1986) might represent a by-product of awareness about group membership. The relatively loose organization of lemur groups, together with the observed attacks and eventual eviction of group members (Vick and Pereira, 1992), might result from limited abilities to communicate about social relationships. That a feature entails consequences with regard to individuals' life and reproductive output does not mean that it is a direct expression of evolutionary pressures (Gould and Lewontin, 1979).

Integrating realistic rules about how social influences are mediated should improve models elaborated in distributed artificial intelligence, and lead to advances in the design of transformable systems. In return, these models may become valuable tools in the task of simulating the morphogenesis of social organizations. They have the potential to show how structurally complex social patterns may emerge from the interaction of individuals pursuing their own goals: this points out the non-adaptiveness of certain features, a null hypothesis difficult to demonstrate in the real world.

## References

- J. J. ABEGGLEN, *On socialization in hamadryas baboons*, Bucknell University Press, Lewisburg, 1984.
- S. A. ALTMANN, Dominance relationships: the Cheshire cat's grin? *Behav. Brain Sci.*, 4, 1981, p. 430-431.
- S. A. ALTMANN, J. ALTMANN, Demographic constraints on behavior and social organization. In I. S. BERNSTEIN and E. O. SMITH (Eds.): *Primate ecology and human origins*, Garland STPM Press, New York, 1979, p. 47-63.
- G. ANZENBERGER, S. P. MENDOZA, W. A. MASON, Comparative studies of social behavior in *Callicebus* and *Saimiri*: behavioral and physiological responses of established pairs to unfamiliar pairs, *Am. J. Primatol.*, 11, 1986, p. 37-51.
- C. BACHMANN, H. KUMMER, Male assessment of female choice in hamadryas baboons, *Behav. Ecol. Sociobiol.*, 6, 1980, p. 315-321.
- I. S. BERNSTEIN, Dominance: the baby and the bathwater, *Behav. Brain Sci.*, 4, 1981, p. 419-457.
- A. H. BOND, L. GASSER (Eds.), *Readings in distributed artificial intelligence*, Morgan Kaufman, San Mateo, 1988.
- D. L. CHENEY, R. M. SEYFARTH, Redirected aggression and reconciliation among vervet monkeys, *Cercopithecus aethiops*, *Behaviour*, 110, 1989, p. 258-275.
- D. L. CHENEY, R. M. SEYFARTH, *How monkeys see the world*, University of Chicago Press, Chicago, 1990.
- M. DAS, J. A. R. A. M. VAN HOOFF, A non-adaptive feedback loop to account for the differences between the macaques' social systems – is it convincing? *J. Theor. Biol.*, 160, 1993, p. 399-402.
- V. DASSER, A social concept in Java monkeys, *Anim. Behav.*, 36, 1988a, p. 225-230.
- V. DASSER, Mapping social concepts in monkeys, In R. W. BYRNE and A. WHITEN (Eds.): *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*, Oxford University Press, Oxford, 1988b, p. 85-93.
- S. B. DATTA, Demographic influences on dominance structure among female primates, In V. STANDEN and R. A. FOLEY (Eds.): *Comparative socioecology*, Blackwell, Oxford, 1989, p. 265-284.
- C. DEMARIA, B. THIERRY, Formal biting in stump-tailed macaques (*Macaca arctoides*), *Am. J. Primatol.*, 20, 1990, p. 133-140.
- F. B. M. DE WAAL, *Chimpanzee politics*, Jonathan Cape, London, 1982.
- F. B. M. DE WAAL, Class structure in a rhesus monkey group: the interplay between dominance and tolerance, *Anim. Behav.*, 34, 1986, p. 1033-1040.
- F. B. M. DE WAAL, L. M. LUTTRELL, The formal hierarchy of rhesus monkeys: an investigation of the bared-teeth display, *Am. J. Primatol.*, 9, 1985, p. 73-85.
- F. B. M. DE WAAL, L. M. LUTTRELL, The similarity principle underlying social bonding among female rhesus monkeys, *Folia Primatol.*, 46, 1986, p. 215-234.
- R. I. M. DUNBAR, *Primate social systems*, Croom Helm, London, 1988.
- J. K. FEIBLEMAN, Theory of integrative levels, *Br. J. Phil. Sci.*, 1954, p. 59-66.
- J. GOODALL, *The chimpanzees of Gombe*, Belknap Press, Cambridge, Mass., 1986.
- S. J. GOULD, R. LEWONTIN, The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme, *Proc. R. Soc. Lond. B Biol. Sci.*, 205, 1979, p. 581-598.

- G. HAUSFATER, S. J. CAIRNS, R. N. LEVIN, Variability and stability in the rank relations of nonhuman primate females: analysis by computer simulation, *Am. J. Primatol.*, 12, 1987, p. 55-70.
- R. A. HINDE, *Biological bases of human social behaviour*, McGraw-Hill, New York, 1974.
- R. A. HINDE, Interactions, relationships and social structure, *Man*, 11, 1976, p. 1-17.
- R. A. HINDE, S. DATTA, Dominance: an intervening variable, *Behav. Brain Sci.*, 4, 1981, p. 442-433.
- P. C. JUDGE, Dyadic and triadic reconciliation in pigtail macaques (*Macaca nemestrina*), *Am. J. Primatol.*, 23, 1991, p. 225-237.
- H. KUMMER, *Social organization of hamadryas baboons*, University of Chicago Press, Chicago, 1968.
- H. KUMMER, Rules of dyad and group formation among captive gelada baboons (*Theropithecus gelada*), In S. KONDO, M. KAWAI, A. EHARA and S. KAWAMURA (Eds.): *Proceedings of the Fifth Congress of the International Primatological Congress*, Japan Science Press, Tokyo, 1975, p. 129-159.
- C. LÉVI-STRAUSS, *Anthropologie structurale*, Plon, Paris, 1958.
- W. A. MASON, Field and laboratory studies of social organization in *Saimiri* and *Callicebus*, In L. A. ROSENBLUM (Ed.): *Primate behaviour*, vol. 2, Academic Press, New York, 1971, p. 107-137.
- W. A. MASON, Ontogeny of social systems, In D. J. CHIVERS and J. HERBERT (Eds.): *Recent advances in primatology*, vol. 1, Academic Press, London, 1978, p. 5-14.
- S. P. MENDOZA, Behavioural and physiological indices of social relationships: comparative studies of New World monkeys, In H. O. BOX (Ed.): *Primates responses to environmental change*, Chapman and Hall, London, 1991, p. 311-335.
- S. P. MENDOZA, W. A. MASON, Primate relationships: social dispositions and physiological responses. In P. K. SETH and S. SETH (Eds.): *Perspectives in primate biology*, vol. 2, Today and Tomorrow, New Delhi, 1989, p. 129-143.
- T. NISHIDA, The social structure of chimpanzees of the Mahale Mountains. In D. A. HAMBURG and E. R. McCOWN (Eds.): *The great apes*, Benjamin/Cummings, Menlo Park, 1979, p. 73-121.
- T. NISHIDA, Alpha status and agonistic alliances in wild chimpanzees (*Pan troglodytes schweinfurthii*), *Primates*, 24, 1983, p. 318-336.
- S. OYAMA, *The ontogeny of information*, Cambridge University Press, Cambridge, 1985.
- T. E. ROWELL, Beyond the one-male group, *Behaviour*, 104, 1988, p. 189-201.
- T. E. ROWELL, What can we say about social structure? In P. BATESON (Ed.): *The development and integration of behaviour? Essays in honour of Robert Hinde*, Cambridge Univ. Press, Cambridge, 1991, p. 255-270.
- R. M. SEYFARTH, A model of social grooming among adult female monkeys, *J. Theor. Biol.*, 65, 1977, p. 671-692.
- R. M. SEYFARTH, Do monkeys rank each other? *Behav. Brain Sci.*, 4, 1981, p. 447-448.
- R. M. SEYFARTH, Grooming and social competition in primates, In R. A. HINDE (Ed.): *Primate social relationships*, Blackwell, Oxford, p. 182-190.
- H. SIGG, A. STOLBA, Home range and daily march in a hamadryas baboon troop, *Folia Primatol.*, 36, 1981, p. 40-75.
- B. B. SMUTS, *Sex and friendship in baboons*, Aldine, New York, 1985.
- E. STAMMBACH, H. KUMMER, Individual contributions to a dyadic interaction: an analysis of baboon grooming, *Anim. Behav.*, 30, 1982, p. 964-971.

- S. B. STRUM, B. LATOUR, Redefining the social link: from baboons to humans, *Soc. Sci. Inform.*, 26, 1987, p. 783-802.
- I. J. A. TE BOEKORST, P. HOGEWEG, The natural history of an artificial CHIMP world: group structure as a side effect, In I. J. A. TE BOEKORST: *Social structure of three great ape species*, Ph. D. Diss., Rijksuniversiteit Utrecht, 1991, p. 135-157.
- B. THIERRY, C. GAUTHIER, P. PEIGNOT, Social grooming in Tonkean macaques (*Macaca tonkeana*), *Int. J. Primatol.*, 11, 1990, p. 357-375.
- B. THIERRY, Feedback loop between kinship and dominance: the macaque model, *J. Theor. Biol.*, 145, 1990, p. 511-521.
- B. THIERRY, Emergent constraints condition the action of ultimate causes, *J. Theor. Biol.*, 160, 1993, p. 403-405.
- E. A. VAITL, Nature and implications of the complexly organized social system in nonhuman primates. In D. J. CHIVERS and J. HERBERT (Eds.): *Recent advances in primatology*, vol. 1, Academic Press, London, 1978, p. 17-30.
- C. P. VAN SCHAIK, J. A. R. A. M. VAN HOOFF, On the ultimate causes of primate social system, *Behaviour*, 85, 1983, p. 91-117.
- L. G. VICK, M. E. PEREIRA, Episodic targeting aggression and the histories of *Lemur* social groups, *Behav. Ecol. Sociobiol.*, 25, 1992, p. 3-12.
- E. VISALBERGHI, W. A. MASON, Determinants of problem-solving success in *Saimiri* and *Callicebus*, *Primates*, 24, 1983, p. 385-396.
- J. WALTERS, Interventions and the development of dominance relationships in female baboons, *Folia Primatol.*, 34, 1980, p. 61-89.
- R. W. WRANGHAM, Evolution of social structure. In B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM and T. T. STRUHSAKER (Eds.): *Primate societies*, University of Chicago Press, Chicago, 1987, p. 282-296.