Introduction

1 Why macaque societies?

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Societies are built through the interactions of the individuals who compose them. In a sense, they look like transparent organisms, which allow us to observe their mechanisms (Kummer, 1984). Significant parts of them, however, remain hidden. We have only indirect access to the motives and strategies pursued by individuals, and the structures and functions produced by the social dynamics go far beyond the behaviors of individuals.

To analyze societies, we commonly distinguish between social networks and demographic structures. Social networks represent the sets of interactions and relationships that link individuals. Demographic structures refer to the size and age-sex composition of social units. Attempts to find out which come first – the social networks or the demographic structures – have given headaches to numerous students. We end up with the same chicken-or-egg problem when we attempt to uncover causal relationships between these structures and other entities like mating and rearing systems.

The main issue is, what is a social organization? In this book we will use the terms social organization and society as synonymous. We define them as sets of conspecifics that are distributed and behave in a structured manner. This is admittedly a minimal definition, but societies are the very object of our studies and we are still learning about their nature. Some go as far as to ask whether societies exist at all (Rowell, 1993). The reason for such a question is that the organization is partly in the eye of the observer (Ashby, 1962; Strum & Latour, 1987). It is the observer who recognizes structures. We do not perceive the social organization per se, we only see what may be called *sociodemographic forms* (Thierry, 1994a). Human observers may disagree with each other about the forms they identify according to their theoretical assumptions and the analytic tools they use. But there is more to it than that. The actors in a society may themselves differ in their views on social organization. What is significant in the physical world of animals depends on their perceptual and cognitive abilities,

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and the same holds true for their social world (von Uexkühl, 1956; Gibson, 1979; Cheney & Seyfarth, 1989). For instance, whether or not a monkey can read the social relationships that link its group-mates will affect the number of dimensions of the society in which it lives (see Dasser, 1988a). There is still more than the observers' and actors' perspectives. By investigating how societies are built, we aim to gain knowledge of how they arise, how they work and how they change through the course of evolution. Evolution primarily shapes societies by acting upon individuals. But how do selective processes see a social organization? We cannot just presume that any sociodemographic forms we perceive are direct targets of selective processes.

The biological study of behavior is usually approached from the four questions envisioned by Tinbergen (1963): immediate factors, ontogenetic development, adaptive function and evolutionary history. Any behavior should be explained in terms of the above questions. These questions are often grouped following the classical distinction between proximate and ultimate causes (Mayr, 1961). Proximate causation includes immediate and developmental causes that take place once the program encoded in DNA is actualized in the individual. In ultimate causation, evolutionary processes determine the genesis of the program itself. Heuristic though this dichotomous scheme may be, it nevertheless has its limits (Dewsbury, 1992). Even leaving aside the difficulties inherent in the concept of genetic program (Oyama, 1985), a considerable problem remains, which is to discern causes and consequences. This is especially true for complex systems like social organizations, which are made up of individuals linked by information flow. Numerous feedback loops make it difficult to distinguish between features relevant to selection and those which are merely their side effects, and between the direct and indirect advantages or disadvantages they may entail. We need thorough knowledge concerning the proximate mechanisms of societies in order to get back to their ultimate causes (Lott, 1991).

To understand the determinism of multifaceted organizations, we have to consider in turn how every facet relates to the core of societies: individual abilities and personalities, life-history traits, mating systems, demographic dynamics, gene flow, social relationships, intergenerational transmission of behaviors, self-organization processes, ecological factors and phylogenetic correlates. A huge amount of knowledge has accumulated on many of these issues in humans and their societies, but *Homo sapiens* is the only extant representative of its genus, and it is further characterized by wide intercultural variations. This precludes any comparative enterprise that would aim to trace social diversity back to its evolutionary foundations. Among animals, knowledge is basically represented by fragmented information, some facets of social organizations are documented in one species or genus, and other facets in another species or genus. In this context, the genus *Macaca* appears as an outstanding exception.

This is the best-studied group of monkeys. There is no insuperable gap in our knowledge regarding their biology and societies. Macaques also feature broad behavioral diversity. They provide us with a Rosetta stone, a unique model allowing researchers to contrast all aspects of primate societies. By model we mean as well the reference animals, the comparative framework attached to their study, and the example to be extended to other species.

A brief look at the history of work on macaques shows that this research has brought a number of prime scientific discoveries. The early studies of rhesus macaques yielded a wealth of information regarding physiology and reproduction (Bourne, 1975). We still use the rhesus name as a label for the Rh blood group. The finding that infant rhesus macaques may prefer warmth to nurture, and that an early separation from mother induces irreversible psychological damage, drastically changed our understanding of feelings in nonhuman primates (Harlow & Harlow, 1965). Japanese macaques were the first wild animals that were individually identified and followed for their whole lifetime by observers. This allowed Japanese primatologists to discover that newly acquired behaviors might be socially transmitted among macaques (Kawamura, 1959; Kawai, 1965). The observations changed our views regarding innovation and change in primate organization. These studies also made us aware of the pivotal role of kin relationships in macaques (Kawai, 1958; Kawamura, 1958). In groups of rhesus and Japanese macaques, females form matrilines, i.e., subgroups of relatives who help one another in contests. As a result of this, the dominance status of individuals depends on the support of their allies, and strict rules of rank inheritance determine the social status of females. Combined with the conclusions reached from the study conducted on baboons and chimpanzees, this, for a time, led to the belief that most primate societies are governed by dominance and nepotism (Strier, 1994). Though there were early hints that some macaques might be ‘nicer’ than others (Rosenblum *et al.*, 1964), two decades passed before interspecific contrasts in the conciliatory dispositions of macaques were directly addressed (Thierry, 1986a, 2000; de Waal & Luttrell, 1989). During the same period, several socioecological models were proposed to explain differences in the social relationships and mating systems of primates by environmental variations (Wrangham, 1980; Caldecott, 1986a; van Schaik, 1989; Sterck *et al.*, 1997).

Macaques are mainly frugivorous, semi-terrestrial primates. They inhabit a wide range of habitats, from equatorial to temperate ecosystems, and from evergreen primary forests to grasslands, mangrove swamps, semi-deserts or areas settled by humans (Fooden, 1982a; Richard *et al.*, 1989). They differ both in their morphology and behavior. As shown in the Plate 1, their morphological diversity looks like variations on the same theme. We may expect similar homologous variations with regard to their behavioral diversity. Macaque species differ in

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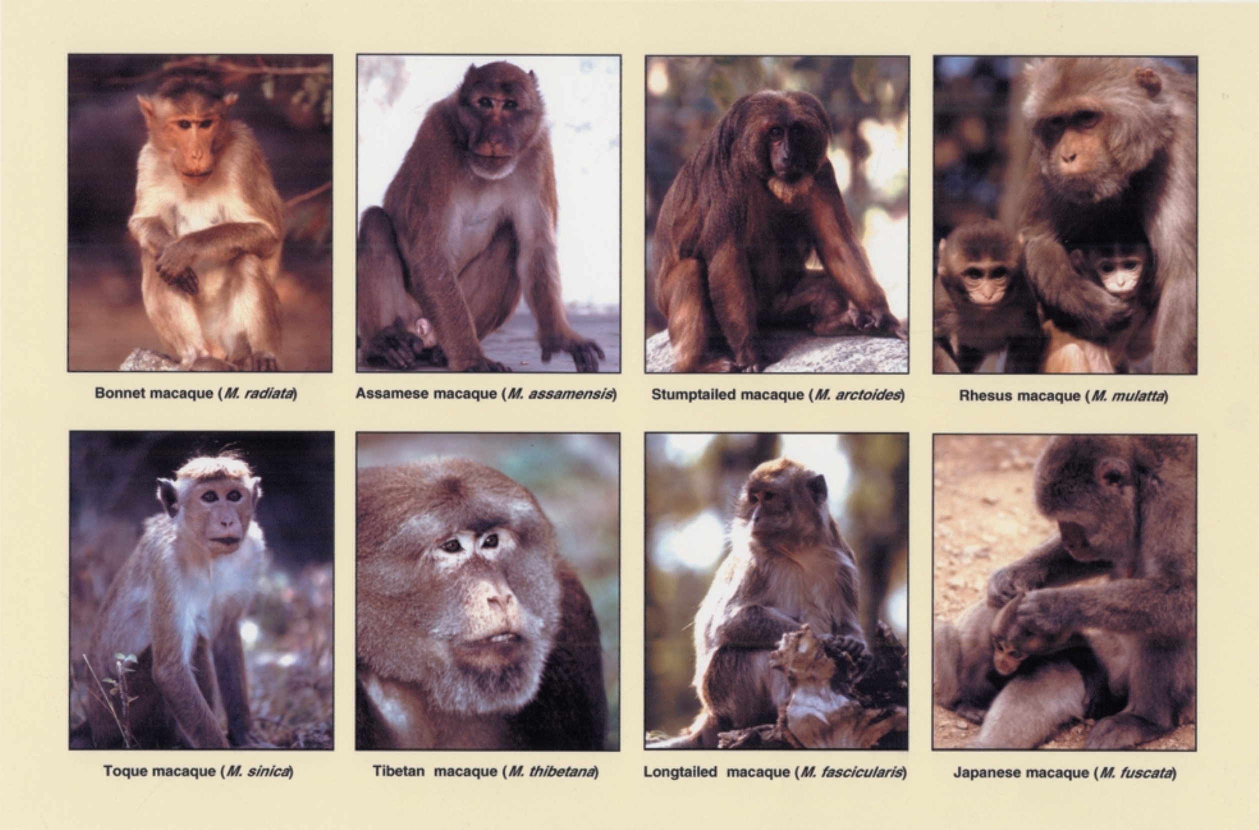
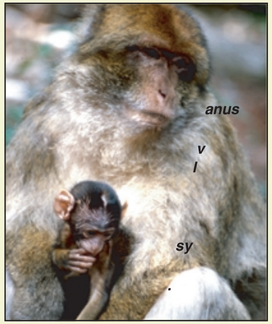


Bonnet macaque (*M. radiata*)
Assamese macaque (*M. assamensis*)
Stumptailed macaque (*M. arctoides*)
Rhesus macaque (*M. mulatta*)
Toque macaque (*M. sinica*)
Tibetan macaque (*M. thibetana*)
Longtailed macaque (*M. fascicularis*)
Japanese macaque (*M. fuscata*)

Plate 1. *How macaques look: 16 of the 20 Macaca* species. (Photographers: C. Abegg, *M. silenus, pagensis siberu, radiata*; R. Seitre, *M. maurus, hecki, nemestrina, sinica, assamensis, arctoides*; B. Thierry, *M. sylvanus, nigra, tonkeana, thibetana, fascicularis, mulatta, fuscata*.)



Barbary macaque (*M*)

Mentawai macaque (*M*)

Moor macaque (*M*) *a*

Heck's macaque (*M*)

Liontailed macaque (*M*)

Crested macaque (*M*)

Tonkean macaque (*M*)

Pigtailed macaque (*M*

Plate 1. (*cont.*)

their styles of affiliation, aggression, dominance, nepotism, maternal behavior and socialization. However, they share the same basic patterns of organization. They form multimale, multifemale groups, that is, groups which permanently contain both adult males and females with offspring. Neighboring groups have overlapping home ranges. The adult sex ratio is biased toward females. Females constitute kin-bonded subgroups within their natal group while most males transfer between groups at maturation.

We are now in a position not only to test the ecological fit of social behaviors, but also to assess their reproductive consequences and phylogenetic correlates. Steroid assays allow recognition of the females' reproductive state from fecal and urine samples collected in the field (Heistermann *et al.*, 1995). DNA analyses enable us to identify males' paternity and measure genetic diversity (Melnick & Hoelzer, 1996). The advent of computer simulations allows us to explore how structures may arise from self-organization processes (Camazine *et al.*, 2001). Phylogenetic analyses make it possible to test the influence of the evolutionary past upon social organization patterns (Brooks & McLennan, 1991; Harvey & Pagel, 1991). We have enough knowledge of macaque systematics and phylogeny (Fooden, 1976; Hoelzer & Melnick, 1996), to provide a firm foundation for examining macaque societies in an historical perspective (Matsumura, 1999; Thierry *et al.*, 2000).

The genus *Macaca* (*Mammalia*: *Cercopithecidae*) is one of the most successful primate radiations. It has the widest geographical range of primates after *Homo*. We presently recognize 20 species of macaques, which are distributed in South and East Asia, with the exception of the Barbary macaque in North Africa (Table 1.1 & Fig. 1.1). The number of species may differ according to taxonomic decisions. If the two subspecies of pigtailed macaques (*Macaca nemestrina nemestrina* and *M. n. leonina*) and the two subspecies of Mentawai macaques (*M. pagensis pagensis* and *M. p. siberu*) are ranked as full species, that would increase the number of macaque species by two (see Groves, 2001). Also, if we recognize six or eight species of macaques on Sulawesi island (Groves, 2001; Froehlich & Supriatna, 1996) instead of seven (Fooden, 1969), that would change the number of species by one. A comprehensive review of the various classification schemes for macaques proposed in the last century may be found in Fa (1989).

Macaques represent a monophyletic group (Delson, 1980; Morales & Melnick, 1998). They are placed within the tribe Papionini, which also includes baboons, geladas, mangabeys, drills and mandrills. The fossil record indicates that macaques diverged from other Papionini in northern Africa in the late Miocene 8–7 millions years ago (Delson, 1980). They invaded Eurasia about 5.5 million years ago probably via the Near East. They then split into several phyletic lineages that have been identified from morphological (Fooden, 1976;

Table 1.1. *Species, phyletic lineages and geographic distribution of the genus* Macaca *Lacépède, 1799*

Species	Distribution
***silenus–sylvanus* lineage**	
Barbary macaque (*M. sylvanus*)	Algeria, Morocco
Liontailed macaque (*M. silenus*)	Southwest India
Crested macaque (*M. nigra*)	North Sulawesi
Gorontalo macaque (*M. nigrescens*)	North Sulawesi
Heck's macaque (*M. hecki*)	North Sulawesi
Tonkean macaque (*M. tonkeana*)	Central Sulawesi
Moor macaque (*M. maurus*)	Southwest Sulawesi
Booted macaque (*M. ochreata*)	Southeast Sulawesi
Muna-Butung macaque (*M. brunnescens*)	Southeast Sulawesi
Mentawai macaque (*M. pagensis*)	Mentawai
Pigtailed macaque (*M. nemestrina*)	Indochinese peninsula, Sumatra, Borneo
***sinica–arctoides* lineage**	
Toque macaque (*M. sinica*)	Sri Lanka
Bonnet macaque (*M. radiata*)	South and West India
Assamese macaque (*M. assamensis*)	Continental Southeast Asia
Tibetan macaque (*M. thibetana*)	East and Central China
Stumptailed macaque (*M. arctoides*)	South China, Indochinese peninsula
***fascicularis* lineage**	
Longtailed macaque (*M. fascicularis*)	Indochinese peninsula, Indonesia, Philippines
Rhesus macaque (*M. mulatta*)	Continental South and East Asia
Japanese macaque (*M. fuscata*)	Japan
Taiwanese macaque (*M. cyclopis*)	Taiwan

(From Fooden, 1976, 1982; Delson, 1980; Groves, 2001.)

Delson, 1980) and molecular evidence (Hoelzer & Melnick, 1996). Three main species groups are distinguished among extant macaques (Fooden, 1976): the *silenus* group, which includes the liontailed, the Sulawesi, the Mentawai and the pigtailed macaques; the *sinica* group, which includes the toque, the bonnet, the Assamese and the Tibetan macaques; and the *fascicularis* group, which includes the longtailed, the rhesus, the Japanese and the Taiwanese macaques. The taxonomic position of two further species is still debated. The Barbary macaque is likely the most ancient taxon of the genus, and is in fact its last African representative. It is alternatively classified as being either the only member of its own species group (Delson, 1980) or one belonging to the *silenus–sylvanus* group (Fooden, 1976). Similarly, the stumptailed macaque is either ascribed to its own species group (Fooden, 1976) or included in the *sinica–arctoides* group (Delson, 1980) (see Deinard & Smith, 2001). We may retain that there are three broad macaque lineages (Table 1.1). Modern macaques most

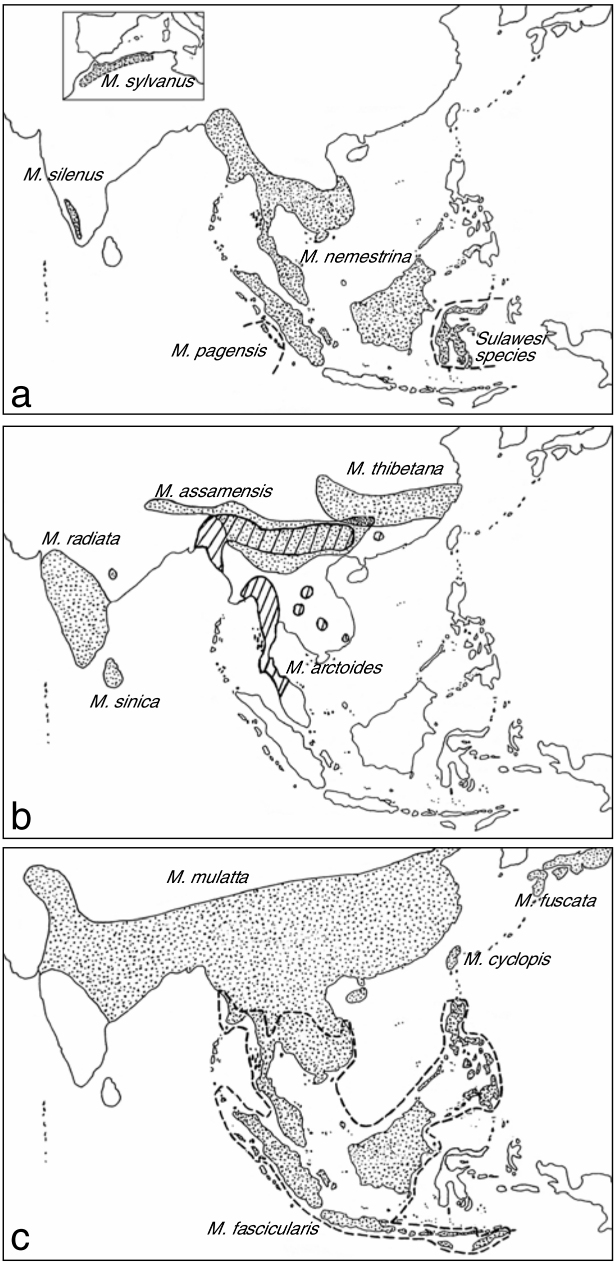


Fig. 1.1. Present geographical distribution of macaques (from Fooden, 1982a). (a) *silenus–sylvanus* lineage, (b) *sinica–arctoides* lineage, (c) *fascicularis* lineage.

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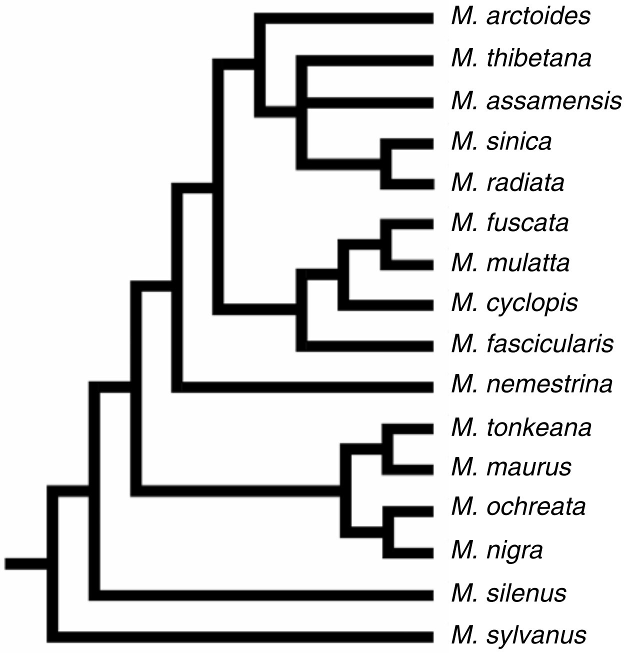

Fig. 1.2. A reconstruction of the phylogenetic tree of macaques (16 of the 20 species), based on a meta-analysis of previously published data, both morphological and molecular (from Purvis, 1995).

likely arose from speciation events that occurred within the last 2 million years (see Fa, 1989). The phylogenetic tree constructed by Purvis (1995) provides a tentative branching order for macaque species (Fig. 1.2).

From the present geographic distribution, it may be inferred that macaques dispersed in three successive waves in Asia (Fooden, 1976). The *silenus–sylvanus* lineage originated from the first macaque radiation. It has the most fragmented geographical distribution (Fig. 1.1a). Its 11 species are situated far away from each other and often present a relict distribution, indicating an early dispersal. The Barbary macaque lives in semi-deciduous montane forests of North Africa. The liontailed macaque is found in the evergreen hill-country forests of South India. The pigtailed macaque is present in the Indochinese peninsula and fringing continental islands of Indonesia that are connected by shallow-waters. Other species inhabit the far-reaching evergreen forests of Sulawesi and Mentawai deep-water oceanic islands. The *sinica–arctoides* lineage is thought to be the second to have dispersed. This lineage has a moderately fragmented distribution in peninsular India and subtropical Southeast Asia (Fig. 1.1b). Bonnet, Tibetan, Assamese and stumptailed macaques are continental. Only the toque