

# Chapter 1

## Recent Developments in Primatology and Their Relevance to the Study of Tibetan Macaques



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## 1.1 Recent Trends and Developments in Primatology

Given their shared evolutionary history with humans, nonhuman primates play an exceptional role in the study of animal behavior, ecology, and evolution. This close phylogenetic relationship has led scholars from a diverse set of disciplines (e.g., biological and social sciences, notably psychology and anthropology) and theoretical perspectives (e.g., kinship theory, multilevel selection, social interactions, cultural traditions, competition, cooperation, innovation) to examine a broad range of research topics and methodologies in primatology. It is hardly an exaggeration to say that primatology is an intellectual “melting pot” in the study of animals.

The integration of different disciplines into the science of primatology has led to a major paradigm shift in the philosophy of science. Traditionally, scientists tended to assume animals had limited agency and behavioral flexibility or were incapable of engaging in complex forms of decision-making. They would be accused of committing a major scientific sin, namely, anthropomorphism, if they empathized with their research subjects or thought animals share emotions, social strategies, or cognitive abilities with humans (e.g., Masson and McCarthy 1996). Such a philosophical standpoint has become increasingly tenuous, as recent evidence in many mammals, especially nonhuman primates, have identified that they do indeed exhibit emotions, empathy, behavioral strategies, social bonding, cognitive abilities, and, in some instances, a moral sense of fairness (e.g., de Waal 1988, 2010; Kappeler and van Schaik 2006; Kappeler and Silk 2009; van Schaik 2016). In light of these findings, anthropomorphism and highlighting the behavioral and cognitive continuity between humans and other mammals may provide a more parsimonious null hypothesis than the alternative view, namely, that mammals in general and primates in particular have limited ability to respond to changes in their social and ecological environments (de Waal et al. 2006).

Primatologists have a keen and profound understanding that the sensations and emotions of researchers, as well as their subjective experiences as primates, are an essential variable in pursuing scientific questions. As in the case of quantum mechanics, where measurements and the behavior of quanta are entwined no matter what controls researchers place on the experiment, scientific objectivity in primatology is accomplished by including their own sensations and emotions as critical variables in research. We argue there exists no clear demarcation between being overtly subjective and being prudently self-reflective, and therefore in the case of primate research, we attempt to balance anthropomorphism without losing scientific objectivity.

Accompanying this philosophical shift, broad comparative studies, grounded in evolutionary, ecological, and behavioral perspectives, have led, in recent years, to new and exciting discoveries focused on social strategies, problem-solving, and cognitive abilities of nonhuman primates including complex social networks, cooperation between kin and nonkin, collective behavior, biological markets, behavioral economics, and culture (Byrne and Whiten 1988; van Schaik et al. 1999; Byrne and Bates 2007; Dufour et al. 2008; Sueur et al. 2010; Balasubramaniam et al.

2011; Sussman and Garber 2011; Pasquaretta et al. 2014; Garber 2019). Using social cognition as an example, major developments have been made in understanding primate intelligence (Machiavelli intelligence), social development, personality, empathy, theory of mind, trading, intuitive moral sense (particularly, fairness), and others (Dufour et al. 2008; Devaine et al. 2017). These discoveries would have been impossible without careful self-examination of our own behaviors, societies, and cognitive abilities. In fact, the study of our focal species in this volume, the Tibetan macaque (*Macaca thibetana*), clearly reflects such introspective, anthropomorphic thinking across a wide range of topics from social interactions and feeding ecology to gut microbe communities and self-medication. Despite the many insights anthropomorphic approaches provide, we must refrain from assuming that all similarities in social behaviors, social organizations, and cognitive abilities are derived from shared ancestry between humans and nonhuman primates because these similarities could also have arisen independently through convergent or parallel evolution. As such, distinguishing between homology and homoplasy will continue to pose a major challenge to primatologists.

## 1.2 Why Macaques, Especially Tibetan Macaques?

New developments in primatology in recent years have reinforced the view that nonhuman primates offer a window for us to look into human behavior, biology, and sociality from an evolutionary perspective (e.g., Kappeler and van Schaik 2006; Kappeler and Silk 2009; van Schaik 2016). Primates not only provide an instructive model to better understand human evolution, they may also provide information and insights into a range of practical issues in our society from promoting cooperation to preventing disease transmission (Romano et al. 2016). In fact, it is hard for us to underestimate how much we can learn from behavioral, ecological, and evolutionary knowledge gained from nonhuman primates.

Although nonhuman great apes represent our closest living relatives, all primate radiations can provide important model systems that unveil evolutionary patterns and processes. Currently there are over 500 species of living primates (Estrada et al. 2017). Many of these species are more abundant and evolutionarily successful (in numbers, populations, and species) than are great apes. As such they can provide a broader range of demographic and socioecological scenarios for testing evolutionary hypotheses, especially using comparative approaches (e.g., Harvey and Pagel 1991). In this sense, macaques (genus *Macaca*) may be unmatched as a model group for evolutionary studies of social behavior, social organization, and social cognition in primates. With 20–23 species, macaques are among the most successful primate radiations, with the largest geographical distribution of any taxa (Thierry et al. 2004; Fleagle 2013). The genus forms a monophyletic clade (Morales and Melnick 1998), and the evolutionary relationships among species have been mapped out with a reasonable level of certainty (Purvis 1995; Li and Zhang 2005; Jiang et al. 2016).

The availability of this critical information has paved the way for pursuing questions about the evolution of their behaviors using comparative methods.

One major challenge now for macaque behavioral ecologists is to obtain quality long-term data on behavioral variability and trade-offs between affiliative and agonistic alliances, social cohesion, and reproductive success. This level of information is missing for virtually all species, including the Tibetan macaque. In an attempt to find a general pattern of social style in macaques, for instance, Thierry (2004) classified all macaque species into four grades of social structure, from despotic (Grade 1) to egalitarian societies (Grade 4). These grades were associated with traits such as degree of social tolerance, symmetrical or asymmetrical conflict, a linear-like dominance hierarchy, and the strength of kin bonds. Clearly, there are significant challenges in attempting to quantify these variables. Based on limited information, Thierry (2004) identified Tibetan macaque as a Grade 3 species. Close examination, however, revealed that the aggressive behavior and dominance hierarchy of this species are more consistent with Grade 2 (Berman et al. 2004, 2006), which led to the revision of Thierry's classification scheme (Thierry 2011). This example illustrates the challenges of attempting to answer evolutionary questions using limited information from little known species. As such, this volume aspires to fill some glaring gaps in our knowledge of Tibetan macaques. Furthermore, several chapters attempt to directly address evolutionary questions from comparative perspectives between the Tibetan macaque and its sister species.

The Tibetan macaque is endemic to China and is listed in the IUCN Red List as near threatened (see Chap. 2). It is one of the most widespread primate species in China, distributed across 13 provinces. Its estimated population size is 20,000 individuals (Li et al. unpublished data). While rhesus macaques have been intensively studied in the field and laboratory, Tibetan macaques are far less known. As such, they provide a good comparison for understanding macaque ecology and behavior across a range of demographic, social, and ecological conditions. Also, Tibetan macaques have several unique features in the genus *Macaca*. They are the largest in body size (adult male body mass ~ 15 kg) and are found at elevations up to 2400 m (see Berman et al. 2006). They live in relatively small groups with a strict linear dominance hierarchy. Home range size is 1.62–3.62 km<sup>2</sup> with a pattern of habitat utilization (feeding in particular) particularly favorable for long-term observation and data collection. These features make the species well-suited for a wide range of studies for testing hypotheses related to behavior, ecology, evolution, conservation, management, human-animal interaction, and infectious disease transmission (see Chap. 14 Balasubramaniam, Sueur, and MacIntosh). Additionally, given that some populations are present in national parks or protected areas, such as those in Mt. Huangshan and Mt. Emei, they are highly accessible for educational and research purposes. (See the elaboration by Jin-Hua Li and Peter Kappeler in Chap. 2.)

### 1.3 A Short History of Tibetan Macaque Research

Primate research in China was largely absent until the nineteenth century, when European and American naturalists and missionaries came to China and reported their discoveries of exotic species. Following these initial descriptions, there remained no systematic studies of the behavior and ecology of Chinese primates until the 1970s, when a small number of pioneers of Chinese zoologists began to study and observe endemic species such as snub-nosed monkeys (*Rhinopithecus* spp.) and Tibetan macaques. During this period, the research was often sporadic and was published principally in Chinese journals.

The Tibetan macaque was first described to the scientific community as *M. thibetanus* by A. Milne-Edwards in 1870 based on a specimen collected by French missionary Abbé Armand David at Baoxing County in Sichuan Province (see Fooden 1983). However, in 1938, G. M. Allen believed it to be a subspecies of the stump-tailed macaque (formerly *M. speciosa* but currently *M. arctoides*) and named it *M. speciosus thibetanus*. It was not until 1983 that the Tibetan macaque regained its current species status as *M. thibetana*. This changed consensus was based on Jack Fooden's work on the anatomy of the reproductive system of the species. Recent studies using mtDNA have corroborated and validated this taxonomic distinction (Liu et al. 2006).

Despite the fact that Tibetan macaques are found in several small and isolated locations across China (a small population was recently found in eastern India) today, they were once widely distributed across a broad strip running from the foothills of southeastern Tibet to the coastal regions of East China including 13 provinces: Zhejiang, Anhui, Fujian, Jiangxi, Hubei, Hunan, Guangdong, Guangxi, Sichuan, Guizhou, Yunnan, Gansu, and Tibet (Jiang et al. 2015). Currently, four geographic subspecies are identified based on morphological characters and mtDNA (Jiang et al. 1996; Liu et al. 2006; Sun et al. 2010). Genomic studies show that the Tibetan macaque diverged from its congeneric species some 0.5 Ma after a long bottleneck for the genus (Fan et al. 2014).

Field studies on Tibetan macaques have been carried out primarily at two sites, Mt. Emei in Sichuan Province and Mt. Huangshan in Anhui Province. Research on the Mt. Emei population has been led by Qikun Zhao and Ziyun Deng based at the Kunming Institute of Zoology of the Chinese Academy of Sciences. The bulk of the data from the population at this site was collected between 1987 and 1999. Research at the Mt. Huangshan site began in 1983 and led by Qishan Wang and Jin-Hua Li from Anhui University, in long-term collaboration (since 2003) with researchers from Central Washington University including Lixing Sun, Lori Sheeran, and colleagues. These research efforts have led to most of our current understanding of the species's social behavior, ecology, and population biology.

Research on ecology and population biology of Tibetan macaques has focused on morphological adaptation to ecological factors in its habitat (Xiong 1984), the current distribution of the species (Wada et al. 1987; Jiang et al. 1996), home range (Wang and Xiong 1989), adaptive relationships between body mass and

elevation (Zhao and Deng 1988a, b; Zhao 1994a), effects of climate, vegetation, and slope on food resources (Zhao et al. 1989), selection of sleeping sites (Li and Wang 1994), ecological factors linked to group fission and reformation (Li et al. 1996a, b), diet (Li 1999; Zhao 1999), social organization (Deng and Zhao 1987; Li and Wang 1996), population dynamics (Wang et al. 1994), age structure and life expectancy and mortality (Li et al. 1995), and population growth in relation to population density, processes of group fission, and disease (Li et al. 1996a, b).

Several other research projects have focused on social bond formation, grooming relationships, social networks, and reproductive strategies. This has been made possible by long-term observation and monitoring of known individuals in several groups, aided by provisioning. This part of research has compared species differences in mating tactics between Tibetan and Japanese macaques (Xiong and Wang 1991; Zhao 1994c), birth timing in relation to socioecological factors such as dominance rank and altitude (Li et al. 1994; Zhao 1994c; Li et al. 2005), birth seasonality (Zhao and Deng 1988a, b; Li et al. 2005), and descriptions and evaluations of behaviors that are critical measures of social relationships such as bridging (defined as two individuals ritualistically lifting an infant accompanied by affiliative behaviors such as teeth chattering, see Zhao 1996) and grooming (Li et al. 1996a, b). These efforts have led to a complete ethogram of Tibetan macaques consisting of 32 distinct patterns of social behavior (Li 1999; Li et al. 2004). Using this ethogram, researchers can conduct in-depth analyses of behavior, social structure, and social dynamics of the species. A series of papers have been published on sociality and group stability analyzed at various levels from the individual, to dyads, social networks (cliques), and to the entire group. The topics addressed include collective decision-making and leadership in group movement (Wang et al. 2015, 2016; Fratellone et al. 2019), personality (Pritchard et al. 2014), benefit-cost analyses of grooming exchanges (Xia et al. 2012, 2013), and social networks among group members (Fratellone et al. 2019).

In recent years, new field and laboratory techniques from other disciplines have been applied to behavioral, ecological, and evolutionary studies of the species. They include the development and application of fecal DNA analysis (Zhao and Li 2008), extraction and analysis of fecal steroid hormones (Xia et al. 2015, 2018), and gut microbe analysis (Sun et al. 2016). Several of the chapters in this volume reflect these new and exciting research developments.

## 1.4 Tibetan Macaques at Mt. Huangshan Research Site

Many advancements in our understanding of primate behavior, biology, and evolution have been made from field studies. In this respect, long-term field studies are particularly valuable (Kappeler and Watts 2012) because they allow us to observe especially rare behaviors and biological events that may be missed based on short-term observations. For instance, long-term field studies have enabled researchers to document the cultural transmission of information within a group of Japanese

macaques on Koshima Island and warfare in chimpanzees (*Pan troglodytes*). Likewise, much of our understanding of the behavior ecology and reproductive strategies of male and female Tibetan macaques reported in this volume would not be possible without long-term field studies and the dedication of primatologists working at Mt. Huangshan.

The Mt. Huangshan research site was first established in 1983, when the late Qishan Wang, then head of the Biology Department at Anhui University, founded a primate research program in collaboration with Kazuo Wada from the Primate Research Institute at Kyoto University in Japan. They jointly led a team to explore southern Anhui for a field site suitable for long-term research of the species. After some scouting, they settled on a location, now known as the Valley of Monkeys, at Yulingken, just a 15-min walk from the village of Fuxi, within the scenic area of Mt. Huangshan. This was the beginning of the first and in the meantime longest running primate research site in China, and long-term systematic observations of the Tibetan macaques have continued for more than 30 years. Today, the site is recognized as one of the eight long-term primatological study sites in the world (Kappeler and Watts 2012). Over the course of three decades, more than 150 primatologists from Japan, the United States, Germany, England, and Canada have come and conducted research in collaboration with Chinese colleagues at Mt. Huangshan.

Kazuo Wada's insights and contributions were essential, especially in getting this long-term research project started. One of the major inaugural events took place in October, 1986, when Wada presented a series of talks during the First Primatological Research Symposium of China hosted by Anhui University. The meeting was attended by only 12 participants (including Jin-Hua Li and Lixing Sun, then both beginning graduate students), representing probably fewer than ten qualified primatological researchers in the nation. At that time, some 27 primate species naturally occurred in China. In comparison, there were about 500 primatologists in Japan, working on a single endemic species, the Japanese macaque (*M. fuscata*). Wada was a dedicated field primatologist who had published extensively about the biology of macaques. Though skeptical about sociobiology, he was quite open in sharing his research ideas and experience, especially under the mild impact of Chinese whiskey. Among what he brought to Chinese primatology were two simple yet brilliant Japanese methodological perspectives that changed the face of Chinese primatological research: he recommended that primates be recognized individually and helped establish a naming system that reflected the sex, generation, and lineage information for all group members. At the time, these practices were still considered an inappropriate use of anthropomorphism by many in the West.

Since then, primatological research has thrived in China with increasingly well-trained primatologists working on virtually all of China's primate species across a range of topics from ecology, behavior, and conservation to molecular genetics and cognitive science with several highly productive and visible research groups. So, a few trickling streams of effort, initiated just a few decades ago, have grown to be a torrent of vibrant primatological research in China today, culminating in the formal launch of the Chinese Primatological Society in 2017. The inauguration conference of the society was attended by well over 200 researchers from all corners of the nation.

The chapters presented here partly illustrate the status quo of Chinese primatology from the research work conducted mainly in Tibetan macaques at Mt. Huangshan. They are also a demonstration for the fruitfulness of international collaboration by sharing research resources, ideas, and methodologies, reflecting the multidisciplinary nature of primatology. We expect that collaborations among researchers from a diverse range of academic and cultural backgrounds will continue to grow and deepen in the future.

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