

Chapter 11

The Gut Microbiome of Tibetan Macaques: Composition, Influencing Factors and Function in Feeding Ecology



Binghua Sun, Michael A. Huffman, and Jin-Hua Li

11.1 Introduction

Microbes dominated the earth for at least 2.5 billion years before multicellular life appeared in the biosphere (Hooper and Gordon 2001; Ley et al. 2008). In fact, animals have been living and evolving in a microbial world (Margaret et al. 2013). Microbes inevitably colonized animals and coevolved through the process of interactions with their hosts (Clayton et al. 2018). Microorganisms can inhabit multiple parts of a host's body, such as the skin, oral cavity, sex organs, and the gastrointestinal (GI) tract. They are usually recognized as the microbiome of a particular host. As an essential part of the host's body, the microbiome plays an important role in host physiology by influencing nutritional intake, metabolic activity, and immune homeostasis (Turnbaugh et al. 2006; Greenblum et al. 2012; Hooper et al. 2012). Thus, the complex relationship between hosts and their microbiomes provides a unique opportunity for understanding mammalian adaptation and evolution (Hird 2017).

As the most complex and diverse ecological system of the mammalian body, the GI tract is colonized by bacteria, archaea, fungi, and viruses (Underhill and Iliev 2014). Previous studies have revealed that the gut microbiota play an important role in immune regulation, vitamin synthesis, energy acquisition, and disease risk

B. Sun

School of Resources and Environmental Engineering, Anhui University, Hefei, Anhui, China

M. A. Huffman

Primate Research Institute, Kyoto University, Kyoto, Japan

e-mail: huffman.michael.8n@kyoto-u.ac.jp

J.-H. Li (✉)

School of Resources and Environmental Engineering, Anhui University, Hefei, Anhui, China

International Collaborative Research Center for Huangshan Biodiversity and Tibetan Macaque Behavioral Ecology, Anhui, China

School of Life Sciences, Hefei Normal University, Hefei, Anhui, China

e-mail: jhli@ahu.edu.cn

© The Author(s) 2020

J.-H. Li et al. (eds.), *The Behavioral Ecology of the Tibetan Macaque*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-27920-2_11

207

reduction of the host (Turnbaugh et al. 2006; Hooper et al. 2012; Sharon et al. 2012). For example, all vertebrates lack cellulase, the enzymes, which help them to digest the fiber in their food, and are reliant upon intestinal microbes for its production (Yokoe and Yasumasu 1964; Mackie 2002). As a result, mammals maintain rich gut microbial communities, which are beneficial for the digestion of cellulose and hemicellulose abundant in the foods they ingest (Amato et al. 2015).

Nonhuman primates (NHPs) evolved in tropical forest habitats and radially spread to woodland, savanna and montane environments (Hanya et al. 2011). In order to adapt to the resultant temporal food resource shifts and to maintain ordinary functions of the body, NHPs have evolved many anatomical and behavioral strategies (Rodman and Cant 1984). For example, some primates have evolved specialized stomachs and teeth, while many others have evolved distinctive habitat use patterns, ranging behavior and social organization (Milton and May 1976; Chivers et al. 1984; Cachel 1989; Yamada and Muroyama 2010; Hanya and Chapman 2013). Generally, NHPs prefer to eat high-quality food rich in lipids, proteins, and carbohydrate, such as fruits and young leaves. However, these foods are not always available year-round (Rodman and Cant 1984; Ungar 1995; Hanya et al. 2011; Hanya and Chapman 2013). NHPs living in temperate environments can only eat mature leaves, gum and roots during winter (Fan et al. 2009). These low-quality foods usually contain high proportions of cellulose and hemicellulose, which are difficult to digest (Coley 1983; Burrows 2010). In response to ecological pressures, many primates also use behavioral strategies such as adjusting their activity budgets and foraging patterns to help overcome periods of food scarcity (Zhou et al. 2007; Starr et al. 2012; Hanya and Chapman 2013; Campera et al. 2014). However, how wild primates digest low-quality foods high in cellulose during the winter has not been well understood (Amato et al. 2014).

Although low-quality foods, including woody plants, mature leaves, fungi, mature leaves, and plant exudates are difficult to digest, more recent research related to the above has revealed that these foods can be broken down and utilized by the intestinal microbes of NHPs. For this reason, the gut microbiota may provide a way to understand how primates adapt to ecological pressures during periods of food scarcity. Since the gut microbiome is dominated by bacteria, many studies on the feeding ecology of mammals have focused solely on the bacterial microbiome (Qin et al. 2010). Other common elements, such as gut fungi, also appear to affect the health and nutrition of animals, but this too is not yet well understood (Huffnagle and Noverr 2013; Underhill and Iliev 2014; Sokol et al. 2017). Although intestinal fungi have a much smaller number of cells compared to bacteria, the evidence suggests that gut mycobiota can also play an important role in host health by affecting gut bacterial composition (Hoffmann et al. 2013), interacting with immune cells, and assisting in the metabolic activity of the host (Hajishengallis et al. 2011; Romani 2011; Iliev and Underhill 2012; Rizzetto et al. 2014). Therefore, it is important to integrate information about the role of gut bacteria and fungi when discussing the role of the gut microbiome in the evolution of animal dietary strategies.

NHPs and humans have extensive similarities in their genetic characteristics, physiology and morphology. Very important animal model systems, NHPs are extremely important for understanding human physiology, behavior, cognition,



Fig. 11.1 A female Tibetan macaque carrying a baby is foraging for food in winter (Photo credit: Qixin Zhang)

health and evolution (McCord et al. 2014; Ren et al. 2015). Therefore, compared with other laboratory animals, NHPs have an advantage in helping us to understand the role of the gut microbiome in human health maintenance, as well as the evolutionary relationships involving the gut microbiome, host diet and evolution.

The free-ranging Tibetan macaque (*Macaca thibetana*) group at Mt. Huangshan (described in Chap. 2) presents a good opportunity for studying this, since all members of the group can be identified individually, allowing for the collection of feces from individuals of known age and sex (Zhang et al. 2010). Our study group lives in a deciduous and evergreen-broadleaf-mixed montane forest. As the temperature fluctuates across seasons (highest in summer: 34.2 °C, lowest in winter: -13.9 °C), the quality of their food also varies accordingly (see Fig. 11.1). For example, from winter to spring, Tibetan macaques experience a switch from low quality food resources (mature leaves, roots and plant stem) to high quality food resources (young leaves and flowers) (Xiong and Wang 1988; Zhao 1999). As a result, our study population is an ideal model for studying the role of the gut microbiome in primate feeding ecology and evolution.

In this chapter, we will summarize our research on the composition of the bacterial/fungal community and microbial diversity of Tibetan macaques and analysis of the factors influencing variation in the microbiome across age, sex and season in this species. Furthermore, we use this information to discuss the role of the Tibetan macaques' gut microbiome in relation to the evolution of their feeding ecology.

11.2 Gut Microbiome of Tibetan Macaque

11.2.1 Composition of Gut Bacteria

Understanding the composition of an animal's gut bacteria helps us to reveal its role in the host's feeding ecology, however, we know little about the Tibetan macaques' gut microbiota. Recently, using the methods of high-throughput sequencing and bioinformatics, Sun et al. (2016) detected 14 known bacterial phyla in this macaque's gut, the most dominant phyla (relative abundance > 1%) being Firmicutes, Bacteroidetes and Proteobacteria Spirochaetes (Sun et al. 2016). Comparing our results to those of the gut microbiome in other NHPs (Table 11.1), we found that the two most dominant phyla (Firmicutes and Bacteroidetes) were commonly reported in many other species as well (Ochman et al. 2010; Mckenney et al. 2015; Xu et al. 2015). At the genus level, the two most dominant genera present in the gut of Tibetan macaques were *Prevotella* and *Succinivibrio*. Although the genus *Prevotella* was also commonly reported elsewhere (Ochman et al. 2010; Mckenney et al. 2015; Xu et al. 2015), *Succinivibrio* has been seldom been detected as a dominant genus. The relative abundance of these main bacterial genera (relative abundance > 1%) are presented in Fig. 11.2a.

Table 11.1 The dominant phyla of gut bacteria detected in several non-human primate species

Monkey's name	Dominant phyla			Captive/ wild	Study
	Firmicutes	Bacteroidetes	Proteobacteria		
<i>Lemur Catta</i>	+	+		Captive	McKenney et al. (2015)
<i>Varecia variegata</i>	+	+		Captive	McKenney et al. (2015)
<i>Propithecus coquereli</i>	+	+		Captive	McKenney et al. (2015)
<i>Rhinopithecus bieti</i>	+	+	+	Wild	Xu et al. (2015)
<i>Nycticebus pygmaeus</i>		+		Wild	Xu et al. (2013)
<i>Gorilla beringei</i>		+	+	Wild	Ochman et al. (2010)
<i>Gorilla gorilla</i>		+	+	Wild	Ochman et al. (2010)
<i>Pan troglodytes</i>	+	+		Wild	Ochman et al. (2010)
<i>Macaca thibetana</i>	+	+		Wild	Sun et al. (2016)

Note: + means the relative abundance was one of the top two

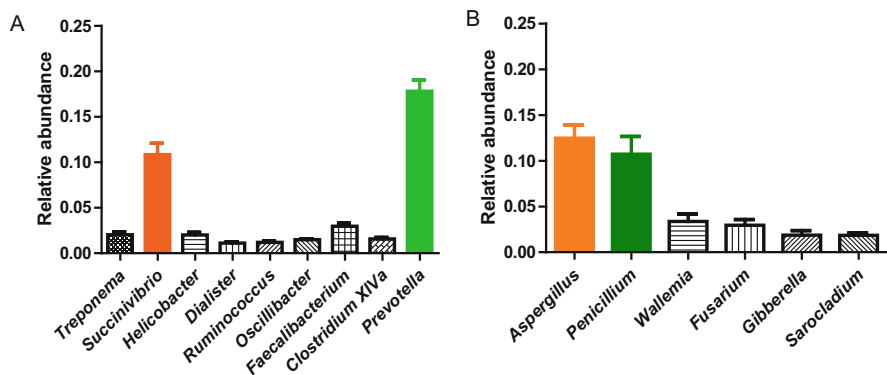


Fig. 11.2 The relative abundance of the main genera of bacteria and fungi. (a) The relative abundance of the major bacterial genera (relative abundance > 1%); data from Sun et al. (2016). (b) The relative abundance of the major fungal genera (relative abundance > 1%), data from Sun et al. (2018)

11.2.2 Composition of Gut Fungi

Previous studies on humans and mice have revealed that the mammalian gut is rich in fungi, dominated by three phyla: Ascomycota, Basidiomycota, and Zygomycota (Iliev and Underhill 2012; Qiu et al. 2015; Mar et al. 2016; Strati et al. 2016; Wheeler et al. 2016; Sokol et al. 2017). However, little is known about the gut fungi in NHPs. Using the Illumina Miseq platform and primers of the ITS region (Bokulich and Mills 2013; Sun et al. 2018) first reported that the gut mycobiota of Tibetan macaques was dominated by two phyla Ascomycota and Basidiomycota (Sun et al. 2018), this is consistent with previous studies on mammalian gut mycobiomes. In addition, other phyla such as Zygomycota, Chytridiomycota, Glomeromycota and Rozellomycota were also detected in this macaque species. At the family level, Trichocomaceae shows the highest relative abundance (24.70%). At the genus level, the gut mycobiota of Tibetan macaques are rich in *Aspergillus* and *Penicillium* (relative abundance more than 10% respectively). Furthermore, by defining the core families and genera (both present in >90% of the samples with an average relative abundance > 0.01), Sun et al. (2018) revealed that six core taxa, namely Trichocomaceae, Nectriaceae, Davidiellaceae, *Aspergillus*, *Penicillium* and *Fusarium* can be detected in the gut of Tibetan macaques. The relative abundances of fungal genera (>1%) are presented in Fig. 11.2b. The presence of core taxa in the gut of this macaque suggests that the fungi in their guts are not random and exist as a relatively stable fungal community.

11.3 Factors Affecting the Gut Microbiome in Tibetan Macaques

11.3.1 *Affects of Age, Sex, and Season on Gut Bacterial Microbiome*

It is well known that many internal and external factors can affect the diversity and composition of an animal's gut microbiota, such as age, sex and seasonal change. Based on data from the Illumina Miseq platform and linear mixed models, Sun et al. (2016) evaluated factors affecting gut microbial diversity in Tibetan macaques. The results showed that sex and age had no significant effect on the alpha diversity (including Shannon index, Chao 1, OTU richness and ACE) of the gut bacterial microbiome, as well as the beta diversity (evaluating by unweighted and weighted UniFrac distances) (Sun et al. 2016). These results differ from previous studies in humans and other vertebrates (Yatsunenkov et al. 2012; Bolnick et al. 2014), but are consistent with those in chimpanzees and baboons (Degnan et al. 2012; Tung et al. 2015).

Seasonal factors on the other hand have a strong effect on the composition and diversity of the gut bacterial microbiome in Tibetan macaques (Sun et al. 2016). For example, the Shannon diversity index of the gut bacterial microbiome was significantly different between winter and spring. In addition, a significant seasonal separation of beta diversity evaluating by weighted UniFrac distances and unweighted UniFrac distances (Permanova tests, $p < 0.05$ and 0.01 respectively) were detected. Furthermore, three phyla and 20 known genera showed significant differences between the two seasons. The representative taxa rich in winter samples were Proteobacteria, Spirochaetia, *Succinivibrio*, *Clostridium* sensu stricto and *Treponema*, but Firmicutes and *Prevotella* were richest in spring samples. Differences in the composition of gut bacteria also resulted in the variations of predicted metagenomes between winter and spring. Using PICRUSt and LEfSe tests, Sun et al. (2016) found that seven KEGG pathways of Tibetan macaques' gut bacterial microbiome, including Glycan Biosynthesis and Metabolism, Amino Acid Metabolism, Signal Transduction, Cell motility, Transport and Catabolism, Neurodegenerative Diseases and Endocrine System, were significantly enriched in the winter. However six other metabolic pathways Energy Metabolism, Carbohydrate Metabolism, Cellular Processes Transcription, Signaling and Metabolism of Cofactors and Vitamins and Enzyme Families were significantly enriched in the spring (Sun et al. 2016). The potential functions of the gut microbiome in different seasons of our study group will be discussed in Sect. 11.4.

11.3.2 Gut Fungal Microbiome Affected by Age, Sex, and Season

Although previous studies in humans have revealed that age and sex can influence the composition and diversity of the gut fungal microbiome (Strati et al. 2016), little information is available for wild living primates. Using LEfSe analysis, Sun et al. (2018) first reported that only one fungal genus *Sarocladium* was enriched in the old age group. By comparing males and females, the family Mycosphaerellaceae and genus *Devriesia* were particularly enriched in females, while the phylum Ascomycota and family Tetracosphaeriaceae were enriched in males (Sun et al. 2018). These results indicated that the effect of sex and age on the composition of gut fungi was not as strong as that found in humans. In addition, we found evidence of marked seasonal variation in the composition of this macaque species' gut mycobiota. Fifteen taxa had significant variation across the four seasons. The abundant taxa in each season were as follows, Autumn: Wallemiaceae, Hypocreaceae, *Wallemia*, *Trichoderma*; Spring: Sclerotiniaceae, Nectriaceae, *Ciboria*, *Fusarium*, *Gibberella*, *Sarocladium* and *Talaromyces*; Summer: Trichocomaceae and *Penicillium*; Winter: *Devriesia* and Teratosphaeriaceae. This result is the first report to find strong seasonal influences on primate gut mycobiota, indicating the potential relationship between gut mycobiota and seasonal changes in host diet.

Different from previous studies in humans, no evidence indicates that age or sex strongly affect the alpha diversity of Tibetan macaque gut mycobiota (Sun et al. 2018). This result is likely because even individuals living in the same environment have differences in their dietary preferences. In addition, using PCoA and PERMANOVA tests, we found that there existed significant variation in beta diversity among different age and sex classes. Interestingly, seasonal change can significantly affect alpha and beta diversity, as well as the composition of the gut fungal microbiome.

11.4 Functions of the Gut Microbiome in Tibetan Macaque Feeding Ecology

Feeding ecology plays an important role in understanding the evolution of NHPs (Lambert 2011). With advances in sequencing technology, many studies have revealed that the gut microbiome aids in the digestion of some food resources, especially those rich in cellulose and hemicellulose, substances which are difficult to digest. Therefore, this important adaptive mechanism has attracted increasing attention in recent years. Tibetan macaques living in a highly seasonal ecosystem with strongly seasonal changes in rainfall, temperature, food resources, and home range shifts (Xiong and Wang 1988; Zhao 1999). Previous studies have suggested that these environmental factors are closely reflected in the composition of the gut

microbiome (Amato et al. 2015; Chevalier et al. 2015; Maurice et al. 2015; Wu et al. 2017). Therefore, our study subjects may provide an important model for understanding the functions of the gut microbiome in primate feeding ecology, especially for primates living in highly seasonal ecosystems.

11.4.1 Gut Bacterial Microbiome and the Feeding Ecology of Tibetan Macaques

It is well known that the gut bacterial microbiome can help hosts to digest food resources more efficiently, and they also can change according to variation in host diet across time and space, helping the host to meet its nutrient and energy requirements (Hooper et al. 2002; Donohoe et al. 2011; Koren et al. 2012; Amato et al. 2014; Chevalier et al. 2015). As a species living in a highly seasonal ecosystem, Tibetan macaques depend mostly on a plant diet for their subsistence, including leaves, grass, roots, fruits, and flowers, and they usually shift home ranges to adapt to seasonal changes in food availability (Xiong and Wang 1988; Zhao 1999). The diverse and responsive gut bacterial community of wild-living Tibetan macaques can be considered an important adaptation for their foraging lifestyle. The presence of the relatively abundant fiber-degrading bacteria of Firmicutes and Bacteroidetes in their gut can help them to utilize the heavily plant-based diet. Some well-known fiber-degrading bacteria genera detected in the gut of Tibetan macaques, such as *Succinivibrio* and *Clostridium*, suggest that the gut bacterial microbiome plays an important role in the Tibetan macaques' feeding ecology.

In seasonal ecosystems, one of the most important questions is how animals adapt to seasonal changes in food composition and availability. From winter to spring, Tibetan macaques experience a switch from low quality food resources (mature leaves, roots and plant stem) to high quality food resources (young leaves and flowers). Generally, low-quality food resources are rich in cellulose and hemicellulose, and high-quality food resources are rich in pectin, carbohydrates and simple sugars. Based on a comparative study of the Tibetan macaque gut bacterial microbiome between winter and spring (Sun et al. 2016), the gut bacterial adaptive mechanism for seasonal food type's changes in the Tibetan macaque diet is summarized in Fig. 11.3.

During winter, the representative gut bacterial taxa Proteobacteria, *Succinivibrio* and *Clostridium* significantly increased, and the predicted metagenomes of glycan biosynthesis and metabolic pathways significantly increased in winter samples (Sun et al. 2016). The genus *Succinivibrio*, which usually is detected in rumen microbial ecosystems, ferment glucose efficiently by producing acetic acid and succinic acid (de Menezes et al. 2011), as well as being beneficial to the metabolism of different types of fatty acids (Van Dyke and McCarthy 2002). Another genus *Clostridium* contains many organisms which produce cellulose and hemicellulose-digestive enzymes (Van Dyke and McCarthy 2002; Zhu et al. 2011). The significant increase



Fig. 11.3 Food type change and adaptive shifts of the gut bacterial microbiome in Tibetan macaques. The predicted metagenomes of KEGG pathway and bacterial taxa of the Tibetan macaque gut microbiome, which significantly increased in winter, are beneficial for the digestion of cellulose and hemicellulose rich foods in winter, and the other bacteria significantly increased in spring, which are beneficial for the digestion of pectin, carbohydrate and simple sugar which are abundant in spring

of the genus *Clostridium* in winter samples is very beneficial for the digestion of cellulose and dietary fiber. In addition, evidence from black howler monkeys, humans and mice reveals that Proteobacteria are highly correlated with energy acquisition (Bryant and Small 1956; Koren et al. 2012; Amato et al. 2014; Chevalier et al. 2015). In response to cold weather, primates experience an increase in energy loss (Tsuji et al. 2013), and Tibetan macaques are no exception. The increase of Proteobacteria is beneficial for coping with cold weather. In conclusion, the gut bacterial microbiome in winter increases the efficiency of dietary fiber digestion in Tibetan macaques, which helps them to meet their energy requirements.

In addition, Sun et al. (2016) found that Firmicutes and *Prevotella* were significantly enriched in the Tibetan macaque gut during spring. During this time, the diet consists mainly of young leaves, flowers and bamboo shoots, foods that are richer in digestible pectin, carbohydrates and simple sugars, compared to mature leaves (Xiong and Wang 1988; Zhao 1999; You et al. 2013). The genus *Prevotella* is associated with the digestion of carbohydrates simple sugars, pectin and hemicellulose (Amato et al. 2014). The significant increase of genes related to carbohydrate metabolism and energy metabolism pathways in spring samples also indicates that the gut bacterial community helps break down and make accessible these high-quality food resources, beneficial for macaques to recover from energy loss experienced during the cold conditions of winter.

11.4.2 Gut Fungal Microbiome and Feeding Ecology of Tibetan Macaques

Compared with the gut bacterial microbiome, there is very little data on the primate gut fungal microbiome, and the role of gut fungi in primate foraging ecology is unknown. Sun et al. (2018) first reported the diversity and composition of Tibetan macaque gut mycobiota. Three genera *Aspergillus*, *Penicillium* and *Fusarium* were detected as normal inhabitants in the gut. The two most dominant genera, were *Aspergillus* (12.46%) and *Penicillium* (10.72%). It has been reported that the anaerobic species of these two genera can produce cellulolytic and hemicellulolytic enzymes, which are beneficial to cellulosic biomass degradation (Boots et al. 2013; Liao et al. 2014; Shuji et al. 2014; Solomon et al. 2016; Trinci et al. 1994). Similarly, as robust cellulose and hemicellulose degrader, the genus *Fusarium* was reported in a recent study (Huang et al. 2015). At certain times of the year, Tibetan macaques depend on a plant diet, high in cellulose and hemicellulose (Xiong and Wang 1988; You et al. 2013; Campbell et al. 2001). Our previous studies indicated that the dominant genera of Tibetan macaque gut mycobiota may play an important role in the digestion of these and other plant items.

In addition, the gut fungal microbiome of Tibetan macaques changed with the seasonal change in dietary food content. Fifteen taxa were detected to be significantly enriched in one of the four seasons (Sun et al. 2018). This result indicates that the gut mycobiota can response to dietary shifts. It has been proposed that the gut mycobiota response to seasonal dietary shift is beneficial to the hosts' nutritional and reproductive needs (Noma et al. 1998; Tsuji et al. 2013). However, knowledge about the functions of the particular fungi in the mammalian gut is limited (Milton and May 1976), as are genomic databases and metabolic maps of gut fungi (Huffnagle and Noverr 2013), making it difficult to explain the relationship between mycobiota composition and primate feeding ecology. Based on the available information about the genus *Penicillium* (Shuji et al. 2014), we hypothesize that this summer season enriched genus may aid in the digestion of mature leaves, which contain a higher proportion of cellulose and hemicellulose. However, a possible explanation as to why this genus was not enriched during winter could be that the ingestion of fallen nuts in winter caused the amount of *Penicillium* to decrease due to some chemical interaction (Maria et al. 2014). Secondly, it has been reported that high diversity of gut mycobiota can improve the utilization efficiency of plant fiber consumption (Bauchop 1981; Akin et al. 1983; Denman and Mcsweeney 2010). Thus, the gut mycobiota with high alpha diversity during the winter, reported in our previous study, may be beneficial for Tibetan macaques to digest dietary fiber. In conclusion, the gut fungal mycobiota detected in Tibetan macaque provides evidence for the role of gut fungi in primate foraging ecology. More attention needs to be paid to this in future studies.

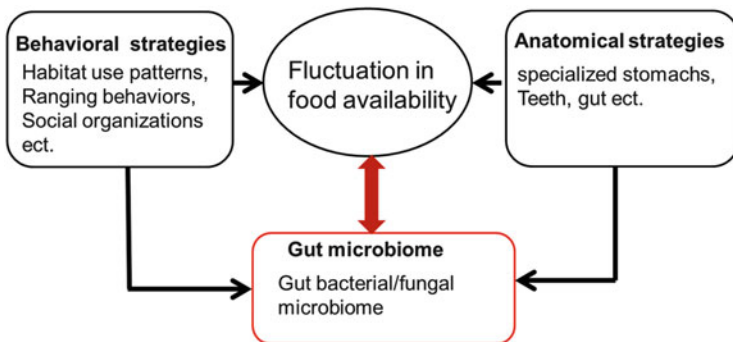


Fig. 11.4 Adaptive mechanisms of wild primates in response to fluctuations in food availability and food quality

11.5 Conclusions and Future Directions

Our studies of the Tibetan macaque gut microbiome reviewed in this chapter add important baseline data for the Tibetan macaque to our knowledge of the mammalian gut microbiome regarding difference in host age, sex and its role in feeding ecology, as well as the role of the gut microbiome in the adaptive radiation of primates. Together with anatomical and behavioral strategies, the gut microbiome is believed to be important factor in the successful evolution of NHPs, particularly as an adaption to the temporal fluctuation in food resource types and their availability. The present data on the wild Tibetan macaque gut microbiome leads us to hypothesize that gut microbiota played an important role in the adaptive radiation of primates, and other animals, which can help them to solve foraging dilemmas in seasonally fluctuating environments (Fig. 11.4). Further research is necessary to test this hypothesis on more mammalian species. In addition, mammals living in a microbial environment, and the microorganisms in the soil and plant foods can also change with seasonal fluctuations. The link between the gut microbiome and environmental microbiomes remain to be elucidated.

Acknowledgments Many thanks to the Huangshan Garden Forest Bureau for their permission and support of this work. We also gratefully acknowledge Paul A. Garber, Lori K. Sheeran and all members of our research group for their excellent work on the gut microbiome of Tibetan macaques. This chapter was supported by grants from the National Natural Science Foundation of China (No. 31870371, 31400330, 31172106), the Special Foundation for Excellent Young Talents in University of Anhui Province, China (No. 2012SQRL018ZD) and the Initial Funding for Doctoral Research in Anhui University (No. J01003229).

References

- Akin DE, Gordon GL, Hogan JP (1983) Rumen bacterial and fungal degradation of *Digitaria pentzii* grown with or without sulfur. *Appl Environ Microbiol* 46:738–748
- Amato KR, Leigh SR, Angela K, Mackie RI, Yeoman CJ, Stumpf RM, Wilson BA, Nelson KE, White BA, Garber PA (2014) The role of gut microbes in satisfying the nutritional demands of adult and juvenile wild, black howler monkeys (*Alouatta pigra*). *Am J Phys Anthropol* 155:652–664
- Amato KR, Leigh SR, Kent A, Mackie RI, Yeoman CJ, Stumpf RM, Wilson BA, Nelson KE, White BA, Garber PA (2015) The gut microbiota appears to compensate for seasonal diet variation in the wild black howler monkey (*Alouatta pigra*). *Microb Ecol* 69:434–443
- Bauchop T (1981) The anaerobic fungi in rumen fibre digestion. *Agric Environ* 6:339–348
- Bokulich NA, Mills DA (2013) Improved selection of internal transcribed spacer-specific primers enables quantitative, ultra-high-throughput profiling of fungal communities. *Appl Environ Microbiol* 79(8):2519–2526
- Bolnick DI, Snowberg LK, Hirsch PE, Lauber CL, Parks B, Lusi AJ, Knight R, Caporaso JG, Svanbäck R (2014) Individual diet has sex-dependent effects on vertebrate gut microbiota. *Nat Commun* 5:4500
- Boots B, Lillis L, Clipson N, Petrie K, Kenny DA, Boland TM, Doyle E (2013) Responses of anaerobic rumen fungal diversity (phylum Neocallimastigomycota) to changes in bovine diet. *J Appl Microbiol* 114:626–635
- Bryant MP, Small NJ (1956) Characteristics of two new genera of anaerobic curved rods isolated from the rumen of cattle. *J Bacteriol* 72:22–26
- Burrows AM (2010) The evolution of exudativory in primates. Springer, New York
- Cachel S (1989) Primate adaptation and evolution. *Int J Primatol* 10:487–490
- Campbell JL, Glenn KM, Grossi B, Eisemann JH (2001) Use of local North Carolina browse species to supplement the diet of a captive colony of folivorous primates (*Propithecus* sp.). *Zoo Biol* 20:447–461
- Campera M, Serra V, Balestri M, Barresi M, Ravaolaha M, Randriatafika F, Donati G (2014) Effects of habitat quality and seasonality on ranging patterns of collared brown lemur (*Eulemur collaris*) in littoral forest fragments. *Int J Primatol* 35:957–975
- Chevalier C, Stojanović O, Colin DJ, Suarez-Zamorano N, Tarallo V, Veyrat-Durebex C, Rigo D, Fabbiano S, Stevanović A, Hagemann S (2015) Gut microbiota orchestrates energy homeostasis during Cold. *Cell* 163:1360–1374
- Chivers DJ, Wood BA, Bilsborough A (1984) Food acquisition and processing in primates: concluding discussion. In: Chivers DJ, Wood BA, Alan B (eds) Food acquisition and processing in primates. Springer, New York, pp 545–556
- Clayton JB, Gomez A, Amato K, Knights D, Travis DA, Blekhan R, Knight R, Leigh S, Stumpf R, Wolf T (2018) The gut microbiome of nonhuman primates: lessons in ecology and evolution. *Am J Primatol* 80:e22867
- Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol Monogr* 53:209–229
- de Menezes AB, Lewis E, O'Donovan M, O'Neill BF, Clipson N, Doyle EM (2011) Microbiome analysis of dairy cows fed pasture or total mixed ration diets. *FEMS Microbiol Ecol* 78:256–265
- Degnan PH, Pusey AE, Lonsdorf EV, Goodall J, Wroblewski EE, Wilson ML, Rudicell RS, Hahn BH, Ochman H (2012) Factors associated with the diversification of the gut microbial communities within chimpanzees from Gombe National Park. *Proc Natl Acad Sci U S A* 109:13034–13039
- Denman S, Mcsweeney C (2010) Development of a real-time PCR assay for monitoring anaerobic fungal and cellulolytic bacterial populations within the rumen. *FEMS Microbiol Ecol* 58:572–582

- Donohoe DR, Nikhil G, Xinxin Z, Wei S, O'Connell TM, Bunger MK, Bultman SJ (2011) The microbiome and butyrate regulate energy metabolism and autophagy in the mammalian colon. *Cell Metab* 13:517–526
- Fan P, Ni Q, Sun G, Bei H, Jiang X (2009) Gibbons under seasonal stress: the diet of the black crested gibbon (*Nomascus concolor*) on Mt. Wuliang, Central Yunnan, China. *Primates* 50:37–44
- Greenblum S, Turnbaugh PJ, Borenstein E (2012) Metagenomic systems biology of the human gut microbiome reveals topological shifts associated with obesity and inflammatory bowel disease. *PNAS* 109:594–599
- Hajishengallis G, Liang S, Payne MA, Hashim A, Jotwani R, Eskan MA, Mcintosh ML, Alsam A, Kirkwood KL, Lambris JD (2011) Low-abundance biofilm species orchestrates inflammatory periodontal disease through the commensal microbiota and complement. *Cell Host Microbe* 10 (5):497–506
- Hanya G, Chapman CA (2013) Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecol Res* 28:183–190
- Hanya G, Qarro M, Tattou MI, Fuse M, Vallet D, Yamada A, Go M, Takafumi H, Tsujino R, Agetsuma N (2011) Dietary adaptations of temperate primates: comparisons of Japanese and Barbary macaques. *Primates* 52:187–198
- Hird SM (2017) Evolutionary biology needs wild microbiomes. *Front Microbiol* 8:725
- Hoffmann C, Dollive S, Grunberg S, Chen J, Li H, Wu GD, Lewis JD, Bushman FD (2013) Archaea and fungi of the human gut microbiome: correlations with diet and bacterial residents. *PLoS One* 8:e66019
- Hooper LV, Gordon JI (2001) Commensal host-bacterial relationships in the gut. *Science* 292 (5519):1115–1118
- Hooper LV, Midtvedt T, Gordon JI (2002) How host-microbial interactions shape the nutrient environment of the mammalian intestine. *Annu Rev Nutr* 22:283–307
- Hooper LV, Littman DR, Macpherson AJ (2012) Interactions between the microbiota and the immune system. *Science* 336:1268–1273
- Huang Y, Busk PK, Lange L (2015) Cellulose and hemicellulose-degrading enzymes in *Fusarium commune* transcriptome and functional characterization of three identified xylanases. *Enzyme Microb Technol* 73–74:9–19
- Huffnagle GB, Noverr MC (2013) The emerging world of the fungal microbiome. *Trends Microbiol* 21:334–341
- Iliev ID, Underhill DM (2012) Interactions between commensal fungi and the C-type lectin receptor Dectin-1 influence colitis. *Science* 336:1314–1317
- Koren O, Goodrich J, Cullender T, Spor A, Laitinen K, Bäckhed HK, Gonzalez A, Werner J, Angenent L, Knight R (2012) Host remodeling of the gut microbiome and metabolic changes during pregnancy. *Cell* 150:470–480
- Lambert JE (2011) Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campbell C, Fuentes A, MacKinnon KC, Panger M, Bearder S, Stumpf R (eds) *Primates in perspective*, 2nd edn. Oxford University Press, Oxford, pp 512–522
- Ley RE, Micah H, Catherine L, Turnbaugh PJ, Rob Roy R, J Stephen B, Schlegel ML, Tucker TA, Schrenzel MD, Rob K (2008) Evolution of mammals and their gut microbes. *Science* 322 (5905):1188
- Liao H, Li S, Wei Z, Shen Q, Xu Y (2014) Insights into high-efficiency lignocellulolytic enzyme production by *Penicillium oxalicum* GZ-2 induced by a complex substrate. *Biotechnol Biofuels* 7(1):162
- Mackie RI (2002) Mutualistic fermentative digestion in the gastrointestinal tract: diversity and evolution. *Integr Comp Biol* 42:319–326
- Mar RM, Pérez D, Javier CF, Esteve E, Maringarcia P, Xifra G, Vendrell J, Jové M, Pamplona R, Ricart W (2016) Obesity changes the human gut mycobiome. *Sci Rep* 6:21679

- Margaret MFN, Hadfield MG, Bosch TCG, Carey HV, Tomislav DLO, Douglas AE, Nicole D, Gerard E, Tadashi F, Gilbert SF (2013) Animals in a bacterial world, a new imperative for the life sciences. *PNAS* 110:3229–3236
- Maria U, Xiaoyu W, Baer DJ, Novotny JA, Marlene F, Volker M (2014) Effects of almond and pistachio consumption on gut microbiota composition in a randomised cross-over human feeding study. *Br J Nutr* 111:2146–2152
- Maurice CF, Cl KS, Ladau J, Pollard KS, Fenton A, Pedersen AB, Turnbaugh PJ (2015) Marked seasonal variation in the wild mouse gut microbiota. *ISME J* 9:2423–2434
- McCord AI, Chapman CA, Weny G, Tumukunde A, Hyeroba D, Klotz K, Koblings AS, Mbori DN, Cregger M, White BA (2014) Fecal microbiomes of non-human primates in Western Uganda reveal species-specific communities largely resistant to habitat perturbation. *Am J Primatol* 76:347–354
- Mckenney EA, Melissa A, Lambert JE, Vivek F (2015) Fecal microbial diversity and putative function in captive western lowland gorillas (*Gorilla gorilla gorilla*), common chimpanzees (*Pan troglodytes*), Hamadryas baboons (*Papio hamadryas*) and binturongs (*Arctictis binturong*). *Integr Zool* 9:557–569
- Milton K, May ML (1976) Body weight, diet and home range area in primates. *Nature* 259:459–462
- Noma N, Suzuki S, Izawa K (1998) Inter-annual variation of reproductive parameters and fruit availability in two populations of Japanese macaques. *Primates* 39:313–324
- Ochman H, Worobey M, Kuo CH, Ndjanga JBN, Peeters M, Hahn BH, Hugenholtz P (2010) Evolutionary relationships of wild hominids recapitulated by gut microbial communities. *PLoS Biol* 8:8
- Qin J, Li R, Raes J, Arumugam M, Burgdorf KS, Manichanh C, Nielsen T, Pons N, Levenez F, Yamada T (2010) A human gut microbial gene catalogue established by metagenomic sequencing. *Nature* 464(7285):59–65
- Qiu X, Zhang F, Yang X, Wu N, Jiang W, Li X, Li X, Liu Y (2015) Changes in the composition of intestinal fungi and their role in mice with dextran sulfate sodium-induced colitis. *Sci Rep* 5:10416
- Ren T, Grieneisen LE, Alberts SC, Archie EA, Wu M (2015) Development, diet and dynamism: longitudinal and cross-sectional predictors of gut microbial communities in wild baboons. *Environ Microbiol* 18(5):1312–1325
- Rizzetto L, De FC, Cavalieri D (2014) Richness and diversity of mammalian fungal communities shape innate and adaptive immunity in health and disease. *Eur J Immunol* 44:3166–3181
- Rodman PS, Cant JGH (1984) Anatomy and behavior. (Book reviews: adaptations for foraging in nonhuman primates). *Science* 226:1187–1188
- Romani L (2011) Immunity to fungal infections. *Nat Rev Immunol* 11:275–288
- Sharon G, Turnbaugh PJ, Elhanan B (2012) Metagenomic systems biology of the human gut microbiome reveals topological shifts associated with obesity and inflammatory bowel disease. *PNAS* 109:594–599
- Shuji T, Takashi K, Tetsuo K (2014) Complex regulation of hydrolytic enzyme genes for cellulosic biomass degradation in filamentous fungi. *Appl Microbiol Biotechnol* 98:4829–4837
- Sokol H, Leducq V, Aschard H, Pham HP, Jegou S, Landman C, Cohen D, Liguori G, Bourrier A, Nionlarmurier I (2017) Fungal microbiota dysbiosis in IBD. *Gut* 66:1039–1048
- Solomon KV, Haitjema CH, Henske JK, Gilmore SP, Borges-Rivera D, Lipzen A, Brewer HM, Purvine SO, Wright AT, Theodorou MK (2016) Early-branching gut fungi possess a large, comprehensive array of biomass-degrading enzymes. *Science* 351:1192–1195
- Starr C, Nekaris KAI, Leung L (2012) Hiding from the moonlight: luminosity and temperature affect activity of Asian nocturnal primates in a highly seasonal forest. *PLoS One* 7:e36396.1–e36396.8
- Strati F, Paola MD, Stefanini I, Albanese D, Rizzetto L, Lionetti P, Calabrò A, Jousson O, Donati C, Cavalieri D (2016) Age and gender affect the composition of fungal population of the human gastrointestinal tract. *Front Microbiol* 7:1227

- Sun B, Xi W, Bernstein S, Huffman MA, Xia DP, Gu Z, Rui C, Sheeran LK, Wagner RS, Li J (2016) Marked variation between winter and spring gut microbiota in free-ranging Tibetan Macaques (*Macaca thibetana*). *Sci Rep* 6:26035
- Sun B, Gu Z, Wang X, Huffman MA, Garber PA, Sheeran LK, Zhang D, Zhu Y, Xia DP, Li JH (2018) Season, age, and sex affect the fecal microbiota of free-ranging Tibetan macaques (*Macaca thibetana*). *Am J Primatol* 80(7):e22880
- Trinci APJ, Davies DR, Gull K, Lawrence MI, Nielsen BB, Rickers A, Theodorou MK (1994) Anaerobic fungi in herbivorous animals. *Mycol Res* 98:129–152
- Tsuji Y, Hanya G, Grueter CC (2013) Feeding strategies of primates in temperate and alpine forests: comparison of Asian macaques and colobines. *Primates* 54:201–215
- Tung J, Barreiro LB, Burns MB, Grenier JC, Lynch J, Grieneisen LE, Altmann J, Alberts SC, Blekhan R, Archie EA (2015) Social networks predict gut microbiome composition in wild baboons. *elife* 4:e05224
- Turnbaugh PJ, Ley RE, Mahowald MA, Magrini V, Mardis ER, Gordon JI (2006) An obesity-associated gut microbiome with increased capacity for energy harvest. *Nature* 444:1027–1031
- Underhill DM, Iliev ID (2014) The mycobiota: interactions between commensal fungi and the host immune system. *Nat Rev Immunol* 14:405–416
- Ungar PS (1995) Fruit preferences of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. *Int J Primatol* 16:221–245
- Van Dyke M, McCarthy A (2002) Molecular biological detection and characterization of *Clostridium* populations in municipal landfill sites. *Appl Environ Microbiol* 68:2049–2053
- Wheeler ML, Limon JJ, Bar AS, Leal CA, Gargus M, Tang J, Brown J, Funari VA, Wang HL, Crother TR (2016) Immunological consequences of intestinal fungal dysbiosis. *Cell Host Microbe* 19(6):865–873
- Wu Q, Wang X, Ding Y, Hu Y, Nie Y, Wei W, Ma S, Yan L, Zhu L, Wei F (2017) Seasonal variation in nutrient utilization shapes gut microbiome structure and function in wild giant pandas. *Proc Biol Sci* 284:20170955
- Xiong C, Wang Q (1988) Seasonal habitat used by Thibetan Monkeys. *Acta Theriol Sinica* 8:176–183
- Xu B, Xu W, Yang F, Li J, Yang Y, Tang X, Mu Y, Zhou J, Huang Z (2013) Metagenomic analysis of the pygmy loris fecal microbiome reveals unique functional capacity related to metabolism of aromatic compounds. *PLoS One* 8(2):e56565
- Xu B, Xu W, Li J, Dai L, Xiong C, Tang X, Yang Y, Mu Y, Zhou J, Ding J (2015) Metagenomic analysis of the *Rhinopithecus bieti* fecal microbiome reveals a broad diversity of bacterial and glycoside hydrolase profiles related to lignocellulose degradation. *BMC Genomics* 16:174
- Yamada A, Muroyama Y (2010) Effects of vegetation type on habitat use by crop-raiding Japanese macaques during a food-scarce season. *Primates* 51:159
- Yatsunenko T, Rey FE, Manary MJ, Trehan I, Dominguez-Bello MG, Contreras M, Magris M, Hidalgo G, Baldassano RN, Anokhin AP (2012) Human gut microbiome viewed across age and geography. *Nature* 486(7402):222–227
- Yokoe Y, Yasumasu I (1964) The distribution of cellulase in invertebrates. *Comp Biochem Physiol* 13:323–338
- You SY, Yin HB, Zhang SZ, Tian-Ying JI, Feng XM (2013) Food habits of *Macaca thibetana* at Mt. Huangshan, China. *J Biol* 30(5):64–67
- Zhang M, Li J, Zhu Y, Wang X, Wang S (2010) Male mate choice in Tibetan macaques *Macaca thibetana* at Mt. Huangshan, China. *Curr Zool* 56:213–221
- Zhao Q-K (1999) Responses to seasonal changes in nutrient quality and patchiness of food in a multigroup community of Tibetan macaques at Mt. Emei. *Int J Primatol* 20:511–524
- Zhou Q, Wei F, Huang C, Li M, Ren B, Luo B (2007) Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. *Int J Primatol* 28:657–671
- Zhu L, Wu Q, Dai J, Zhang S, Wei F (2011) Evidence of cellulose metabolism by the giant panda gut microbiome. *PNAS* 108:17714–17719

Open Access This chapter is licensed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence and indicate if changes were made.

The images or other third party material in this chapter are included in the chapter's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the chapter's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

