The digesta particle size of Japanese macaques in Yakushima: Variation, determinants and its potential influence on digestion

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Background

Chewing is a signature behavior and the major step in reducing digesta particle size in mammals. It is a critical step in the feeding of mammalian herbivores. As the result of chewing, digesta particle size reflects the interaction between the properties of food and the chewing ability of the animals while influencing digestion. Documenting such data can provide insight into both feeding ecology and digestive adaptation in herbivores. Researchers usually use fecal particle size as a proxy for digesta particle size during studying feeding ecology and digestion because chemical digestion only has a minor influence.

Previous studies recognized potential factors that influence digesta particle size including factors related to diet such as the mechanical properties of food, and factors related to chewing ability, such as tooth wear. However, most of these studies focus on folivores. Results from fruit-eating primates showed a different pattern. With their complicated diet, it is difficult to generalize the conclusion from previous studies to primates. This thesis aims to clarify the variation pattern, the determinants, and the potential influence of digesta particle size on digestion in primates that are dietary generalists by using the Japanese macaques in Yakushima, Japan (*Macaca fuscata yakui*) as a model.

Methods

In Chapter 2, to clarify the pattern of variation of digesta particle size in Japanese macaques, I compared their fecal particle size in the lowland, highland, and summit zone of Yakushima. In Chapter 3, to reveal the determinants, I collected data on feeding behavior, fecal particle size, and the dietary toughness in the lowland zone. I compare the dietary toughness and fecal particle size among months and age-sex classes. I also examined the influence of diet composition, dietary toughness, and age-sex classes on fecal particle size by GLMM. In Chapter 4, to examine the influence of digesta particle size on

digestion when consuming a generalist diet, I conducted *in vitro* digestibility and fermentation assay on five typical foods from the Japanese macaque diet. Finally, I used GLM analysis to compare the importance of particle size in explaining the variations in digestibility and fermentation speed between food items.

Results

Chapter 2 found that although there were variations in digesta particle size, it is limited to specific conditions. I only found fecal particle size in the summit zone was significantly higher than it was in the other zones in autumn (two-way ANOVA, p=0.0002, Tukey HSD: summit vs lowland, p=0.0015, summit vs highland, p=0.0021). Chapter 3 found significant differences across months in the dietary toughness (Kruskal-Wallis test, $P < 0.001$) and fecal particle size (Kruskal-Wallis test, $P < 0.001$). I did not find significant fecal particle size difference across age-sex classes (Kruskal-Wallis test, $P = 0.28$) or absolute ages(Kruskal-Wallis test, $P = 0.06$). In GLMM analysis, however, only the intake of fruits showed a marginally significant negative effect. Chapter 4 demonstrates that in the five typical foods of Japanese macaques, the influence of particle size on digestion depends on food types. The influence of particle size on digestibility is more obvious in seeds and mature leaves compared to fruits and young leaves. The influence on the speed of fermentation is more obvious in fruits and seeds compared to mature leaves and young leaves.

Discussion

The determinants and the potential influence of digesta particle size are different in Japanese macaques in Yakushima compared to folivores. The results showed the mechanical properties of foods, and the chewing ability was not important in the variation of digesta particle size while the influence of reducing particle size on digestion may be more relevant. In a leaf-dominated diet, the major factors are the mechanical defenses of plants against herbivory and the animals' ability to overcome such defenses. When dietary generalists eat mechanically unchallenging foods, the major factor may be whether chewing is necessary to improve digestion.

Predicting food quality from digesta particle size should be treated with caution. For generalist primates, large digesta particle size does not necessarily correspond to low-quality food. These also suggest new perspectives for explaining food selection. For eating leaves, selecting leaves that are easier for reducing digesta particle size may be critical as the particle size of leaves strongly influences digestion. This can help us understand the avoidance of tough and fiber-rich food in primates. For generalist primates, selecting foods that do not require chewing may be important. This can explain the preference for fruits in primates. Besides, the factors that influence digesta particle size may also influence feeding through influencing chewing behavior.

It is necessary to conduct more digesta particle size studies in more species of primate while including the influence of chewing on digestion as a factor. For generalist primates, considering whether chewing matters for the study subject may be more relevant than asking whether they face challenges in chewing. It is necessary to further examine the factors that decide the effects of particle size on digestion. As a proximate determinant of digesta particle size, the observation of chewing behavior is also worth further investigation.

Conclusions

This thesis used Japanese macaques in Yakushima as a model to explore the determinants and the potential influence on digestion of digesta particle size in generalist primates. They indicate that digesta particle size mainly reflects the mechanical resistance of food and the chewing ability during eating leaves while reflecting the influence of reducing particle size on digestion in generalist primates. The latter is an important but rarely explored perspective to interpret relevant data, especially in primates that have complicated diets. Further study is required to clarify the details in this perspective.