Feeding competition in Japanese macaques in Yakushima: effects of intergroup hostility and group size

Yosuke Kurihara

Introduction

Among the factors determining fitness of group-living animals across a wide range of species, feeding competition is the most prevalent. Intragroup scramble competition and intergroup contest competition are group-size-dependent, and their combination could cause variations in fitness across group sizes. Most studies have shown feeding and reproductive disadvantages in larger groups, suggesting that costs of intragroup scramble competition outweigh benefits of intergroup contest competition. Despite the presumed benefits of group living, the importance of intergroup feeding competition remains unclear. Japanese macaques (*Macaca fuscata yakui*) in Yakushima Island, Japan, are ideal subjects to study intergroup feeding competition. The island has two long-term research sites (coastal and highland forests), where macaques are genetically identical, but subjected to different levels of intergroup feeding competition. Comparing the food conditions and food patch use between the two sites can help in understanding the ecological basis and behavioral mechanisms underlying intergroup feeding competition. Additionally, birth rates increase with group size in macaques of the coastal forest in contrast to the general trend in primates. Revealing mechanisms of group-size effects on reproductive success will contribute to understanding the costs and benefits of group living. The aim of the present study is to reveal the costs and benefits of group living in Japanese macaques in Yakushima Island from the perspective of feeding competition.

Methods

To reveal the ecological basis and behavioral mechanisms of intergroup feeding competition, I compared food patch characteristics and food patch use between coastal and highland forests. Behavioral data were collected from adult females of three groups (larger coastal group: 30–33 individuals; smaller coastal group: 8–13 individuals; highland group: 24–27 individuals) by using focal animal sampling, and vegetation survey was conducted in the two sites. To reveal the mechanisms of group-size effects on reproductive success in the coastal forest, I compared feeding behavior and energy budgets (energy intake, expenditure, and balance) between two different-sized groups of macaques. Energy budgets were estimated by conducting nutritional analysis of the food items.

Results and Discussion

Intergroup relationships were hostile when food patches were worth defending and easy to defend. In the coastal forest characterized by intense intergroup conflict, the smaller subordinate group increased the number of co-feeding individuals in response to location-specific risk of intergroup encounters. Feeding duration in one patch, frequency of visual scanning, and number of co-feeding adult males did not depend on such risk even in the coastal forest. The highland group did not modify food patch use based on such risk. Additionally, I found differences in feeding behaviors between two different-sized groups of macaques in the coastal forest. The larger group had a bigger home range and spent more time feeding, especially on mature leaves, suggesting more intense intragroup scramble competition. Mature-leaf feeding did not lead to a longer duration of feeding in one patch, but enabled the macaques to stay with a larger number of co-feeding individuals in the larger group. The smaller group traveled longer distances and spent more time traveling despite the similarities of the number of visited

patches and inter-patch distance between the two groups, suggesting greater costs of intergroup contest competition. However, the energy budgets did not differ between the two groups.

Conclusion

The present study revealed the ecological basis of intergroup feeding competition. Additionally, I found variation in feeding behavior depending on group size in the coastal forest characterized by intense intergroup conflict; however, such variation was not translated into energy budgets of the macaques. The present study emphasizes the necessity of long-term research for critically assessing the importance of intergroup feeding competition as a selective force of group living.