Effects of the habitat differences on feeding behavior and co-feeding relationships in infant Japanese macaques (*Macaca fuscata*) during weaning period

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Introduction

Many primate socioecological studies have revealed that food conditions affect the social relationships between adult females. Although the infancy is the significant period that develops the social relationships, the effect of food conditions on social relationships of infants is unknown. During weaning, infants need to develop co-feeding relationships with group members. Compared with adults, infant primates prefer foods that are easy to access and process; thus, their mothers may not always be suitable co-feeding partners. Regional differences in food conditions exist among habitats of Japanese macaques (Macaca fuscata), especially in winter. Infants need to eat solid foods before the onset of winter. In this study, I compared between the northern (41°N, Shimokita) and southern limits (30°N, Yakushima) of their distribution. In Shimokita, a region covered with deciduous forests and snow, macaques feed on bark, dormant buds, and sedges. In the lowland Yakushima, which is covered with evergreen forests, macaques can feed on leaves and fruits even during winter. This study aimed to provide a comprehensive examination of the physical properties that influence food selection by infants. Furthermore, the influence of habitat differences on suckling and feeding behavior and co-feeding relationships of infants were also investigated by comparison between sites.

Methods

Four mother–infant pairs were studied in Shimokita and Yakushima during winter. I simultaneously followed an infant and its mother. Their activities, the distance between them, and the individual within 2 m of the focal animal were recorded. The size, need for processing, and height of food items were recorded by direct observation, whereas the fracture toughness of food items was measured using a rheometer. In addition, the crown sizes and densities of the food trees were recorded by a vegetation survey. I examined the effects of 4 physical properties (i.e., food size, need for processing, height, and fracture toughness) on the dietary differences of mothers and infants by using generalized linear mixed models. Following this analysis, I calculated food physical property scores (FPS) based on the abovementioned physical properties, weighting by the degree of infants' preference, in order to comprehensively evaluate the degree of difficulty in accessing and processing food items for infants.

Results

Compared to mothers, infants at both sites fed more frequently on items that could be eaten in a single bite, at lower positions in trees, and that did not require processing. In addition, infants spent less time feeding on food items that were tougher than 2000 J/m² than did their mothers. Infants in Shimokita spent more time in contact with the mother's nipple than did infants in Yakushima, and the average time spent feeding was equivalent to that spent by their mothers. The ratio of time spent feeding on large food items was higher in infants in Shimokita than those in Yakushima. Infants at both sites spent more time apart from their mothers when the mothers fed on food items that were

more difficult to access or process (i.e., higher FPS). When infants were away from their mothers, they fed mainly in close proximity to other infants and juveniles that fed on food items that were easier to access or process (i.e., lower FPS) than the food items eaten by their mothers. Compared to infants in Yakushima, infants in Shimokita spent more time co-feeding with the mothers, and mothers fed more on food items that were easy to access or process. When away from their mothers, the time spent co-feeding with other infants was shorter in infants in Shimokita than those in Yakushima. The density and crown size of food trees was lower and smaller in Shimokita than in Yakushima.

Discussion

In both habitats, infants fed more frequently on food items that were easy to access or process because of the low physical ability compared with that of their mothers. Such food selection by infants reduces the costs of feeding and allows them to avoid falling from high trees. The dietary difference in terms of food physical properties causes separation between mothers and infants. When infants are separated from their mothers, other infants that have similar physical abilities are important co-feeding partners in terms of searching for food items and avoiding losing other group members. In addition, infants that co-feed with other infants reduce the level of food competition because the overall food requirement of infants is smaller than that of other age classes. Food conditions in terms of not only the nutritional quality of foods but also the food physical property (food size) were severer in Shimokita than in Yakushima. Under poor food conditions and low temperatures (Shimokita), infants spent more time feeding and

suckling and tended to keep in close proximity to their mothers during feeding for their survival. In addition, it was easier for infants in Shimokita than those in Yakushima to co-feed with their mothers because of lower FPS of foods eaten by mothers. When infants were away from their mothers, the smaller crown size of food trees in Shimokita limited co-feeding with other infants.

Conclusion

In both habitats, the physical properties of food items affected food selection of infants.

The habitat differences (food conditions and the climate) affected the suckling and feeding time, and co-feeding time spent with mothers and other infants.

離乳期のニホンザル (Macaca fuscata) のアカンボウにおける 採食行動と伴食関係に生息環境が及ぼす影響

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霊長類において、食物環境がオトナメス間関係に与える影響を調べる社会生態学的研究が盛んに行われてきたが、アカンボウの社会関係に及ぼす影響については注目されてこなかった。アカンボウ期は、群れ他個体との関係が形成される重要な時期であり、特に離乳期は、伴食を通じた関係が生じる。アカンボウは、入手や処理の容易な食物を好むことが示唆されている。ニホンザルのアカンボウは、離乳期に当たる冬には採食を行う必要が生じるが、冬季の食物環境は地域によって異なる。彼らの分布北限の下北半島は、落葉樹林帯で、積雪があり食物は樹皮や冬芽などに限定される。一方で、南限の屋久島は、常緑樹林帯で、冬でも葉や果実が利用できる。本研究は、食物の物理的性質がアカンボウの食物選択に及ぼす影響を検討後、それを含めた生息環境の違いがアカンボウの吸乳・採食行動と伴食関係に与える影響を明らかにすることを目的とした。

下北と屋久島において、冬季に母子 4 組を対象に、母子の採食行動と近接相手を記録した。また、食物樹の密度と樹冠の大きさを検討するため植生調査を行った。各食物を 4 つの物理的性質(食物の大きさ、操作の有無、高さ、かたさ)により評価し、母子の食物利用の差にそれらの物理的性質が与える影響を総合的に検討した。その後、アカンボウに好まれる寄与度に応じ重みづけをした 4 つの物理的性質を使用し、食物の物理的性質を総合的に評価するスコアを

作成した。

両地域共にアカンボウは母親と比較し、一口で利用できる(小さい)、操作がない、低い位置にある、2000J/m² 未満のかたさの食物を好んだ。屋久島と比較し、下北のアカンボウは、乳首接触時間が 2 倍程度長く、採食時間も母親と同等程度まで延ばしていた。また、下北のアカンボウは、大きな食物を利用する比率が高かった。両地域共に、母親が入手や処理の難しい食物を利用した際は、アカンボウは母親から離れる傾向にあった。母親から分離後、アカンボウは、母親より入手や処理のしやすい食物を利用する他のアカンボウやコドモと伴食することが多かった。屋久島と比較し下北では、アカンボウは母親と近接し採食する時間が長く、また母親は入手や処理のしやすい食物に長い採食時間を費やしていた。また、母親と分離時に、下北のアカンボウは他のアカンボウとの伴食時間が短かった。食物樹の密度や樹冠サイズは下北の方が小さかった。

両地域共に、身体能力が未熟なアカンボウは、母親と比較し入手や処理の容易な食物に採食時間を費やし、また高木からの落下の危険を回避していた。こうした食物利用の違いにより、母子の分離が生じることが示唆された。また、アカンボウにとって他のアカンボウは、採食量が少ないため採食競合が生じにくく、はぐれる危険を回避しつつ伴食する相手として適していた。屋久島と比較し、下北では、母親が入手や処理の容易な食物に長い採食時間を費やしていたため、アカンボウは母親と伴食しやすく、また気温が低く、大きな食物に依存せざるを得ない点も含み食物環境が厳しいため、下北のアカンボウは吸乳時間を延ばし、採食時に母親の保護を受けやすい距離に留まることが示唆された。また、下北では食物の樹冠サイズが制限となり、アカンボウは他のアカンボウと伴食しにくかったと考えられる。

以上のことから、食物の物理的性質は、アカンボウの食物選択に生息環境によらない一貫した影響を及ぼす一方で、母親による処理や入手の容易な食物の利用の程度の差に生息環境による違いをもたらし、気温や食物条件などの他の生息環境の違いと相まって、アカンボウの採食行動と伴食関係に影響を与えていた。