

Abstract of thesis

Male-to-female aggression shapes fission–fusion dynamics in wild Japanese macaques (*Macaca fuscata*): Female counterstrategies utilizing high-ranking males as “protectors”

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INTRODUCTION

In primates, fission–fusion dynamics (FFD)—which are characterized by temporal variation in three dimensions: (a) subgroup size, (b) subgroup composition, and (c) spatial cohesion among group members—are a key component of social systems. Identifying the factors that shape FFD is essential for understanding the diversity and evolution of primate societies. Although various ecological and social factors that influence FFD have been identified, the effect of an important social factor—male-to-female aggression as a form of sexual coercion—has rarely been examined. Given its widespread occurrence across primates and the costs it imposes on females, clarifying how male-to-female aggression influences FFD addresses a major gap in our understanding of primate social systems.

Japanese macaques (*Macaca fuscata*) generally form cohesive groups; yet subgrouping occasionally occurs, and spatial cohesion among individuals fluctuates over time. Moreover, intense male-to-female aggression is frequently observed during the mating season. In this thesis, I investigated how male-to-female aggression during the mating season affects the three dimensions of FFD in a wild group of Japanese macaques. Crucially, the effect of male aggression on FFD is generally expected to depend on how females counter such aggression. Accordingly, I hypothesized that the high-ranking males (alpha and beta males) functioned as “protectors” of females against male aggression, and that females adjusted their spatial associations with these males in response to aggression risk to utilize their protective effects, thereby influencing group FFD.

METHODS

I conducted field observations from October 2018 to March 2022. The study period was divided into eight observation periods: four mating and four non-mating seasons. The study group was the B₁ group on Kinkazan Island. All observed aggregations of B₁ group members were defined as “subgroups” and their daily membership was recorded. The

subgroup that contained more than 50% of the adult females was defined as the “main subgroup.” An individual was defined as having “left” the main subgroup when present on day $t - 1$ but absent on day t , and as having “returned” when absent on day $t - 1$ but present on day t . I recorded all male-to-female aggression using behavioral sampling and monitored each adult female’s reproductive state (estrous or anestrus).

I also collected behavioral data on adult females using the focal animal sampling method. I recorded the following data at one-minute intervals: (1) focal female’s activity, (2) IDs of individuals within 3-m proximity, (3) IDs of grooming partners, and (4) membership of the resting unit—a cluster of resting or grooming adults defined using the 3-m chain rule—to which the focal female belonged. To quantify affiliative relationships between the high-ranking males and adult females, I calculated the dyadic Composite Sociality Index (CSI) using proximity and grooming data.

RESULTS

During the study period, the alpha male, *TY*, and the beta male, *IT*, exhibited an unusual behavioral pattern for Japanese macaques: repeatedly leaving and returning to the main subgroup. First, I provided a detailed description of the frequent subgrouping events observed during the 2019 mating season and showed that subgrouping tended to occur when the alpha male, *TY*, left the main subgroup and only a subset of females—typically those who had high CSI values with him, along with their maternal relatives—followed him.

Building on these findings, I conducted quantitative analyses to examine the factors that influenced two dimensions of FFD: temporal variation in subgroup size and subgroup composition. During the mating season, anestrus females who had higher CSI values with the high-ranking males, especially with *TY*, were more likely to follow the corresponding male when he left or returned to the main subgroup, thereby influencing the size and composition of subgroups. Importantly, anestrus females experienced less male aggression on days when the high-ranking males were present than on days when they were absent from the main subgroup, suggesting that these males functioned as “protectors” of anestrus females.

Finally, I investigated whether the risk of male aggression influenced the remaining dimension of FFD: spatial cohesion among individuals within subgroups. During the mating season, *TY* played a key role in maintaining cohesion within the resting-unit network. Moreover, on days when *TY* was present, anestrus females tended to increase their spatial proximity to *TY* and other females while resting or grooming as the risk of male aggression increased (indexed by the number of observed males). Notably,

anestrous females were able to reduce the male aggression they received through such spatial adjustments.

DISCUSSION

The results of this study suggest that male-to-female aggression shaped FFD in Japanese macaques by prompting anestrus females to adjust their subgrouping patterns and spatial cohesion according to the risk of male aggression. When the high-ranking males, particularly *TY*, who functioned as “protectors” against male aggression, left the main subgroup, females closely associated with them tended to follow them, likely to maintain such protection. Additional analyses showed that even anestrus females who did not follow the high-ranking males were more likely to leave the main subgroup when these males were absent, presumably to avoid the increased risk of male aggression in their absence. In contrast, when *TY* was present, anestrus females were able to mitigate their risk of male aggression by increasing their spatial cohesion with other females around *TY*.

This study thus highlights the critical, yet often overlooked, role of female counterstrategies against male-to-female aggression in shaping group FFD. Future comparative studies are expected to provide a more comprehensive understanding of how male-to-female aggression affects FFD across primates.