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学位論文題目 Behavioral flexibility in physical and social contexts in Asian elephants

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博士論文の要旨

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論文題目：Behavioral flexibility in physical and social contexts in Asian elephants
(アジアゾウの物理的文脈および社会的文脈における行動柔軟性)

Behavioral flexibility has been receiving attention in studies of cognition and behavior in animals (reviewed in Lefebvre 2017; Lea et al. 2020; Strier 2017). In the studies of comparative cognition, behavioral flexibility has been regarded as a reflection of complex and sophisticated cognition (Lea et al. 2020). On the other hand, in behavioral ecology, behavioral flexibility refers to an individual's flexible ability to change behavior in response to external pressures (Kappeler et al. 2013; Strier 2017; Lea et al. 2020). Thus, the broad applicability of the definition of behavioral flexibility enables researchers to bridge different disciplines such as comparative cognition and behavioral ecology.

Elephants have been attracted attention for their advanced cognitive abilities and complex sociality (Bates and Byrne 2007; Plotnik and Jacobson 2022) and have been believed to have a high degree of behavioral flexibility (Plotnik and Jacobson 2022). Therefore, elephants are a suitable research subject for studying behavioral flexibility. However, there have been a limited number of studies on behavioral flexibility in Asian elephants (*Elephas maximus*). One possible reason is that their habitat is dense forests in which continuous observation is difficult. Because of this inevitable limitation, it is important to conduct studies both in captive and wild conditions, whose results compensate each other. Also, studying behavioral flexibility in both the physical and social contexts is important because it can provide valuable insights into how elephants solve problems in physically changing environments and how social roles are adjusted in changing situations.

In this thesis, I conducted three independent studies and examined behavior that requires flexibility in captivity and the wild. In chapter 2, I reported a novel example of behavioral flexibility, spontaneously manipulating invisible air to achieve their goals, found during the natural observation of captive Asian elephants (Mizuno et al. 2016). While the use of sticks by animals, including primates and birds, to retrieve inaccessible objects has been well-documented (for recent reviews, see Bentley et al. 2010; Shumaker et al. 2011), there has been no report of the use of air which has no physical substance. I found that two captive Asian elephants regularly blew to drive food items within their reach. This behavior was spontaneously acquired by the elephants, without any guidance by humans. A detailed analysis of this behavior revealed that elephants blew to attract food when the distance between themselves and

the food was long. This result suggests that elephants use their breath to achieve their goals. Animals that move objects with non-solid are more commonly seen in water than on land (Schulz et al. 2021). The elephants, living on land, probably acquired the flexibility to manipulate their breath. As such, these findings provided valuable insights into how animals manipulate invisible and low-resistance pneumatics, as well as their possession of behavioral flexibility in the physical context.

In chapters 3 and 4, I examined behavioral flexibility in collective movement in different situations, such as group movement in a risky situation (crossing artificial roads) and group departure after a rest at a water body. Collective movement is defined as "a group of animals that decide to depart/move quite synchronously, move together in the same direction ... and maintain cohesion..." (Petit and Bon 2010). Hockings (2011), who examined the position of progressive group members during road crossing in chimpanzees (Hockings et al. 2006; Hockings 2011), suggested that the collective movement provides a nice opportunity to examine the degree of behavioral flexibility. That is, individuals may cope with the degree of the risk not by relying on a regularized spatial pattern but rather by altering its position. If there is only one fixed leader, collective movement can be considered to be less flexible. Some research on African savanna elephants (*Loxodonta africana*) highlights the protective role or leading role of the oldest female (McComb et al., 2001; Foley et al. 2008; McComb et al. 2011; Mutinda et al. 2011). In contrast, it is predicted that Asian elephants exhibit more remarkable flexibility in their collective behavior than African savanna elephants. The reason is that Asian elephants have a more fluid social system and weaker dominant relationships than African savanna elephants. I examined whether the progression order was stationary and whether an individual who engages in multiple initiative behavior was fixed.

In chapter 3, I examined how a group handles risky circumstances (Mizuno et al. 2017). Free-ranging wild Asian elephants in Mudumalai Wildlife Sanctuary and National Park, southern India, must frequently cross busy roads. I assessed if measures of road and traffic characteristics serve as indicators of risk and compared behaviors of different age classes during road-crossing events. As a result, more individuals displayed excitable behavior on wider roads. Additionally, adults were more likely to cross the road first, which is considered the most dangerous position, compared with non-adults. Non-adults tended to move ahead of others on the road, suggesting that it is more important for non-adults to follow adults at the beginning of a crossing than to follow along for the entire crossing. These findings may suggest that less experienced group members derive benefits by following the decisions of experienced ones under risky situations.

In chapter 4, I focused on the multiple initiative behaviors during the collective movement of wild Asian elephants at water bodies where individuals visit to drink water and take a bath or rest (Mizuno et al. 2023). Although many studies have

explored initiative behavior during collective movements (for a review, see Petit and Bon 2010), most studies have focused on a single initiative behavior (Bourjade et al. 2015). Rather than focusing on a single initiative behavior, examining multiple types of initiative behavior can provide deeper insights into the mechanisms of collective behavior (Bourjade et al. 2015) and consequently behavioral flexibility. I conducted behavioral observations of wild Asian elephants visiting a water body in Udawalawe National Park, Sri Lanka. I found that adults were more likely to exhibit such behavior than the expected frequencies. Regarding the role of the oldest, I found the oldest individual took the initiative more often than by chance only in one of three types of initiative behavior (the first long-walk). The number of cases in which the oldest female performed all three types of initiative behavior consecutively was greater than expected, but its occurrence was rare (4/23 cases). Although these results can be interpreted as weak evidence of the oldest individual's role in collective movements, it is possible that the examined initiative behaviors may differ in their degree of influence on collective movement. I also found that a single female, generally the oldest female, consecutively engaged in three types of initiative behavior more frequently than expected, although their occurrence did not constitute the majority of cases (6/23). This low consecutiveness among Asian elephants may be related to their fission–fusion dynamics and lack of core groups. Our results highlight the importance of analyzing multiple initiative behaviors associated with collective movement.

Chapters 3 and 4 are the first studies to examine collective movement in Asian elephants and showed that Asian elephants display fluid and adaptive social roles when crossing roads and visiting water bodies. It can be said that Asian elephants, whose leadership was not completely fixed, showed more flexibility in their collective movements than African savanna elephants, where the daily movement of other group members is influenced by the decisions of the oldest female in a group (Mutinda et al. 2011). These differences may be related to the fact that Asian elephants have a more fluid social system compared to African savanna elephants (de Silva and Wittemyer 2012). Moreover, other social characteristics of Asian elephants, such as less strong dominant relationships and less frequent social interactions (de Silva et al. 2017) compared to African savanna elephants (Archie et al. 2006; Wittemyer and Getz 2007), could be related to the inter-specific differences in the pattern of collective movements.

This thesis, which studied behavioral flexibility in both physical and social contexts, provided a better understanding of how Asian elephants adapt to their surroundings. High problem-solving skills allow them to successfully find and acquire resources in their habitats. Individuals would be able to act flexibly in complex societies and various situations. Thus, I provided new examples of behavioral flexibility in Asian elephants and emphasized how this species can solve problems in physically changing environments as well as how they can adjust their social roles in different situations.

博士論文審査結果

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Title
論文題目 Behavioral flexibility in physical and social contexts in Asian elephants

出願者（水野佳緒里氏）は、アジアゾウの認知行動に関する三篇の学術論文をもとに行動柔軟性(behavioral flexibility)を主題とした博士論文を提出した。

第一章では、博士論文の構成と行動柔軟性に関する説明がなされた。行動柔軟性は比較認知学や行動生態学といった複数の学問分野で注目されている概念であり、物体の物理学的特性や因果関係に関する理解、および社会的状況における行動選択において重要な役割を果たす。アジアゾウは、道具使用に代表される洗練された認知能力を持ち、集団の構成個体が柔軟に変化する離合集散社会を形成する。これらの特徴から、アジアゾウが行動柔軟性の研究対象として適していることが本章では述べられた。また、密林に生息する野生のアジアゾウの行動観察は難しいため、野生状態のみならず飼育状態での観察を併用することの意義が説明された。

第二章では、物理学的な現象の理解にみられる行動柔軟性の例として、飼育アジアゾウによる空気使用に関する行動実験が解説された。出願者は動物園に飼育されているアジアゾウ二頭が、届かない位置にある餌に鼻息を吹きかけて、近くに移動させる新規な行動を発見した。出願者は餌までの距離と空気使用の関係を分析し、本行動が効率的に餌を獲得するための合目的な行動であることを明らかにした。また、二頭の間で鼻息の使用方法に違いがあり、その結果、餌を獲得する効率に個体差があることを明らかにした。本研究は、陸生動物が気体を合目的に用いることを報告した初めての研究であり、動物の行動柔軟性と知性に関する新たな側面を明らかにしたものである。本研究成果は *Animal Cognition* 誌に掲載された(Mizuno et al. 2016)。

第三章と第四章では、社会的状況における行動柔軟性の例として、集団移動における個体の役割を明らかにした二つの研究が、それぞれ報告された。複数個体が同期して同じ方向に移動する集団移動は様々な動物でみられる。ある種の動物では、個体が持つ単純な行動ルールと局所的な相互交渉の集積として集団移動が起きる。個体間でその特性や行動ルールが異なる種であっても、順位関係が強く凝集性の高い集団を形成するアフリカゾウなどの種では、特定の個体がおもに先導役となるという役割の固定化がみられる。これらの種に対して、離合集散社会を形成するアジアゾウでは、先導個体となる個体が固定されておらず、行動柔軟性が発揮されると出願者は考えた。この発想に基づき、アジアゾウにおいて集団のどの個体が移動を先導するかを調べた。

第三章では、危険な道路を集団が渡る状況に着目し、成体個体が移動を先導するかどうかを、インドにおける野外調査に基づいて検証した。その結果、成体個体が未成体個体よりも高い割合で群れを率いていた。ただし、最年長個体が集団移動の先導役を行う傾向は見出されなかった。また、道路を横断中に、進行する未成体個体の順番が入れ替わるとい

う現象も発見した。本研究成果は *Behaviour* 誌に掲載された(Mizuno et al. 2017)。

第四章では、スリランカにおいて、アジアゾウの集団が水場を訪問・出発する際の各段階を詳細に観察し、第三章と同様に個体の年齢と集団移動における先導役との関係を調べた。その際、集団移動に含まれる四つの先導行動に分離し、各段階における個体の行動を詳細に調べた。その結果、第三章と同様に成体個体が未成体個体よりも高い割合で先導役となっていたが、最年長個体が先導役となる事例は多くなかった。本研究成果は *Journal of Ethology* 誌に掲載された(Mizuno et al. 2023)。

第三章と第四章の研究は、アジアゾウの集団移動に関する世界初の研究であり、離合集散社会という柔軟性の高い社会構造を持つ本種における個体の役割を明らかにした貴重な研究例である。

総合考察にあたる第五章では、三つの研究の意義づけと過去の研究との比較が行われた。とくに集団移動に関して、近縁種であるアフリカゾウとの比較が行われ、アジアゾウにみられる行動柔軟性の社会生態学的背景が議論された。また、未解明な点、今後の展望が簡潔に述べられた。

本博士論文は、アジアゾウの認知行動に関する新たな知見が多く含まれており、飼育下と野生状況、物理学および社会的状況において発揮される行動柔軟性についての独特の視点が含まれている。これらの点から、学術的価値が極めて高いと評価した。以上の理由により、審査委員会は、本論文が学位の授与に値すると判断した。