Behavioral flexibility in physical and social contexts in Asian elephants

Kaori Mizuno

Doctor of Philosophy

S O K E N D A I

The Graduate University for Advanced Studies, SOKENDAI

2023

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Abstract

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; Jacobson et al. 2023). Therefore, elephants are a suitable research subject for studying behavioral flexibility. However, the number of behavioral studies on Asian elephants (*Elephas maximus*) is limited. 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. The studies of collective behavior in African savanna elephants (*Loxodonta africana*) have revealed the protective behavior or leadership of the oldest female (McComb et al., 2001; Foley et al. 2008; McComb et al. 2011; Mutinda et al. 2011). In contrast, the collective behavior of Asian elephants has not been studied. There is a possibility that Asian elephants exhibit a different type of collective behavior because the patterns of social behavior differ between the two species: Asian elephants have a more fluid social system (de Silva and Wittemyer 2012) and weaker dominant relationships (de Silva et al. 2017) 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 dominance 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. Being flexible and cooperative with others in complex societies might assist an individual in obtaining benefits of group-living. As such, behavioral flexibility plays a crucial role in the adaptation and success of individuals. 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.

Chapter 1: General introduction

Behavioral flexibility

Behavioral flexibility has been receiving attention in studies of behavior and cognition in animals (reviewed in Lefebvre 2017; Lea et al. 2020; Strier, 2017). There are several definitions of behavioral flexibility, which vary among research disciplines. In the studies of comparative cognition, behavioral flexibility has been regarded as a reflection of complex and sophisticated cognition (Lea et al. 2020), and this is primarily studied in the physical context, i.e., whether animals understand physical laws and causal understanding. More specifically, it has been believed that species with high behavioral flexibility can accomplish reversal learning tasks (Lucon-Xiccato and Bisazza 2014; Pintor et al. 2014; Szabo 2018), problem-solving (Webster and Lefebvre 2001; Loukola et al. 2017; Chow et al. 2018; Daniels et al. 2019), and innovation (Sol 2002; Huebner 2015; Reader 2016). Additionally, species with a larger brain size relative to their body size are suggested to have higher behavioral flexibility (Sol et al. 2007; Boussard et al. 2021). 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). This has been primarily studied in the topics relating to social behavior in behavioral ecology, such as intra-specific variation in group size (Strier et al. 2014), social structure (Amici et al. 2008), and the pattern of group movement (Hockings 2011). Thus, the definition of behavioral flexibility encompasses a wide range of interpretations (Audet and Lefebvre 2017; Lea et al. 2020), and its broad applicability enables researchers to bridge different disciplines such as comparative cognition and behavioral ecology.

Behavioral flexibility in elephants

Elephants have been attracted attention for their advanced cognitive abilities and complex sociality (Bates and Byrne 2007; Plotnik and Jacobson 2022). Elephants have been believed to have a high degree of behavioral flexibility as evidenced by their responses to rapidly changing environmental conditions caused by human activities (Plotnik and Jacobson 2022; Jacobson et al. 2023). Therefore, elephants are a suitable research subject for studying behavioral flexibility.

At present, there are three extant species of elephants in a family Elephantidae: African savanna elephants (*Loxodonta africana*), African forest elephants (*Loxodonta cyclotis*), and Asian elephants (*Elephas maximus*). Each species is believed to have distinct social structures (Fishlock et al. 2015; Wittemyer and de Silva 2012) and cognitive abilities (Plotnik and Jacobson 2022). Among elephant species, forest elephants are the least studied (Goldenberg et al. 2021; Scalbert et al. 2023) because of difficulties in observing in dense forests. Research on wild African savanna elephants is relatively advanced, and many aspects associated with this species are now better understood (Moss et al. 2011). African savanna elephants maintain a coherent core unit based on matrilineal kin and those units sometimes fuse into a large herd (Wittemyer et al. 2005). Male elephants disperse from their natal units at roughly 14 years of age, after which males have multiple trajectories such as living alone, living in an all-male group, or a mixed herd with females (Chiyo et al. 2011; Lee et al., 2011). The dominance relationship among females is linear, with the oldest female in a group being the most dominant (Archie et al. 2006; Wittemyer and Getz 2007). Moreover, field experiments on wild African savanna elephants provided evidence of sophisticated cognitive abilities,

such as extensive memory capacity (McComb et al., 2001; McComb et al. 2011), discrimination by olfactory and color cues (Bates et al. 2007), acoustic cues (McComb et al. 2014), and recognition of out-of-sight associates' relative locations (Bates et al. 2008c). Compared to African savanna elephants, there have been a limited number of behavioral studies in Asian elephants, as seen in Table 1.1.

Group structure of Asian elephants

In Asian elephants, variations in grouping patterns among the areas and seasons have been observed, which indicates that their social environment can flexibly change according to the local ecological conditions. Asian elephants form a matrilineal society as females associate with their natal group members (Fernando and Lande 2000). Males leave their natal group after they aged around eight years old (Sukumar 2003) and stay alone or temporally associates with other males or females (McKay 1973; Keerthipriya et al. 2018). Typically, a group is composed of adult females and their offspring, but its social-ties seem to be loose compared to that of African savanna elephants. Fernando and Lande (2000), who conducted behavioral observations and genetic analyses in Ruhuna National Park (RNP), Sri Lanka, suggested that females in a group were highly related. According to Fernando and Lande (2000), a group of Asian elephants do not interact with other groups. In contrast, de Silva et al. (2011a) suggested that the group composition of Asian elephants changes by day or season based on the research in Udawalawe National Park, Sri Lanka. This means that Asian elephants exhibit a "fission-fusion" social system. de Silva and Wittemyer (et al. 2012), which took data from the same study site as de Silva et al. (2011a), stated that Asian elephants develop extensive networks through interacting with various individuals. In addition, de Silva

and Wittemyer (et al. 2012) suggested that Asian elephants do not have a hierarchical group structure. On the other hand, Nandini et al. (2018), which investigated three populations of wild elephants in India, suggested that they have a hierarchical group structure and that the differences might arise from variation in average group size.

As such, the social structure of Asian elephants exhibits intra-specific variation but remains unclear and controversial, although matrilineal social structure and fission-fusion society seem to be common characteristics of this species. Recent studies highlight a relationship between fission-fusion and behavioral flexibility (Amici et al. 2008, 2018). As the fluid and changing nature of individuals and groups involved in fission-fusion societies, it is essential for an individual to consistently evaluate and update social connections with various members and the social relationships among third parties (Aureli et al. 2008). This could result in selective pressure to be flexible and adapt one's behavior while evaluating their current relationships with various individuals.

Because of these unique characteristics, Asian elephants with sophisticated intelligence and social complexity based on the fission-fusion social system are particularly valuable in the studies of both comparative cognition and behavioral ecology. However, the number of behavioral studies on Asian elephants is limited (Table 1.1). 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.

Outlines of Chapter 2, 3, and 4

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, to attract an inaccessible object. Therefore, the air-using behavior described in chapter 2 was a notable finding. More specifically, two captive Asian elephants that 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 yields valuable insights on 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). It means that decisions of movement by each individual are not made independently of one another

but depend on communication within the group as well as on social relationships (Petit and Bon 2010). In groups of some species, such as colonies of social insects (Couzin and Franks 2003; Carlesso et al. 2023), schools of fish (Herbert-Read et al. 2011; Katz et al. 2011), and flocks of birds (Ballerini et al. 2008), collective movement are accomplished by an emergence process of self-organization. This means that each group member follows simple behavioral principles, and the accumulation of local interactions results in collective behavior. One reason for this is that individuals in a large group would not communicate directly with all of the other group members, but rather must rely on local contact with physically close individuals (Conradt and Roper 2005). Compared to such groups, relatively smaller groups in which individuals can interact with any of their members would show a flexible way of collective movement. Additionally, in the case of groups composed of individuals with different characteristics, levels of knowledge, ages, status, and power, each individual might not follow a simple behavioral rule but behave differently during the group movement. 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. The studies of collective behavior in African savanna elephants have revealed the protective behavior or leadership of the oldest female (McComb et al., 2001; Foley et al. 2008; McComb et al. 2011; Mutinda et al. 2011) and the leadership of older males in all-male groups (Allen et al. 2020). In contrast, the collective behavior of Asian elephants has not been studied. There is a possibility that Asian elephants exhibit a different type of collective behavior

because the patterns of social behavior differ between the two species as follows. First, Asian elephants have a more fluid social system compared to African savanna elephants (de Silva and Wittemyer 2012), as mentioned above. An individual needs to adjust their behavior by consistently evaluating and updating their social connections with different members in the fluid group composition (Aureli et al. 2008). Therefore, within the fluid social system of Asian elephants, individuals were predicted to flexibly change their positions in collective behavior. Second, the dominant relationship between individuals of Asian elephants is not transitive, unlike African savanna elephants (Archie et al. 2006; Wittemyer and Getz 2007), which means that a > b and b > c does not always establish a > c (de Silva et al. 2017). Additionally, aggression from young to old individuals is also relatively common in Asian elephants, compared to African savanna elephants (de Silva et al. 2017). Third, daily social interactions among Asian elephants seem less intense than those of African savanna elephants: Asian elephants are about a third less likely to exhibit aggressive behavior than African savanna elephants (de Silva et al. 2017). Thus, studying the collective behavior of this species is valuable. More generally, the study of collective movement adds a new perspective to the studies of social interactions among wild Asian elephants (Table 1.1). 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. Due to human development, elephants, which are originally from the forests, are occasionally forced to cross over busy roads with heavy traffic. In fact, the elephants that use the area are

disturbed by motorists who stop to look at them around the road (Vidya and Thuppil 2010). In adjusting to circumstances brought on by human activity, elephants would have been assumed to exhibit great behavioral flexibility (Plotnik and Jacobson, 2022).

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). However, collective movements usually feature several steps that involve consecutive initiative behaviors. 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.

In general discussion, I highlighted the elephant's flexibility traits in both physical and social contexts based on what I revealed in chapters 2, 3, and 4.

Table 1.1 Examples of behavioral studies in Asian elephants

Physical or social	Behavior	Research field	Citation
physical	innovation in food acquisition	captive	Jacobson et al. 2021; Barrett and Benson-Amram 2020
		wild	Jacobson et al. 2023
physical	insightful problem solving	captive	Foerder et al. 2011
physical	food manipulation	captive	Kaufmann et al. 2023
social	empathic responses to distress	captive	Plotnik and de Waal 2014
social	association with elephant handlers	captive	Yasui and Idani 2020
social	visual signal by a trunk	captive	Yasui and Idani 2017
social	dominance relationships	wild	de Silva et al. 2017
social	vocal repertoires	wild	de Silva 2010; Nair et al. 2009
social	vocal learning	captive	Stoeger et al. 2012

Chapter 2: Asian elephants acquire inaccessible food by blowing

Abstract

Many animals acquire otherwise inaccessible food with the aid of sticks and occasionally water. As an exception, some reports suggest that elephants manipulate breathing through their trunks to acquire inaccessible food. Here, we report on two female Asian elephants (*Elephas maximus*) in Kamine Zoo, Japan who regularly blew to drive food within their reach. We experimentally investigated this behaviour by placing foods in inaccessible places. The elephants blew the food until it came within accessible range. Once the food was within range, the elephants were increasingly less likely to blow as the distance to the food became shorter. One subject manipulated her blowing duration based on food distance: longer when the food was distant. These results suggest that the elephants used their breath to achieve goals; that is, they used it not only to retrieve the food but also to fine-tune the food position for easy grasping. We also observed individual differences in the elephants' aptitude for this technique, which altered the efficiency of food acquisition. Thus, we added a new example of spontaneous behaviour for achieving a goal in animals. The use of breath to drive food

is probably unique to elephants, with their dexterous trunks and familiarity with manipulating the act of blowing, which is commonly employed for self-comfort and acoustic communication.

Introduction

Many animals acquire otherwise inaccessible food with the aid of sticks (e.g. rodents: Okanoya et al. 2008; corvids: Taylor et al. 2010; elephants: personal observations; primates: Giudice and Pave 2007; Pollack 1998; Lethman 1982. For recent reviews, see Bentley-Condit and Smith 2010; Shumaker et al. 2011) and occasionally with water (e.g. archerfish: e.g. Bekoff and Dorr 1976; stingrays *Potamotrygon castexi*: Kuba et al. 2010; orangutans *Pongo abelii*: Mendes et al. 2007). However, some reports suggest that elephants manipulate their breathing through their trunks to acquire inaccessible food (Jesse 1834 cited in Romanes 1883; Darwin 1874; Nissani 2004). Darwin (1874) reported that when a small object was inaccessible, an elephant blew on the ground beyond the object such that "the current reflected on all sides may drive the object within his reach". It is important to investigate how elephants use blowing to achieve goals because a detailed analysis of this phenomenon will provide extremely rare data on how animals manipulate invisible and low-resistance pneumatics. However, researchers have had few opportunities to study elephants that spontaneously blow to acquire inaccessible food. Here, we report two captive Asian elephants (*Elephas maximus*) that regularly blew to drive food items within their reach (Fig. 2.1). By placing foods in inaccessible locations, we observed how elephants blow to drive food. Our main purpose was to determine whether this behavior was goal-directed. If it was, the elephants might change their behavior according to the distance to the food; that is,

they would blow frequently when the food was still distant (even if the food was within reach) and until the food came close enough to grasp easily. To test this idea, the relationship between food distance and behavior (blowing or grasping) was investigated. We further investigated individual differences in aptitude for this technique and the efficiency of food acquisition. Based on these results, we discuss whether blowing can be regarded as tool use, and cognitive underpinnings of this behavior.

Material and methods

Subjects and housing

Our subjects were two female Asian elephants, Mineko and Suzuko, born in 1981 and 1980 in Myanmar, respectively, and both transported to Japan in 1987. They reside in Kamine Zoo, Ibaraki Prefecture, Japan. One individual (Mineko) was regularly seen blowing to acquire otherwise inaccessible foods while the first author observed them for another study in 2011 (six times by all occurrence measures over a 12.8-h observation; Martin and Bateson 1986). Note that Suzuko was not observed doing this behavior during the same observation, although this short observation precluded our knowing whether Suzuko was able to acquire food by blowing. Behavioural observations of aggressive behavior suggested that Mineko was dominant over Suzuko. Neither elephant has been the subject of previous behavioral or cognitive experiments. They have been kept under "free contact" conditions, wherein zookeepers enter the enclosures and share direct contact with the elephants. For treatment and management, both elephants have received daily behavioral training (lying, standing, lifting a foot, walking with a keeper, etc., following keepers' commands).

Experimental setting

The experiment was conducted for 32 days from late August to early October 2013. Each day, the subjects were released into the outdoor exhibition compound (approximately 38 × 15 m), which was surrounded by a dry moat (2-m depth). The foods were placed in two areas (locations a and b, separated by 4 m) within a U-shaped ditch (50-cm width, 1.8 and 1.3-cm maximum depth, respectively, and minimum distances of 150 and 155 cm from the compound) of the dry moat. This means that two subjects could attempt to acquire food at the same time in separate areas.

We used five types of food (apples, bamboo, hay, fallen leaves, and potatoes). The subjects had regularly consumed all of these foods prior to the experiment. The foods varied in size and weight, although we attempted to minimise these differences (Table 2.1). Apples and potatoes were not altered. Bamboo (6–7-cm diameter) was cut into 15–20-cm lengths. Hay was offered in volumes of approximately 40 × 60 cm, and fallen leaves were measured using a basket (25 × 40 × 15 cm). We used mostly the leaves of cherry and Sawleaf Zelkova trees, as they grew around the compound, and the subjects were already familiar with them.

Apples, bamboo, and potatoes were placed sideways in locations a and b at a distance of 180 cm from the compound prior to the respective sessions (defined as "initial positon"). Hay was placed so that its nearest side was 170 cm from the compound. Fallen leaves were scattered over a range that encompassed locations a and b and that spanned both accessible and inaccessible distances. Leaves were occasionally moved by wind, but we did not fix their position.

To record the position and movement of food in the experiments, we conducted preliminary setup before the experiments. We placed grid sheets (10-cm increments) on

the ground around locations a and b when the elephants were elsewhere. The grid sheets were pre-recorded using a stationary video camera (Canon iVIS HF or Sony HDR-CX170), and the sheets were then removed. During the experiments, we consistently placed the video camera in the same position. By superimposing the pre-recorded image of the grids onto experimental video data (processed with Adobe Photoshop Elements 9 and Adobe Premiere Elements 9; Adobe Systems Inc., San Jose, California), we were able to continuously record the positions of the food items.

Experimental procedures

In each experimental session, we chose two pieces/clumps of one of the five types of food (not always the same type) and placed it in the two inaccessible locations. Foods were set out one to four times daily. Each day, the first food was set out before the elephants entered the compound at 08:45. The subjects could attempt to acquire the food *ad libitum* while they were in the compound. If the food was removed, a zookeeper set out new food at 10:30, 12:00, or 13:30 following our instructions. Hay was set out only before 8:45, as it was challenging to place it while the elephants were present. A "session" started when food was set out, and ended when the food was taken by a subject or when the elephants returned to their rooms. A "trial" started when a subject began blowing at a food item, and ended when the subject acquired the food (defined as "success") or aborted the attempt by leaving the area for more than 1 minute ("not success"). Of these trials, an "initial trial" was defined as a trial that started when the food was in the initial position. The period between the beginning of a session and the time an elephant began a trial varied according to the food type, with apples, potatoes and bamboos taking relatively longer times (apple: mean $\pm$ SE: 73.23 $\pm$ 13.44 min,

potato: 68.56 ± 16.90 min, bamboo: 62.45 ± 19.53 min, fallen leaves: 16.40 ± 3.68 min, hay: 6.43 ± 1.67 min). This difference may reflect the elephants' preference and motivation for each type of food. If the food moved due to the subject's blowing but was not taken, we did not restore it to its initial position. We conducted multiple sessions with each food and attempted to perform >10 initial trials with each subject for each food type.

During this study period, we did not change the amount of regular food given each day. Neither we nor zookeepers approached the elephants during trials, but we did not control for behavior by zoo visitors; however, it is unlikely that their presence affected the elephants' behavior. We did not give extra rewards or praise when they acquired food in the trials.

All trials were recorded using two cameras at each location, one focused on the subject and food together, and the other focused on food only. In total, we conducted 101 sessions, during which 128 trials were observed (Mineko: 68, Suzuko: 60; Table 2.1).

Data coding

Recorded movies were analyzed using Adobe Premiere Elements 9. Frame-by-frame playback (1/30-second increments) was used when necessary.

For each trial, we recorded the following:

  (1) The individual that initiated the trial (Mineko or Suzuko).

  (2) Whether the individual succeeded

  (3) The frequency of blows within each trial.

(4) The duration of each blowing bout, measured by ear in 0.2-second increments based on the start and end of audible blowing, using frame-by-frame playback.

(5) The food position on the grid (nearest point, 5-cm increments) after the end of each blowing bout; by comparing food positions (only grid rows were measured) before and after blowing, we calculated the distance of food movement.

(6) The direction of food movement immediately after the start of blowing, classified as forward, backward, right, or left.

In the experimental sessions using hay, we also recorded the following for each blowing bout:

(7) The target of blowing. The position, classified into three types (near, centre, or far side of the hay), was assessed by recording which portion of the hay blew away at the start of each blowing bout.

(8) Whether the direction of food movement changed: if the hay moved continuously forward it was classified as "no change". In contrast, when the direction of hay movement changed from forward to backward, it was classified as "change".

(9) The trunk-tip position at the start of each blowing bout, classified into four types (not reaching for the hay, at the front edge, at the back edge, or over the hay). We drew three vertical lines over the hay in our video recordings to judge trunk position.

(10) The trunk shape at the start of each blowing bout. Based on which part of the trunk was bent, this was classified into two types (tip turned down, or trunk bent approximately 30 cm from the tip).

With help from a blind coder, we calculated inter-observer reliabilities for (3) blowing frequency and (4) blowing duration. Using Pearson's correlation coefficient

(Martin and Bateson 1986), we found high reliabilities for both data sets (blowing

frequency: r = 0.93; blowing duration: r = 0.96).

Data analysis

Unless otherwise noted, we used a (general) linear model (LM) or a generalised linear

model (GLM). We used R 2.14.1 (R Development Core Team 2011) for all analyses, at

$\alpha = 0.05$ (two-tailed). Trials on potatoes were excluded from most analyzes because

Suzuko did not attempt to acquire a potato (Table 2.1). The trials with fallen leaves were

used only for an analysis of success rates because the non-cohesive nature of this food

presumably required a qualitatively different gathering technique (i.e. collecting leaves

into one place; Video 2.S1).

(i) Goal-directed behavior

Relationship between behavior (blowing vs. grasping) and food distance

For each subject, a GLM with binomial error structure was used to investigate the

relationship between food distance and behavior (blowing or grasping). Blowing data

from periods when food was inaccessible were excluded, as grasping would be

impossible (even when an individual stretched, keeled her forelegs, and raised one of

rear legs; see Video 2.S1). In location a, the inaccessible area was defined as >175 cm

from the compound because Suzuko could grasp food at a maximum distance of 175 cm

in all trials. Mineko grasped food at a maximum distance of 160 cm, but appeared

capable of reaching at least 175 cm, as her trunk was longer than Suzuko's. In location b,

the inaccessible area was defined as >130 cm for Suzuko and 165 cm for Mineko

because they grasped food at these respective maximum distances. We analyzed trials

with four types of food (Mineko: number of behaviors, i.e. blowing or grasping: n = 114 in 44 trials; apple: n = 50 in 21 trials; bamboo: n = 10 in 5 trials; hay: n = 43 in 13 trials; potato: n =11 in 5 trials; Suzuko: apple: n = 11 in 3 trials; bamboo: n = 12 in 6 trials; hay: n =34 in 14 trials). Whether the subject blew or grasped was set as a dependent variable, and the distance between the subject and food as an independent variable.

Relationship between blowing duration and food distance

We further investigated whether the subjects altered their blowing duration according to food distance for four types of food, expecting that they would blow for longer when the food was distant. Blowing data for four types of food were analyzed using a LM after excluding trials during rain (Mineko: n = 161, apple: 85, bamboo: 11, hay 41, potato: 24; Suzuko: n = 155, apple: 73, bamboo: 24, hay: 58). Blowing duration was set as the dependent variable, and the distance between subject and food as an independent variable. We controlled for any effects of blowing bout order (RESULTS) and subject pose (standing or kneeling; RESULTS) by setting these variables as additional independent variables.

(ii) Individual differences in blowing skill

We compared the success rates and blowing skills (see Data coding) of the two individuals.

Success rate (Table 2.1)

The success rates of the two elephants were compared for the four types of food using a GLM with binomial error structure. Trials in which Suzuko's attempts were disturbed

by Mineko were excluded (N = 109; apples: 40, Mineko: 27, Suzuko: 13; bamboo: 12, Mineko: 5, Suzuko: 7; fallen leaves: 25, Mineko: 11, Suzuko: 14, hay: 32, Mineko: 13, Suzuko: 19). Whether the subject succeeded was set as the dependent variable, and individual identity was set as an independent variable. Food type was also set as an independent variable to control for differences among foods.

Blowing duration

The blowing durations of the two subjects were compared for three types of food using a two-sample unpaired t-test. We compared the durations of the first blow in each initial trial (n = 73; apple: 31, Mineko: 18, Suzuko: 13; bamboo: 12, Mineko: 5, Suzuko: 7; hay: 30, Mineko: 11, Suzuko: 19). Trials performed during rain were excluded because the camera did not clearly record the sound of blowing.

Blowing frequency

The frequencies of blows per trial for the three types of food were compared between the subjects using a GLM with Poisson error structure based on data from the initial and successful trials (N = 55; apples: 20, Mineko: 17, Suzuko: 3; bamboo: 11, Mineko: 5, Suzuko: 6; hay: 24, Mineko: 11, Suzuko: 13). Blowing frequency was set as the dependent variable, and individual identity and food type as independent variables.

Distance of food movement

The distances of food movement between two subjects were compared for the three types of food using a LM on the first blowing bouts in the initial trials (n = 76: apple: 34, Mineko: 20, Suzuko: 14; bamboo: 12, Mineko: 5, Suzuko: 7; hay: 30, Mineko: 11,

Suzuko: 19). The distance of food movement was set as a dependent variable, and individual identity and food type as independent variables.

Direction of food movement

The direction of food movement between subjects was compared for the three types of food using Fisher's exact test. Not all foods could move equally well with blowing, depending on their shape and structure (e.g. bamboo). To address this, we analyzed only data in which the food could potentially move vertically. Moreover, we included only data for when the food actually did move (n = 140; apple: 62, Mineko: 37, Suzuko: 24; bamboo: 33, Mineko: 10, Suzuko: 23; hay: 46, Mineko: 28, Suzuko: 18). We compared the proportions of food that moved forward versus food that moved in other directions between the two elephants.

Target of blowing

We compared the target positions and whether the hay was continuously driven forward using Fisher's exact test for data collected from the subjects when the hay was in the initial position (n = 59, Mineko: 13, Suzuko: 46). We compared the proportion of blowing bouts targeting the far side of the hay versus those targeting other positions and the proportion of cases in which the hay was continuously driven forward versus those in which its direction changed from forward to backward.

Position and shape of trunk

We compared the position and shape of the subjects' trunks while blowing using blowing data on hay in the initial position (n = 56: Mineko: 11; Suzuko: 45). To analyze

the position, we used Fisher's exact test to examine the proportion of cases in which the trunk-tip was held over the hay versus when it was in other positions.

Results

(i) Goal-directed behavior

On average, subjects blew 3.18 times (SE: 0.34) to drive the food from its initial position to an accessible range.

Subjects were less likely to blow when food was nearby (based on data from only cases where food was within reach; Fig. 2.2; binomial GLMs, Mineko: b $\pm$ SE = -0.013 ± 0.004, $z = -3.52$, $P < 0.001$; Suzuko: b $\pm$ SE = -0.071 ± 0.022, $z = -3.25$, $P = 0.001$). Moreover, Mineko manipulated her blowing duration based on food distance; she blew for a longer duration when the food was distant than when it was near (LM: Mineko: b $\pm$ SE = 0.003 ± 0.0004, $z = 9.65$, $P < 0.001$). We found no such relationship for Suzuko (b $\pm$ SE = 0.0008 ± 0.002, $z = 0.46$, $P = 0.64$).

(ii) Individual differences in blowing skill

Individual differences in blowing skill between the two subjects were found, with Mineko being more proficient than Suzuko. First, Mineko's overall success rate (81%) was higher than Suzuko's (70%) (binomial GLM, b $\pm$ SE = -2.68 ± 0.76, $z = -3.55$, $P < 0.001$; Table 2.1). Second, the food was moved a significantly longer distance per blow by Mineko (average $\pm$ SE: 42.57 ± 7.11 cm) than by Suzuko (15.19 ± 5.81 cm) (LM: b $\pm$ SE = -34.42 ± 8.69, $t = -3.96$, $P < 0.001$; Fig. 2.3). These results may be due to differences in both blowing duration and the target. Mineko's blowing duration (average $\pm$ SE: 1.18 ± 0.02 s) exceeded Suzuko's (0.69 ± 0.02 s) (*t*-test: $t = 16.19$, *d.f.* = 71, $P <$

0.001), although the frequency of blows per trial was similar (Mineko: average ± SE: 3.45 ± 0.34, Suzuko: 3.18 ± 0.45; Poisson GLM: b ± SE = 0.043 ± 0.17, $z = 0.26$, $P = 0.80$). The direction of food movement also differed between subjects. Mineko always drove food forward (75/75), whereas Suzuko sometimes drove it to the right or left (2/65) or backward (8/65) (Fisher's exact test: forward versus other directions: $P < 0.001$). We investigated the blowing target using trials with hay because the large surface area allowed easy target identification. To drive hay toward the elephant, it was necessary to blow on its far side. The frequency of blowing at each target location did not differ between subjects (Mineko: far: 10, centre: 3, near: 0; Suzuko: far: 31, centre: 11, near: 4; Fisher's exact test comparing far versus other positions: $P = 0.74$). However, the direction of hay movement occasionally changed during blowing for Suzuko (30/46), whereas it did not for Mineko (no change: Mineko, 13/13; Suzuko, 16/46; Fisher's exact test: $P < 0.001$). This suggests that Mineko was able to consistently aim for and hit the far side of the hay, whereas Suzuko was less consistent. These results may be due to differences in trunk-tip position between the subjects during blowing, as Mineko held the tip of her trunk over the hay in all cases (11/11), whereas Suzuko did not (over: 11, back edge: 15, front edge: 13, not reaching for hay: 6). The relative proportions of these trunk positions differed significantly between subjects (Fisher's exact test: over hay versus other positions: $P < 0.001$). Trunk shape also differed between subjects (Video 2.S1). Mineko turned the tip of her trunk down (11/11), whereas Suzuko bent her trunk at ~30 cm from the tip (45/45). Mineko's proficiency was also clear in other behaviors; for example, she seemed to manipulate her blowing speed to collect fallen leaves efficiently (Video 2.S1).

Discussion

The blowing behavior we observed was goal-directed. Both elephants blew the inaccessible food until it reached an accessible range and blew even more to drive food towards them. However, Suzuko sometimes ceased blowing after the food reached an accessible range (Fig. 2.2), and grasped the food by stretching and sometimes raising one of her rear legs. On the other hand, Mineko blew food until the food came close enough to grasp easily as we expected. It might be that blowing was less demanding for Mineko than kneeling on her forelegs and stretching her body, although we do not know why Mineko was reluctant to stretch her body.

This study not only replicates Darwin's observation but also adds a new example of the spontaneous behavior for achieving a goal in animals. The use of breath for driving food is probably unique to elephants, due to their dexterous trunks. Additionally, they are familiar with manipulating the act of blowing, as they commonly use this technique for self-comfort (Chevalier-Skolnikoff and Liska 1993) and acoustic communication (Olson 2004), which might underpin their skilful use of breath.

Does this blowing behavior count as tool use? A classic and standard definition of tool use by Beck (1980) is "the external employment of an unattached environmental object to alter more efficiently the form, position…" (See also St Amant and Horton 2008 for an extension of this definition). Breath or air may not fit this definition because it is part of the environment. However, several types of behavior have been difficult to define or rule out as tool use (e.g. water shooting in archerfish: Bekoff and Dorr 1976; use of a water jet in the stingray: Kuba et al. 2010; producing bubbles to form a barrier for herding fish in humpback whales *Megaptera novaeangliae* and dolphins: Wiley 2011; Leighton 2004; using water to manipulate objects in bottlenose dolphins *Tursiops*

truncatus: Yamamoto et al. 2014). For example, Kuba et al. (2010) suggested that the use of a water jet by the stingray can be regarded as tool use. Based on studies of water use in archerfish, Brown (2012) also suggested that if aquatic animals have "control over the water and use it effectively to achieve a goal, then it may count as true tool use." If we follow Brown's criterion that goal-directedness is sufficient for defining a tool, the blowing behavior of elephants can be counted as tool use. The definition of a tool has also been controversial among researchers. Although it is tempting to discuss whether air is tool, we think that such a simple dichotomy is less fruitful because the conclusion strongly depends on the definition that researchers employ. Working from the standpoint of comparative psychology, Seed and Byrne (2010) suggested that determining whether a given behavior constitutes tool use is less important than analysing examples in which animals need to exhibit their cognitive abilities in a flexible way to solve a problem. We agree with this opinion and think that it would be more fruitful to consider the psychological processes underlying the use of air. Seed and Byrne (2010) raised four elements as the cognitive underpinnings of the uses of tools. Of these, our results suggest that elephants seem to understand causality and physical reasoning. Our experiments were not designed to test the other two elements, insight and planning; therefore, the question of whether these were involved in the use of air remains unexplored. In addition, the concept of an extension of the body is also important for understanding the cognitive aspects. For example, Maravita and Iriki (2004) analyzed the neural activities and behaviors/postures of macaques trained to use a tool and concluded that the tool can be regarded as an extension of the body. It remains an open question whether animals manipulating water or air use these non-solid media as extensions of the body, as they are detached from their body. As such, reports

of new instances of tool or tool-like uses will provide an opportunity to infer psychological processes, which will ultimately lead researchers to critically rethink the definition of tool use in a more sophisticated manner. This study offers such an opportunity.

We found several differences in the techniques used for and the consequences of blowing between the two elephants. Mineko's success rate was higher than Suzuko's. Mineko drove food forward in all cases, and the distance over which she drove the food was significantly greater than the distance Suzuko was able to achieve. Mineko held her trunk-tip over the food and kept blowing at the far side of the food. This suggests that she was aware of the physical consequence of blowing on the far side, knowing that it was an efficient way to drive the food towards her. Additionally her blowing duration was longer than Suzuko's, and Mineko manipulated her blowing duration based on food distance. She may have learned that longer-duration blowing drives food further. Mineko's sophisticated skills may imply that she learned or understood the physical principles underlying the effects of blowing. Mineko's skills likely explain her higher success rate and distance per blowing. In contrast to Mineko, Suzuko sometimes drove food backward. One reason for this might be that she bent her trunk ~30 cm from the tip and her trunk-tip was not held over the food in all blowing bouts.

Manipulating air might be difficult because of its nature (i.e. it is invisible and has less resistance than other substances). Our study provided a rare observation of two captive Asian elephants manipulating air as a problem-solving technique, with one of the two employing sophisticated skills. Recently, many reports have suggested that elephants have advanced cognitive abilities, including knowledge about the physical environment (e.g. Wickler and Seibt 1997; Hart et al. 2001; Irie-Sugimoto et al. 2008;

Bates et al. 2008a; Smet and Byrne 2015. For a review see Byrne et al. 2009; Irie and Hasegawa 2009), which are comparable to those of apes and corvids (Bates et al. 2008b; Plotnik and Clayton 2015). Our study provides additional, previously unreported data demonstrating physical intelligence in elephants. At the same time, however, this study raised several questions. It is unclear whether the subjects acquired blowing behavior through trial-and-error, insight problem solving, or social learning. However, the fact that two co-habiting females show the same behavior raises the possibility of social learning. Other remaining questions are whether this use of breath for problem solving is common in elephants and the degree to which individuals can manipulate blowing duration and speed. To answer these questions, it would be fruitful to conduct additional experiments with this study's subjects, to look for other individuals who can use air in similar ways, and to conduct new experiments of problem solving that are designed to elicit individuals to the use of air.

Ethical statement

This experiment was approved by the Research Ethics Committee of The Graduate University for Advanced Studies (2014A002) and by Kamine Zoo.

Table 2.1 Success rates

Food	Weight(g)			Total session (a/b*1)	Initial trial*2		Trial*3		Success		Displacement*4	% Success	
	Range	Average	S.E.		Mineko	Suzuko	Mineko	Suzuko	Mineko	Suzuko	Suzuko	Mineko	Suzuko*5
Potato	62–110	82.4	4.4	10 (5/5)	8	0	12	0	5	-	-	42	-
Apple	114–204	174.2	3.7	27 (10/17)	18	11	27	17	21	3	4	78	23
Hay	243–298	274.6	3.2	27 (12/15)	11	19	13	20	13	14	1	100	74
Bamboo	170–253	214.0	7.1	11 (4/6)	5	6	5	7	5	6	0	100	86
Fallen leaves	-	-	-	26 (26/0)	9	16	11	16	11	14	2	100	100
All foods	-	-	-	101 (57/44)	51	52	68	60	55	37	7	81	70

*1 Number of sessions in which the food was placed at location a or b.

*2 Number of trials in which the food was placed in the initial position by a person.

*3 Number of trials, including initial trials and subsequent trials, in which the food was moved from the initial position by either of the two subjects.

*4 Number of times Suzuko was displaced by Mineko during Suzuko's trials.

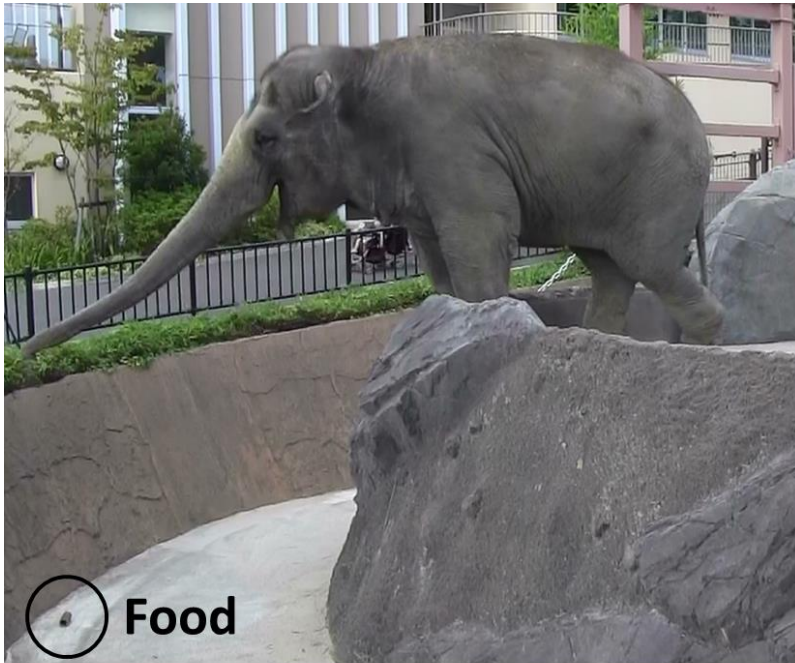*5 Success rate divided by the number of trials, excluding the number of displacements.

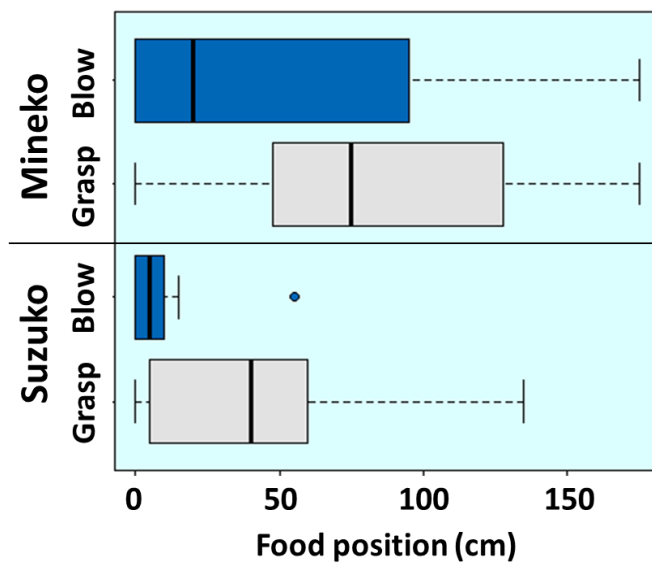**Fig. 2.1** Mineko blowing at bamboo.

Fig. 2.2 Boxplots showing food distance when each subject grasped or blew after the food reached within an accessible distance.

On the *horizontal axis*, ''0'' indicates the maximum distance elephants could reach. Positive values on the horizontal axis indicate the distance of the food from the point ''0''
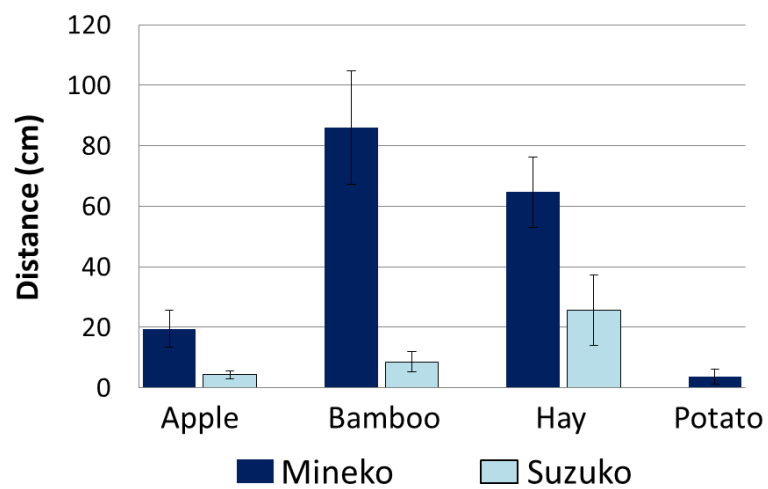
Fig. 2.3 Individual mean distances of food movement per blow for each food. Error bars indicate 1 S. E.

Video 2.S1 The online version of this article (doi:10.1007/s10071-015-0929-2) contains supplementary material, which is available to authorized users.

Chapter 3: Collective behaviour of wild Asian elephants in risky situations: How do social groups cross roads?

Abstract

Among group-living animals, some members may derive benefit by following the decisions of other members. Free-ranging wild Asian elephants in Mudumalai National Park, southern India, must often cross roads and can be disturbed by vehicles. We assessed if measures of road and traffic characteristics serve as indicators of risk, and compared behaviours of different age classes during road-crossing events. More individuals displayed excitable behaviour on wider roads. A larger number of adults entered the road first, which is considered the most dangerous position, compared with immature elephants. Immature individuals tended to move ahead of others on the road, suggesting that it is more important for immature individuals 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 benefit by following the decisions of experienced ones under risky situations.

Introduction

In group travel, the order of progression may depend on individual characteristics or on the situation. (for a review, see Petit and Bon, 2010). In some species, dominance hierarchy is associated with progression order: dominant individuals take the front

position (e.g. grey wolves, *Canis lupus*: Peterson et al. 2002; sheep, *Ovis aries*: Squires and Daws, 1975; yellow baboons, *Papio cynocephalus*: Rhine, 1975, Rhine and Westlund, 1981; grey-cheeked mangabeys, *Lophocebus albigena*: Waser, 1985). In some species, physiological status is associated with position. Female buffalo with calves become more aggressive and tend to take the front position during their lactation period (Prins, 1989). In white-handed gibbons, reproductively cycling females take the front position more often than do pregnant and lactating females, seemingly to increase mating opportunities (Barelli et al. 2008). In golden shiners (*Notemigonus crysoleucas*), personality is associated with progression order: individuals at the front tend to be bolder, and are more prone to enter new places (Leblond and Rees, 2006).

Advantages of taking the front position are to increase opportunities to obtain food (e.g. roach fish, *Rutilus rutilus*: Krause et al. 1992, Krause et al. 1998; buffalo, *Syncerus caffer*: Prins, 1989; white-handed gibbons, *Hylobates lar*: Barelli et al. 2008) or to mate (e.g. Barelli et al. 2008). Sometimes, it may provide benefits for all group members that an individual having specific attributes, such as knowledge or power takes the front position. A study revealed true leadership by older females of killer whales (*Orcinus orca*): post-reproductive females, which are considered to have more knowledge than reproductive females, take the front position and lead their herd members to resource-rich sites (Brent et al. 2015). In risky situations, taking the front position by a powerful group member may reduce the risk for all group members. Some researchers have suggested a protection theory, according to which powerful individuals take the front or end positions that are more exposed, and vulnerable (e.g. immature or injured) individuals take centre positions in risky situations (e.g. Washburn and DeVore 1961; Rhine 1975; Rhine and Westlund 1981; for a review see Sueur and Petit 2008).

Extending Hamilton's suggestion that all individuals occupying the periphery have the same risk (Hamilton, 1971), Bumann et al. (1997) suggested that occupying the forward position in group movement is more risky than occupying the rear. Behaviours involved during travel in a potentially dangerous situation are less well-known because there are few opportunities to observe such situations (Altman, 1979; Rhine and Westlund, 1981). There are very few reports about group movements in risky situations. When chimpanzees (*Pan troglodytes*) travel through areas inhabited by predators (Tutin et al. 1981), they form a large party and move silently and quickly (Tutin et al. 1983). When chacma baboons retreat after predatory alarm calls, adult males take the end position, which is relatively close to the perceived location of the predator (Rhine, 1975; Rhine and Tilson, 1987). In recent years, animals have been forced to cross artificially constructed roads in their day-to-day movements, and several studies have reported the collective behavior of various species during such events. In chimpanzees, adult males cross roads first more frequently than do juveniles or adult females, and a high-ranking male or female takes the end position (Hockings et al. 2006). In meerkats (*Suricata suricatta*), a dominant breeding female leads subordinates to a roadside and waits until some individuals cross ahead, in order to reduce her own risk (Perony and Townsend, 2013). Additionally, a few reports have illustrated behavior of animals in a normal compared to risky or dangerous situations. For example, α-male chimpanzees take the front position more frequently in road-crossings (i.e. risky situations) than in climbing trees (i.e. normal situations; Cibot et al. 2015). Forest elephants (fitted with collars) move faster while crossing a road than in other normal situations (Blake et al. 2008).

Forest elephants form a matrilineal group with two to three individuals (Schuttler et al. 2014; Fishlock et al. 2015). Occasionally, some individuals associate

with non-relatives (Schuttler et al. 2014) or multiple groups interact temporarily (Fishlock and Lee, 2013). African elephants (*Loxodonta africana*) live in hierarchical social structures, based on matrilineal kin (Wittemyer et al. 2005). Asian elephants (*Elephas maximus*) do not maintain a coherent core group: each female associates with multiple females, and the composition of a group changes over time (de Silva et al. 2011). Elephants mature slowly and have a long life expectancy (approximately 60 years or more; Moss, 1988; Sukumar, 2003; de Silva et al. 2013; Lee et al. 2016; Turkalo and Wittemyer, 2017); they are also reported to have an extensive memory capacity (Rensch, 1957; McComb et al. 2001; Bates et al. 2008; Foley et al. 2008). The matriarch, the oldest female elephant in a group, is the most dominant individual in African elephant (Archie et al. 2006). Furthermore, reproductive success is higher in groups with an older matriarch (McComb et al. 2001). An anecdotal report mentioned the guarding role of an older female when a group encountered a predator (Douglas-Hamilton, 1972). McComb et al. (2011) demonstrated that elephant family groups with older matriarchs were better at discriminating increased threats posed by male lions, and Mutinda et al. (2011) noted that the oldest female's decisions affect all other individuals in their daily travel. However, this study did not focus on movements in potentially dangerous situations. In contrast with African savanna elephants, there have been no reports on the role of the oldest individual in a group of Asian elephants (Vidya and Sukumar, 2005). Given some differences in social organization between African savanna elephants and Asian elephants (de Silva and Wittemyer, 2012), there could be differences in the latter species with respect to collective behavior in risky situations.

Free-ranging wild Asian elephants in Mudumalai Wildlife Sanctuary and

National Park, southern India, must frequently cross busy roads (Video 3.S1). Vidya and Thuppil (2010) found that elephants standing by roadsides are disturbed by motorists who stop to look at them. Sometimes, elephants made a mock charge at motorists or retreated from the road. Using a same location, we examined behaviors of female groups of Asian elephants in this risky situation of crossing a road. Due to poor visibility within the forest where the elephants spend most of their time, we were unable to observe variables such as travel order, leading behavior, or starting and stopping movement in non-risky situations. We assessed if measures of road and traffic characteristics serve as indicators of risk by examining associations between the degree of risk and elephant behavior, with the prediction that elephants would show excitement or nervousness on higher-risk roads. We measured whether an elephant tail was raised as an index of excitable behavior because there are some reports suggesting that tail raising was observed when an elephant was apprehensive or alarmed (Poole, 1999; Poole and Granli, 2011).

During a road-crossing event, we considered the front position to be most risky, as Bumann et al. (1997) suggested that, for a moving prey group, front positions are more risky than rear positions, especially when a predator is stationary. Although, road crossing differs from predator-prey situations, the last position of a crossing group is considered relatively safe. We hypothesized that more experienced animals would take the first position to lead other group members; less experienced animals would derive benefits by following experienced individuals. First, we compared adults with immature individuals. In Asian elephants, weaning occurs at approximately three years of age (Sukumar, 2003) and maturity at approximately 10 years (Sukumar, 2003; de Silva et al. 2013). Therefore, we defined adults as older than 10 years in this study. We made the

following predictions: (1-1) immature individuals would exhibit greater excitement than adults, as indicated by tail raising. (1-2) A larger number of adults would enter the road first, as compared to immature individuals. (1-3) A larger number of immature individuals, as compared to adults, would follow other members when deciding on the timing of road-crossing; inter-individual intervals of immature individuals would be shorter than those of adults. (1-4) Immature individuals would reduce their duration of stay in a high-risk area, as compared to adults. Second, the effect of age for mature elephants was examined by comparing the behavior of the oldest female with non-oldest adult females. We predicted that the oldest female, which might be the most experienced group member, (2-1) would exhibit less excitement than other adult females, (2-2) cross first, and (2-3) take longer to cross in order to let other group members pass her on the road.

Methods

Study sites

Observations were carried out on roads passing through Mudumalai Wildlife Sanctuary and National Park (henceforth, Mudumalai; also designated as a Tiger Reserve) in Tamil Nadu, India (Fig. 3.1; 321 km^2, 11°30'N–11°42'N, 76°30'E–76°45'E; the general altitude ranges from 900 to 1200 m above mean sea level). The mean density of elephants is approximately 2.5 individuals/km^2 (2012 figures from the state forest department). Roads were classified into two types based on location and traffic: "*major roads*" from Masinagudi to Theppakadu (traffic density: c. 1500 vehicles per day), and from Thorapally to Bandipura (c. 3750 vehicles per day); and "*secondary roads*" from Moyar to Singara (c. 225 vehicles per day). Traffic is permitted on roads passing

through the park only between 6 A.M. and 9 P.M. We defined "*roads*" as tracks that vehicles can pass through, including lanes made of concrete and unpaved edges that are nonetheless flat with no obstacles (e.g. trees or signboards). Secondary roads have broader edges but denser roadside vegetation, that obstructs visibility, whereas major roads have narrower edges but better visibility, because vegetation (approximately 10 m from the road edge) is managed to control fires during the dry seasons.

Field methods

Observations were conducted for 33 days, beginning in August, 2014, and spread over several months from January to October, 2015. We searched for free-ranging elephants from vehicles by driving along roads at low speed. When we found elephants standing by the roadside, we stopped our vehicles and began observations, maintaining a distance of at least 20 meters from the elephants. After all individuals had finished crossing, we waited for 5 min in case any other elephants appeared; if none did, we left the location.

In total, we observed eight crossing events by solitary elephants (three adult females, four adult males, and one immature male over 7 yr of age) and 55 events by multiple elephants (defined as "a group crossing") in total. Of these 55 events, 28 events were recorded by video camera (Sony HDR-XR550V; Sony, Tokyo, Japan), and 27 events were recorded by taking notes. In five events, six adult males (one male in the > 30 yr age class, one male in the 16–30 yr age class, and four males in the 10–15 yr age class) crossed the road with females. We could not observe the entire group crossing in two events. In one of these events, some group members had already crossed the road when we sighted them; in the other, some members did not cross at all. These two events were excluded from some parts of our analyses (see below).

Age estimation

We estimated age class (< 1, 1–5, 6–10, 11–15, 16–30, > 30 yr) by criteria based on previous studies (Sukumar, 1989; Arivazhagan and Sukumar, 2008). We did not record any behavior of calves (< 1 yr) because their crossing speed is much slower than that of other immature individuals (1–10 yr) and they appear to concentrate on following their mothers. We defined adult as the > 10 yr age class and immature individuals as the 1–10 yr age class. We also attempted to identify the oldest individual in a group through several criteria. We used the relative height method (Sukumar 1989). The broadly consistent relationship between height and age-class is well established in Asian elephants (Sukumar et al. 1988). However, height alone cannot be used as a measure of age among female elephants older than about 20 years (average of 228 cm height at withers). Among the largest individuals in the group, we thus used several other age-related morphological characteristics such as temporal depression, buccal depression, skull size, skin folds, degree of ear folding and skin depigmentation as indicators of older age among female elephants. If two or more relatively old individuals within a group were very similar in physical characteristics, we did not attempt to identify the oldest, and we excluded any data for such individuals from comparisons between oldest and non-oldest adults. We were able to assign the oldest individual in 44 groups.

Data coding

Of 55 events, two were excluded; 53 were treated as independent for the following reasons. We considered the probability that different groups were observed to be

sufficiently high (92%; see below). We attempted to identify adults by examining the tail and the side of a pinna from 28 video-recorded events, and then calculated the probability. We were unable to examine these features in two events due to the low quality of the video image. We could examine the left pinna and the tail in 10 crossing events and found that two of these events involved the same adults. We also were able to examine the right pinna and the tail in 16 crossing events and found that two of these events were performed by the same group; in each case, we excluded one of these crossing events (i.e. two of 28 video recording events were excluded). From these results, the probability that different groups were observed was 92% (= (9 / 10 + 15 / 16) / 2 * 100).

53 events (26 events by video recording and 27 events by taking notes) were analyzed to examine "*order of individuals' entering and leaving the roads*". If the progression positions changed on the road, "*order change score*" of such an individual was calculated as follows (in case some elephants moved ahead of others on the road):

$(X_e - X_l) / (G - 1 - C)$,

where X_e is the order in which the individual entered the road, X_l is the order in which the individual left the road, G is the group size (number of members), and C is number of calves in the group. Group size and composition were examined from 51 events, in which we were able to observe the entire group crossing. The average group size was 5.9 ± 3.1 (SD, N = 51), and the group composition is available in Table 3.1.

In addition to the order of crossing, more detailed behaviors were examined from 26 video-recorded events (9 events on major roads and 17 events on secondary roads), using Adobe Premiere Elements 9 (Adobe Systems, San Jose, CA, USA or Observer XT 11; Noldus, Wageningen, Netherlands). Frame-by-frame playback

(1/30-second increments) was performed when necessary.

Each "*road width*" was measured in increments of one-half of the body length of an adult female, by watching an adult crossing the road on video (road width of major roads: average $\pm$ SD = 2.39 $\pm$ 0.26 adult body lengths, N = 9; secondary roads: 4.50 $\pm$ 0.35 adult body lengths, N = 17). "*Crossing duration of a group*" began when the first crosser began to cross and ended when the last crosser left the road. "*Crossing duration*" of an individual started when a subject entered the road and ended when it left the road. A group took on average 100.0 $\pm$ 115.4 (SD, N = 25) seconds to cross the road. The "*inter-individual interval*" at the moment of entering the road was also calculated: any subsequent individual's entering time was subtracted from the previous individual's entering time. "*Tail raising*" was counted if the individual raised its tail more than 15 degrees from the vertical and for more than one second. "*Stop*" was counted if an individual was completely stationary. In case any other individuals stopped while following another one, we counted only the individual which stopped first.

We also counted the number of vehicles (e.g. motorbikes, cars, jeeps, buses) that passed for three minutes before the first crosser began to cross in each event if video data were available (average $\pm$ SD: major road: 6.7 $\pm$ 3.0 vehicles, N = 7, secondary road: 2.0 $\pm$ 1.2 vehicles, N = 9). Occasionally, vehicles stopped to watch the elephants standing by the roadside or crossing the road. The average number of vehicles that stopped during each individual's crossing was 2.0 $\pm$ 1.1 (SD, N = 116; 26 crossing events). Of the 26 video-recorded events, five crossing events were recorded in the morning (9:00–12:00), 17 events in the afternoon (12:00–18:00), and four events during sunset (18:00–19:30). We could not determine whether the number of vehicles or the crossing time was associated with any behavior of elephants due to these narrow

distributions.

Statistical analysis

We used R 3.2.2 (R Development Core Team, 2015) for all analyses. We applied generalised linear models (GLMs) to determine which factors were related to the crossing duration of a group. We applied generalised linear mixed models (GLMMs) using the *glmer* function from the lme4 package version 1.1–10 (Bates et al. 2015) to examine behavioral differences between adults and immature individuals and between the oldest and non-oldest adult females. The statistical significance of each coefficient in the models was examined by a Wald test ($\alpha = 0.05$; two-tailed). Although we estimated five age classes, we compared the behavior only of adults (> 10 yr) and immature individuals (1–10 yr) due to the small sample size of each age class.

Behavioural differences between adults and immature individuals, and between oldest and non-oldest adult females

The ratio of individuals entering the road first or last, or leaving the road last, were examined in adult and immature individuals and in oldest and non-oldest adults using a G-test with William's correction (Sokal and Rohlf, 1995). When comparing the ratio of the oldest and non-oldest adult females, we excluded data for crossing events performed by groups involving single adults. The observed value in each age class was calculated by summing the individuals that entered or left the road first or last in all events. In cases where multiple individuals entered the road at the same time, we did not include the ranking, as we could not specify which individual entered the road first or last. The expected value in each age class was calculated according to group composition. First,

the probability that any given individual in the age class would cross first (or last) was calculated for each event. For example, if the group had two adults and one immature individual, the probability that the adult would cross first is 2/3. Second, all of the probabilities for each event were summed for each age class. We excluded an event in which some group members had already crossed from our analyses of the ratio of the number of individuals entering the road first (N = 47 for comparisons between adult and immature individuals; N = 32 for comparisons between oldest and non-oldest adult females). To analyze the ratio of the number of individuals entering the road last, and that of individuals leaving the road last, we excluded one event in which some elephants did not cross and other two events in which there were only two group members (entering the road last: N = 48 for comparisons between adult and immature individuals; leaving the road last: N = 47 for comparisons between adult and immature individuals, N = 32 for comparisons between oldest and non-oldest adult females).

The order change scores of adult and immature individuals were compared for 114 subjects (adult: 56, immature: 58) of 34 events in which progression positions changed during crossing, using the asymptotic Wilcoxon rank sum test.

We used GLMM with a binomial probability distribution and the logit link function to compare the proportion of individuals that raised their tails or stopped on the road among adults and immature individuals, and among oldest and non-oldest adult females. We excluded data for individuals whose tails were hid by other individuals (adult: 55, immature: 61; 26 events; oldest: 24, non-oldest adult: 29; 26 events). Event was set as the random effect. Age class (adult vs. immature or oldest adult vs. non-oldest adult), road type, and road width were set as explanatory variables.

We assessed whether inter-individual interval was associated with age class,

tail raising, road width, and road type using GLMM with a gamma probability structure and the log link function. The sample size was N = 86 (32 adults, 54 immature; 26 events). Group size, road type (major road vs. secondary road) and road width were set as explanatory variables. Event was set as the random effect. The crossing durations of adults and immature individuals and of oldest and non-oldest adult females were compared using GLMM with a gamma probability structure and the log link function, with event was set as the random effect. We excluded data for four adult females with calves (< 1 yr) because their crossing speed appeared to be influenced by their calves' crossing speed (adult: 47, immature: 56; 25 events; oldest: 19, non-oldest adult: 26; 23 events). Age class, tail raising (relaxed vs. raised), road width, and road type were set as explanatory variables.

Results

There was an association between road characteristics and elephant behavior, as we predicted. More individuals raised their tails while crossing wider roads (Fig. 3.2; Table 3.2a; $P = 0.005$). On the other hand, road type (which was classified into two types based on location and traffic) was not associated with elephant behavior.

Adults vs Immature individuals

Adults, which are more experienced than immature individuals, exhibited slightly less excitement and displayed leading behavior, as compared to immature individuals. The number of immature individuals that raised their tails was nearly significantly greater than that of adults (Fig. 3.3; Table 3.2a; $P = 0.056$). The ratio of adults entering the road first compared to that of immature individuals was higher than expected by chance (Fig.

3.4a; adults: observed: 38 expected: 24.0; immature individuals: observed: 9, expected: 23.0; G-test with William's correction; $G = 9.3$, df $= 1$, $P = 0.002$). The ratio of individuals entering the road last was similar in both age classes (Fig. 3.4b; adults: observed: 31, expected: 25.4; immature individuals: observed: 17, expected: 22.6; G-test with William's correction; $G = 1.3$; df $= 1$, $P = 0.25$). The ratio of adults leaving the road last compared to that of immature individuals was higher than expected (Fig. 3.4c; adults: observed: 34, expected: 24.5; immature individuals: observed: 13, expected: 22.5; G-test with William's correction; $G = 4.1$, df $= 1$, $P = 0.044$).

The inter-individual interval of immature individuals (average $\pm$ SD $= 18.1 \pm 44.6$ seconds; N $= 54$) was shorter than that of adults (28.7 ± 69.6 seconds; N $= 32$; Table 3.2c; $P = 0.03$). In 34 of 53 events, 114 individuals (56 adults, 58 immature individuals) changed their progression positions on the road. The order change score of immature individuals was higher than that of adults: more immature individuals moved ahead of adults on the road (Fig. 3.5; asymptotic Wilcoxon rank sum test; $W = 2474$; $P < 0.001$). In three of 53 events, elephants that crossed first and left the road last (order change score $= -1$: one oldest adult in the > 30 yr age class, two non-oldest adults in the 15–30 yr age class; see also Video 3.S2). Although the staying duration of immature individuals (average $\pm$ SD $= 5.7 \pm 3.2$ seconds/adult body length) was slightly shorter than that of adults (6.1 ± 3.2 seconds/adult body length), the staying duration was not significantly associated with age class (Table 3.2d; $P = 0.15$). Similarly, the proportions of individuals stopping on the road were similar in both age classes (Table 3.2b; $P = 0.83$).

Oldest vs. non-oldest adults

We examined the effect of age among mature elephants, with the prediction that the oldest female (which might be the most experienced individual in a group) would display leading behavior, as compared to non-oldest adult females. The number of crossing events performed by groups involving single adult and multiple immature individuals was eight. In seven of these events, the adult (i.e. oldest) crossed the road either first or last. The number of events performed by groups involving multiple adults was 34. Although the oldest individual entered the road first or last in 68% (23 of 34) of crossing events, we found no significant differences between oldest and non-oldest adults in entering the road first (Fig. 3.6a; oldest: observed: 9, expected: 6.6; non-oldest adult: observed: 19, expected: 11.6; *G*-test with William's correction; $G = 0.08$, df = 1, $P = 0.78$); or leaving the road last (Fig. 3.6b; oldest: observed: 14, expected: 6.8; non-oldest adult: observed: 11, expected: 11.7; *G*-test with William's correction; $G = 1.5$, df = 1, $P = 0.22$). The proportion of tail raising (Table 3.3a; $P = 0.44$) or stopping (Table 3.3b; $P = 0.90$), and crossing duration (Table 3.3c; $P = 0.21$) was similar between the oldest and non-oldest adults.

Discussion

We found that the degree of risk was associated with the behavior of wild Asian elephants, which live in social groups, are long lived, and mature slowly, and we found some behavioral differences between adults and immature individuals; however, we did not find an age effect for mature elephants. A wider road was considered riskier for the elephants, as they displayed excited behavior on wider roads. Traffic did not significantly affect the behavior of elephants in this study. Loud human voices, nearby

vehicles, the number of vehicles, and crossing time appeared to trigger nervous behavior in elephants, but we were unable to determine a definite relationship between these factors and any behavior.

More adults entered the road first, and fewer adults tended to display tail raising behavior than immature individuals. We cannot separate age from experience because the possibility that some adults have less road-crossing experience than immature individuals cannot be excluded. That said, elephants have relatively fixed home ranges in unfragmented forests (Baskaran et al. 1995), use familiar paths during day-to-day movement, and have long-term memory; they are likely familiar with roads and vehicles, and have more experience in crossing busy roads as they age. Therefore, adults might not be as excited as immature elephants, assessed the timing of crossing the road and crossed first. The inter-individual interval at the moment of entering the road of immature individuals was shorter than that of adults, suggesting that immature individuals may rely on adults to decide the timing of a road-crossing. Although staying duration on the road is not significantly associated with age class, immature individuals moved ahead of other members on the road after initially following adults. The results suggest that it may be more important for immature individuals to follow adults at the beginning of the crossing, rather than to follow along for the entire crossing. However, we cannot make this conclusion, as immature individuals seem to move fast and slow, and change their position more often than adults, even in normal situations. It is also possible that adults may take a role to ensure all members cross safely by leaving the road last. In three events, adult females entered the road first and left the road last. Additionally, the ratio of adults leaving the road last compared to that of immature individuals was higher, while the ratio of individuals entering the road last was similar

in the two age class.

We did not find any significant differences in the leading behavior of the oldest adult females compared to that of non-oldest adult females. In African savanna elephants, when a group with an older matriarch encounter a dangerous situation, the elephants bunch together (McComb et al. 2011). This finding suggests that a matriarch acts to protect her group members. When African savanna elephants travel in groups, an older adult moves first and is followed by young adults (Mutinda et al. 2011). However, in our study, the number of events in which oldest females crossed the road first was not greater than expected by chance. This behavioral variation between the two species could be related to differences in their social structures. Asian elephants do not maintain a coherent core group (de Silva et al. 2011) and have a weaker linear hierarchy (de Silva et al. 2017) than African savanna elephants, which maintain a coherent core family unit (Wittemyer et al. 2005) and have a strong linear hierarchy (de Silva et al. 2016, Archie et al. 2006; Wittemyer and Getz, 2007). Therefore, Asian elephants may not have a clearly identifiable leader; all adult members may take up the role according to the circumstances. However, it is too early to conclude this based only on this study of risky situations. An individual's familiarity with particular roads may highly influence some behaviors such as crossing duration, nervous behavior, and order of entry to the road. Due to poor visibility in the dense vegetation, we were unable to observe which individual initiated road-crossing movement while the group waited along the roadside. Occupying the leading position of a progression can sometimes be different from being the initiator that moves first in a group departure, or that produces a signal or cue for departure (Ramseyer et al. 2009; Dumont et al. 2005). In African savanna elephants, the oldest female typically initiates group movement but takes the last position of the group

progression, while the 15–20 yr age class takes the front position (Mutinda et al. 2011). It is possible that an individual produces a signal and controls the movement of group members from any number of possible positions (Kummer, 1968; Byrne, 2000).

This study showed that adult female elephants, which are more experienced and less excitable than immature individuals, crossed the road first, which is regarded as the most dangerous progression position. More immature individuals moved ahead of other members on the road after initially following adults. Immature individuals may derive benefit by following an adult's decision to cross a road. Our hypotheses, that more experienced animals were predicted take the first position in risky circumstances to lead group members, and that less experienced animals would follow other members, were supported by our comparisons of adults with immature individuals, but not for mature adults. However, we recognize that our sample size and identification of groups/individuals were limited. Future work should involve the collection of more types of road-crossing observations as well as collective behavior in non-risky situations, such as movement in forests; observing such group behaviors would improve our insight into the response of Asian elephants to potentially risky situations.

Table 3.1 Age composition of elephant groups (N = 51) observed crossing roads in Mudumalai, including six adult males that crossed with female groups in five crossing events (four males in the 10–15 yr age class, one male in the 16–30 yr age class, and one male in the > 30 yr age class). Crossing events by solitary elephants were excluded.

Age	<1	1–5	6–10	11–15	16–30	>30	All
Average	0.4	1.3	1.2	0.5	1.0	1.4	5.9
SD	0.7	1.0	1.1	0.7	0.9	1.1	3.1

Table 3.2 Effects of age class (adult vs. immature individual) and other explanatory variables on (a) tail raising (N = 116: 55 adults and 61 immature individuals; 26 events), (b) stopping (N = 116: 55 adults and 61 immature individuals; 26 events), (c) inter-individual interval (N = 86; 26 events), (d) crossing duration (N = 103: 47 adults and 56 immature individuals; 25 events) analyzed by GLMMs. Variables displaying significant differences are indicated in bold.

Explanatory variables	Estimate ± SE	*Z* value	*P* value
(a) Response value: whether a subject raised its tail			
Intercept	-3.35 ± 1.11	-3.02	0.003
Age class (adult vs immature)	-0.88 ± 0.46	-1.91	0.056
Road type (major road vs secondary road)	-1.52 ± 1.00	-1.52	0.13
Road width (body length of an adult)	**1.18 ± 0.42**	**2.83**	**0.005**
(b) Response value: whether a subject stopped or not			
Intercept	-2.46 ± 1.37	-1.79	0.07
Age class (adult vs immature)	0.12 ± 0.55	0.21	0.83
Road type (major road vs secondary road)	0.29 ± 0.47	0.62	0.53
Road width (body length of an adult)	-1.06 ± 1.26	-0.84	0.40
		T value	
(c) Response value : inter-individual interval at the moment of entering road			
Intercept	3.24 ± 0.91	3.56	4.E-04
Age class (adult vs immature)	**0.60 ± 0.27**	**2.20**	**0.03**
Tail raising (relaxed vs raised)	0.22 ± 0.33	0.68	0.50
Road width (body length of an adult)	-0.51 ± 0.34	-1.51	0.13
Road type (major road vs secondary road)	0.72 ± 0.88	0.82	0.41
(d) Response value: crossing duration			
Intercept	2.01 ± 0.37	5.36	8.15E-08
Age class (adult vs immature)	0.10 ± 0.07	1.46	0.15
Tail raising (relaxed vs raised)	**-0.17 ± 0.08**	**-2.12**	**0.03**
Road width (body length of an adult)	**0.28 ± 0.14**	**2.04**	**0.04**
Road type (major road vs secondary road)	0.72 ± 0.88	0.82	0.41

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Table 3.3 Effects of age class (oldest vs. non-oldest adult) and other explanatory variables on (a) tail raising (n = 53: 24 oldest adults and 29 non-oldest adults; 26 events), (b) stopping (n = 53: 24 oldest adults and 29 non-oldest adults; 26 events), and (c) crossing duration (n = 45: 19 oldest adults and 26 non-oldest adults; 23 events) analyzed by GLMMs.

Variables displaying significant differences are indicated in bold.

Explanatory variables	Estimate	±	SE	*Z* value	*P* value
(a) Response value: whether subjects raised its tail					
Intercept	-2.47	±	1.34	-1.84	0.07
Age class (oldest vs non-oldest adult)	0.47	±	0.61	0.77	0.44
Road type (major road vs secondary road)	-0.62	±	1.13	-0.55	0.58
Road width (body length of adult)	0.54	±	0.45	1.20	0.23
(b) Response value: whether subjects stopped or not					
Intercept	-2.44	±	1.82	-1.34	0.18
Age class (oldest vs non-oldest adult)	-0.09	±	0.79	-0.12	0.90
Road type (major road vs secondary road)	-0.68	±	1.51	-0.45	0.65
Road width (body length of an adult)	0.31	±	0.58	0.52	0.60
				T value	
(c) Response value: crossing duration					
Intercept	2.00	±	0.43	4.64	3.53E-06
Age class (oldest vs non-oldest adult)	0.13	±	0.10	1.25	0.21
Tail raising (relaxed vs raised)	**-0.42**	**±**	**0.14**	**-3.00**	**0.003**
Road width (body length of an adult)	0.33	±	0.17	1.90	0.06
Road type (major road vs secondary road)	-0.27	±	0.47	-0.58	0.56
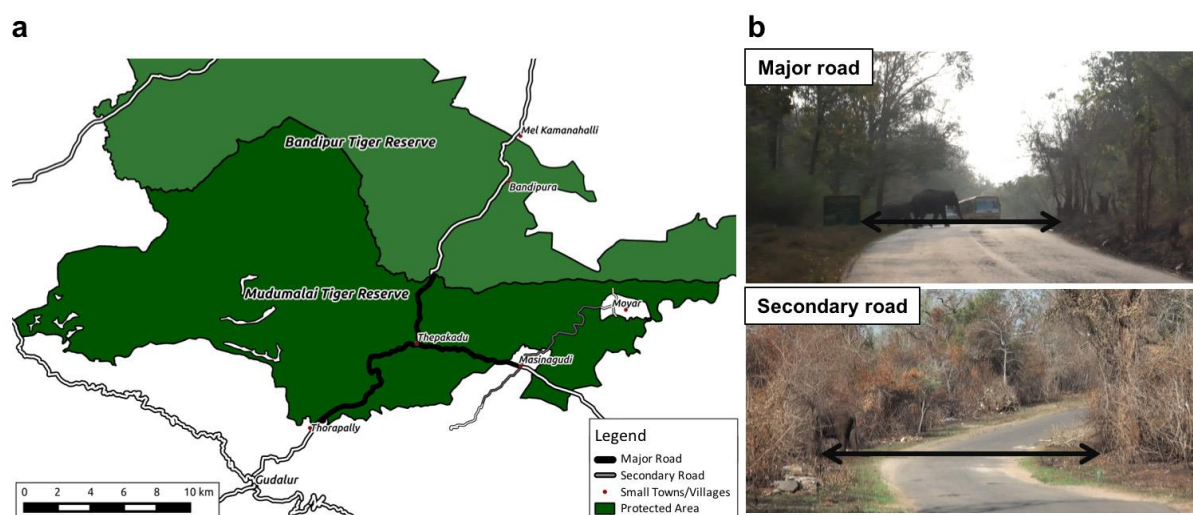
Fig. 3.1 (a) Map of roads through the Mudumalai Wildlife Sanctuary and National Park. Roads that we travelled to search for elephants are shown in colour; black indicates a major road and grey indicates a secondary road. (b) Photographs of major and secondary roads; arrows indicate road widths.
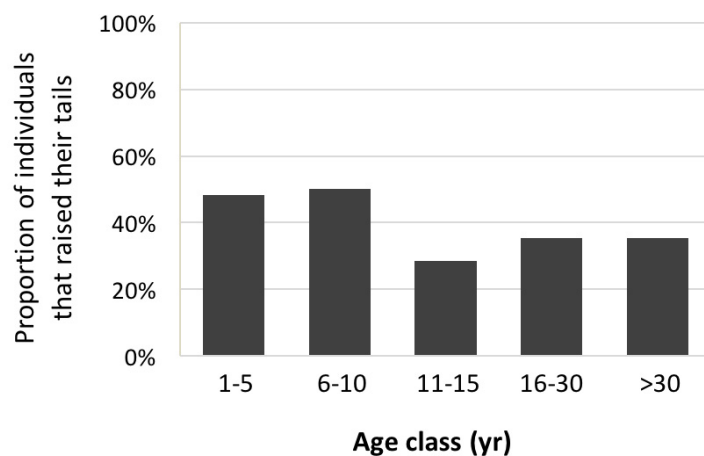

Fig. 3.2 The proportion of individuals that raised their tails during road-crossing in different age classes (N = 116; 26 events).
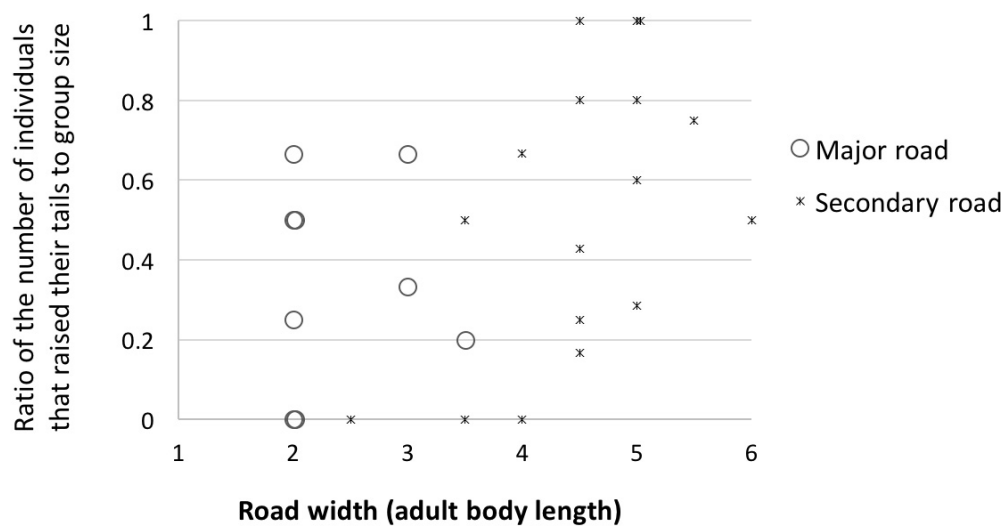
Fig. 3.3 Ratio of individuals that raised their tails to group size in each road (N = 26).
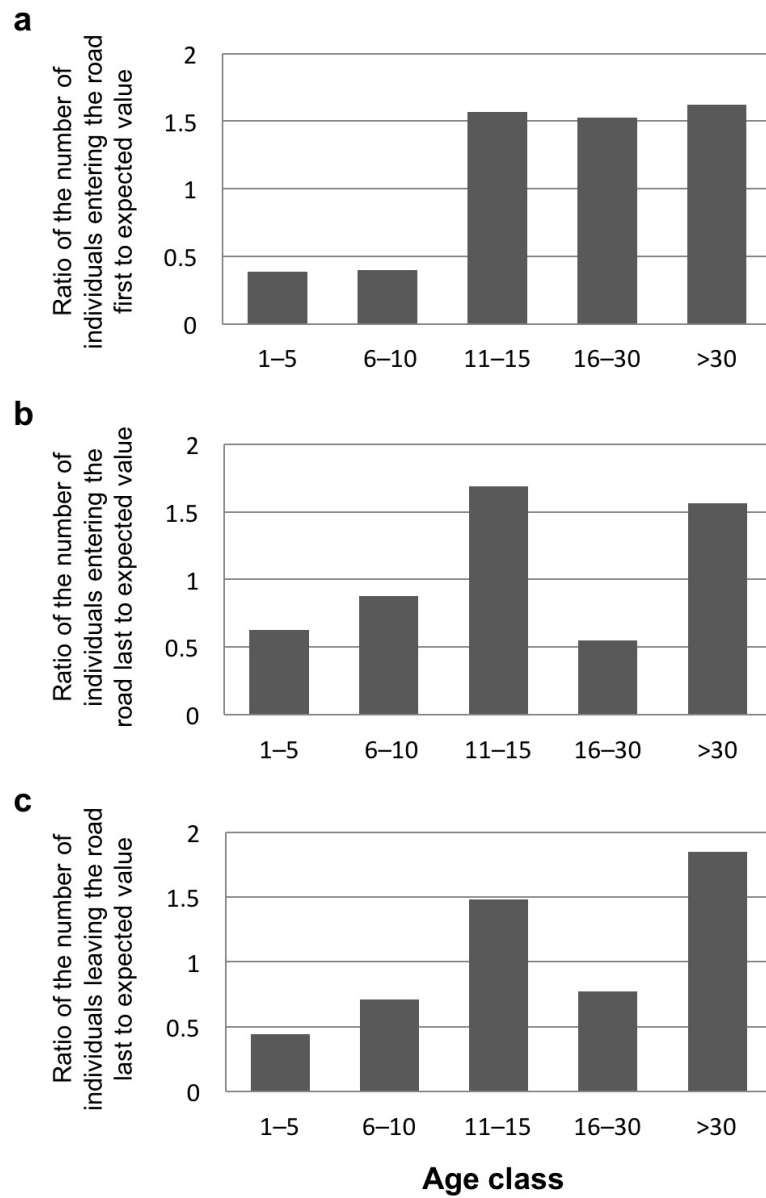
Fig. 3.4 Ratios of observed to expected values in each age class (a) entering the road first (N = 47), (b) entering the road last (N = 48), and (c) leaving the road last (N = 47).
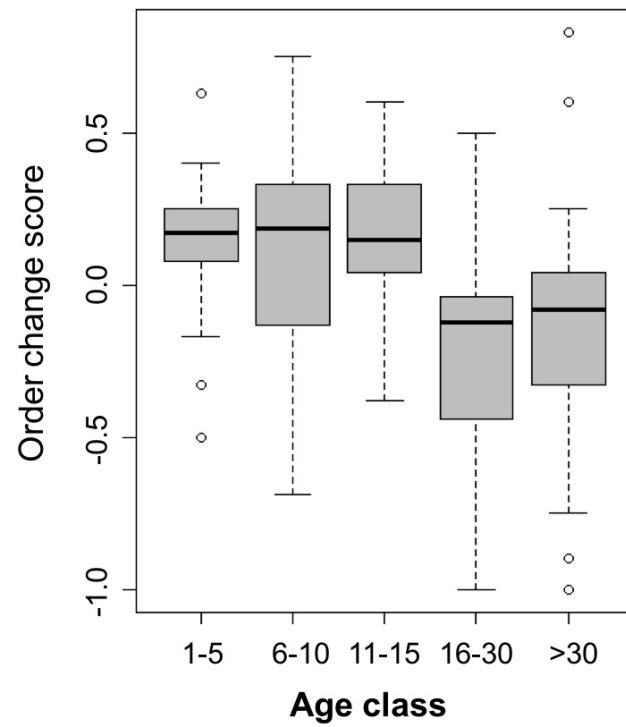
Fig. 3.5 Boxplots of order change score in each age class (N = 114 individuals; progression positions changed on the roads in 34 events). Positive values indicate that an individual passed another elephant on the road.
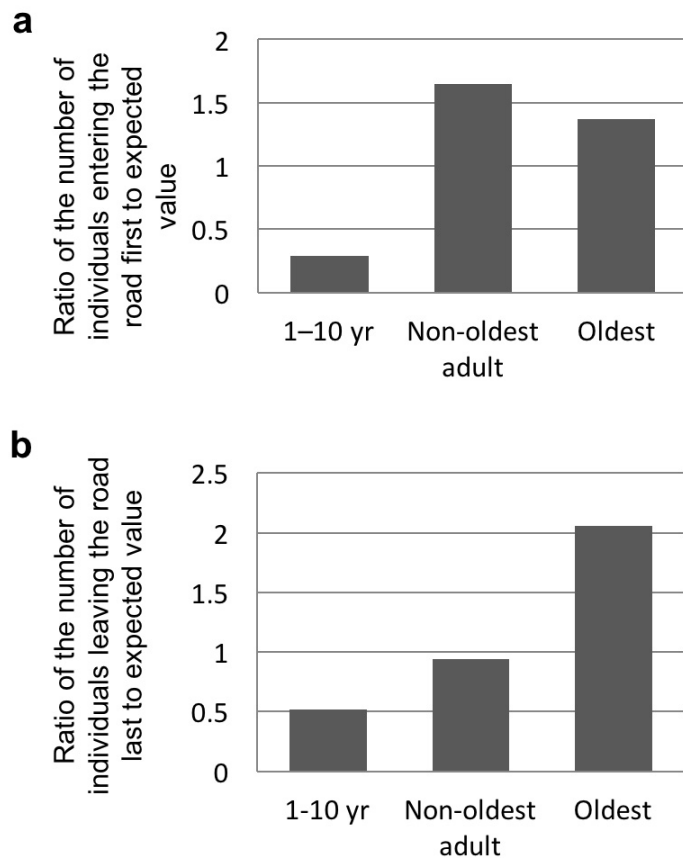
Fig. 3.6 Ratio of observed to expected values in each category (a) entering the road first (N = 32) and (b) leaving the road last (N = 32).

Video 3.S1 and Video 3.S2 The online version of this article (doi: 10.1163/1568539X-00003465) contains supplementary material, which is available to authorized users.

Chapter 4: Collective movements during visits to water bodies in wild Asian elephants

Abstract

Collective movements feature multiple consecutive processes involving different types of initiative behavior. It remains unclear whether, and to what extent, the same individual consecutively performs different initiative behaviors in a single collective-movement event. We conducted behavioral observations of wild Asian elephants (*Elephas maximus*) visiting a water body in Udawalawe National Park, Sri Lanka. We analyzed 32 collective-movement events involving 51 individually identified adult females. We used randomization tests to compare the observed and expected frequencies of initiative behavior by a particular individual. We found that adults were more likely to exhibit such behavior than the expected frequencies. We 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.

Introduction

The evolutionary origin of leadership has attracted the interest of both biological and social scientists (Smith et al. 2016). In previous studies on collective movement, the initiation of group movement and occupation of the front position have often been used as indicators of leadership (Ramseyer et al. 2009; Bonanni et al. 2010; Ramos et al. 2015; but see Allen et al. 2020). The behavior of other individuals also determines a leader, because individuals have a behavioral choice of whether to follow an initiator (Uhl-Bien et al. 2014). In studies examining relationships between individual attributes and leadership, dominant individuals (Squires and Daws 1975; Peterson et al. 2002), bolder individuals (Reebs and Leblond 2006; Harcourt et al. 2010), and older individuals (Brent et al. 2015; Nesterova et al. 2015; Tokuyama and Furuichi 2017) were more likely to emerge as leaders of groups.

Although many studies have explored leadership during group movements (for a review, see Petit and Bon 2010), most studies have focused on a single initiative behavior, such as successful initiation of group movements (Bourjade et al. 2015). In these studies, initiative behavior was defined as a cue, signal, or behavior indicating the initiation and direction of group movement. Group movements usually feature several steps that involve consecutive initiative behaviors. It is also possible that individuals other than the initiator may change the direction of movement (Strandburg-Peshkin et al. 2015). However, whether a particular individual consecutively undertakes multiple types of initiative behavior and other individuals follow those behaviors remains poorly understood. 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). This study used multiple measures to

examine group movement in Asian elephants.

Elephant leadership is a notable research topic because elephants are highly social and long-lived animals (de Silva et al. 2013; Lee et al. 2016); thus, older individuals are more experienced and knowledgeable than younger individuals (McComb et al. 2001; Bates et al. 2008; Foley et al. 2008), and older elephants often take on the leadership of their groups using their knowledge (McComb et al. 2001; McComb et al. 2011). Older female African savanna elephants are better at making decisions that are crucial to group survival (McComb et al. 2001; Foley et al. 2008) and are more successful at initiating group movements (Mutinda et al. 2011). Older males are more likely to lead all-male traveling groups (Allen et al. 2020).

Whether older individuals play leading roles in Asian elephant societies remains unclear (Vidya and Sukumar 2005). Asian elephants form a matrilineal society in which females associate with their natal group members (Fernando and Lande 2000). However, a core group may be absent, with group composition changing daily or seasonally, i.e., a fission–fusion social system (de Silva et al. 2011a). This social structure differs from that of African savanna elephants, which maintain a coherent core family unit based on matrilineal kinship (Wittemyer et al. 2005). In contrast to African savanna elephants, which live in open savanna areas, Asian elephants generally live in moist, dense forests with low visibility. In such habitats, food and water resources are relatively widespread and spatially continuous, and predation pressure is low compared to African savanna elephant habitat (Silva et al. 2017). Asian elephants have small home ranges, and do not migrate large distances compared to the African species (Fernando et al. 2008). Due to these differences, group members may not follow older individuals that attempt to initiate group movement, or older individuals may not always

take leadership.

To our knowledge, leadership in Asian elephants has been explored in only one study (Mizuno et al. 2017), which found that adult females walked in the front position more often than did non-adults when the group was in the potentially dangerous situation of crossing a vehicular road. Mizuno et al. (2017) focused only on the positions of individuals within groups in risky situations. They analyzed neither the process of group decision-making, such as how elephants decide when to cross a road, nor whether the oldest female led the group. Therefore, examination of group decision-making and analysis of multiple types of initiative behavior in different contexts are important research topics.

Free-ranging Asian elephants in Udawalawe National Park (UWNP) regularly visit permanent water bodies to drink and bathe, particularly during the dry season. These water bodies have multiple entry and exit points. Thus, elephants probably seek the safest and easiest paths before entering and leaving the water bodies. We observed group movements around water bodies in UWNP and tested three predictions derived from Mizuno et al. (2017) and the socioecological characteristics of the elephants. First, we examined which individuals engaged in initiative behavior during their arrival at and departure from water bodies. Similar to Mizuno et al. (2017), we predicted that adult females would engage in initiative behavior more frequently than non-adults (Prediction 1). Second, we predicted that the oldest female would not engage in initiative behavior more frequently than other adult females (Prediction 2). Next, we examined whether the same individual consecutively engaged in multiple types of initiative behavior. We predicted that multiple individuals would perform multiple types of initiative behavior on group departure, such that consecutiveness would be low (Prediction 3). Predictions

2 and 3 are based on the fluid fission–fusion society of elephants. In such a society, the degree to which one individual (e.g., the oldest female) affects the behavior of other group members is not so strong that other individuals may elect not to follow the decisions of the initiator.

Methods

Study area

The study was conducted in UWNP, located in south-central Sri Lanka (Fig. 4.1). UWNP covers approximately 308 km^2; the annual rainfall is approximately 1500 mm and the average annual temperature is approximately 32°C (Kotagama 2014). The natural vegetation of the park is tropical dry evergreen forest. There are two large man-made reservoirs inside the park. Approximately 1,000 elephants use the park, and studies on their social behavior and communication have been conducted at this site (e.g., de Silva 2010; de Silva et al. 2011a). Crocodiles (*Crocodylus palustris*) and leopards (*Panthera pardus kotiya*) are considered potential predators, although predation on elephants has not been reported (de Silva et al. 2011b, 2013). Numerous domestic and international tourists visit the park, so the elephants are habituated to tourist vehicles.

Observation procedure

Field observations were conducted at small human-made water tanks and the Udawalawe Reservoir inside the park by driving a 4×4 vehicle and making opportunistic observations (Fig. 4.1) between 06:30 and 18:30 from May to October 2016 (74 days). The visibility at water bodies is good, but surrounding forests are dense

and may hinder observation of elephant behavior. We visited the water bodies on an *ad hoc* basis. In 15 cases, some elephants were already present at the water body when we found the group (Table 4.1). Otherwise, we waited for aggregations of elephants to arrive and then used a handheld video camera to record all behaviors. The recording commenced with the appearance of the first individual and continued until the last individual left the water body, and each recording was defined as an event. As the elephants did not disperse widely in the water body, we were able to check for all the types of behavior defined below. Following the group after departure from the water bodies was impossible due to the dense forest.

Using the video data, we extracted all events in which the group consisted of three or more individuals. For analytical convenience, we chose events in which we could clearly confirm that the elephants had departed based on the following criteria: First, the group *rested*; no animal took more than 10 consecutive steps for more than 1 min near the water body. Then, all the elephants *turned* their bodies through more than 45º and *walked* more than 10 steps ("*long-walk*"). We used 45º as the threshold for turning toward a new direction for departure following a previous study of primates (Sueur et al. 2010) because we could readily observe whether an elephant had turned (Fig. S4.1). We also extracted events in which the arrival interval between individuals was less than 5 min, to ensure that the observed individuals belonged to the same group. A closer examination of the 27 events that met these criteria showed that the arrival interval between individuals was less than 150 s, as 97.3% (108/111) of all arrivals by subsequent individuals occurred within 150 s of the preceding individual's arrival (arrivals $N = 111$, range 0–101 s, median 4, mean 10.42, three outliers: 291, 293, and 298). Therefore, we further excluded the remaining three events from the analyses as

outliers. Including 15 cases in which individuals were present at the start of observation, a total of 39 departure events met these criteria (Table 4.1). To control for the possible effect of sex within a group, we excluded two cases that included adult males more than 10 years old (see below for method of age estimation). The results of analyses including these two cases did not differ qualitatively from those that excluded them (see Table S4.1, S4.2 and S4.3 in Supplementary Materials). Additionally, to check events with fully overlapping group composition, we attempted to identify all adults using morphological features such as ear shape and tail length (de Silva et al. 2011b). Nine individuals could not be identified due to insufficient information (e.g., only one photograph was available or no distinct physical features were visible). In total, K.M. identified 51 adult females. During 27 of the 37 events, group composition did not fully overlap any other events (7 events: some adults overlapped; 20 events: adults that appeared only once or adults that could not be identified). During the other 10 events, five groups appeared twice, with all adults overlapping. The overlapping groups appeared either a few hours after their first departure or on another day. We were initially concerned that if group members overlapped completely, those data could bias the results; indeed, the same individual did not always perform the multiple types of initiative behavior in such cases (Table S4.4). For these overlapped cases, only the first five events were used (the other five were excluded). Thus, we analyzed 32 events in which the group compositions did not completely overlap (Table 4.1). The results of analyses including the overlapping five cases did not qualitatively differ from those that excluded those cases (Table S4.1, S2 and S3 in Supplementary Materials). In addition, we analyzed 17 events in which the same adult(s) was included in a group to test whether the same individual performed multiple types of initiative behavior in a

different setting. For these cases, we also found that the same individual did not always perform the initiative behaviors (Table S4.4).

We defined the age classes of adult females ($\geq$ 10 years), non-adult females and males (< 10 years) based on the apparent height of an adult female (Table 4.2; Arivazhagan and Sukumar 2008; Fernando et al. 2022). If a group contained more than one adult, the oldest was identified by one researcher (A. D. G. Ranjeewa), who has studied elephants in the park for over 10 years.

We recorded the identities of individuals that performed the following four types of initiative behavior and their timing for each individual. First, we recorded the timing of all individuals when the group arrived at the water tank.

(1) Arrival: we recorded when for each individual that touched the water. We defined the first individual that touched the water as the "first arrival".

We also observed three types of initiative behavior related to group departure from the water tank. For (2) and (3), the initiator was not necessarily in the front position of the group.

(2) Turn: an individual's turning more than 45º toward the direction of future departure (Sueur et al. 2010). This turn behavior was observed in all individuals. If an individual turned in the direction of departure, turned in another direction, and then turned again in the direction of departure, only the first turn was counted. We defined the first individual that turned as the "first turn".

(3) Long-walk: the first individual that walked in the direction of travel for more than approximately 10 m (10–15 continuous steps) without stopping for more than 5 s of rest. The number of steps varied by age class due to both body size and step length variation: 10 steps for adults, 13 for those aged 5–10 years, and 15 for those aged <

5 years. Note that this long-walk was not always performed by all individuals, but all group members walked in the same direction as the initiator (i.e., we did not observe failed initiation).

(4) Walking in front: an individual at the front of a moving group at 1 min after the first long-walk started. Occasionally, the first long-walk continued without stopping for long enough for it to be recorded as walking in front.

Statistical analysis

All statistical procedures were performed with R ver. 4.0.5 (R Core Team 2021). The significance level of all tests was set to 0.05. The data were analyzed in relation to three predictions.

Prediction 1: adult females would engage in initiative behavior more frequently than non-adults

Using a randomization test, we tested whether adults were more likely to engage in initiative behavior during arrival (first arrival) and departure (first turn, first long-walk, and walking in front) than would be expected by chance. First, we generated an artificial dataset of 20 (for first arrival) or 32 (for first turn, first long-walk, and walking in front) cases in which the individual performing each type of initiative behavior was determined randomly. The numbers of adults and non-adults for each case were obtained from corresponding observational data. In the artificially generated data for each case, we examined whether an adult was the initiator. By repeating this procedure for all cases, we obtained the number of cases in which an adult performed initiative behavior. We further repeated these procedures 10000 times and obtained a null

distribution of the number of cases of adults performing initiative behavior. Finally, we examined whether the numbers of observed cases (16 for first arrival, 21 for first turn, 26 for first long-walk, and 27 for walking in front) were in the upper 2.5% (two-tailed test) of the obtained null distribution.

Prediction 2: the oldest female would not engage in initiative behavior more frequently than other adult females

Similarly, we used a randomization test to explore whether the number of events in which the oldest female engaged in initiative behavior was higher than the generated null distribution. First, we excluded events involving a single adult female from the observational data; thus, we used 18 for first arrival, 23 for first turn, first long-walk, and walking in front. We conducted a randomization test to generate a null distribution. The fundamental structure of the randomization test was as described above, but we designed the dataset so that adults performed initiative behavior following the probabilities obtained from the observational data (15/18 for first arrival, 17/23 for first turn, 20/23 for first long-walk, and 20/23 for walking in front). This process was adopted because we found that adults were more likely to take an initiative role than were non-adults (Table 4.3).

Prediction 3: multiple individuals would perform multiple types of initiative behavior on group departure

In 6 of 23 cases, one individual consecutively performed three types of initiative behavior for departure. Using a randomization test, we tested whether these six cases might have occurred because the three types of initiative behavior was distributed

randomly among group members. The fundamental structure of the randomization test was as described above. For cases in which all three behaviors were performed by adults, we examined whether the artificially generated dataset had a single adult performing all three behaviors. After repeating this procedure for all 23 cases, we obtained the number of cases in which a single adult female performed all three types of initiative behavior. We repeated these procedures 10000 times to obtain a null distribution of the number of cases with consistent adult leadership. Finally, we examined whether the number of observed cases (6) was in the upper 2.5% (two-tailed test) of the null distribution.

We conducted a similar randomization analysis of the oldest female and non-oldest adult female, and examined whether the observed cases (four and two, respectively) might have occurred by chance.

Finally, to confirm the consecutiveness of initiative behaviors between arrival and departure, we checked whether an individual that consecutively performed three types of initiative behavior was the first individual that had arrived at the water tank. We did not conduct the randomization test for the first arrival because the sample size was insufficient (Table 4.1).

Results

The median duration of all events from the first arrival to the departure of the last individual was 7.34 min (4.8–35.3 min, $N = 20$). The median time latency between the first and last arrivals was 33 s (5–139 s, $N = 20$; Fig. S4.1) and that between the first and last turns was 65.5 s (4–551 s, $N = 32$). The time latencies between two consecutive behaviors are shown in Fig. S4.1.

Prediction 1: adult females would engage in initiative behavior more frequently than non-adults

The number of observed cases in which adults performed the four types of initiative behavior was in the upper 2.5% of the null distribution obtained from randomization (Table 4.3; first arrival, $P < 0.001$; first turn, $P = 0.011$; first long-walk, $P < 0.001$; and walking in front, $P < 0.001$).

Prediction 2: the oldest female would not engage in initiative behavior more frequently than other adult females

The oldest individual took the first long-walk in 14 of the 23 cases, which was in the upper 2.5% of the null distribution (Table 4.4; $P = 0.014$). However, the number of observed cases involving the oldest individual was not in the upper 2.5% of the null distribution for the other three behaviors (first arrival, $P = 0.27$; first turn, $P = 0.76$; and walking in front, $P = 0.17$).

Prediction 3: multiple individuals would perform multiple types of initiative behavior on group departure

The number of observed cases (six) in which the same adult female performed three behaviors (first turn, first long-walk, and walking in front) was significantly higher than the upper 2.5% of the null distribution (Table 5; $P = 0.024$) according to the randomization test. In four of the six cases, the same individual was the first to arrive at the water body. In the other two cases, the individual that arrived first was another adult, out of three adults in one case and was unknown in the other case.

Of these six events, four were performed by the oldest female and two by other adults. Based on the randomization test, the number of observed cases (four cases) in which the oldest female performed three types of initiative behavior was significantly higher than the upper 2.5% of the null distribution (Table 5; $P = 0.018$), while the number of observed cases (two cases) in which a non-oldest adult female was a consecutive initiator did not differ from the null distribution ($P = 0.36$). In three of the four cases, the oldest was the first to arrive at the water body; in the remaining case, the individual that arrived first was unknown.

Discussion

This study examined the consecutiveness of three types of initiative behavior in group-movement events of Asian elephants. Through comparison of the observed and null distributions, we found that adults exhibited four types of initiative behavior (first arrival, first turn, first long-walk and walking in front) more frequently than expected. This result supports Prediction 1. The movement patterns of Asian elephants did not appear to vary with environmental context: adults took the front position more frequently than did non-adults both when crossing roads (38/47 events; Mizuno et al. 2017) and when moving around water bodies (27/32 events in the present study). Although road crossings may be more dangerous than movements around a water body, both studies imply that adult elephants exhibit initiative regardless of the degree of danger.

In contrast to the effects of age class, we did not find clear evidence that the oldest adult female performed multiple types of initiative behavior. The randomization test showed that the frequency of the first long-walk deviated from the null distribution,

whereas that of the other three types of initiative behavior did not differ significantly. Although these results support Prediction 2, it is possible that the examined initiative behaviors may differ in their degree of influence on group movement. In particular, walking a relatively long distance after standing still for a long period appeared to be a crucial group behavior indicating the intention to move, rather than the subtler first turn. If this possibility is true, the role of the oldest female may be more important than the results of this study suggest. Testing this idea will require examination of whether the influence on group movement differs among types of initiative behavior.

In terms of the three consecutive initiative behaviors that occurred at the time of departure (first turn, first long-walk, and walking in front), the numbers of cases in which adult females (6/23 cases) or the oldest female (4/23 cases) performed all three types of initiative behavior were greater than expected. This result does not strongly support Prediction 3, but the fact that the individuals performing the three types of behavior differed in the other 17 cases suggests that consecutive initiative is not a strong characteristic of group movement in Asian elephants.

Building on our previous research (Mizuno et al. 2017), this study was a rare and valuable attempt to examine group movement in Asian elephants that provides quantitative data implying a weak role of the oldest female in initiating group movement in this species. A unique feature of this study is that we focused on multiple types of initiative behavior related to group departure, allowing us to examine the consecutiveness of initiative behaviors. Nonetheless, our study has several limitations. First, we could not observe the same group repeatedly because of practical difficulties in observation, which prevents from analyzing the consistency of initiative behavior, i.e., whether the same individual takes an initiative role at different times or in different

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contexts in groups consisting of the same members. Leadership can occur in other contexts such as food acquisition, within-group conflict resolution, between-group interactions, and group defense (Smith et al. 2016). Therefore, it is necessary to observe the same groups repeatedly in different situations over a longer period. Second, our small sample size and different observational methods prevent a comparison of results between Asian and African savanna elephants. Finally, low visibility and our observational design did not allow us to record the behavior of group members before and after visits to water bodies, which hindered our ability to determine whether contextual differences influenced the initiator of group movement. Future studies that overcome these limitations will help to elucidate group movement and leadership in Asian elephants.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The field observations complied with the guidelines for animal studies in the wild issued by the Wildlife Research Center of Kyoto University, Japan.

Table 4.1 Numbers of events used for each analysis

Event type	Events with at least one adult		Events with multiple adults	
	All events including PRE	Events excluding PRE	All events including PRE	Events excluding PRE
All events including AM and OGC	39[*1]	24[*1]	27[*2]	20[*2]
Events excluding AM, but including OGC	37[*1]	24[*1]	26[*2]	20[*2]
Events excluding AM and OGC	32[*3]	20[*3]	23[*4]	18[*4]
Events with adults that were observed more than once	17[*5]	14	11	9

AM: events attended by adult males, OGC: events with all adults overlapping, PRE: events in which individuals were present at the water body at the start of the observation

[*1] Data used in Table S4.1 in Supplementary Material

[*2] Data are used in Table S4.2 and S4.3 in Supplementary Material

[*3] Data used in Tables 4.2 and 4.3

[*4] Data used in Tables 4.4 and 4.5

[*5] Data used in Table S4.4 in Supplementary Material

Table 4.2 Age class composition of the elephant groups ($N = 32$)

	Adult female	Immature	Total
Average	2.16	2.78	4.94
SD	1.02	1.41	2.00
Range	1 ~ 5	1 ~ 7	3 ~ 10

Table 4.3 Occurrence of initiative behavior by adults, and the results of randomization tests (null distribution and *P*-value)

Behavior (*N*)	Observed occurrence	Expected occurrence		*P*
		Median	95% confidence interval	
First arrival (20)	16	9	5 ~ 13	**0.0008**
First turn (32)	21	14	9 ~ 20	**0.011**
First long-walk (32)	26	14	9 ~ 20	**0**
Walking in front (32)	27	14	9 ~ 20	**0**

The significant results are shown in bold

Table 4.4 Occurrence of initiative behavior by the oldest individuals, and the results of randomization tests (null distribution and *P*-value)

Behavior (*N*)	Observed occurrence	Expected occurrence		*P*
		Median	95% confidence interval	
First arrival (18)	8	6	3 ~ 10	0.27
First turn (23)	6	7	3 ~ 11	0.76
First long-walk (23)	14	8	4 ~ 13	**0.014**
Walking in front (23)	11	8	4 ~ 13	0.17

The significant results are shown in bold

Table 4.5 Observed occurrence of three types of initiative behaviors (turn, long-walk, and walking in front) performed by the same individual, and the results of randomization tests (null distribution and P-value) ($N = 23$)

Observed occurrence		Expected occurrence		P
		Median	95% confidence interval	
Adult	6*	2	0 ~ 5	**0.024**
Oldest adult	4	1	0 ~ 3	**0.018**
Non-oldest adult	2	1	0 ~ 4	0.361

*4 cases were performed by the oldest females and 2 cases were performed by non-oldest adult females

The significant results are shown in bold
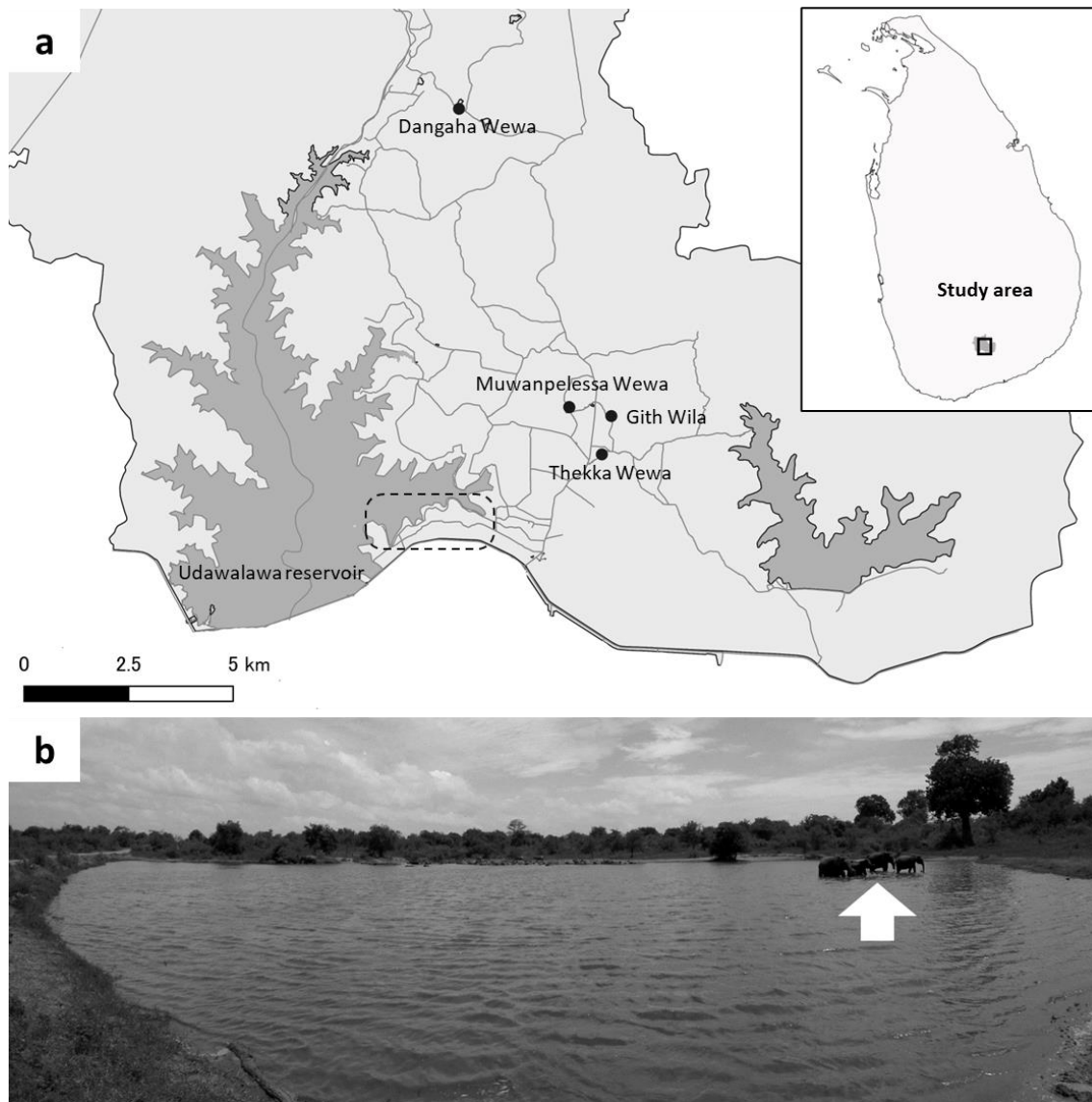
Fig. 4.1 a The research sites in Udawalawe National Park, Sri Lanka. Dots indicate water bodies. The periphery of the lake, surrounded by dotted lines, was the area where we observed groups of elephants. The base map and data were obtained from OpenStreetMap and the OpenStreetMap Foundation (https://www.openstreetmap.org/copyright). b Thekka Wewa and a group of elephants pointed by a white arrow

Supplementary materials

Table S4.1 Occurrence of initiative behavior by adults, and the results of randomization tests (null distribution and *P*-value)

Behavior	All events including AM and OGC					Events including OGC				
	Number of events	Observed occurrence	Expected occurrence		*P*	Number of events	Observed occurrence	Expected occurrence		*P*
			Median	95% confidence interval				Median	95% confidence interval	
First arrival	24	20	11	6 ~ 15	**0.0001**	24	20	11	6 ~ 15	**0**
First turn	39	24	17	12 ~ 23	**0.020**	37	24	17	11 ~ 22	**0.007**
First long-walk	39	31	17	12 ~ 23	**0**	37	30	17	11 ~ 22	**0**
Walking in front	39	33	17	12 ~ 23	**0**	37	31	17	11 ~ 22	**0**

AM: events attended by adult males, OGC: events with all adults overlapping
The significant results are shown in bold

Table S4.2 Occurrence of initiative behavior by the oldest individuals, and the results of randomization tests (null distribution and *P*-value)

Behavior	All events including AM and OGC					Events including OGC				
			Expected occurrence					Expected occurrence		
	Number of events	Observed occurrence	Median	95% confidence interval	*P*	Number of events	Observed occurrence	Median	95% confidence interval	*P*
First arrival	20	9	7	3 ~ 11	0.249	20	9	7	3 ~ 11	0.251
First turn	27	7	8	4 ~ 13	0.731	26	7	8	4 ~ 13	0.723
First long-walk	27	15	10	5 ~ 14	**0.025**	26	15	10	5 ~ 14	**0.025**
Walking in front	27	13	10	5 ~ 15	0.131	26	13	9	5 ~ 14	0.083

AM: events attended by adult males, OGC: events with all adults overlapping
The significant results are shown in bold

Table S4.3 Observed occurrence of three types of initiative behavior (turn, long-walk, and walking in front) performed by the same individual, and the results of randomization tests (null distribution and *P*-value)

	All events including AM and OGC ($N = 27$)				Events including OGC ($N = 26$)			
	Observed occurrence	Expected occurrence		*P*	Observed occurrence	Expected occurrence		*P*
		Median	95% confidence interval			Median	95% confidence interval	
Adult	6	2	0 ~ 6	**0.039**	6	2	0 ~ 6	**0.038**
Oldest adult	4	1	0 ~ 4	**0.029**	4	1	0 ~ 4	**0.026**
Non-oldest adult	2	1	0 ~ 4	0.412	2	1	0 ~ 4	0.411

AM: events attended by adult males, OGC: events with all adults overlapping
The significant results are shown in bold

Table S4.4 List of events in which the composition of adults in a group was the same or in which the same individual appeared more than once

Event ID	Group ID in case all adults completely overlapped in two events*1	ID of adults that observed more than once	ID of the oldest individual	Initiative behaviors*2				Proportion that the same individual did initiative behavior	Number of individuals			Group size
				First arrival	First turn	First long-walk	Walking in front		Adult female	Adult male	Non-adult	
1	G1	A, D	**D**	A	**D**	**D**	j-X1*3	1/4	2	0	4	6
2	G1	A, D	**D**	**D**	j-X2*3	**D**	**D**		2	0	4	6
3	-	A, D	**D**	**D**	**D**	**D**	**D**	-	3	0	4	7
4	G2	M, N	**M**	**M**	**M**	**M**	**M**	1/4	2	0	1	3
5	G2	M, N	**M**	unknown	j-1	N	**M**		2	0	1	3
6	G3	I, J, K	**I**	**I**	K	K	**I**	0/3	3	0	1	4
7	G3	I, J, K	**I**	unknown	j-1	**I**	J		3	0	2	5
8	-	I, J, K	unidentified individual	J	j-1	I	j-1	-	5	0	3	8
9	-	A	**A**	ad-1	ad-1	j-1	ad-1	-	2	0	3	5
10	-	B	**B**	**B**	**B**	**B**	**B**	-	2	0	4	6
11	-	B	**B**	**B**	ad-1	ad-2	ad-2	-	4	0	6	10
12	-	C	**C**	ad-1	ad-1	j-1	j-2	-	2	0	7	9
13	G4	C	-*4	j-1*5	C	C	C	1/4	1	0	2	3
14	G4	C	-*4	C	j-2*5	j-2*5	C		1	0	3	4

15	G5	L	-*4	L	L	L	j-1	3/4	1	0	2	3
16	G5	L	-*4	L	L	L	L		1	0	2	3
17	-	A	-*4	unknown	j-1	A	A	-	1	0	3	4
18	-	-	-*6	oldest	ad-1	ad-1	ad-1	-	3	0	4	7
19	-	-	-*6	j-1	ad-1	oldest	ad-1	-	2	0	3	5
20	-	-	-*6	oldest	j-1	j-1	j-2	-	4	0	5	9
21	-	-	-*6	ad-1	j-1	oldest	oldest	-	2	0	1	3
22	-	-	-*6	unknown	oldest	ad-1	oldest	-	3	0	2	5
23	-	-	-*6	unknown	oldest	oldest	oldest	-	2	0	1	3
24	-	-	-*6	oldest	oldest	oldest	ad-1	-	2	0	2	4
25	-	-	-*6	ad-1	ad-1	ad-1	oldest	-	2	0	2	4
26	-	-	-*6	ad-1	ad-2	oldest	oldest	-	3	0	3	6
27	-	-	-*6	j-1	ad-1	oldest	oldest	-	3	0	3	6
28	-	-	-*6	unknown	ad-1	oldest	oldest	-	2	0	2	4
29	-	-	-*6	ad-1	ad-1	ad-1	ad-1	-	2	0	1	3
30	-	-	-*6	j-1	ad-1	oldest	ad-1	-	2	0	2	4
31	-	-	-*6	unknown	j-1	oldest	ad-1	-	3	0	2	5
32	-	-	-*4	unknown	j-1	j-1	ad-1	-	1	1	2	4
33	-	-	-*4	unknown	j-1	ad-1	ad-1	-	0	1	2	3
34	-	-	-*4	unknown	ad-1	ad-1	ad-1	-	1	0	2	3
35	-	-	-*4	unknown	j-1	j-2	j-2	-	1	0	3	4
36	-	-	-*4	unknown	j-1	j-1	ad-1	-	1	0	4	5
37	-	-	-*4	unknown	j-1	j-1	ad-1	-	1	0	2	3

| 38 | - | - | -[*4] | unknown | ad-1 | ad-1 | ad-1 | - | 1 | 0 | 2 | 3 |
| 39 | - | - | -[*4] | unknown | j-1 | ad-1 | ad-1 | - | 1 | 0 | 2 | 3 |

The letter was highlighted in gray if it was unknown who had performed the behavior or if a juvenile had performed it. The average percentage of events in which the same individual performed initiative behavior among different groups in which all adults overlapped was 30%. See the table for the initiative behavior of the groups in which one or more adults overlapped

[*1] Group IDs (G1–G5) were assigned in cases where all adults overlapped completely

[*2] If an initiative behavior was performed by an adult who appeared more than once, the ID is shown. The oldest individual is indicated in bold. Otherwise, ad- indicates an adult and j- indicates a juvenile; ad-1 is the same individual within a single event, but not across multiple events

[*3] In G1, j-X1 and j-X2 may have been the same individual; we could not be certain without a clear photograph

[*4] Since there was only one adult, that individual became the oldest

[*5] In G4, j-1 and j-2 are different individuals

[*6] The oldest ID was not written for events in which the same adult appeared more than once. However, if the oldest took the initiative behavior, it indicated "oldest" is shown there. Like ad-1 and j-1, "oldest" is not the same individual across events
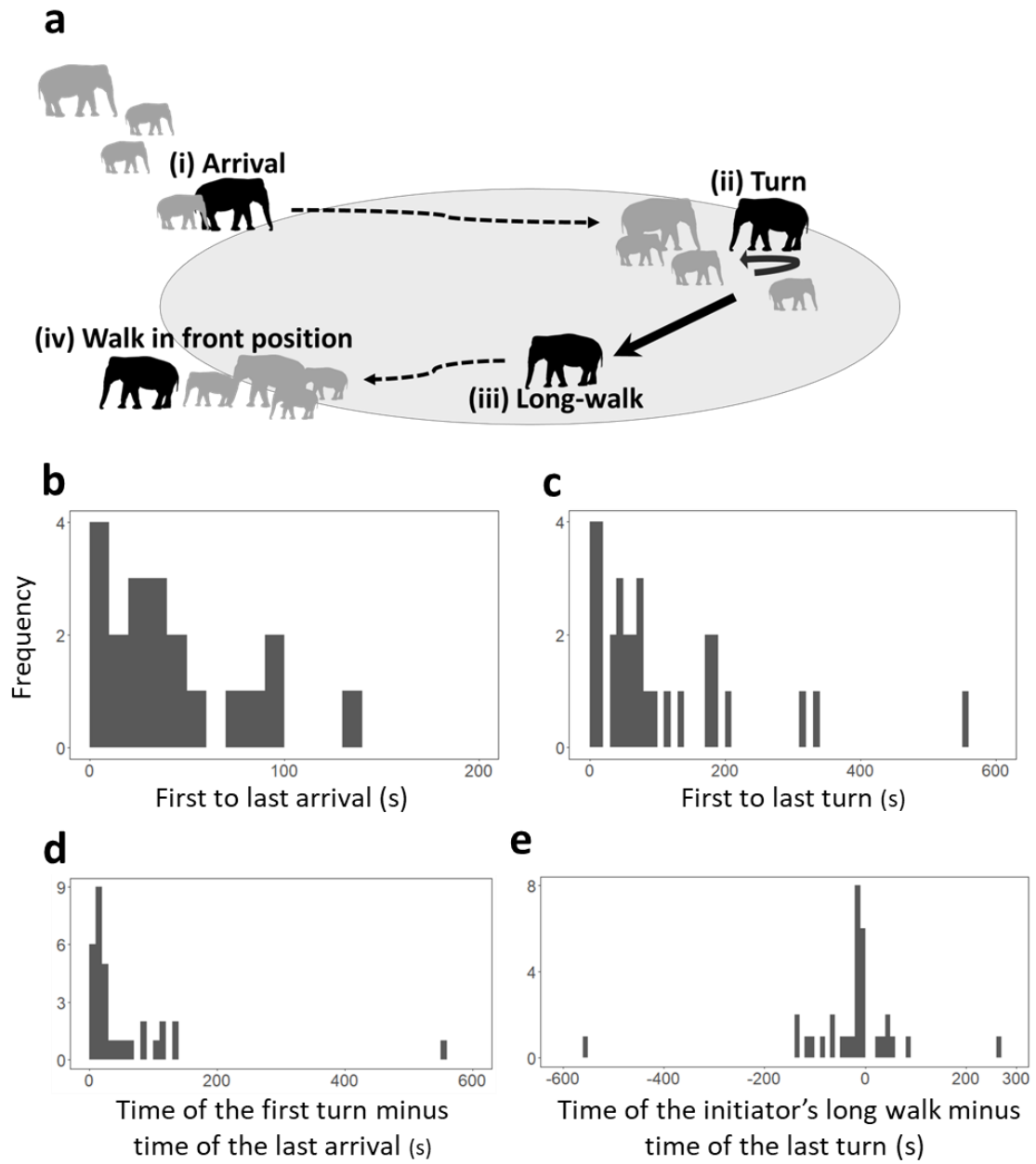
Fig. S4.1 (a) Schematic of the four types of initiative behaviors. (b, c) Time latencies between the first and last individuals that performed each initiative behavior. (b) First to last arrivals. (c) First to last turns. (d, e) Time latencies between two consecutive behaviors. (d) Time of the first turn minus time of the last arrival. (e) Time of the initiator's long-walk minus time of the last turn

Chapter 5: General discussion

In this thesis, I added new examples of the behavioral flexibility of Asian elephants. In Chapter 2, I found 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. In chapters 3 and 4, I discovered that Asian elephants display fluid and adaptive social roles when crossing roads and using water bodies, showing their ability to adjust to the situation flexibly.

General discussion and implication of chapter 2

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 because of the unique environment of this zoo. The roaming area was surrounded by moats, and when food accidentally fell into the moat, the elephants' trunks could not reach it. In this problem-solving circumstance, the elephant may have learned the behavior that was not originally part of its behavioral repertoire.

From the standpoint of behavioral flexibility, this study has three important implications. The first point is social learning. The fact that the two females living together exhibited identical behavior may suggest that the second female acquired the behavior through social learning. No experimental evidence of observational learning of elephants has yet been found, but it is known that African savanna elephants exhibit social facilitation (Greco et al. 2013; Barrett and Benson-Amram 2020) and that Asian and savanna elephants mimic vocalizations (McComb et al. 2005; Stoeger et al. 2012).

It is crucial to assess the ability to do social learning of physical movements such as tool use and breath control.

The second point is intentional, strategic, and subtle modifications in their trunk movements. The African elephant has been estimated to increase its trunk volume by up to 64% in order to carry huge amounts of water and to suck at speeds of over 150 m/s, about 30 times quicker than a human sneeze (Schulz et al. 2021). The gripping force of an African elephant's trunk-tip is estimated to be 32N (Cornette et al. 2022). It would be interesting to examine how much the trunk volume increases, how much the trunk tip narrows, and how much force is applied when the Asian elephant injects breath. One subject seemed to adjust the amount and speed of blowing depending on the food (personal observation, see supplemental materials of Mizuno et al. 2016). There is no clear empirical evidence that Asian elephants can modify their sucking, grasping, and blowing forces according to the objects. Therefore this type of behavioral flexibility should be studied further in the future.

The third point is the relationship between vocal learning and flexible breathing control. It is thought that the capacity for vocal learning and adaptive vocal behavior is related to the control and coordination of the pulmonic system, which includes the diaphragm and lungs, i.e., voluntary control of breathing (Perlman and Clark 2015). However, little direct research has been done on less audible non-vocal behaviors (Perlman and Clark 2015). The report of chapter 2 is valuable as it demonstrates that elephants, which are known to be rare vocal learners among mammals (Stoeger et al. 2012), can flexibly control their breathing.

As such, these findings provided a novel example of behavioral flexibility in a physical context in Asian elephants. The ability to manipulate breath to attract objects

has not been reported in African savanna or forest elephants. There are subtle differences between Asian and African elephants in how they grasp objects with their trunks and in the distribution of neurons in their trunks (Kaufmann et al. 2022). It is also suggested that some of their cognitive abilities differ (Plotnik and Jacobson 2022). Further research is needed to determine if these species can perform the same behavior.

General discussion and implication of chapters 3 and 4

The chapters 3 and 4 examined collective movement in Asian elephants under different circumstances. In some species with large group size, individuals follow simple behavioral principles, and the accumulation of local interactions results in significant collective behavior (Couzin and Franks 2003; Ballerini et al. 2008; Herbert-Read et al. 2011; Katz et al. 2011; Carlesso et al. 2023). On the other hand, elephants form relatively small groups, which allow one individual to communicate with all other group members. Additionally, their group composition is not stable, with individuals having varying characteristics. These aspects might relate to the collective behavior deviated from fixed patterns.

There was a similarity and a dissimilarity between the two studies. Regarding the similarity, I found that adults made decisions to initiate collective movement often, and immature individuals followed them. In chapter 3, adults were more likely to cross the road first than non-adults. In chapter 4, adults were more likely to initiate the departure than non-adults. Decisions by older individuals might relate to that they are more experienced and have greater knowledge than younger individuals. A group needs to make a good decision about an appropriate destination or an appropriate timing based on a group member's knowledge and experience. Additionally, occupying the forward

position in a group progression is considered to be risky (Bumann et al. 1997). Adults, that are larger and stronger than immature individuals, can assume these costs more effectively than younger individuals (Sueur and Petit 2008).

Regarding the dissimilarity between the two studies, the role of the oldest female was different. In chapter 3, I could not find any evidence that the oldest individual played a leading role. In chapter 4, 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 the collective movements, it is possible that the examined initiative behaviors may differ in their degree of influence on collective movements. In particular, walking long distances after standing still for a long period appears to be a crucial behavior indicating the intention to move rather than the subtler first turn. If this possibility is true, the role of the oldest female may be more important than the results of this study suggest. Testing this idea will require an examination of whether the influence on collective movement differs among types of initiative behavior. The oldest female may become a leader in a particular context. In addition, the collective movement performed when crossing a road or leaving a water body may differ from that in other situations.

Chapters 3 and 4 are the first studies to examine collective movement in Asian elephants. 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 dominance 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. Nonetheless, several questions remain. For example, the sample size was smaller than that of the previous study of African savanna elephants (Mutinda et al. 2011), and we could not compare the frequency of initiative behavior of all group members during certain departure events. The low visibility and our observational design did not allow us to record the behavior of group members before and after the water rest, hindering the examination of whether contextual differences affected the individuals' roles, such as leadership, during the collective movement. More generally, leadership can occur in other contexts, such as food acquisition, within-group conflict resolution, between-group interactions, and group defense (Smith et al. 2016). Therefore, it is necessary to explore whether leadership is distributed among adults by repeatedly observing certain groups in those different situations over a longer period.

Conclusion

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. Being flexible and cooperative with others in complex societies might

assist an individual in obtaining benefits of group-living. Thus, behavioral flexibility plays a crucial role in the adaptation and success of individuals.

Behavioral studies of Asian elephants had been limited despite their unique characteristics, such as intelligence and social complexity, which make them particularly valuable in the studies of both comparative cognition and behavioral ecology. This thesis 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. Even though I highlighted the value of studying behavioral flexibility, more studies are still required to comprehend the variety of behaviors exhibited by elephants that can live for decades in a constantly changing environment.

Acknowledgments

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