Collective movements during visits to water bodies in wild Asian elephants

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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 dawalawe 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 fre uencies of initiative behavior by a particular individual. We found that adults were more likely to exhibit such behavior than the expected fre uencies. We also found that a single female, generally the oldest female, consecutively engaged in three types of initiative behavior more fre uently 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.

Keywords Collective movement Departure Multiple types of initiative behavior *Elephas maximus*

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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 (hl-Bien et al. 2014). In studies examining relationships between individual attributes and leadership, dominant individuals (S uires 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 uruichi 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 initia-tive 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 oley et al. 2008), and older elephants often take on the leader-ship 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 oley 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 (ernando 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 ele-phants, 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 preda-tion 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 (ernando et al. 2008). Due to these differ-ences, 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 posi-tion 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 old-est 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.

ree-ranging Asian elephants in dawalawe National Park (WNP) 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 WNP and tested three predictions derived from Mizuno et al. (2017) and the socio-ecological characteristics of the elephants. irst, we exam-ined 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 fre uently than non-adults (Prediction 1). Second, we predicted that the oldest female would not engage in initiative behavior more fre uently than other adult females (Prediction 2). Next, we examined whether the same individual consecutively engaged in mul-tiple types of initiative behavior. We predicted that multiple individuals would perform multiple types of initiative behav-ior 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 WNP, located in south-central Sri Lanka (ig. 1). WNP covers approximately 308 km2 the annual rainfall is approximately 1500 mm and the aver-age annual temperature is approximately 32 C (Kotagama 2014). The natural vegetation of the park is tropical dry ever-green 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 interna-tional tourists visit the park, so the elephants are habituated to tourist vehicles.

Observation procedure

ield observations were conducted at small human-made water tanks and the dawalawe Reservoir inside the park by driving a 4 4 vehicle and making opportunistic observa-tions (ig. 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 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.

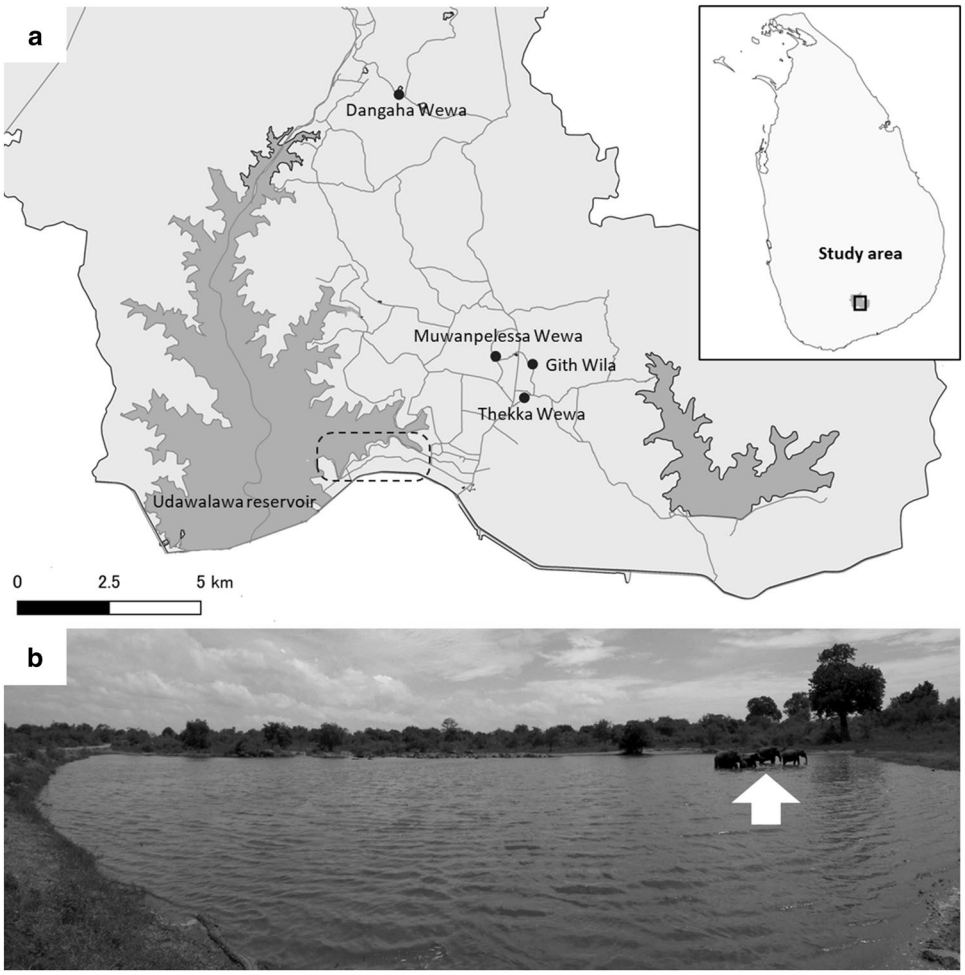

Fig. 1 **a** The research sites in dawalawe National Park, Sri Lanka. Dots indicate water bod-ies. The periphery of the lake, surrounded by dotted lines, was the area where we observed groups of elephants. The base map and data were obtained from OpenStreetMap and the OpenStreetMap ounda-tion (https: www.openstreet map.org copyright). **b** Thekka Wewa and a group of elephants pointed by a white arrow

Table 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 S1 in Supplementary Material

[*2]Data are used in Tables S2 and S3 in Supplementary Material

[*3]Data used in Tables 2 and 3

[*4]Data used in Tables 4 and 5

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

Table 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

As the elephants did not disperse widely in the water body, we were able to check for all the types of behavior defined below. ollowing the group after departure from the water bodies was impossible due to the dense forest.

sing the video data, we extracted all events in which the group consisted of three or more individuals. or analytical convenience, we chose events in which we could clearly con-firm that the elephants had departed based on the following criteria: irst, 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 45 and walked more than 10 steps (long-walk). We used 45 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 (ig. S1). 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 subse uent 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 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 ualitatively from those that excluded them (see Tables S1, S2 and S3 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. iden-tified 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 over-lapping. 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 individ-ual did not always perform the multiple types of initiative behavior in such cases (Table S4). or 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 1). The results of analyses including the overlapping five cases did not ualitatively differ from those that excluded those cases (Tables S1, 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 differ-ent setting. or these cases, we also found that the same individual did not always perform the initiative behaviors (Table S4).

We defined the age classes of adult females (10 years), non-adult females and males (10 years) based on the apparent height of an adult female (Table 2 Arivazhagan and Sukumar 2008 ernando et al. 2022). If a group con-tained 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 tim-ing for each individual. irst, 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. or (2) and (3), the initiator was not necessarily in the front position of the group (2010).

(2) Turn: an individual s turning more than 45 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 10-15 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 stop-ping 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

sing 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. irst, 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 10,000 times and obtained a null distribution of the number of cases of adults performing initiative behavior. inally, 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. irst, 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 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 behav-ior 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.

Table 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	
irst arrival (20)	16	9	5 13	**0.0008**
irst turn (32)	21	14	9 20	**0.011**
irst long-walk (32)	26	14	9 20	**0**
Walking in front (32)	27	14	9 20	**0**

The significant results are shown in bold

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 10,000 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.

inally, 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 randomi-zation test for the first arrival because the sample size was insufficient (Table 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 ig. S1) 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 ig. S1.

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 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 distribu-tion (Table 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.

Table 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	
irst arrival (18)	8	6	3 10	0.27
irst turn (23)	6	7	3 11	0.76
irst 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 5 Observed occurrence of three types of initiative behaviors (turn, long-walk, and walking in front) performed by the same indi-vidual, 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 per-formed by non-oldest adult females

The significant results are shown in bold

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 dis-tribution (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 distribu-tion (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 fre uently than expected. This result supports Prediction 1. The movement patterns of Asian ele-phants did not appear to vary with environmental context: adults took the front position more fre uently 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 stud-ies 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 fre uency 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 re uire 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 uantitative data implying a weak role of the oldest female in initiating group movement in this species. A uni ue 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. irst, 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 contexts in groups consisting of the same members. Leadership can occur in other contexts such as food ac uisition, 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. inally, 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. uture studies that overcome these limitations will help to elucidate group movement and leadership in Asian elephants. 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 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.

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