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

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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.

Keywords

collective behaviour, Asian elephant, ontogenetic difference, risky situation, order of progression.

1. Introduction

In group travel, the order of progression may depend on individual characteristics or on the situation (for a review, see Petit & 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 & Daws, 1975; yellow baboons,

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Papio cynocephalus: Rhine, 1975, Rhine & 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 & Reebs, 2006).

Advantages of taking the front position are to increase opportunities to obtain food (e.g., roach fish, *Rutilus rutilus*: Krause et al., 1992, 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 & DeVore, 1961; Rhine, 1975; Rhine & Westlund, 1981; for a review see Sueur & 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 & 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 & 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 behaviour 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 & Townsend, 2013). Additionally, a few reports have illustrated behaviour 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 & 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 et al., 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 & Sukumar, 2005). Given some differences in social organization between African savanna elephants and Asian elephants (de Silva & Wittemyer, 2012), there could be differences in the latter species with respect to collective behaviour in risky situations.

Free-ranging wild Asian elephants in Mudumalai Wildlife Sanctuary and National Park, southern India, must frequently cross busy roads (see Video 1 in the online edition of this journal). Vidya & 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 behaviours 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 behaviour, 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 behaviour, 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 behaviour because there are some reports suggesting that tail raising was observed when an elephant was apprehensive or alarmed (Poole, 1999; Poole & 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 behaviour 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.

2. Methods

2.1. 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 (Figure 1; 321 km^2, 11°30′–11°42′N, 76°30′–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 ca. 1500 vehicles per day), and from Thorapally to Bandipura (ca. 3750 vehicles per day); and ‘secondary roads’ from Moyar to Singara (ca. 225 vehicles per day). Traffic is permitted on roads passing through the park only between 6 AM and 9 PM. 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.

2.2. 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

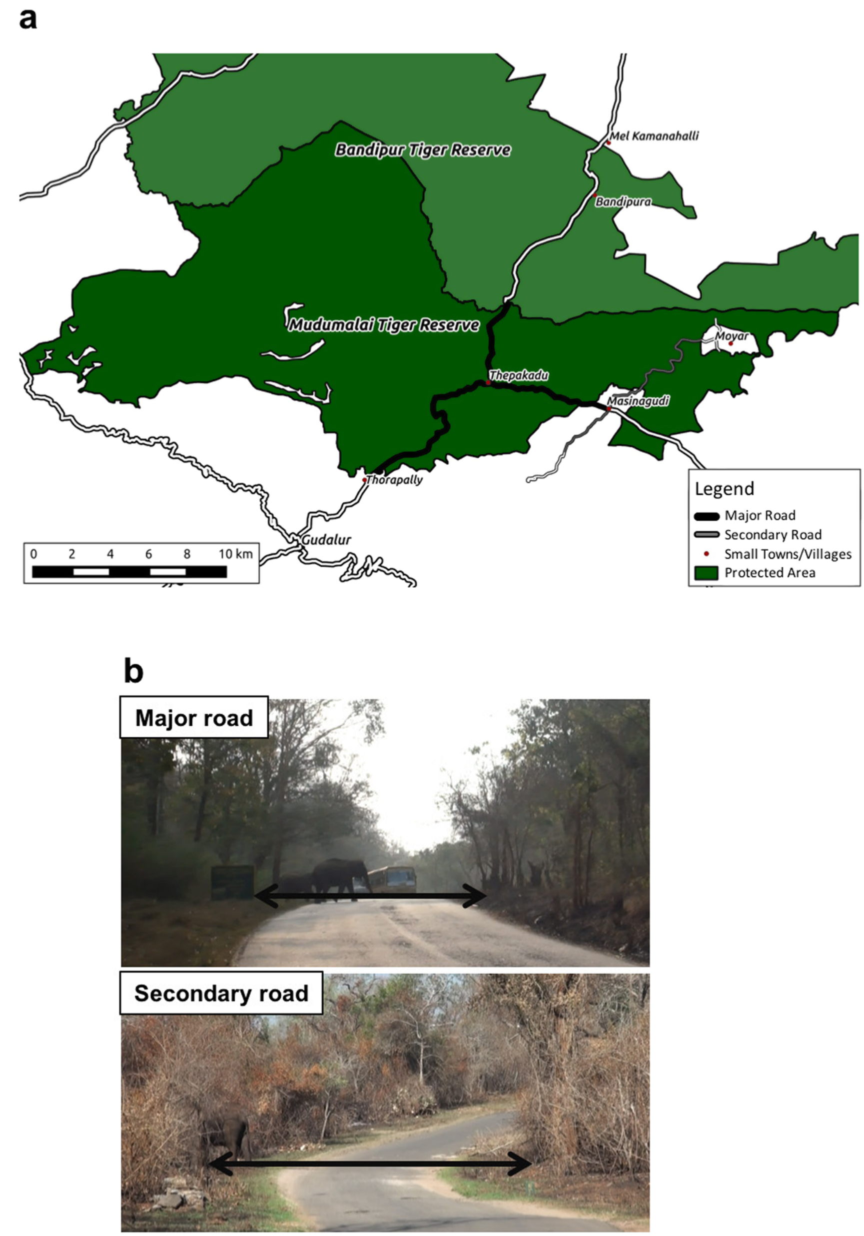

Figure 1. (a) Map of roads through the Mudumalai Wildlife Sanctuary and National Park. Roads that we travelled to search for elephants are shown in colour; black indicates a major road and grey indicates a secondary road. (b) Photographs of major and secondary roads; arrows indicate road widths.

and began observations, maintaining a distance of at least 20 m 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 years 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 year age class, one male in the 16–30 year age class, and four males in the 10–15 year 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 analysis (see below).

2.3. Age estimation

We estimated age class (<1, 1–5, 6–10, 11–15, 16–30 and >30 years) by criteria based on previous studies (Sukumar, 1989; Arivazhagan & Sukumar, 2008). We did not record any behaviour of calves (<1 year) because their crossing speed is much slower than that of other immature individuals (1–10 years) and they appear to concentrate on following their mothers. We defined adult as the >10 year age class and immature individuals as the 1–10 year 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.

2.4. 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% $(= (9/10 + 15/16)/2 \times 100)$.

53 events (26 events by video recording and 27 events by taking notes) were analysed 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):

$$(X_{\mathrm{e}} - X_{\mathrm{l}})/(G - 1 - C),$$

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 $\pm$ SD group size was 5.9 ± 3.1 ($N = 51$), and the group composition is given in Table 1.

In addition to the order of crossing, more detailed behaviours 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, The Netherlands). Frame-by-frame playback (1/30-s 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 ± 0.26 adult body lengths,

Table 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 year age class, one male in the 16–30 year age class and one male in the >30 year age class).

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

Crossing events by solitary elephants were excluded.

$N = 9$; secondary roads: 4.50 ± 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 $\pm$ SD 100.0 ± 115.4 s ($N = 25$) 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 ± 3.0 vehicles, $N = 7$, secondary road: 2.0 ± 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 ± 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 behaviour of elephants due to these narrow distributions.

2.5. *Statistical analysis*

We used R 3.2.2 (R Development Core Team, 2015) for all analyses. 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 behavioural 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 behaviour only of adults (>10 years) and immature individuals (1–10 years) due to the small sample size of each age class.

2.5.1. 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 & 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 analysis 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 analyse 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 (56 adults, 58 immature) 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 (55 adults, 61 immature; 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 GLMMs 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 year) because their crossing speed appeared to be influenced by their calves' crossing speed (47 adults, 56 immature; 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.

3. Results

There was an association between road characteristics and elephant behaviour, as we predicted. More individuals raised their tails while crossing wider roads (Figure 2; Table 2; $p = 0.005$). On the other hand, road type (which was classified into two types based on location and traffic) was not associated with elephant behaviour.

3.1. Adults vs immature individuals

Adults, which are more experienced than immature individuals, exhibited slightly less excitement and displayed leading behaviour, as compared to immature individuals. The number of immature individuals that raised their tails was nearly significantly greater than that of adults (Figure 3; Table 2;

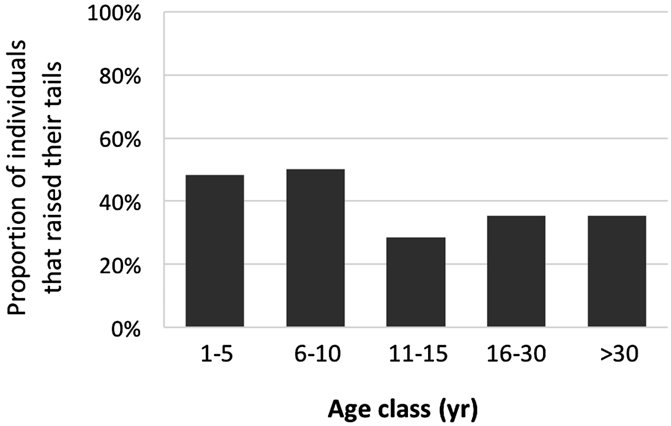

Figure 2. The proportion of individuals that raised their tails during road-crossing in different age classes ($N = 116$; 26 events).

$p = 0.056$). The ratio of adults entering the road first compared to that of immature individuals was higher than expected by chance (Figure 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 (Figure 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 (Figure 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 ± SD = 18.1 ± 44.6 s; $N = 54$) was shorter than that of adults (28.7 ± 69.6 s; $N = 32$; Table 2; $p = 0.03$). 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 (Figure 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 year age class, two non-oldest adults in the 15–30 year age class; see also Video 2 in the online edition of this journal). Although the staying duration of immature individuals (average ± SD = 5.7 ± 3.2 s/adult body length) was slightly shorter

Table 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) analysed by GLMMs.

Explanatory variable	Estimate ± SE	Z	T	p
(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
(c) Response value: inter-individual interval at the moment of entering the road				
Intercept	3.24 ± 0.91		3.56	0.0004
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

* Significant difference.

than that of adults (6.1 ± 3.2 s/adult body length), the staying duration was not significantly associated with age class (Table 2; $p = 0.15$). Similarly, the proportions of individuals stopping on the road were similar in both age classes (Table 2; $p = 0.83$).

3.2. 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 fe-

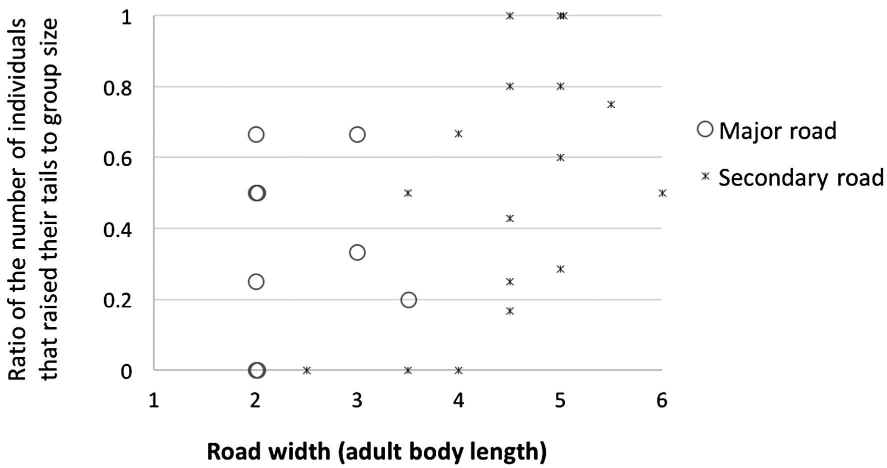

Figure 3. Ratio of individuals that raised their tails to group size in each road ($N = 26$).

Table 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) analysed by GLMMs.

Explanatory variable	Estimate ± SE	Z	T	p
(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
(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

* Significant difference.

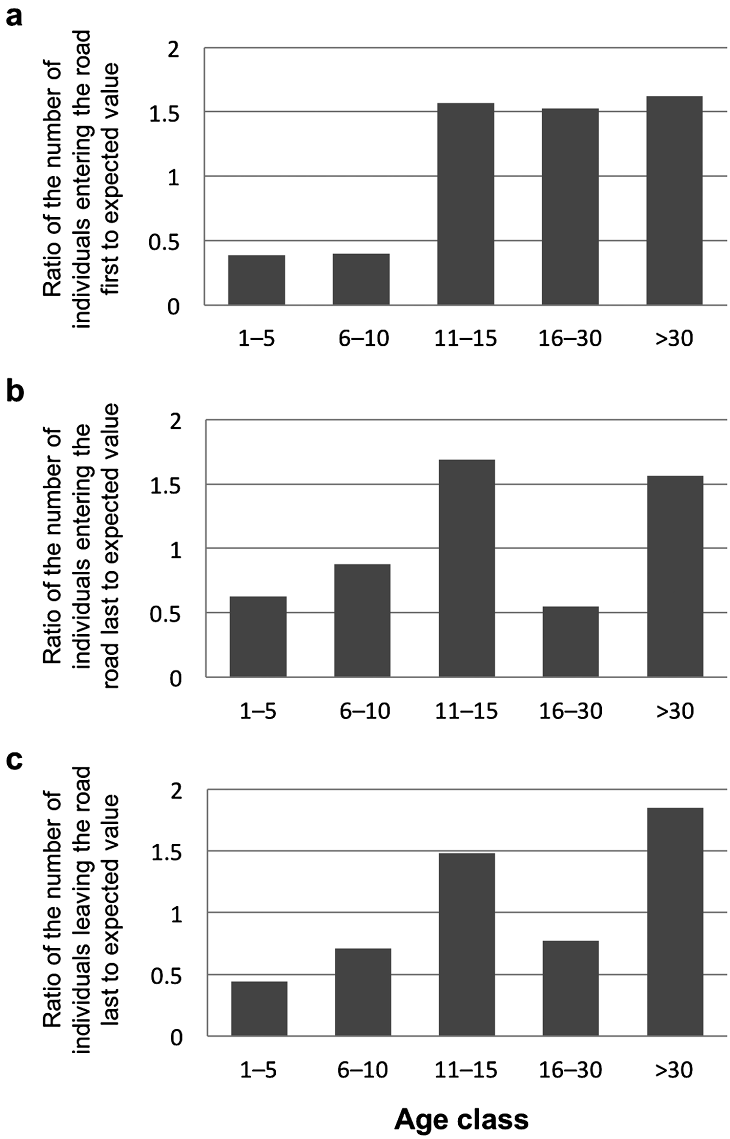

Figure 4. Ratios of observed to expected values in each age class (a) entering the road first ($N = 47$), (b) entering the road last ($N = 48$) and (c) leaving the road last ($N = 47$).

males. 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

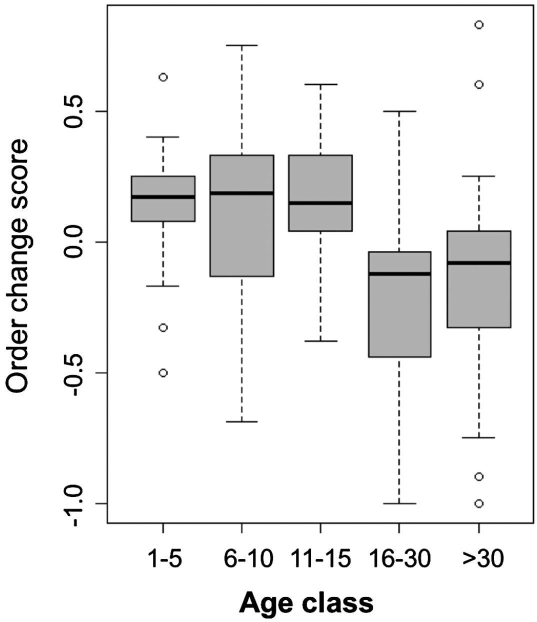

Figure 5. Boxplots of order change score in each age class ($N = 114$ individuals; progression positions changed on the roads in 34 events). Positive values indicate that an individual passed another elephant on the road.

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 (Figure 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 (Figure 6c; 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; $p = 0.44$) or stopping (Table 3; $p = 0.90$) and crossing duration (Table 3; $p = 0.21$) was similar between the oldest and non-oldest adults.

4. Discussion

We found that the degree of risk was associated with the behaviour of wild Asian elephants, which live in social groups, are long lived and mature slowly, and we found some behavioural differences between adults and

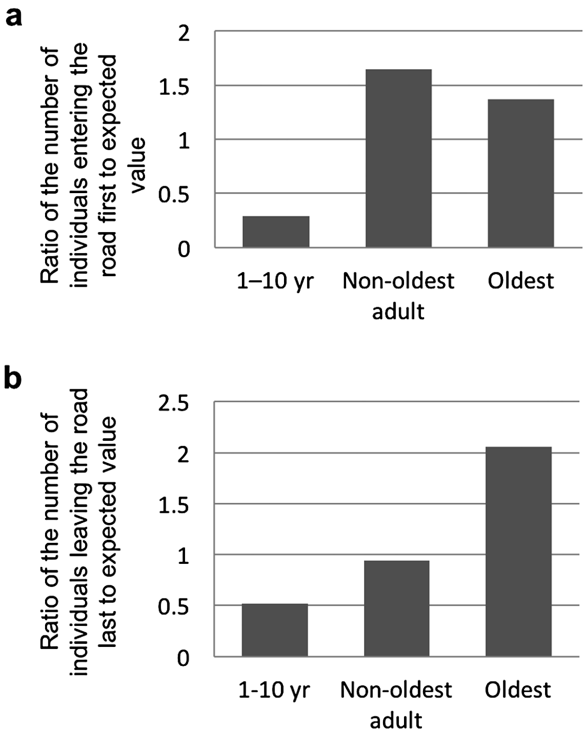

Figure 6. Ratio of observed to expected values in each category (a) entering the road first ($N = 32$) and (b) leaving the road last ($N = 32$).

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 behaviour on wider roads. Traffic did not significantly affect the behaviour of elephants in this study. Loud human voices, nearby vehicles, the number of vehicles, and crossing time appeared to trigger nervous behaviour in elephants, but we were unable to determine a definite relationship between these factors and any behaviour.

More adults entered the road first, and fewer adults tended to display tail raising behaviour 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 behaviour 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 behavioural 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 (Archie et al., 2006; Wittemyer & Getz, 2007; de Silva et al., 2016). 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 behaviours such as crossing duration, nervous behaviour, 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 (Dumont et al., 2005; Ramseyer et al., 2009). In African savanna elephants, the oldest female typically initiates group movement but takes the last position of the group progression, while the 15–20 year 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 behaviour in non-risky situations, such as movement in forests; observing such group behaviours would improve our insight into the response of Asian elephants to potentially risky situations.

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