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Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants

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BEHAVIOR RATHER THAN DIET MEDIATES SEASONAL DIFFERENCES IN SEED DISPERSAL BY ASIAN ELEPHANTS

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Abstract. Digestive physiology and movement patterns of animal dispersers determine deposition patterns for endozoochorously dispersed seeds. We combined data from feeding trials, germination tests, and GPS telemetry of Asian elephants (*Elephas maximus*) to (1) describe the spatial scale at which Asian elephants disperse seeds; (2) assess whether seasonal differences in diet composition and ranging behavior translate into differences in seed shadows; and (3) evaluate whether scale and seasonal patterns vary between two ecologically distinct areas: Sri Lanka's dry monsoon forests and Myanmar's (Burma) mixed-deciduous forests. The combination of seed retention times (mean 39.5 h, maximum 114 h) and elephant displacement rates (average 1988 m in 116 hours) resulted in 50% of seeds dispersed over 1.2 km (mean 1222–2105 m, maximum 5772 m). Shifts in diet composition did not affect gut retention time and germination of ingested seeds. Elephant displacements were slightly longer, with stronger seasonal variation in Myanmar. As a consequence, seed dispersal curves varied seasonally with longer distances during the dry season in Myanmar but not in Sri Lanka. Seasonal and geographic variation in seed dispersal curves was the result of variation in elephant movement patterns, rather than the effect of diet changes on the fate of ingested seeds.

Key words: Asian elephant; dispersal distance; *Elephas maximus*; mechanistic model; Myanmar; seasonal differences; seed dispersal curves; seed shadow; Sri Lanka.

INTRODUCTION

Seed dispersal is a key process for population and community dynamics in plants, with profound implications for succession, regeneration, and conservation of ecosystems (Wang and Smith 2002). The spatial distribution of dispersed seeds (seed shadow) sets the template for future demographic processes, such as predation, germination, growth, and reproduction (Nathan and Muller-Landau 2000). Despite their importance, knowledge of factors affecting seed shadows and their consequences for dispersal outcomes is limited (Nathan and Muller-Landau 2000, Westcott et al. 2005).

One critical determinant of spatial patterns of seed dispersal is the distance of dispersal events, summarized by the dispersal curves (Levin et al. 2003). In seeds dispersed by endozoochory, dispersal curves depend on

gut passage time (time from ingestion to defecation), and speed and direction of animal movements during this period (Janzen et al. 1976, Holbrook and Smith 2000, Westcott et al. 2005). In addition, nonrandom use of space by animal dispersers causes dispersal of disproportional amounts of seeds to particular locations, such as feeding patches (Janzen et al. 1976), latrines (Fragoso 1997), display sites (Wenny and Levey 1998), and resting places (Russo and Augspurger 2004). Post-dispersal seed germination and seedling establishment are affected by the effects of gut passage on seed viability and germination (Traveset and Verdú 2002).

In seasonal environments many animal dispersers show pronounced temporal variations in diet, habitat use, or foraging behavior. These can alter the shape and scale of dispersal curves. For instance, seasonal changes in diet composition can affect gut passage rate (e.g., Spalinger et al. 1993, Schabacker and Curio 2000), modifying seed retention time (Levey and Karasov 1992). Similarly, seasonal changes in spatial arrangement of resources may influence movement patterns of dispersers, and therefore dispersal outcomes. The effect of seasonal variation on spatial patterns of endozoocho-

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rous seed dispersal and the relative importance of the factors modulating it (digestive physiology vs. animal behavior) remains largely to be tested (but see McConkey and Chivers 2007).

Elephants are efficient seed dispersers and are likely to play an important role for long-distance dispersal (Corlett 1998). Yet, there is no data on the spatial scale at which elephants actually disperse seeds. Asian elephants (*Elephas maximus*) occur in a wide range of habitats: from the dry, thorny forests of southern India and Sri Lanka to the tropical moist forests of Southeast Asia (Sukumar 2006). They consume and defecate large amounts of viable seeds (Sivaganesan and Johnsingh 1995, Kitamura et al. 2007, Campos-Arceiz et al. 2008; Samansiri and Weerakoon 2008), have long gut passage times (up to at least 73 h; Weerasinghe et al. 1999) and large home ranges (50–1000 km²; Sukumar 2006), potentially allowing for seed dispersal distances over several kilometers. Asian elephants also show drastic seasonal changes in diet composition, with less nutritious diets that are rich in indigestible fiber during the dry season (McKay 1973, Sivaganesan and Johnsingh 1995). Increases in indigestible fiber during the dry season may result in seasonal variation in dispersal distances by altering the rate of passage of digesta and perhaps the scarification of seeds in the gut.

We combine data from feeding trials, seed germination tests, and GPS telemetry of Asian elephant movements to (1) describe the spatial scale at which Asian elephants disperse seeds, (2) assess whether seasonal differences in diet and ranging behavior translate into seasonal differences in seed shadows, and (3) evaluate whether dispersal scale and seasonal variation vary between two ecologically distinct elephant habitats (Sri Lankan dry monsoon forest vs. Myanmar's (Burma) mixed-deciduous forest). We analyzed (1) the effect of seasonal diet switches on gut retention time and seed germination, using captive animals, (2) seasonal changes in the displacement rates of wild elephants from Sri Lanka and Myanmar, and (3) the combined effect of these factors on the seed dispersal curves.

METHODS

Selection of plant species for feeding and germination experiments

We used tamarind *Tamarindus indica* as a model species for feeding trials and germination tests. Native to Africa, this leguminous tree was naturalized in tropical Asia in ancient times, where it is now a common plant. The fruits are bean-like, irregularly curved pods. We chose tamarind seeds (hard, glossy-brown, 1.10–1.25 cm diameter) because elephants are known to consume many leguminous seeds of comparable size, including tamarind itself (McKay 1973, Sivaganesan and Johnsingh 1995; Samansiri and Weerakoon 2008). Tamarind seeds have known germination requirements and can be counted in intact pods.

Seed passage experiments with captive elephants

Feeding trials were conducted at Ueno Zoo (Tokyo) using four captive Asian elephants with body size ranging between 2040 and 4270 kg, including three females (9–28 years) and one male (11 years). We tested the effect of diet on seed survival and retention time using two different treatments during feeding trials. We modified the composition of elephants' regular diet to simulate seasonal differences in diet, while keeping the total mass constant (Table 1).

Feeding trials were conducted during two weeks, each week involving a different diet type. The order of treatments varied among individual elephants: two randomly selected individuals had dry-season diet followed by wet-season diet, and two had the reverse sequence. For a period of 15 min on the first day after diet switches we offered each elephant tamarind pods containing a known number of seeds mixed with vegetable pellets. Unconsumed seeds were removed and counted. Uniquely colored plastic beads (300–400 beads) fed twice daily to each elephant allowed us to identify which elephant each dropping belonged to. We regularly collected dung piles, recording their origin (individual elephant) and defecation time. During the daytime (09:00–15:00) elephants were housed in outdoor enclosures and feces were collected every two hours for females, and once for the male. During the afternoon and night, elephants were housed separately in indoor enclosures and video-recorded. We used the video tapes to identify defecation time of each pile. When several piles were mixed, we assigned these feces the mean time between the first and the last defecations associated with the pile. Feces were sieved in situ (3-mm mesh size) with the aid of high pressure hoses. Defecated seeds retrieved intact were noted and stored in paper envelopes for further germination tests. Dung collection from each elephant ceased when no seed had been retrieved for at least 36 h.

Germination test

Seeds retrieved from elephant feces and 385 control seeds were randomly assigned to 4 × 4 × 5 cm cells in germination trays in a greenhouse three weeks after the start of feeding trials. Time of germination (radicle emergence) and establishment (appearance of first pair of true leaves) was recorded three times per week. Monitoring was discontinued after 10 weeks, and all non-germinated seeds were found to be either rotten or decayed.

To assess the effect of individual seed size on germination and establishment, seeds were weighed individually before planting (accuracy 0.01 g). Following gut passage, seeds were retrieved with various degrees of hydration and we used the fully hydrated fresh mass as a surrogate of their initial mass. Seeds were initially inserted in individual cells with ~1.5 cm of water-saturated vermiculite and their mass measured every two days. Once the seed mass stabilized (mass change

TABLE 1. Composition of Asian elephant diet in Ueno Zoo, Tokyo, Japan.

Diet	Fresh grass (%)	Bamboo (%)	Hay (%)	Vegetal pellets (%)	Rice straw (%)	Banana (%)	Bread (%)	Total (%)
Regular	59.7	6.5	8.8	7.1	13.6	2.8	1.4	100
Dry season	45.2	13.1	8.8	1.4	27.3	2.8	1.4	100
Wet season	74.2	0.0	8.8	12.8	0.0	2.8	1.4	100

Note: We modified the relative composition of different elements of the regular diet, while keeping the total mass constant (50–87 kg/d, depending on the elephant's body size), to simulate seasonal diet differences.

between consecutive measures <10%) or the seed germinated (radicle emergence), the seed was considered fully hydrated and transferred to cells filled with two centimeters of horticultural mixture. To evaluate whether this procedure influenced seed germination, one-half of the control seeds were set to hydrate until mass stabilized (as for ingested seeds) while the other half were directly planted on horticultural mixture. Germination did not differ between both planting methods ($Z_{1,383} = 0.513$; $P = 0.61$) so we will treat them as a pooled control treatment hereafter.

Telemetry and movement analysis

Telemetry data were obtained from the locations of six radio collars with Telonics GPS-satellite transmitters (TGW-3780, Telonics 2004) attached to three wild elephants from Yala National Park (southeastern Sri Lanka) and three from Bago Yoma (central Myanmar). Yala is dominated by dry monsoon forest whereas Bago Yoma is dominated by mixed-deciduous forests. Both areas show distinct dry and rainy seasons. Elephant locations were recorded every four hours and transmitted via the ARGOS satellite system. We used data from two three-week periods, at the peaks of the dry and wet seasons in each area, respectively. For each season the displacement of individuals was estimated from 15 different tracking series of 116 h. These series were created by randomly sampling 15 different starting points from the three-week data set (Westcott et al. 2005). Subsamples were chosen to have a minimum time lag of 12 hours to avoid temporal autocorrelation. For one Myanmar elephant we were only able to sample two and seven displacement series for the dry and wet season, respectively. For one Sri Lankan elephant we sampled only the wet season due to the installation of an electric fence, altering the animal's movements during the dry season.

Dispersal curve estimation

For each ingested seed that survived gut passage and germinated, dispersal distance was estimated substituting the value of the seed's retention time by the value of elephant displacement in each displacement series (Westcott et al. 2005). Seasonal differences in dispersal distance were assessed comparing the estimated dispersal curves of the dry season (which combined seed retention times from dry-season diet with dry-season displacement values) and the wet season (which com-

bined retention times from wet-season diet and wet-season displacement values).

Data analysis

All analyses were conducted using R statistical environment (version 2.40, R Development Core Team 2006). The survival, retention time, germination probability, and germination time of ingested seeds were separately fitted to generalized linear mixed models (GLMMs) using the Laplace approximation and the maximum likelihood (ML) method in the lmer function of the package lme4 (Bates and Sarkar 2007). When appropriate, we fitted models using several error distributions and function links, selecting the best model on the basis of Akaike Information Criterion (AIC) values. Significance of effects was assessed by means of likelihood ratio tests of reduced models lacking the factor being tested against the full model (LRT; Pinheiro and Bates 2000, Venables and Ripley 2002). Diet was included as a fixed factor and elephant as a random factor. The interaction between diet and elephant also was included. Elephant mass was used as a covariate in the analyses of seed survival, retention time, germination probability, and germination time. Seed mass and seed retention time were incorporated as covariates in the analyses of germination probability and germination time.

In addition, we compared the germination probability and germination time of control and ingested seeds by means of GLMs, which included the factorial combination of treatment (control vs. ingested seeds) with seed mass as a covariate.

The curves of elephant displacement and seed dispersal distance were examined using linear mixed models with the function lme from the package nlme (Pinheiro et al. 2006). Displacement curves were analyzed as a repeated-measures model for longitudinal data, in which time (elapsed time since the beginning of the displacement series until each location measurement) was the longitudinal factor. Region, season, and their interaction were included as fixed factors, elephant (nested within region) as a random factor, and their effects on displacement rates were assessed based on the significance of their interactions with the longitudinal factor, time. To account for the complex shape of the examined relationships between time and distance, we fitted models including time in its linear, quadratic, and cubic form, and selected the model with the lowest AIC

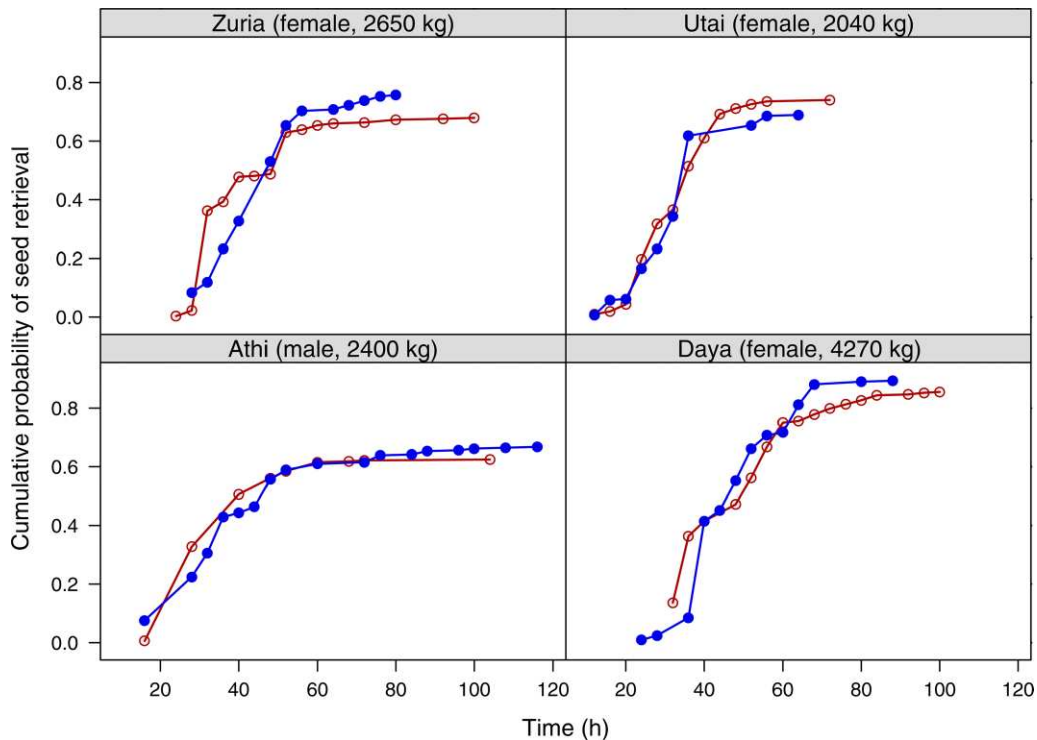


FIG. 1. Cumulative retrieval of ingested tamarind seeds in elephant dung. Type of diet: fiber-poor, wet season = blue solid circles; fiber-rich, dry season = red open circles. $N = 328/352$, $202/318$, $343/330$, and $309/208$ seeds for Daya, Zuria, Athi, and Utai (wet/dry season diet), respectively.

value. The model of seed dispersal curves was similar to the previous but without the inclusion of the longitudinal term. In both analyses, the significance of fixed factors was assessed applying the anova function over the full model (Pinheiro and Bates 2000), whereas the significance of the random effects was tested using LRTs (Pinheiro and Bates 2000). Models to be compared by LRTs were fitted using ML to allow for comparisons.

RESULTS

Seed survival and gut passage rates

Diet differences resulted in a 70% difference in fresh fecal mass between dry-season and wet-season diets (72.0 ± 14.7 kg/d, dry season vs. 42.5 ± 3.6 kg/d, wet season, mean \pm SD), which was not caused by changes in fecal water content (dry-to-fresh mass ratio: 26.7% vs. 27.2%, respectively). Elephants consumed a total of 2390 tamarind seeds, of which 75.1% survived gut passage. An estimated 6.1% of seeds was recovered as large seed fragments (>50% of a seed) and the remaining seeds were either broken into smaller fragments (not quantified) or completely digested. Mean seed retention time was 39.5 h (median = 36.5 h, range = 9.3–113.8 h). Both seed survival ($\chi^2_1 = 5.735$, $P = 0.017$) and retention time ($\chi^2_1 = 14.553$, $P = 0.0001$; Fig. 1) increased with elephant body mass, but were unaffected by diet ($\chi^2_1 = 1.65$, $P = 0.20$ and $\chi^2_1 = 0.99$, $P = 0.32$, respectively; Appendix: Table A1).

Germination and germination time

Germination probability was higher ($Z_{1,2152} = 8.678$, $P < 0.001$) for control (89.4%, $N = 385$ seeds) than for ingested (65.5%, $N = 1769$) seeds. Seedling establishment was also higher ($Z_{1,1409} = 3.355$, $P < 0.001$) for control (98.8%, $N = 344$ seeds) than for ingested (87.3%, $N = 1067$) seeds. Germination probability of seeds defecated by elephants was positively affected by elephant body mass ($\chi^2_1 = 5.577$, $P = 0.018$) and seed mass ($\chi^2_1 = 1107.1$, $P < 0.001$), negatively affected by retention time ($\chi^2_1 = 10.81$, $P = 0.001$; Appendix: Fig. A1) and not affected by diet ($\chi^2_1 = 0.380$, $P = 0.54$; Appendix: Table A1). Seed germination time was shorter ($T_{1,1230} = -14.331$, $P < 0.001$) for seeds defecated by elephants (14.7 ± 3.4 d, mean \pm SD) than for uningested, control seeds (18.5 ± 4.0 d), and was not affected by the elephant's diet ($\chi^2_1 = 2.13$, $P = 0.14$), elephant's body size ($\chi^2_1 = 1.13$, $P = 0.29$), or the seed retention time ($\chi^2_1 = 2.232$, $P = 0.14$; Appendix: Table A1).

Elephant movements

The best model fit for the observed displacement curves retained the longitudinal factor (time) in its quadratic and cubic forms, indicating that the relationship between time and displacement was strongly nonlinear. Elephant displacements were longer in Myanmar than in Sri Lanka (Fig. 2; significant region \times time² and region \times time³ interactions; Appendix:

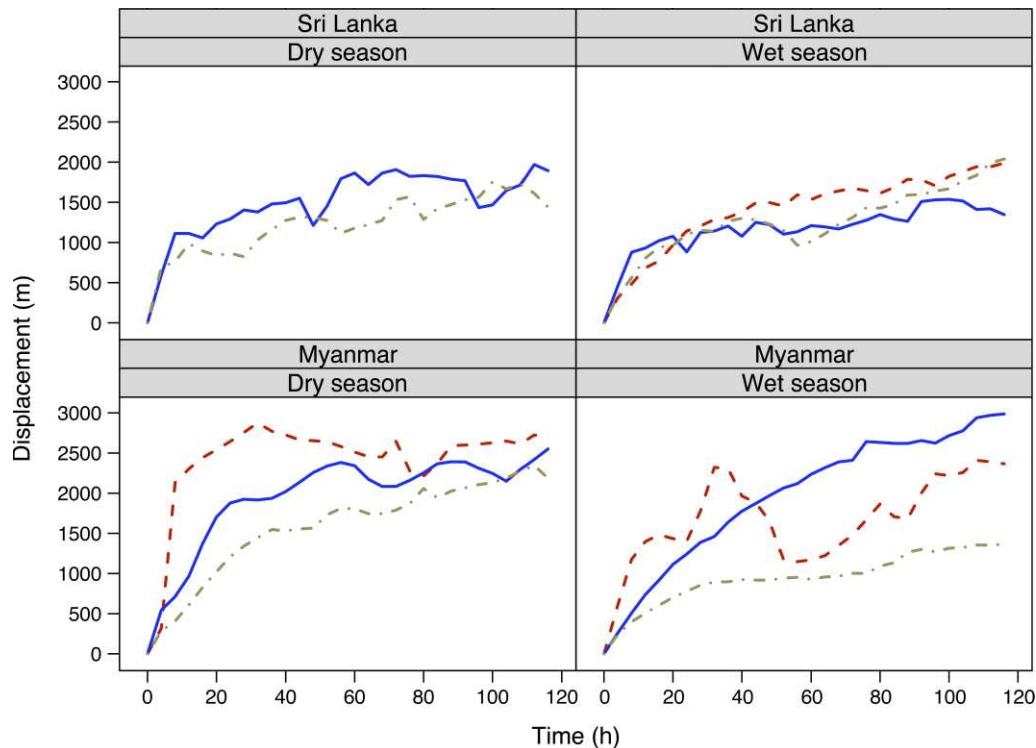


FIG. 2. Mean displacement curves of Asian elephants for the two study regions and seasons.

Table A2). Elephants tended to move longer distances during the dry season, but the strength of seasonal differences varied among regions (significant region \times season \times time² and region \times season \times time³ interactions; Appendix: Table A2) owing to the existence of smaller, though still significant differences in Sri Lanka than in Myanmar (Appendix: Table A3). The highly significant interaction between elephant, season, and time ($\chi^2_9 = 143.4$, $P < 0.0001$; Appendix: Table A2) is caused by the strong variation in seasonal patterns among individual elephants from Myanmar, and its absence from those from Sri Lanka (Fig. 2; Appendix: Table A3).

Seed dispersal curves

Estimated seed dispersal distances were considerably longer in Myanmar during the dry season (mean \pm SD, 2105 \pm 1181 m; maximum value, 5447 m), as compared to Myanmar's wet season (1462 \pm 1174 m; maximum, 5772 m) or to Sri Lanka's dry (1300 \pm 929 m; maximum, 3968 m) and wet (1222 \pm 639 m; maximum, 5164 m) seasons (Fig. 3). Dispersal distances were longer in the dry season ($F_{1,78207} = 9.22$, $P = 0.0024$) and they did not vary between regions ($F_{1,4} = 1.95$, $P = 0.2350$; Appendix: Table A4). However, the significant season \times region interaction ($F_{1,78207} = 6.15$, $P = 0.0132$) indicates that the effect of season varied between regions, being significant in Myanmar ($F_{1,37381} = 11.40$, $P = 0.0007$) but not in Sri Lanka ($F_{1,40886} = 0.40$, $P = 0.5145$) when analyzed separately. The effect of season varied also among

individual elephants (elephant \times season interaction, $\chi^2_2 = 720.95$, $P < 0.0001$, Appendix: Table A4).

DISCUSSION

This study provides the first detailed description of seed shadows produced by a megaherbivore. Asian elephants dispersed 50% of seeds over 1.2 km with maximal distances of 4–6 km. We also provide, for the first time, information on the effects of seasonal variation in disperser diet and behavior on endozoochorous seed dispersal curves. We found seasonal variation in seed dispersal curves, resulting from differences in elephant behavior (movement patterns) rather than digestive physiology (modulation of gut passage times as a consequence of dietary shifts). This seasonal variation was not congruent between the two geographic areas. In Myanmar, elephants showed stronger seasonal differences in displacement patterns and seed dispersal distances (e.g., a 30% increase in mean seed dispersal distance during the dry season; Fig. 3), whereas Sri Lankan elephants showed little seasonal variation in displacement, resulting in a lack of seasonal variation in seed dispersal. The local availability of key resources such as water during the dry season, which is extensively available to elephants in southern Sri Lanka owing to the presence of numerous, ancient man-made ponds (Fernando et al. 2008), could explain regional differences. In addition, individual differences in seed retention time and displacement rates resulted in considerable

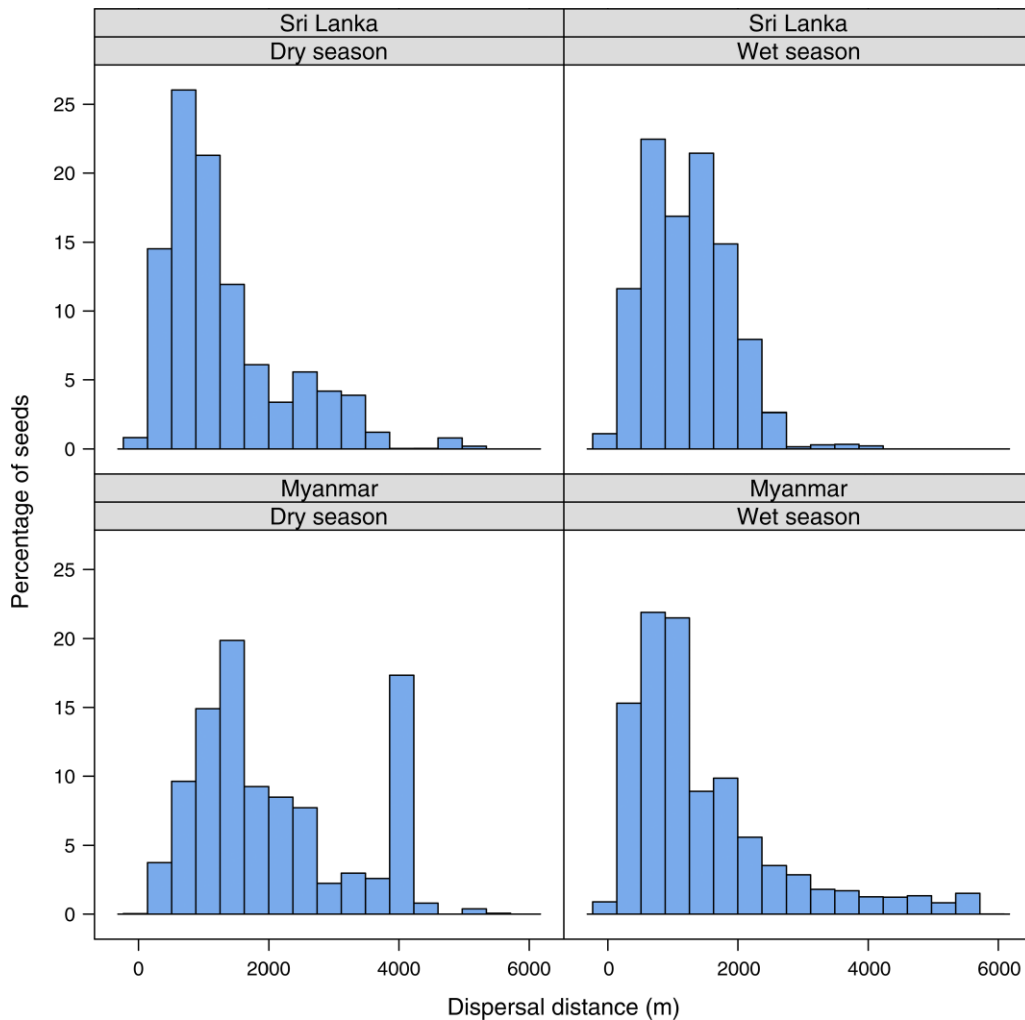


FIG. 3. Dispersal curves produced by Asian elephants for the two study regions and seasons. Graphs are based on the retention times and dispersal distances of 1046 and 3919 seeds (dry and wet season, respectively) for each collared elephant.

individual variations in seed dispersal curves among elephants. Understanding the determinants of landscape use by (individual) dispersers may therefore hold the key to predict the characteristics of the resulting seed shadows.

The lack of effects of major diet shifts on the gut passage, survival, and germination of ingested seeds is at odds with the mainstream focus of dispersal literature, which emphasizes the importance of gut passage effects on dispersal distance and quality (e.g., Traveset 1998, Traveset and Verdú 2002, Samuels and Levey 2005). Instead, our results suggest that the importance of disperser behavior may supersede the effects of disperser physiology and/or body size (similar to Spiegel and Nathan 2007 and Santamaría et al. 2007). The generality of this result is however questionable; instead, it should be taken to demonstrate that these factors play off against one another. While in our case, animal behavior had a greater effect on dispersal outcomes, it is not

difficult to imagine other cases in which size or physiology will.

A number of limitations arise from the simplifications necessarily adopted in our study. First, long-term inactivity of captive zoo animals might affect seed gut passage rates. It is unclear whether such effects exist, and even in which direction. The lack of differences in retention time under our diet treatments (in spite of strong alteration of defecation patterns) suggests that they might not be relevant, at least in this case. Second, long-term gut acclimation to diet shifts was not considered, but it could also modify gut-passage rates and deserves further attention. Third, we used a small number of individuals, both in the feeding experiments and ranging studies, an unavoidable limitation when working with megaherbivores. Fourth, the strong individual differences in gut passage and movement rates (probably related to factors such as body size, age, and sex) introduce considerable noise in our analysis. Its

removal would require a much larger number of experimental and collared individuals. Despite these limitations, our data clearly show the potential of combined experimental (gut passage) and field (telemetry) studies to identify the factors that are most likely to modulate seed dispersal patterns by megaherbivores, and the scales at which such dispersal is likely to occur.

Owing to the high survival of their seeds to gut passage (62–89%) and the high palatability of their pods for wild and captive elephants, tamarinds proved a suitable test species for the experimental study presented here. Captive elephants retained tamarind seeds for a mean of 40 h (maximum 114 h). This is shorter than smaller nonruminant ungulates such as horses and donkeys, which have mean seed retention times of 42–80 h (Cosyns et al. 2005). Though food passage rate decreases with increasing body size among ruminants (Illius and Gordon 1992), megaherbivores may have fast passage rates to reduce energy losses from methanogenic bacteria activity (Clauss et al. 2003). Another Asian megaherbivore, the Indian one-horned rhinoceros *Rhinoceros unicornis*, has longer seed retention times (peaks of 64–88 h and maximum of 172 h; Dinerstein and Wemmer 1988). The mean displacements of our study elephants in the forests of Sri Lanka and Myanmar were in the order of 1.5–3 km in five days. These displacements are shorter than available data for African savanna *Loxodonta africana* (4–6 km/d during daylight; Owen-Smith 1988) and forest *L. cyclotis* (Blake et al. 2001) elephants. The combination of seed retention times and elephant displacements resulted in a spatial scale of dispersal probably larger than that provided by sympatric large dispersers such as hornbills (peaks of 300–700 m and tails up to 3 km for several Asian species; Kinnaird and O'Brien 2007), primates (<1.5 km in different regions; Stevenson 2000, Wehncke et al. 2003, Russo et al. 2006), or deer (25% of seeds >1 km and tails up to 3.7 km by white-tailed deer in North America; Vellend et al. 2003).

Elephants can disperse large amounts of seeds from many plant species (29 species in Myanmar and >60 species in Sri Lanka; Campos-Arceiz et al. 2008; A. Campos-Arceiz, unpublished data) at distances of 1–6 km (see *Results*) and across different habitats, depositing them in large clusters that are (potentially) subject to secondary dispersal (Magliocca et al. 2003). In tropical Asia, elephants are probably unique in dispersing seeds over such long distances and in such a complex way. This important service comes however at a cost, in terms of reduced seed viability and germination probability (particularly at long retention times). Negative effects of gut treatment on germination probability seem to be a general feature for dry and leguminous fruits (Traveset and Verdú 2002), but they might be attenuated by the decreased germination time of ingested seeds (four days on average for tamarinds ingested by elephants), which tends to increase plant fitness in perennial species (Verdú and Traveset 2005). More information is necessary on

other aspects of elephant dispersal service, such as its importance for large-seeded plants, its role in succession processes, and its effects on the spread of invasive species.

Further research is also necessary to test the predicted seed dispersal patterns. New tools and technologies, including remote sensing and GIS, submetric georeferencing, GPS telemetry, and individual-based modeling, offer great promise for this complex undertaking. Their use may provide essential insights on the environmental impacts of the accelerated disappearance of the largest of all animal dispersers.

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APPENDIX

Results of statistical models (*Ecological Archives* E089-151-A1).