SEED DISPERSAL BY AFRICAN SAVANNA ELEPHANTS

Seed dispersal kernel of the largest surviving megaherbivore – the African Savanna Elephant.

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ABSTRACT

Owing to the late Pleistocene extinctions, the megafauna of Europe, Australia and the Americas disappeared and with them the dispersal service they offered megafaunal fruit. The African Savanna Elephant, the largest remaining megaherbivore, offers valuable insights into the seed dispersal services provided by extinct megafauna in prehistoric times. Elephant seed dispersal studies have for the most part concentrated on African and Asian forest elephants. African savanna elephants are morphologically distinct from their forest counterparts. Like the forest elephants they consume large quantities of fruit from a large number of tree species. Despite this little is known of the savanna trees that rely on elephants for their dispersal or the spatial scale at which these seeds are dispersed. We combined information from feeding trials conducted on four park elephants with field telemetry data from 38 collared elephants collected over an 8-year period in APNR/Kruger National Park to assess the seed dispersal service provided by savanna elephants. This study provides the first detailed account of the spatial scale at which African savanna elephants disperse seeds. Our mechanistic model predicts that 50% of seeds are carried over 2.5km, and distances up to 65km are achievable in maximum gut passage time. These findings suggest the savanna elephant as the longest distance terrestrial vertebrate disperser yet investigated. Maintaining their ecological role as a seed disperser may prove a significant factor in the conservation of large-fruited tree diversity within the savannas. These results suggest that extinct megafauna offered a functionally unique dispersal service to megafaunal fruit.

Key words: African savanna elephant; dispersal distance; dispersal kernel*; Loxodonta africana africana* ; maximum gut passage time; mechanistic model; megaherbivore; megafaunal fruit; Pleistocene megafauna.

INTRODUCTION

Owing to their size and behaviour, megaherbivores (>1000kg; Owen-Smith, 1988) may form a unique functional group with regard to certain ecological processes such as seed dispersal (Sekar and Sukumar, 2013). In particular, large vertebrates are thought to play a pivotal role in the dispersal of large specialised fruits (‘megafaunal fruits’ - Gautier-Hion *et al.* 1985; Blake *et al.*, 2009). Megafaunal fruits are typically large in both mass and dimension and exhibit a high degree of mechanical protection (Janzen and Martin, 1982; Guimares *et al.*, 2008). Based on African forest tree examples, Guimares *et al.* (2008) defined megafaunal fruit as fruit either 4–10 cm in diameter with up to five large seeds or fruits greater than 10 cm diameter with numerous small seeds.

Unfortunately, due to a series of extinction events at the end of the Pleistocene (50 to 10 thousand years ago) the large vertebrate communities of Europe, non-tropical Asia, Australia and the Americas vanished almost in their entirety and with them the dispersal services they offered megafaunal fruit (Martin, 1984). While the age of large vertebrates might have seen its end on most continents, Africa and small patches of tropical Asia remain the exception (Barlow, 2001). Five genera of Africa’s megafaunal community; *Ceratotherium* (white rhinoceros), *Diceros* (black rhinoceros), *Giraffa* (giraffe), *Hippopotamus* (hippopotamus), and *Loxodonta* (African elephant) still exist (Owen-Smith, 1988/9) while two genera; *Elephas* (Asian elephant) and *Rhinoceros* (one-horned rhinoceros) remain in Asia.

In Africa and Asia we are thus in the singular position of being able to investigate the seed dispersal service that extant large vertebrates offer megafaunal fruit. Importantly these investigations will also provide insights into the seed dispersal service once provided by extinct megafauna in prehistoric times. The urgency of such studies is underlined by the fact that large vertebrates are disproportionately likely to be extirpated by the drivers of the ongoing extinction crisis (Duffy, 2009).

We selected the African savanna elephant (*Loxodonta africana africana*) as an analogue for extinct large vertebrate dispersers as the majority of known fossils of extinct megafauna have been discovered in regions that were known to be savannas during the Pleistocene (Doughty *et al*., 2013; Prado *et al*, 2001). Elephant seed dispersal studies have largely focused on African and Asian forest elephants. These studies have firmly established forest elephants as prolific seed dispersers, consuming more seeds from more species than any other taxon of large vertebrate disperser (Campos-Arceiz and Blake, 2011). African forest elephants are also the principal, and in some cases sole extant, seed dispersal agent for a number of large-fruited and large-seeded trees (e.g. *Cola spp*., *Tieghemella heckelii* and *Balanites wilsoniana*; White, 1994; Blake, 2009).

Savanna elephants are morphologically distinct from the elephants of the tropical forests of Africa. They weigh between six and seven tonnes, roughly double the weight of the forest elephant (Roca *et al.*, 2001). African savanna elephants have been the subject of far fewer seed dispersal studies. Like the African forest elephants, they disperse large quantities of seeds (2054 seeds/km^2/day in Hwange National Park; Dudley, 2000) from a large number of plant species (221 species in Shimba Hills, Kenya; Engel, 2000). In addition, African savanna elephants are involved in obligate seed dispersal mutualisms with at least seven tree species (*Sclerocarya birrea, Adansonia digitata, Schinziophyton rautanenii, Balanites aegyptiaca, Balanites* *wilsoniana, Hyphaene coriacea* and *Borassus aethiopum*; Bunney, 2014; Cochrane, 2003, Dudley, 2000).

Megafaunal dispersers such as the elephant are important not only because they are capable of processing and swallowing large fruits but also owing to the fact that they can move large numbers of seeds over considerable distances (Campos-Arceiz and Blake, 2011). For example, Campos-Arceiz *et al.* (2008) found that Asian forest elephants in Southeastern Sri Lanka and Myanmar dispersed *Tamarindus indica* seeds up to 6km from the parent tree. Long distance dispersal influences large-scale ecological processes, including some of major conservation concern, such as connectivity in fragmented landscapes and range shifts following climate change (Clark *et al.* 1998; Peres *et al.*, 2016). Despite this there are no data on the spatial scale at which the African savanna elephants disperse seeds.

A practical means of examining the spatial distribution of seeds is to focus on the vertebrate providing the dispersal service rather than concentrating on the fate of individual seeds. By combining the gut passage rates of the vertebrate with its movement data, one can estimate entire seed dispersal kernels (Holbrook and Smith, 2000; Wang and Smith, 2002; Levin *et al.*, 2003, Westcott *et al.,* 2005). In this study we utilise this approach and combine information from feeding trials on African savanna elephants with movement data for wild individuals to: (1) assess the capacity of elephants to disperse the seeds from different types of megafaunal fruits and (2) estimate the spatial scale over which they disperse these seeds.

METHODS

IDENTIFICATION OF MEGAFAUNAL FRUIT PROXIES AND SEED PASSAGE EXPERIMENTS

To quantify seed passage rates through the elephant gut, we conducted a feeding trial at the Elephant Whispers Sanctuary in Mpumalanga, South Africa. The park elephants spend the majority of the day roaming and feeding freely within the park. Since exposure to indigenous megafaunal fruit is possible within the park it was necessary to use market fruit varieties.

Market fruits were selected to represent the two megafaunal fruit types as defined by Guimares *et al*. (2008) and applied to the South African tree flora (Bunney, 2014). The first type includes fleshy fruits that are 4–10 cm in diameter with up to 5 large seeds. The mango (*Mangifera indica*) was chosen to represent Type 1. The second type includes fleshy/dry fruits that are greater than 10 cm in diameter and have numerous small seeds. The Honeydew Melon (C*ucumis melo*) was selected to represent Type II. Feeding trials were conducted on four African elephants (2 males, 2 females) with body size ranging between 2400 and 6000 kg.

The fruits were fed to the elephants in one bout during the regular evening feed. Every faeces was collected and the hourly time interval in which it was dropped was recorded. Faeces were thoroughly teased apart by hand; the large seeds were counted and collected while the small were assigned a quantity score of present (less than 5), few (5-20) and many (greater than 20). Dung collection and analysis was stopped on day 5 as all Type I seeds had been accounted for and we were confident all the Type II seeds had been passed.

TELEMETRY AND MOVEMENT ANALYSIS

Telemetry data were obtained from the locations of 38 radio-collared wild elephants (27 males, 11 females) in the Associated Private Nature Reserves (APNR) on the western boundary of the Kruger National park over a period of 8-years (Elephants Alive). These elephants were fitted with GPS-satellite or GPS/GSM transmitters. Collars were set to acquire positions at 3, 6, 8 or 12-hour intervals (model code; Supplementary Data A). The displacement of individual elephants (i.e. the shortest distance from the initial to the final position) was estimated across tracking intervals of 12-hour multiples (12- 192 hours). This was achieved by randomly sampling 50-100 different starting points across all movement data for each individual elephant. From each of these starting points, the telemetry data series was then moved through until the location closest to the relevant time interval was obtained. The net displacement of the elephant was calculated as the distance between the first and final GPS position. Time series were non-overlapping and were a minimum of 2 days apart.

SIMULATION MODEL AND DISPERSAL KERNEL ESTIMATION

We designed a stochastic model to simulate the dispersal of seeds ingested by wild savanna elephants. The input data for the model was a simulation of the gut passage regimen of the Type II seeds and the telemetry locations of 38 individual elephants (418,001 records). The Type II gut passage curve was the only one utilised as the Type I curve did not have an adequate amount of data for the simulation. A normal distribution curve (mean=31; SD =15) provided the best fit to the melon gut passage time (GPT) data. This curve allowed for the random generation of GPTs (~12 000). For each of these simulated GPTs the model would randomly select an elephant starting location with a time stamp. The model would then move through the ordered elephant co-ordinates until the elapsed time across these co-ordinates equated to or exceeded the GPT. Where the GPT was overshot the model would perform a rounding calculation. The model then calculated the straight line distance between the starting and final location. These ~12,000 distance measures were then used to produce a dispersal kernel that expresses the probability density of seeds deposited at various distance intervals from the parent tree.

RESULTS

SEED PASSAGE EXPERIMENTS

The four park elephants consumed a collective total of 28 mangoes and 5 melons (approx. 2450 seeds; Paillan *et al*, 2004). Gut passage curves were produced for the mango and the melon seeds (Fig. 1).

Mean gut retention time for the mango and melon seeds was similar at ~ 34.7 h and 33.5h respectively. The difference between the two seed types lay in the gut passage range; mango seeds first appeared 15 hours after ingestion and were present up until 66 hours. In contrast, the melon seeds were evident 7 hours after ingestion and were still present up until 96 hours – a 43% greater time radius.

TELEMETRY AND MOVEMENT ANALYSES

Maximum dispersal distances are one of the most important aspects of seed dispersal ecology, certainly in terms of the time it takes for plants to move across landscapes over generations (Nathan *et al.*, 2008). A total of 34,210 displacement events spanning 12 to 192 hours were taken into account. The maximum dispersal distances achieved for each 12-hour time class is expressed in a box and whisker plot (Fig. 2). The maximum dispersal distances are consistently 7 (SD=0.01) times that of the 90th percentile value. Accordingly, a small subset of elephant movement events is of a significantly long range. Based on this movement data, large seeds can potentially achieve a maximum dispersal distance of 59km while the small seeds could potentially exceed the 65km mark (Fig. 2). Maximum dispersal distances appear to reach a ceiling of 70-75km between 4.5 –8 days.

Another crucial aspect of seed dispersal ecology is the median dispersal distance, i.e. the distance at which the majority of seeds will be dispersed to. The median distance that an elephant moves in a 96 hour period is 6.5km (Fig. 2).

DISPERSAL KERNEL ESTIMATION

Our seed dispersal kernel was highly leptokurtic (Kolmogorov-Smirnov $d = 0.177$, $p < 0.01$, Lilliefors $p < 0.01$; Fig. 3) and had a fat tail. Our model predicted that 23% (peak dispersal) of seeds were deposited between 1 and 2km from their parent tree. The mean dispersal distance was 3.7km.

DISCUSSION

The extinction of megafauna in the Pleistocene is likely to have altered ecosystem processes and disturbance regimes at continental scales (Dirzo *et al.*, 2014; Johnson, 2009; Gill *et al.*, 2009). Here we focus on seed dispersal as one of these ecosystem processes and employ the African savanna elephant, one of the last remaining megaherbivores, to better understand their role.

Specifically, this study provides the first detailed account of the spatial scale at which African savanna elephants disperse seeds. Our results indicate that 50 percent of seeds are carried over 2.5km, and one percent of seeds are deposited at distances greater than 20km. Since the average African savanna elephant in Hwange National Park, Zimbabwe defecates over 3200 woody plant seeds per day (Dudley, 2000) then the number of seeds likely to reach distances in excess of 20km is proportionally very large. In addition, distances up to 65km are achievable in maximum gut passage time. Dispersal distances in this range are an order of magnitude greater than the 5-6 km maximum dispersal distance achieved by their counterparts – the Asian forest elephants

(Campos-Arceiz *et al*., 2008). This difference can be attributed to the fact that elephant home range size increases with decreasing rainfall and with a switch from closed to open habitats (Thoules, 1996; Blake *et al*, 2003; Campos-Arceiz and Blake, 2011).

The established theory in long distance dispersal research maintains that the 'standard' dispersal agent determines the short distance dispersal events but is not responsible for long distance dispersal. Long distance dispersal is thought to be brought about by infrequent chance events i.e. nonstandard dispersal events like tropical storms or accidental attachment to a vertebrate (Higgins *et al,* 2003; Myers *et al.*, 2004; Nathan *et al*., 2008; Nathan *et al.* 2012). In the case of African savanna elephants, however, the dispersal agent effects both local and long distance dispersal of large-fruited savanna trees. About 1% of seeds are deposited at distances in excess of 20km from the parent tree. Distance figures of this magnitude are in line with those simulated by stochastic migration models in order to explain the rapid plant migrations seen in the Holocene paleo-records (Nathan and Muller-Landau, 2000). This suggests that extinct megafauna played a significant role in facilitating the movement of vegetation in past millennia.

When one considers that male savanna elephants in their sexual prime can make treks in excess of 100km when in musth or as part of their exploratory behaviour when young (Henley, 2003; Henley, 2014) it is understandable that months if not years of telemetry data is necessary to capture these extreme long distance dispersal events. As this study employed 8 years of movement data from 38 elephants it likely allowed for the comprehensive characterisation of the long-distance component of the dispersal kernel. The other constituent of the dispersal kernel is the gut passage curve. Our maximum gut passage time for the melon seeds (4 days) is in line with a gut passage study that was conducted on captive Asian elephants with a maximum gut passage time of 4.75 days for seeds of *Tamarindus indica* (Campos-Arceiz *et al.*, 2008).

Maintaining the ecological role of the African savanna elephant as a seed disperser may prove to be a significant factor in the conservation of large-fruited tree diversity within the savannas. Within our study site (APNR/Kruger National Park) there are several tree species that possess large fruit (> 4cm) that are actively sought out by elephants. One of these is the Lala Palm fruit (*Hyphaene coriacea*), which has a large single seed with a hard endosperm (Bax and Sheldrick, 1963). According to Nichols (2001) all *Hyphaene coriacea* seeds he found in elephant dung were cracked and when planted germinated within 30 days. Uncracked seeds, in contrast took 90 days or longer to germinate. Another example is that of the Borassus Palm (*Borassus aethiopum*), which has a very large drupe with a diameter of 15-20 cm and possesses 1-3 seeds each enclosed in a woody endocarp. Elephants are particularly fond of this fruit and are thought to be largely responsible for their dispersal (Zona and Henderson (1989).

The African savanna elephant can be considered a suitable proxy for the mammoths (*Mammathus columbi*, *Mammathus imperator* and *Mammathus primigenius;* Doughty *et al*., 2010) and the gomphotheres (*Cuvieronius spp*., Janzen and Martin, 1982) as they were all mixed feeders that occurred in savanna habitats and shared a similar gut physiology (Table 1). The African Black Rhinoceros (*Diceros bicornis*) would however be a better analogue for Merck's Rhinoceros (*Stephanorhinus kirchbergensis*) (Table 1) and warrants the attentions of a seed dispersal study. Although these animals do not appear to consume great quantities of fruit (relative to leaf and branch matter; Dierenfeld *et al*., 1995) they are likely to have excessively long seed retention times – the Indian one-horned rhinoceros (*Rhinoceros unicornis*) has a maximum gut passage time of 172 h (7 days - Dinerstein and Wemmer, 1988). Another African megaherbivore that merits further study is the giraffe (*Giraffa camelopardalis*) as it is considered the modern analogue to the Rusconi's Ground Sloth (*Eremotherium rusconii;* McDonald, 2005). Giraffes consume large quantities of *Acacia* pods (Burtt and Salisbury, 1929; Miller, 1994). In addition, giraffe bulls have been known to undertake long distance movement events – in excess of 50km - between river systems (Fennessey, 2014).

Large vertebrates have likely been providing a vehicle for the large-scale movement of megafaunal fruit seeds for millennia. Understanding the scale of the dispersal service proffered by the African savanna elephant gives us a measure of the ecosystem services that were lost along with the Pleistocene megafauna.

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TABLE 1

Continent	Order	Family	Genus	Species	Open vs Closed Habitat	Grazer/Browser/Intermediate	Body Mass (kg)	References
Africa	Artiodactyla	Bovidae	*Pelorovis*	*antiquus*	Open	Grazer	1000	Klein, 1994
Africa	Perissodactyla	Rhinocerotidae	*Stephanorhinus*	*kirchbergensis*	Closed	Browser	2000	Ecker *et al.*, 2013
Africa	Proboscidea	Elephantidae	*Elephas*	*iolensis*	Open	Grazer	6500	Faith, 2014; Todd, 2010
Australia	Diprotodontia		*Diprotodon*	*optatum*	Open	Browser	1500	Murray, 1984
North America	Artiodactyla	Camelidae	*Camelops*	*hesternus*	Open	Intermediate	1100	Dompierre and Churcher, 1996; Semprebon and Rivals, 2010
North America	Proboscidea	Elephantidae	*Mammathus*	*columbi*	Open	Intermediate	8000	Pérez-Crespo *et al.*, 2012; Lister and Bahn, 2007
North America	Proboscidea	Elephantidae	*Mammathus*	*imperator*	Open	Intermediate	10000	Pérez-Crespo *et al.*, 2012; Lister and Bahn, 2008
North America	Proboscidea	Elephantidae	*Mammathus*	*primigenius*	Open	Intermediate	5500	Bocherens *et al.*, 1994
North America	Proboscidea	Gomphotheriidae	*Cuvieronius*	*spp.*	Open	Intermediate	5000	Prado *et al.*, 2001
North America	Proboscidea	Mammutidae	*Mammut*	*americanum*	Closed	Browser	4523.8	Green *et al.*, 2005
North America	Xenarthra	Glyptodontidae	*Glyptotherium*	*floridanum*	Open	Intermediate	1100	Gillette and Ray, 1981; Vizcaíno, 2000
North America	Xenarthra	Glyptodontidae	*Glyptotherium*	*mexicanum*	Open	Intermediate	1100	Gillette and Ray, 1981; Vizcaíno, 2001
North America	Xenarthra	Mylodontidae	*Glossotherium*	*harlani*	Open	Intermediate	1587	Ruez, 2005
South America	Artiodactyla	Camelidae	*Hemiauchenia*	*paradoxa*	Open	Intermediate	1000	Kohn, 2005; Feranec, 2003
South America	Artiodactyla	Camelidae	*Palaeolama*	*spp.*	Variable	Browser	1000	Marcolino *et al.*, 2012
South America	Notoungulata	Toxodontidae	*Mixotoxodon*	*spp.*	Variable	Intermediate	1000	McFadden, 2005
South America	Notoungulata	Toxodontidae	*Toxodon*	*bilobidens*	Variable	Intermediate	1100	McFadden, 2006
South America	Notoungulata	Toxodontidae	*Toxodon*	*burmeisteri*	Variable	Intermediate	1100	McFadden, 2007
South America	Notoungulata	Toxodontidae	*Toxodon*	*platensis*	Variable	Intermediate	1642	McFadden, 2008
South America	Notoungulata	Toxodontidae	*Toxodon*	*paradoxus*	Variable	Intermediate	1000	McFadden, 2009
South America	Proboscidea	Gomphotheriidae	*Cuvieronius*	*spp.*	Open	Intermediate	5000	Prado *et al.*, 2001

South America	Proboscidea	Gomphotheriidae	*Haplomastodon*	*chimborazi*	Open	Intermediate	6000	Prado *et al.*, 2003
South America	Proboscidea	Gomphotheriidae	*Stegomastodon*	*superbus*	Open	Intermediate	7580	Prado *et al.*, 2001
South America	Proboscidea	Gomphotheriidae	*Notiomastodon*	*spp.*	Variable	Intermediate	6193	Asevedo *et al.*, 2012
South America	Xenarthra	Glyptodontidae	*Doedicurus*	*clavicaudatus*	Variable	Intermediate	1468	de Maria, 2010
South America	Xenarthra	Glyptodontidae	*Glyptodon*	*clavipes*	Open	Grazer	2000	Farina and Vizcaíno, 2001; Zurita *et al.*, 2012
South America	Xenarthra	Glyptodontidae	*Neothoracophorus*	*depressus*	No information	No information	1100	
South America	Xenarthra	Glyptodontidae	*Panochthus*	*tuberculatus*	Open	No information	1061	Vizcaíno et al., 2011
South America	Xenarthra	Glyptodontidae	*Plaxhaplous*	*canaliculatus*	No information	No information	1300	
South America	Xenarthra	Megatheriidae	*Eremotherium*	*rusconii*	Closed	Browser	3500	McDonald, 1995
South America	Xenarthra	Megatheriidae	*Megatherium*	*americanum*	Open	Browser	6265	Bargo, 2001
South America	Xenarthra	Megatheriidae	*Paramegatherium*	*spp.*	No information	No information	3500	
South America	Xenarthra	Mylodontidae	*Glossotherium*	*robustum*	Open	Intermediate	1713	Naples, 1989
South America	Xenarthra	Mylodontidae	*Glossotherium*	*myloides*	Open	Intermediate	1200	Bargo *et al.*, 2006
South America	Xenarthra	Mylodontidae	*Lestodon*	*armatus*	Open	Intermediate	3397	Bargo *et al.*, 2006
South America	Xenarthra	Mylodontidae	*Mylodon*	*listai*	Open	Intermediate	1000	Dani *et al.*, 1994
South America	Xenarthra	Mylodontidae	*Scelidodon*	*spp.*	Open	Intermediate	1000	Miño-Boilini *et al.*, 2009; de Melo França *et al.*, 2015
South America	Xenarthra	Mylodontidae	*Scelidotherium*	*leptocephalum*	Open	Intermediate	1119	Bargo *et al.*, 2006; Janzen and Martin, 1982

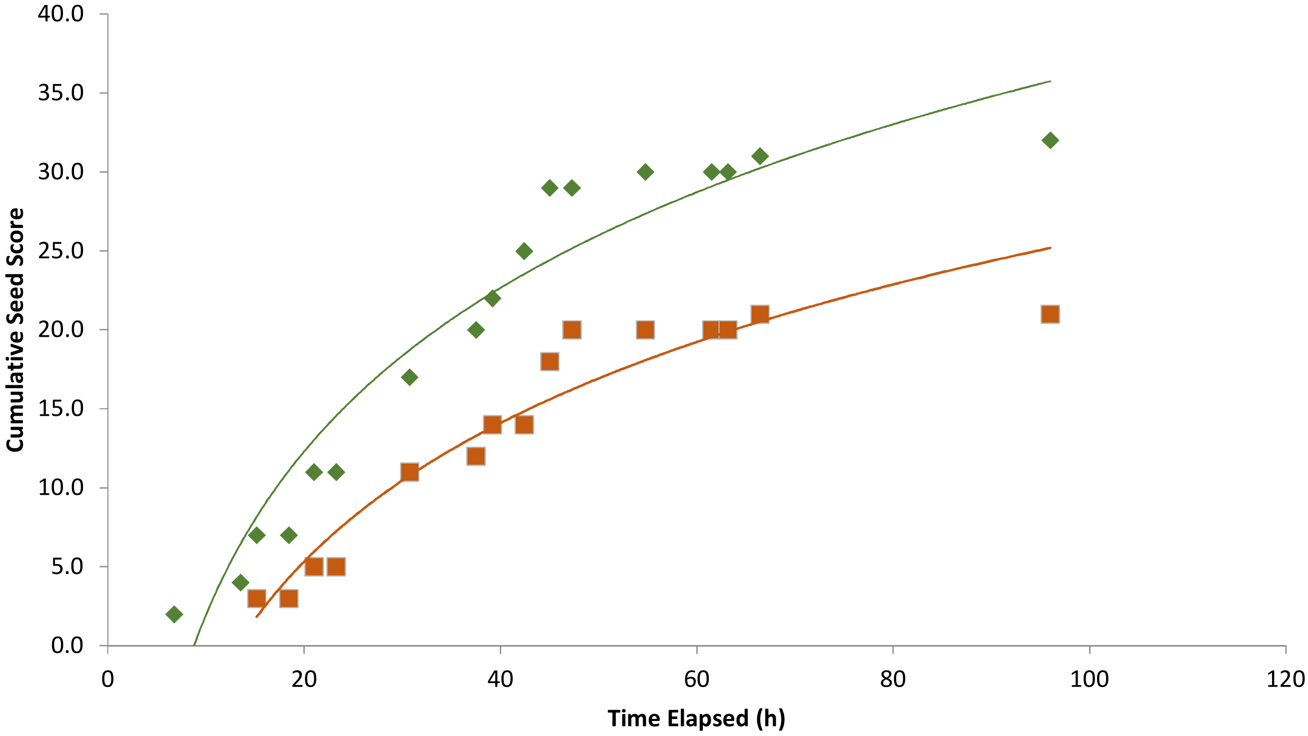
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Cumulative Seed Score
0
20
40
60
80
100
120
Time Elapsed (h)

FIGURE 1

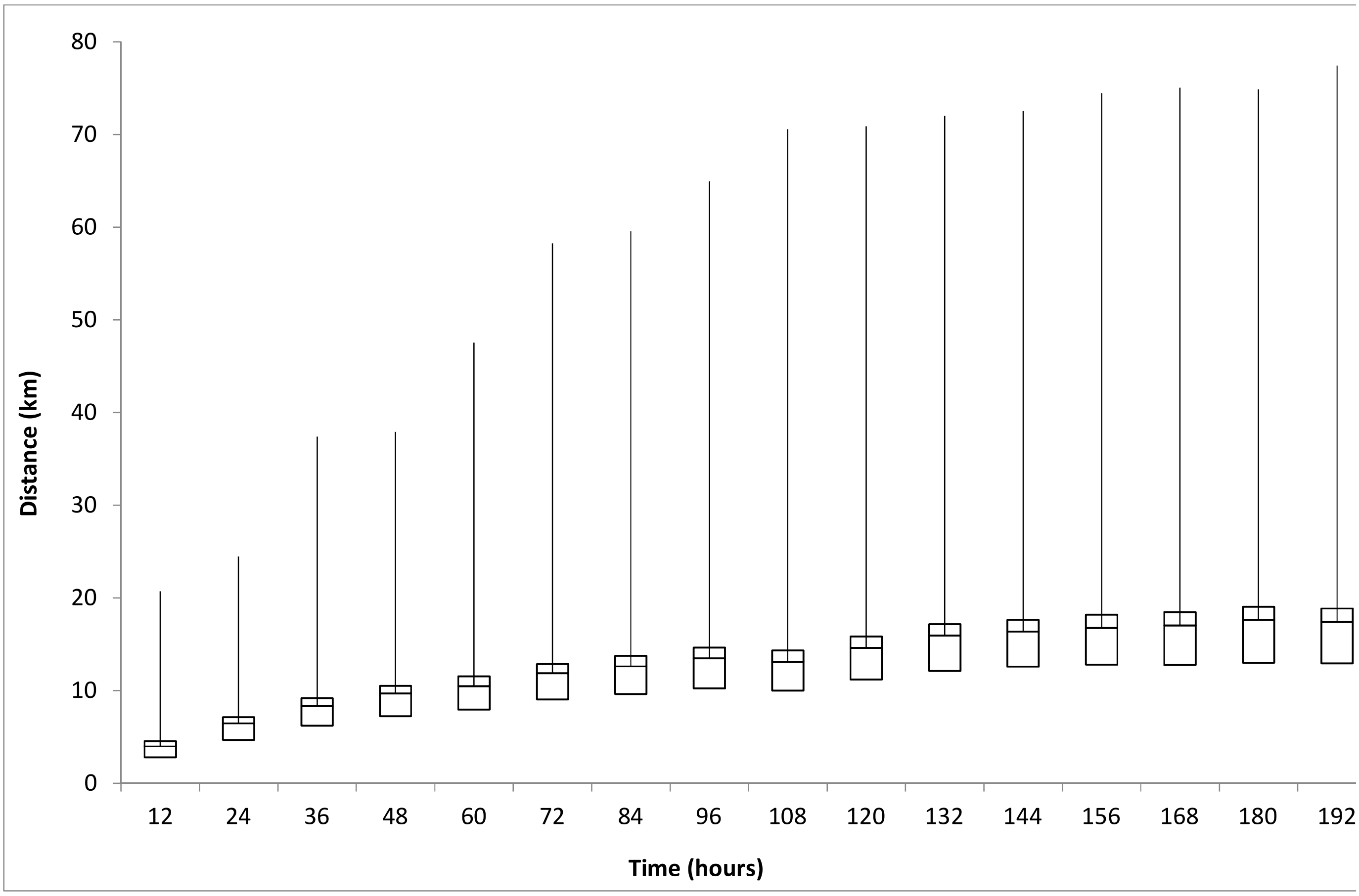
80
70
60
50
40
30
20
10
0
Distance (km)
12
24
36
48
60
72
84
96
108
120
132
144
156
168
180
192
Time (hours)

FIGURE 2

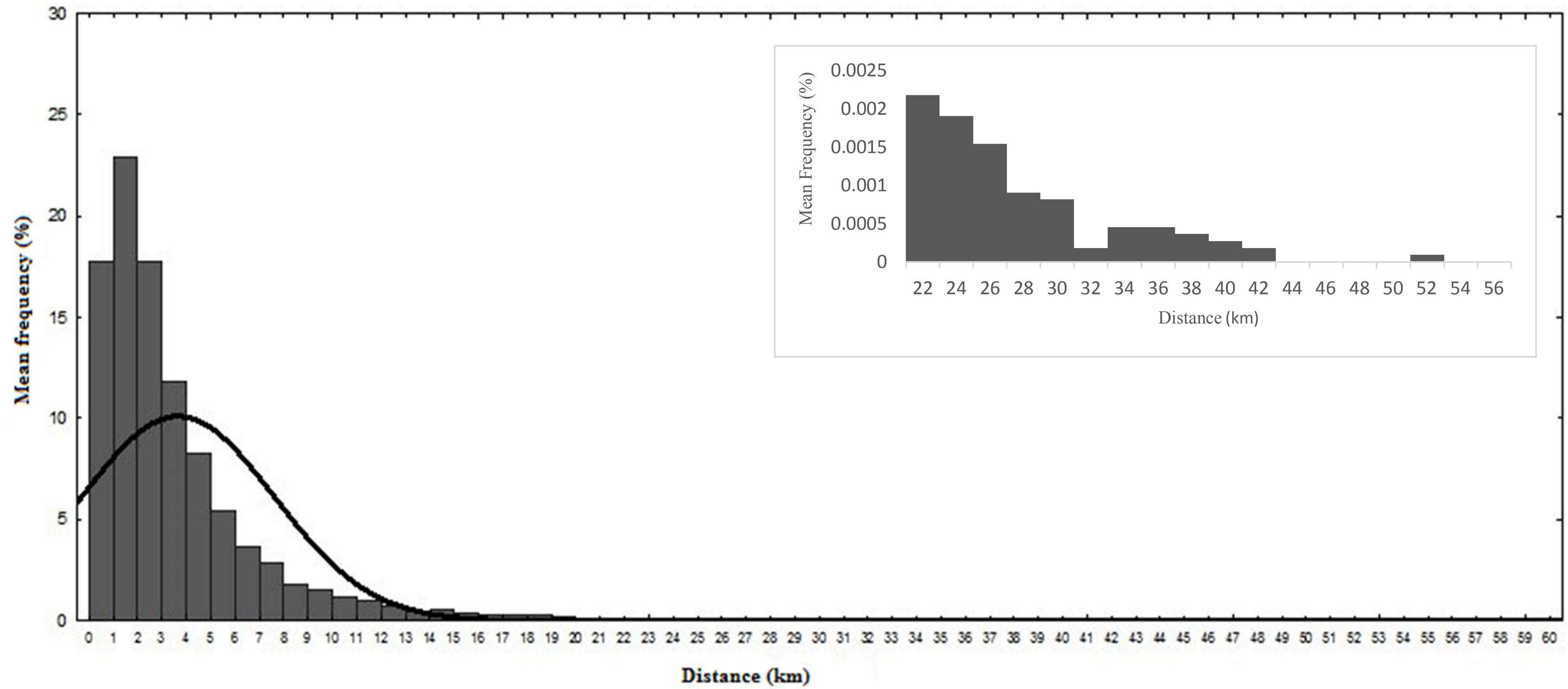
Mean frequency (%)
Distance (km)
0
5
10
15
20
25
30
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60
Mean Frequency (%)
0.0025
0.002
0.0015
0.001
0.0005
0
22 24 26 28 30 32 34 36 38 40 42 44 46 48 50 52 54 56
Distance (km)

FIGURE 3