ASIAN ELEPHANTS ARE ESSENTIAL AS SEED DISPERSERS IN A DISTURBED TROPICAL FOREST

Nitin Sekar

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Abstract

Large animals are disproportionately prone to extinction, and the resulting effects on ecosystem processes are unclear. Megaherbivores—animals weighing over 1000 kg—are thought to be functionally unique in their contribution to many ecological processes. One such ecosystem process is seed dispersal, but few studies have measured the relative importance of a megaherbivore species and sympatric seed dispersers. This dissertation explores how the loss of Asian elephants (*Elephas maximus*) would affect the dispersal of three large-fruited tree species. Research was conducted in Buxa Tiger Reserve, India, a disturbed tropical forest system resembling much of the region. I found that elephants were a top frugivore of all three tree study species: *Dillenia indica* (chalta), *Careya arborea* (kumbhi), and *Artocarpus chaplasha* (lator). The main alternative frugivores were domestic bovids (the cow, *Bos primigenius*, and the buffalo, *Bubalus bubalis*), and Rhesus macaques (*Macaca mulatta*). Elephants consumed the most *D. indica* fruit; once eaten, seeds from *D. indica* were over 16 times more likely to pass undigested into elephant dung than into the dung of domestic bovids. Elephants ate 18% and 10% of frugivore-consumed kumbhi and lator fruits, respectively, defecating 2-3 times as many seeds per fruit as domestic bovids. I show that seed predation of *D. indica* seeds from elephant dung is unlikely to negate elephants’ role in their dispersal. Seeds taken from elephant dung germinated as well or better than seeds from bovid dung or directly from fruit. Elephants were calculated to move seeds up to 10 times as far as domestic bovids. An empirical probability model estimated that the loss of elephants would result in reductions of about 66%, 42%, and 26% in the number of successfully dispersed seeds of each species without compensation. In compensation scenarios, other frugivores could ameliorate reductions in dispersal, making them as low as 6% if species such as gaur (*Bos gaurus*) persist. Thus the importance of elephants as seed dispersers is amplified by the population reductions of other large disperser species throughout tropical Asia. My findings suggest that losing the largest and most physiologically unique species is likely to have measurable effects on ecological processes.
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Introduction

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Earth may be on the verge of a mass extinction event precipitated by our own species’ rapid economic and cultural development. While mass extinction events have happened five times before, this would be the first time humanity is experiencing such a rapid reduction in the planet’s biodiversity (Barnosky et al. 2011), leading to widespread concerns related to both specific species and ecosystem function more generally. Many of the individual species at risk of widespread extirpation either have long been of great cultural value (e.g., Walston et al. 2010, Maisels et al. 2013), or would inspire the human imagination once mysteries about their biology and behavior are unraveled. At the ecosystem level, while we know that our species’ happiness and well-being are premised on the existence of a host of ecosystem processes and services—ranging from nutrient cycling to pollination to erosion prevention—we do not know the extent to which the ongoing extinction event will undermine these ecosystem functions (Loreau et al. 2001, Naeem et al. 2009).

This dissertation explores the functional ecology of a species pertinent to both these concerns: the Asian elephant. While the cultural value of elephants is self-evident, their relative importance in ecosystem function requires explanation. Ecological theory suggests that species loss should lead to deterioration of an ecological process unless other species are able to compensate for the extirpated species’ role in that process (Naeem and Li 1997). For instance, the loss of one nitrogen-fixing plant species may not affect levels of bio-available soil nitrogen if another nitrogen fixer fills the niche space once occupied by the departed species. Empirical work has shown that while the relationship between species loss and ecological function is not straightforward (Naeem et al. 2009), the loss of all species that serve a similar function—i.e., a functional group—may be predicted to affect ecological processes (e.g., Tilman et al. 1997).
challenge for researchers is thus to identify the characteristics that differentiate functional groups from each other for a given ecosystem function.

One biological characteristic that may be relevant across ecosystem functions is size (e.g., Hansen and Galetti 2009). Simulation studies and field observations have shown that while random extinctions may not affect key ecosystem processes, the loss of a system’s largest animal species may lead to the deterioration of ecological functions ranging from bioturbation (Solan et al. 2004), to reduction in disease transmission (Ostfeld and LoGiudice 2003), to population control of larger herbivores (Terborgh and Estes 2010). If size helps delineate functional groups, then the Asian elephant may well be its own functional group. Weighing around 4 metric tons (Sukumar 2003), it is more than twice as large as the next biggest sympatric animal species (the one-horned rhinoceros) and four times as large as the third-place finisher (gaur, *Bos gaurus*) (Dinerstein 2003, Smith and Xie 2008). Given the rarity of both rhinos and gaur across the Asian elephant’s habitat, its relative importance in ecosystem processes should be even greater. So do elephants actually form their own functional group in their ecosystems?

Elephants’ size and other ecological properties may allow them to contribute uniquely to seed dispersal (Campos-Arceiz and Blake 2011), a process thought to determine what plant species are able to persist in an area, thus shaping the species composition and character of the ecosystem (Wang and Smith 2002). Research suggests that megaherbivores (particularly African forest elephants) eat a great deal of fruit, move seeds far from their parent tree, and often deposit viable seeds in dung that acts as fertilizer (Campos-Arceiz and Blake 2011). Their ability to disperse large-seeded species may be exceptional, since smaller frugivores may not be able to ingest or carry larger seeds (such as the pit of the wild mango, *Mangifera indica*) far enough to disperse them (Corlett 2011). Yet understanding whether elephants are functionally unique as seed dispersers requires empirical comparison between them and the other frugivores in their habitat (Jordano and Schupp 2000). I endeavored to conduct just such a comparison through this dissertation. The central question of my thesis is this: if Asian elephants go missing, can the remaining species compensate for them as seed dispersers?

My work was conducted in Buxa Tiger Reserve, a forest habitat that faces disturbances typical for forests across the Indian subcontinent and region. With the help of local assistants, I identified three large fruited, mammal-dispersed trees: the chalta (*Dillenia indica*), the lator
(Artocarpus chaplasha), and the kumbhi (Careya arborea). I then worked to address several questions:

1. What are the main arboreal and terrestrial frugivores of these plant species? What proportion of available fruit does each frugivorous species remove? (Chapters 1 and 2)

2. How do elephants and their main alternative dispersers handle these fruits? (Chapters 2 and 3)
   - Are seeds dropped, spit, or otherwise discarded while feeding, or are they ingested?
   - If seeds are ingested, what proportion of them emerge whole in the feces of these animals?

3. For those seeds that are defecated, what proportion are likely to germinate and survive early distance- and density-dependent sources of mortality? (Chapters 3, 4, and 5)

4. How far are seeds likely to be dispersed by elephants and their main alternative dispersers? (Chapter 3 and 5)

Using the information from Chapters 1-3 and a set of conservative assumptions, I develop a model that calculates how the number of seeds and distance of seed dispersal changes in the absence of elephants. As such, this dissertation aims to qualitatively and quantitatively assess the relative role of Asian elephants as seed dispersers through empirical comparison with their main alternative dispersers in a disturbed landscape. The results presented here further inform our understanding of how body size relates to functional groups and the types of ecological changes we may expect when the largest animal species in an ecosystem disappear.
References:


CHAPTER 1:

Waiting for Gajah: an elephant mutualist’s contingency plan for an endangered megafaunal disperser

AUTHORS: Nitin Sekar, Raman Sukumar.

Summary

1. Large animals are disproportionately likely to go extinct, and the effects of this on ecosystem processes are unclear. Megaherbivores (weighing over 1000 kg) are thought to be particularly effective seed dispersers, yet only a few plant species solely or predominantly adapted for dispersal by megaherbivores have been identified.

2. The reasons for this paradox may be elucidated by examining the ecology of so-called megafaunal fruiting species in Asia, where large-fruited species have been only sparsely researched. We conducted focal tree watches, camera trapping, fruit aging trials, dung seed counts, and germination trials to understand the ecology of *Dillenia indica*, a large-fruited species thought to be elephant-dispersed, in a tropical moist forest (Buxa Tiger Reserve, India).

3. We find that the initial hardness of the fruit of *D. indica* ensures that its small (~6-mm) seeds will primarily be consumed and dispersed by elephants and perhaps other megaherbivores. Elephants removed 63.3% of camera trap-monitored fruits taken by frugivores.

4. If the fruit of *D. indica* is not removed by a large animal, the seeds of *D. indica* become available to successively smaller frugivores as its fruits soften.

5. Seeds from both hard and soft fruits are able to germinate, meaning these smaller frugivores may provide a mechanism for dispersal without megaherbivores.

6. Synthesis: *Dillenia indica*’s strategy for dispersal allows it to realize the benefits of dispersal by megaherbivores without becoming fully reliant on these less abundant species. This risk-spreading dispersal behavior suggests *D. indica* will be able to persist even if its megafaunal disperser becomes extinct.

**Key-words:** Asian elephant (*Elephas maximus*), *Dillenia indica*, dispersal, ecological redundancy, ecological resilience, frugivory, megafaunal fruit

Introduction

Larger animal species are disproportionately likely to be extirpated by the drivers of the ongoing extinction crisis (Duffy *et al.* 2009). Megaherbivores—species weighing over 1000 kg such as elephants and rhinoceroses (Owen-Smith 1988)—are a high conservation priority due to their charisma and cultural significance, and evidence of their ecological significance has been
growing (Owen-Smith 1988; Skarpe 2004). Yet, we are far from understanding the extent to which megafauna extirpation affects biodiversity and ecosystem function (Corlett 2013). Due to their size and singular behaviors, megaherbivores may often form a unique functional group with respect to certain ecological processes (Owen-Smith 1988). Understanding whether megaherbivores are functionally unique would provide an opportunity for us to examine our concepts of ecosystem resilience in the face of ecological change.

Seed dispersal is one ecosystem process for which megaherbivores may be particularly important (Campos-Arceiz and Blake 2011). Megaherbivores often consume large amounts of fruit (Campos-Arceiz and Blake 2011), and fruits are a particularly prominent part of the diets of the African forest elephant (*Loxodonta cyclotis*) and the one-horned rhinoceros (*Rhinoceros unicornis*) (Dinerstein and Wemmer 1988; Tchamba and Seme 1993). Animals such as elephants are able to swallow both small and large seeds without damaging them (Chapman *et al.* 1992; Campos-Arceiz and Blake 2011). Asian and African elephants are capable of taking seeds far from the negative effects of proximity to adult conspecifics (Campos-Arceiz *et al.* 2008a; Blake *et al.* 2009), and seeds of many plants found in megaherbivore dung typically germinate, sometimes better than seeds taken directly from fruit (Chapman *et al.* 1992; Theuerkauf *et al.* 2000; Dinerstein *et al.* 2003).

Given the advantages of dispersal by megaherbivores, one might predict that many plant species sympatric with megaherbivores would be adapted for dispersal by them. Several researchers have described a “megafaunal syndrome” (Janzen and Martin 1982; Gautier-Hion *et al.* 1985) based primarily on size, hardness, and color of fruits that indicates proclivity to dispersal by megaherbivores. *Balanites wilsoniana*, whose fruits each contain a single 8.8-cm-long seed and consist of pulp somewhat toxic to smaller animals, appears to be solely dispersed by African elephants in Uganda and West Africa (Hawthorne and Parren 2000; Cochrane 2003). *Trewia nudiflora* appears heavily reliant on the one-horned rhinoceros in Nepal (Dinerstein 2003). Barlow (2000) and Zaya and Howe (2009) suggest that the Kentucky coffee tree (*Gymnocladus dioicus*) was once dispersed by North America’s extinct rhinoceroses, camels, and gomphotheres.

Despite these insights, it is unclear whether there is in fact a swathe of species that will face serious population declines due to the loss of megaherbivore dispersers. On the one hand, research by Cochrane (2003) on *B. wilsoniana* indicates that the species could face catastrophic
reductions in range and population without elephants, and work by Blake et al. (2009) suggests that Africa’s forests are home to at least 13 species that require elephants for their dispersal. On the other hand, there is evidence suggesting that many megafaunal fruit-bearing species may be resilient to the loss of megaherbivores. *T. nudiflora* has been shown to be dispersed by animals smaller than the rhinoceros (Dinerstein 2003); as yet, no plant species in Asia has been demonstrated to have an exclusive relationship with elephants as dispersers (Kitamura et al. 2002; Kitamura et al. 2007). The persistence of the Kentucky coffee tree and other megafaunal fruits millennia after the extinction of their purported principal dispersers in the Americas (Janzen and Martin 1982; Guimarães et al. 2008; Zaya and Howe 2009), though possibly in much reduced numbers or ranges, calls into question the functional importance of forest-dwelling megaherbivores. Hawthorne and Parren (2000) suggest that, in the short time since elephant ranges have contracted substantially in Ghana, *Balanites wilsoniana* is the only tree species to have shown unequivocal reductions in dispersal ability. While the available evidence is limited, it raises interesting questions. Is it possible that megaherbivores, which tend to be voracious frugivores and potent dispersers, are ecologically redundant as seed dispersers? If so, how are trees apparently adapted for dispersal by the largest mammals dispersing their seeds without these partners?

These mysteries can be better addressed through more research on the extent to which individual extant megafaunal fruit-bearing species depend on megaherbivores for dispersal (Howe 1985). To this end, we provide the first detailed natural history of the dispersal of an Asian megafaunal fruit tree: *Dillenia indica*, a native to south and southeast Asia. Known as the “elephant wood apple” in English and “chalta” in Bengali and Hindi, *D. indica* produces large, hard fruit, which are eaten by elephants and are thought to be largely inaccessible to smaller animals. We attempt to understand i) whether elephants are the principal or sole frugivore and disperser of the chalta tree and ii) whether hardness of fruits—purportedly an element of a megafaunal fruit syndrome—is a barrier to dispersal by smaller animals, even though the seeds of chalta are small—that is, whether the chalta is a true megafaunal fruit. Overall, our aim is to better understand the extent of *Dillenia indica*’s dependence on elephants for dispersal and uncover aspects of *D. indica*’s dispersal ecology that may extend to megafaunal fruits more generally.
Materials and methods

Study species:

The chalta tree (*Dillenia indica*), a member of the Dilleniaceae family endemic to Asia, is an evergreen tree found throughout much of south and southeast Asia (Abdille *et al.* 2005; Campos-Arceiz *et al.* 2012). The tree’s distribution coincides with that of the Asian elephant. The chalta’s wood has multiple uses, and its indehiscent fruits are edible to people, used in local curries, jellies, and shampoo (Mabberley 1997).

The chalta is also appetizing to elephants. Sukumar *et al.* (2003) report that 90% of the elephant dung piles found in Buxa Tiger Reserve, India, during the dry months from December to March contained fruit remains of *D. indica*. Campos-Arceiz *et al.* (2008b) and Datta and Rawat (2008) confirm that captive elephants eat both the bark and fruit of *D. indica* in Burma and India, respectively. The literature also indicates that *D. indica* is a water-dispersed species (Mabberly 1997; Datta and Rawat 2008), making the degree of its dependence on elephants unclear.

The chalta fruit’s seeds are about 6 mm long. Yet the size and hardness of chalta fruits are thought to make them inaccessible to smaller frugivores, and the clear affinity elephants have for them make them a sensible candidate for an Asian megaherbivore-dispersed species.

We counted the number of seeds in each fruit, measured the diameter and mass of fruits, and used a “fruit penetrometer” (see Appendix S1 in Supporting Information) to measure the hardness of fruit from 50 trees. Hardness measurements ranged from 0 to 5.0 “penetrometer units.” We also made qualitative observations of the chalta fruits’ structure.

Study area—Buxa Tiger Reserve:

Buxa Tiger Reserve (henceforth Buxa) is located in the northern region of the Indian state of West Bengal (mostly between 80-200 m asl, 26°30’- 23°50 N and 89°25’- 89°55’ E, 761 km²). With an average annual rainfall of c. 4500 mm, the reserve is predominantly a tropical moist forest habitat. More details in Appendix S2.) Chalta trees are found throughout Buxa. Chalta fruit mature in late November and December, with some trees retaining fruit until mid-May (pers. observation).

In 2003, elephant density in the region was estimated to be 0.31 per square kilometer, or about 217 elephants throughout Buxa (Sukumar *et al.* 2003); the 2010 census by the Forest
Department estimates 228 elephants (pers. comm.). In addition to elephants, many other potentially frugivorous mammals (and potential dispersers) occupy Buxa, including wild boar (*Sus scrofa*), sambar (*Rusa unicolor*), chital deer (*Axis axis*), barking deer (*Muntiacus muntjak*), Rhesus macaques (*Macaca mulatta*), common palm civets (*Paradoxurus hermaphroditus*), and Himalayan crestless porcupines (*Hystrix brachyura*). Gaur (*Bos gaurus*), which occasionally surpass 1000 kg and thus can qualify as a megaherbivore, also occur in Buxa, though in lower numbers than elephants. Finally, domestic animals, particularly domestic buffalo (*Bubalus bubalis*) and cattle (*Bos primigenius*), often penetrate deep into the reserve, and in some areas they are present at greater population densities than large wild ungulates.

**Focal Watches**

Scheduled focal watches (n=46 at 35 trees) totaling 109.5 hours of diurnal observation were conducted from December 2010 to April 2011 and from December 2011 to March 2012 to identify any diurnal arboreal frugivores of the chalta tree and to quantify their relative consumption of fruits. Focal watch trees were selected such that a) they were scattered throughout Buxa, b) they were located en route to (but >200m from) camera trap trees (see next section), and c) substantial proportions of their canopies (minimum 15%) were visible from a safe vantage point (see Appendix S3 for more details).

Fruit fall was detected by sight and sound, and the number of fruits that fell over the course of focal watches was monitored for comparison with fruit consumption rates. In addition, opportunistic focal watches (n=14 at 12 trees totaling 3.9 hours over our 2 field seasons) were conducted when potential arboreal frugivores were seen on chalta trees.

**Camera trapping, fruit counts**

Camera trapping and fruit counts were conducted to identify the main terrestrial frugivores of *D. indica* and to determine the relative quantities of fruit removed by each. First, individual chalta trees were found using a systematic search on foot and by vehicle in Buxa in November of 2010. We then randomly selected 60 trees for camera trapping; up to 4 trees were camera trapped at a time (see Appendix S4).

At each tree, fruits around the tree were counted and the date marked with a pen (Prasad *et al.* 2010). A rough map of the locations of the fruits was made. This made possible the
identification of newly fallen fruits the following day. Partial fruits (fruits that had part of the hard mesocarps removed and pulp exposed) and free pulps (inner pulp packets of chalta fruit with no surrounding layer) were found under the tree (see Fig. 1); their origins were not immediately clear, and they were counted separately. Empty fruits (fruits from which the pulp and seeds had been removed via excavation by a small animal) were also counted. During the second field season, the mesocarps of fruits that had been removed from the canopy, had their contents removed, and dropped were observed; these fruit pieces, qualitatively different from fruits which had been emptied on the ground, were designated “splits.” Splits were counted and removed so that newly dropped splits would be identifiable upon return to a tree.

It was observed that many fruits not taken by frugivores became brown and soft with age, but the seeds inside them appeared viable. Fruits that were i) 25% brown and very soft or ii) more than 75% brown in color (not necessarily soft, but drier and easier to peel open) were classified as “Stage 2” fruits, as they no longer possessed the hard impenetrability that characterized yellow-green “Stage 1” fruits and could be more easily accessed by animals smaller than megafauna. Stage 2 fruits were distinguished from rotten fruits by their smell and texture (see Fig. 1).

Camera traps were used to quantify fruit removal by terrestrial frugivore species (Prasad et al. 2010; see Appendix S4). 1-25 (mean 3.4) stage 1 and stage 2 fruits were placed in front of the camera, and camera traps were programmed to take one picture when triggered and then one picture every 15 seconds for 6 minutes, helping us ascertain whether the animal that triggered the camera also removed fruit. In our second season, we used our fruit penetrometer to measure the hardness of fruits placed in front of the camera. We returned the following day to count fruit and replace fruit in front of the camera if necessary. We rotated to the next group of trees after 2-3 days.

For analysis, we divided the total number of fruit removed by each animal species (on camera) by the total number of fruit-days monitored (e.g. a single fruit watched for two days by a camera trap was two fruit-days). This gave us an estimate of the average proportion of fruit removed per day by each frugivore species. Nonparametric bootstrapping using the boot package in R was used to create bias-corrected and accelerated confidence intervals for these estimates (Davison and Hinkley 1997). In order to deduce what animal species were responsible for leaving free pulps under the chalta trees, we used a general linear model (Gaussian distribution,
identity link) where the initial predictors were dummy variables representing the triggering of the camera traps by the various frugivores in the previous day and the response was the change in number of free pulps over the last day. Akaike information criterion (AIC) was used to select the most parsimonious model (Burnham and Anderson 2002).

In situ fruit fate trial

Chalta fruits proceeded from stage 1 to stage 2 to rotting very slowly and experienced a variety of fates. To understand the proportion of fruits that experienced each fate, ribbons were tied above up to ten fruits which had fallen in the last day to allow tracking of these fruits during future visits. These fruits were also marked. After 2-3 weeks we returned to the tree to find all the marked fruit, coding each fruit as “remaining—stage 1”, “remaining—stage 2”, “removed”, “emptied” (meaning a hole had been made in the fruit and the pulp and seeds extracted), or “rotten.” If neither a ribbon nor its corresponding fruit could be found (as happened if, say, an animal had heavily affected vegetation), the fate of the corresponding fruit was noted as unknown. This exercise provided us an estimate of the proportion of fruits that ultimately faced each fate.

We used the fruits that ultimately passed to stage 2 or rotted to calculate an in situ estimate of the average time taken for fruit to progress from stage 1 to stage 2 or rotten and from stage 2 to rotten. We assumed that the fruit transitioned from one phase to the next half way between the time we last saw the fruit in its previous state and the time we found the fruit in its current state.

Ex situ fruit aging trial

To estimate the approximate amount of time required for chalta fruits to progress from stage 1 to stage 2 to rotten more precisely, we collected 110 fruits that had fallen within the last day from 15 chalta trees. We kept them outside our field station and monitored how long it took for them to progress from stage 1 to stage 2 and from stage 2 to rotten (see Appendix S5 for details).

Germination trials:
To ensure that stage 2 fruits’ seeds were still viable despite the softening of their mesocarps, we collected 65 stage 1 fruits and 52 stage 2 fruits from 33 chalta trees. A total of 259 stage 1 fruit seeds and 268 stage 2 fruit seeds (four to eight seeds from each fruit) were individually planted in an outdoor nursery in Buxa. The seeds were monitored every 2-3 days for germination until a month after the last chalta seed had germinated.

**Elephant dung seed counts:**

In order to ensure that elephants were in fact dispersing seeds, we opportunistically counted the number of chalta seeds in 79 piles of elephant dung found in the forest or on forest roads between November and May of 2010-2012.

**Results**

Chalta fruit averages 9.8 cm in diameter (sd=1.1cm, range: 7.4-18.3 cm, N=281). The mean mass was 447 grams (SD=100, N=448) for stage 1 fruit and 350 grams (SD=88.5, N=112) for stage 2 fruit. The fruit was found to be structured such that the seeds, though small, were difficult to access. For the purposes of this study, chalta fruit is composed of two main types of tissue (see Fig. 1). On the outside are thick, tough layers of protective tissue, the chalta’s epicarp and mesocarp. In the center is a soft pulp sack composed of about 15-20 carpels with up to 313 6mm seeds (mean= 103.1, std. dev.=56.0, N=179) embedded in a sticky liquid that made separating seeds difficult. Many fruits had insects or insect eggs inside them in place of some or all the seeds.

Fruit penetrometer measurements confirmed the difference in hardness between stage 1 and stage 2 fruits. Stage 1 fruits had a mean hardness of 3.40 penetrometer units (sd=0.79, N=800), while stage 2 fruits had an average hardness of 0.88 penetrometer units (sd=0.62, N=250); the difference was statistically significant (student t-test, \( P<0.001 \)).

**Focal watches and arboreal frugivory**

Scheduled focal watches revealed no significant arboreal frugivores for *Dillenia indica*. In 109.5 hours of observation, only 10 Rhesus macaques and 3 Malayan giant squirrels (*Ratufa bicolor*) visited these trees. Macaques occupied the focal trees for a total of 75 minutes, and giant squirrels for 29 minutes. Only one individual—a giant squirrel—even made an attempt to
Fig 1: The structure of the fruit (top left) of the chalta tree (Dillenia indica) is such that the ~6-mm seeds are embedded in a very hard mesocarp, which is thought to prevent frugivory by small animals. On the top right is a “free pulp”—like the seed-containing structure on the left, but somehow naturally released of its woody container and found under the parent tree. On the middle right is a stage 1 chalta fruit whose pulp and seeds have been removed, perhaps by a seed predator. The bottom panel shows the progressive softening of chalta fruit after falling from the tree. The first four fruits from the left would have been classified as stage 1, the fifth as stage 2, and the sixth as either stage 2 or rotten depending on the fruit’s smell. The seventh are the totally decomposed remnants of a chalta fruit.
consume any chalta fruit; it handled four fruits, but discarded each fruit before it had chewed its way to the fruits’ seeds. Giant squirrels and macaques were often heard nearby and passed the focal chalta tree without showing any interest in its fruits; thus the lack of fruit removal was not due to low populations of these two species. The gradual loss of fruits from the crowns of trees observed over the season suggested that no arboreal frugivore, diurnal or nocturnal, was consuming a notable number of fruits from the tree tops.

Nonetheless, we observed an additional 15 macaques and 11 giant squirrels in the crowns of chalta trees during the opportunistic focal watches. Macaques attempted to eat a total of 28 fruits on these occasions, but they never reached the fruit’s seeds. Fruits whose mesocarp had been partially eaten but whose seeds had not been extracted were commonly found below trees during fruit counts and camera trapping. Giant squirrels were observed penetrating the mesocarp and consuming the seeds of 6 of the 10 chalta fruit they handled during opportunistic focal watches, finally discarding the fragmented mesocars—or splits—under the crown of the tree. It was not possible to observe whether the giant squirrels were swallowing the seeds (potential dispersers) or chewing the seeds (seed predators).

Our counts of these splits and newly fallen fruits under trees revealed that an average of 3.37 new fruits (N=262 tree-days, sd=4.48) with seeds untouched fell under each tree each day, while an average of 0.13 split fruits with seeds removed (N=238 tree-days, sd=0.48) were found under each tree each day. This meant that roughly 26.7 times (95% confidence bias-corrected accelerated bootstrap confidence interval: [16.54,44.58]) as many fruits fell to the ground intact as were consumed by arboreal frugivores.

Camera trap and marked fruit data

In total, camera traps monitored 68 trees, 646 tree-days, and 2186 fruit-days. While a variety of species, including frugivores such as sambar deer and civets, triggered the trap, fruits were removed by only a few animals: elephant, gaur, domestic buffalo, domestic cattle, Rhesus macaque, small squirrel (either orange-bellied Himalayan squirrel, Dremomys lokriah, or hoary-bellied squirrel, Callosciurus pygerthythus), and rats (Rattus spp.). Based on their ability to access chalta fruit seeds (but not necessarily on their potential contribution as seed dispersers), the frugivores can be divided into four groups based on their ability to handle chalta fruits and access their seeds: elephants, bovids (gaur, buffalo, cattle), macaques, and rodents (rats and squirrels).
Of the 130 stage 1 and 28 stage 2 fruits removed by frugivores from the camera traps, elephants consumed 76.9% of the stage 1 fruits and 0% of the stage 2 fruits; bovids consumed 22.3% and 14.3%, respectively; macaques removed 0% and 33.9%, respectively; and rodents removed 0.8% and 51.8%, respectively (Fig. 2a). Having triggered the camera, bovids were less likely than elephants to remove stage 1 fruits in front of the camera, apparently due to the hardness of the fruit. Generally, the greater the body-size of the frugivore, the more stage 1 fruits removed, and the smaller the frugivore, the more stage 2 fruits removed. Details observed in the camera trap photographs and our monitoring of fruits under each tree away from the camera traps supported this trend (see Appendix S6).

Fruit counts suggest that stage 2 fruit formed an average of 19% of the fruit under a tree on any given day (N=329 days), On two occasions macaques unpeeled stage 2 fruit and extracted the pulp and seeds in front of the camera, confirming that stage 2 fruits had edible pulp. Rodents showed a clear preference for stage 2 fruits but on one occasion chewed open a stage 1 fruit; it appears that rodents were most responsible for the “empty” stage 1 mesocarps found under trees during counts. Emptied chalta fruits were sometimes found with the remnants of seed coats next to them, suggesting that rodents may often be seed predators.

Free pulps were taken by domestic buffalo, gaur, and rats, but not by elephants. To the contrary, the number of pulps seemed to go up after an elephant visited a tree, as confirmed by our general linear model. In the most parsimonious model, elephants accounted for the appearance of an average of 1.42 pulps each day they visited ($P=2.11\times10^{-14}$). The triggering of the camera trap by bovids and rodents did not predict a decrease in the number of free pulps around the tree, probably because the free pulps were removed whether or not an animal triggered the trap.

**Hardness of fruits removed**

Elephants removed 29 fruits whose hardness had been measured from the camera trap, bovids removed 17, and small mammals removed 8 fruits (see Fig. 2b). Fruits removed by elephants (mean 3.49 penetrometer units, sd=0.62) were harder on average that those removed by bovids (mean 3.03 penetrometer units, sd=0.99); the difference was almost statistically significant (Wilcoxon test, $P=0.069$). The fruits removed by bovids were much harder than those
Fig 2: (a) The proportion of chalta fruit (total, stage 1, and stage 2) removed by each frugivore per day, calculated by taking the total fruit removed from camera traps by a frugivore group over two seasons and dividing that by the number of fruit-days monitored. The 95% BCa confidence intervals, calculated using non-parametric bootstrapping, are large since removal of chalta fruit from a camera trap on any given day was a relatively rare event. (b) The percentage of chalta fruit from each of 10 hardness classes removed by each functional group. A total of 54 fruits whose hardness had been measured by fruit penetrometer were removed from camera traps by frugivores; thus, some hardness classes have a small number of fruit. These graphs illustrate the trend of the hardest fruits being removed by large animals and the softest fruits being removed by rodents and macaques. Elephants are clearly the most important frugivore (and possibly disperser) overall and for stage 1 fruit.
removed by macaques, squirrels, and rats (mean 0.66 penetrometer units, Wilcoxon test $P<0.001$). (See Appendix S7 for notes on fruit penetrometer results).

In situ fruit fate and ex situ aging trials

The fruits in our ex-situ aging trial spent an average of 32.4 days in stage 1 (sd=13.9, range= 9-68, N=110). These fruits then spent an average of 28.7 days in stage 2 (sd=13.5, range=4-56, N=107). As the fruits were placed together, most of the stage 2 fruits began rotting at the same time due to termite infestation, reducing the independence of fruits in our sample.

Ribbons were used to track 466 marked chalta fruits from 33 trees. Of these, at least 75 (16%) passed into stage 2 before rotting, being removed, or being emptied; since trees were only visited once every 2-3 weeks, other fruits probably reached stage 2 before meeting their fate, making this a conservative estimate. Thirty-one fruits and their ribbons were lost after marking (most likely removed by large animals, but excluded from analysis). For fruits that were neither removed nor emptied while in stage 1, the average length of stage 1 was approximately 22.5 days (sd=19.1, range=2.5-88, N=109). For stage 2 fruits that eventually rotted, the average length of stage 2 was about 24.3 days (sd=12.7, range=6-57, N=24). While these periods were somewhat less than those found during the ex situ fruit aging trial, they both point to widely varying stage 1 and stage 2 periods that on average are roughly equal in length (see Table 1).

Overall, of the 435 fruit whose fate we could discern in situ, 314 (72%) were apparently removed by a frugivore, 63 (14%) were emptied by a seed disperser or predator, and 58 (13%) rotted with their seeds inside. Examining the different fates faced by stage 1 and stage 2 fruit is instructive. Of the 391 fruit that met their fate while in stage 1 (were never detected in stage 2), 304 (81.9%) were removed by frugivores, 33 (8.9%) were emptied by seed predators or dispersers, and 34 (9.2%) rotted, meaning that the seeds rotted before the tough mesocarp of the fruit softened to stage 2. Of 64 stage 2 fruits whose final fates were deducible, ten (15.6%) were removed by a frugivore, 30 (46.9%) were emptied, and 24 (37.5%) rotted. This means that, for fruits left behind by the large animals that can chew through the hard mesocarps of stage 1 fruit, about 49.3% of fruits in stage 1 were emptied, providing at least some chance of seeds escaping and germinating, and 50.7% rotted (see Table 1). If a fruit moved to stage 2, presumably due to an absence of large frugivores, 62.5% of fruits were either taken or emptied and 37.5% rotted. Seeds thus had a 26.8% better chance of escaping a fruit left behind by elephants and bovids if
Table 1: A summary of findings from the in situ fruit fate and ex situ fruit aging trials. Both in situ and ex situ trials show substantial variation in the amount of time spent in stage 1 and stage 2, but that on average the stages are roughly equal in duration. In Buxa, the majority of fruits are removed when hard (in stage 1) by elephants and some bovids (as shown by camera traps). Remaining fruits increase the probability of having their seeds removed by softening to stage 2. 33 of 67 (49.3%) stage 1 fruits left by large frugivores were emptied by rodents, whereas 40 of 64 (62.5%) of stage 2 fruits were either emptied or removed by mostly smaller frugivores (as indicated by camera trap data). Presumably, in the absence of elephants, substantially more fruit would progress to stage 2 and face the fates indicated in the third row of the table.

<table>
<thead>
<tr>
<th>Fruit Stage</th>
<th>Length (Days + SD)</th>
<th>Removed (%)</th>
<th>Interpretation</th>
<th>Emptied (%)</th>
<th>Interpretation</th>
<th>Rotted (%)</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(391 fruit in situ)</td>
<td>22.5 +19.1 (in situ)</td>
<td>304 (81.9%)</td>
<td>Most hard fruit taken by elephants, some by bovids</td>
<td>33 (8.9%)</td>
<td>Rodents occasionally able to penetrate hard stage 1 mesocarp</td>
<td>34 (9.2%)</td>
<td>Fungi, termites, insects cause some fruits to rot from inside before softening to stage 2</td>
</tr>
<tr>
<td></td>
<td>32.4 +13.9 (ex situ)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(64 fruit in situ)</td>
<td>24.3+12.7 (in situ)</td>
<td>10 (15.6%)</td>
<td>Softer fruits consumable by many smaller frugivores, including macaques who remove fruit</td>
<td>30 (46.9%)</td>
<td>If not removed while hard, softening to stage 2 allows high-% chance of seed removal by rodents</td>
<td>24 (37.5%)</td>
<td>Some fruits fall in places unlikely to be found by any frugivores.</td>
</tr>
<tr>
<td></td>
<td>28.7+13.5 (ex situ)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(435 in situ)</td>
<td>46.6+23.6 (in situ)</td>
<td>314 (72%)</td>
<td>Substantial elephant population ensures most fruits removed while hard; bovids also contribute.</td>
<td>63 (14%)</td>
<td>When large animals miss fruit, rodents and other small animals pick up the slack.</td>
<td>58 (13%)</td>
<td>If fruit not taken by frugivore, destroyed by fungal pathogens and insects before rainy season.</td>
</tr>
<tr>
<td></td>
<td>60.3+6.3 (ex situ)</td>
<td></td>
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</tr>
</tbody>
</table>
the fruit’s mesocarp softened before the seeds rotted (i.e. the fruit transitioned to stage 2) than if the fruit remained hard until the seeds decayed (i.e. the fruit remained in stage 1).

As the fruiting period encompasses the dry season in Buxa, the vast majority of fruits fell on dry ground as opposed to a water body, and if not removed by dispersers or seed predators rotted months before water from the monsoon was available to carry them away. Any perennial water bodies near trees were often stationary during the fruiting season. Thus, at least in Buxa, it seems unlikely that chalta seeds could rely on water dispersal.

*Germination trials:*

Of 259 seeds from stage 1 chalta fruit, 186 (71.8%) germinated and 177 (68.3%) sprouted true leaves. Of 268 seeds from stage 2 chalta fruit, 175 (65.3%) germinated and 171 (63.8%) sprouted true leaves. The proportions of seeds germinating from stage 1 and stage 2 fruits’ seeds were not significantly different (Chi-squared test, \( P=0.107 \)). See Appendix S8 for more details.

*Elephant dung seed counts:*

Of the 79 elephant dung piles we opened, 78% contained seeds of *Dillenia indica*, and an additional 5.1% contained undigested parts of chalta fruit. The average number of seeds per dung pile was 45.3 (SD: 84.0, range: 0-554). Late in the season, chalta seeds that had germinated were often found in elephant dung, suggesting that chalta seeds could survive gut passage.

*Discussion:*

Our study suggests that megaherbivores, in particular elephants, are the principal consumers of *Dillenia indica* fruits (Fig. 3). Elephants in Buxa consumed 63.3% of the fruit removed from camera traps, more than double that consumed by wild and domestic bovids combined. The chalta fruit’s structure and natural history appear to predispose it to consumption by elephants. Due to its tough mesocarp, the fruit appears initially inaccessible to most frugivores smaller than elephants; Malay giant squirrels, Rhesus macaques, and terrestrial rodents are rarely able to access its seeds. Gaur, domestic buffalo, and domestic cattle also eat chalta fruits, but the hardness of the stage 1 fruit seems to be a barrier for some individuals of those species. This fits with the few other available accounts of chalta frugivory. Campos Arceiz
Fig. 3: The strongly sequential nature of frugivory of the chalta’s hard fruit. The percentage of fruits estimated to follow each path from each source is next to each arrow (with the percentage of all fruits following that path in parentheses). Dotted lines indicate proportion is unknown. Some fruits in the canopy are consumed by giant squirrels, but the vast majority fall to the ground. Of those, most are consumed as stage 1 fruit, which due to hardness are most accessible to elephants. Large bovids and an occasional rodent also consume stage 1 fruits. Most of the fruits that proceed to stage 2 are consumed by macaques, rats, small squirrels, and perhaps other common animals that can now access the chalta seeds due to the softened mesocarp. A few of these stage 2 fruits are eaten by larger frugivores, and the rest rot. Elephants sometimes drop the pulp of the fruit they are eating; these are then consumed by other frugivores.
et al. (2012) recounted the great difficulty Malayan tapirs (*Tapirus indicus*) experienced eating chalta fruits during feeding trials; while all other fruits were consumed or discarded by tapirs within an hour, tapirs were given 1.5 to 21 hours to eat chalta fruits as they repeatedly struggled to consume the (presumably stage-1) fruit’s mesocarp. Similarly, a sambar deer (*Rusa unicolor*), India’s largest deer species, was once spotted struggling to consume a chalta fruit in Kaziranga National Park, Assam (K. Chelliah pers. comm.). Thus, even where such large wild frugivores are available in higher densities than in Buxa, elephants are likely the most important consumer of chalta fruits. Curiously, the release of free pulps, which can then be consumed by a much wider array of frugivores and seed predators, also appears to be mediated by elephants.

This frugivory likely makes the elephant *Dillenia indica*’s most important seed disperser wherever elephants are in adequate supply. The majority (78.5%) of elephant dung piles opened contained chalta seeds. While it is possible that other species that consume less fruit are more effective dispersers (McConkey and Brockelman 2011), what we know about elephants as dispersers thus far makes this unlikely. The generally high passage and germination rate of seeds consumed by elephants and the large area over which free-ranging elephants tend to deposit seeds (Campos-Arceiz and Blake 2011) suggest that, unless seed survival is substantially lower in elephant dung than other deposits due to seed predation or competition, other dispersers may be unable to make up for their inferiority to elephants in consuming chalta fruit. Bovids, macaques, and rodents may complement elephants in the dispersal of chalta, but they probably cannot compensate for elephants.

In addition to hardness, the chalta tree shows several other characteristics of a species designed primarily for an uncommon, terrestrial disperser. Its fruits are capable of waiting long periods of time on the forest floor, a characteristic of a fruit with a rare disperser (Tang et al. 2005) and an element of Zaya and Howe’s “refined megafaunal fruit syndrome” (2009). The tree fruits in the winter and early dry season, when decay and rotting of fruit are much slower processes. The chalta fruit also possesses high levels of phenolic compounds, which could act as antioxidants to retard the rotting process (Abdille et al. 2005) or perhaps even as antifungal compounds, like danielone in the papaya (Echeverri et al. 1997). Based on our camera trap data and *in situ* fruit fate trial, this strategy of patience seems to work—even though elephants only eat an average of 4.6% of the available fruit (stage 1 and stage 2) a day and other dispersers eat a combined 3.1% daily, 72% of fruit in our *in situ* fruit fate trial were removed by non-rodent
frugivores and only a mere 13% rotted. Finally, individual chalta trees drop their fruits over a prolonged period of time—they do not seem to expect a common disperser or a seasonal dispersal event, but instead are hedging their bets. If water, the other proposed disperser of chalta (Datta and Rawat 2008), makes an appearance at all during *D. indica*’s fruiting season in Buxa, it is only after the vast majority of fruits have rotted or been eaten.

Ironically, the same adaptations that facilitate the chalta’s wait for its preferred disperser provide it alternative avenues for dispersal if the megaherbivore never arrives. If insects fail to penetrate the fruit, the chalta’s mesocarp softens gradually instead of rotting quickly, providing access to successively smaller classes of frugivores. Our observations suggest that bovids seem more able and inclined to eat somewhat softer chalta fruits than do elephants. More markedly, fruits that pass into stage 2 are far more accessible to macaques, rodents, and perhaps other common frugivores that provide at least some chance of escape for the chalta’s seeds. Macaques and rodents are relatively unimportant players, together consuming about 17% of the fruit removed from camera traps. This was because stage 2 fruits were rare, averaging 19% of the fruits under a tree. In the absence of elephants and other large herbivores, stage 2 fruits would become more common, thus becoming a more reliable and sought after source of food for potential dispersers like macaques, civets, and rodents. Unlike *Balanites wilsoniana*’s 8.8 cm seeds (Cochrane 2003), the chalta’s 6 mm seeds could be ingested and passed by smaller dispersers; Rhesus macaques at Buxa ingest and defecate viable seeds up to 1.5 cm long (N. Sekar unpublished data). The chalta fruit’s sticky pulp may also play a role in promoting ectozoochorous dispersal by these small animals. Macaques in one series of photos struggled to discard the seeds while eating the pulp, and we experienced similar difficulties while counting seeds.

Along with the fruit’s seed size, the variation in the chalta’s physiology and phenology suggests it is capable of persisting without megafauna. Our *ex situ* aging trial, in which the environment experienced by fallen fruits after the first day was roughly constant, still resulted in widely varying stage 1 lengths, with some fruits transitioning to stage 2 in as little as nine days; this suggests that the varied softening rate of fruits may in part be hereditary. Finally, the variation in the timing of fruit fall in chalta is substantial, with some individuals dropping all their fruits by early February and others keeping fruit into May and the early monsoon. In nearby Arunachal Pradesh, Datta and Rawat (2008) found that some *D. indica* were water-dispersed,
and N. Velho (pers. comm. 2012) observed that chalta trees were evenly split between dry season and monsoon fruiting. The combination of this phenotypic and phenological variation, the chalta fruit’s small seeds, and our observations of stage 2 fruit frugivory by macaques and rodents suggest that chalta trees would have a reasonable chance of successful dispersal without elephants.

Elements of the chalta’s mixed strategy fit into our existing understanding of large fruit ecology. Kitamura et al. (2002) note that large fruits with small seeds are consumed by just as many frugivores as smaller fruits so long as they are soft. The osage orange (*Maclura pomifera*), a purported megafaunal fruit that has survived in the Americas, starts bright green and very hard, gradually softening such that a human or squirrel can reach inside and extract its pulp and relatively small seeds (Barlow 2000). Rodents and even small marsupials from both the neotropics and paleotropics have been shown to cache a percentage of the seeds they remove, often leading to germination (Forget and Wall 2001; Nyiramana et al. 2011). Most dramatically, thieving agoutis on Barro Colorado Island, Panama, were shown to move a third of *Astrocaryum standleyanum*’s seeds over 100 meters, with 14% of cached seeds left uneaten for a year (Jansen et al. 2012). Since our camera trap photos and *in situ* fruit fate trials suggest rodents carry chalta pulps away, it is plausible that Buxa’s rodents play a similarly effective role as forgetful predators/dispersers. Finally, while the chalta’s use of fruit hardness to mediate frugivory may be a novel tactic, its strategy of persisting in the environment for an extended period of time to allow for rare dispersal events is common. For instance, the purported megafaunal species *Maclura pomifera* and *Gymnocladus dioicus* can reproduce vegetatively with sufficient success to extend their effective generation time (Barlow 2000; Zaya and Howe 2009), providing sufficient opportunity for dispersal by floods or a typical seed predator in the absence of the ideal megaherbivore disperser.

While the chalta’s natural history in Buxa suggests that *Dillenia indica* is yet another megafaunal fruit that can struggle on without megafauna, research on this species at other sites would provide complementary insights. At sites with similar population densities of *Dillenia indica* from which elephants or other megaherbivores have recently been lost, studies of the fate of chalta fruits would be expected to find that a significantly larger proportion of chalta fruit rot or are emptied by rodents and other small animals. Conversely, at sites with higher densities of megafauna such as the floodplains of Kaziranga National Park, controlling for density of chalta
trees, one may expect to see even fewer fruits rotting or being emptied than in the forests of Buxa. Finally, and most informatively for our understanding of functional redundancy and adaptability in dispersal systems, one would expect that in sites that lost elephants and other megaherbivores long ago, chalta fruits would show an increase in the proportion of time spent in stage 2, a softening of fruits while in the tree, and potentially a shortening of the period over which fruits ripen and drop. Alternatively, in sites where seasonal flooding occurs, chalta phenology may change such that fruits are dropped in the rainy season and dispersed by water.

**Conclusions**

Our research on the ecology of *Dillenia indica* focused primarily on the quantity of fruit removed by frugivores at one site. Nonetheless, our findings on *Dillenia indica*’s natural history strongly support two broad ideas. First, at least some plants should be adapted to be preferentially dispersed by megaherbivores. Second, such plants should be partially “pre-adapted” to dispersal by other mechanisms due to the potential unreliability of a wide-ranging species whose abundance varies over time. Unlike species regularly dispersed by rodents, birds, or macaques, trees dispersed by megafauna need to produce fruit that can withstand relatively long periods on the ground, allowing otherwise rare events to become sufficiently probable to facilitate occasional dispersal. In addition, many individual trees could end up rooted where megaherbivores rarely or never forage, selecting for back-up dispersal mechanisms or the ability to reproduce vegetatively. If the dynamics we observed in Buxa are representative of the chalta’s natural history across its range, it is conceivable that animals as common as macaques, bovids, and even rodents allow the chalta tree to persist long enough to fully adapt to a megaherbivore-free landscape. However, while *Dillenia indica* and other megafaunal symbionts may be resilient to the extirpation of elephants, the concomitant loss of other dispersers, changes in climate, and fragmentation of habitat may add up to too much for these species to withstand (Kitamura et al. 2005, McConkey et al. 2012).

**Acknowledgments**

We thank the West Bengal Forest Department for permissions to carry out this research in Buxa Tiger Reserve, and for their support in the field. We owe thanks to Dr. Andrew Dobson, Dr. Soumya Prasad, Dr. Andre Pittet, Dr. Ahimsa Campos-Arceiz, Dr. David Wilcove, and Dr.
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References


**Supporting Information**

**Appendix S1:** *Use of fruit penetrometer to measure hardness of Dillenia indica*

**Appendix S2:** *Additional details about study area, Buxa Tiger Reserve*

**Appendix S3:** *Focal Watches*

**Appendix S4:** *Camera trapping, fruit counts*

**Appendix S5:** *Ex situ fruit aging trial*

**Appendix S6:** *Camera trap and marked fruit data*

**Appendix S7:** *Fruit Penetrometer and Hardness of Fruits*
Appendices S1-S7: Further details on methods and results:

Appendix S1: Use of fruit penetrometer to measure hardness of Dillenia indica:
We used a “fruit penetrometer” to measure the hardness of fruit from 50 trees. The fruit penetrometer was constructed by attaching a 6-32 Phillips pan-head machine screw to the end of a pocket penetrometer (generally used for measuring soil compressive strength) using glue and electric tape. The fruit penetrometer was then pressed one centimeter into each fruit at the same structural point, where three parts of epicarp met, and a reading from 0 to 5 kg/cm$^2$ was taken (unadjusted for the surface area of the point of the screw, hereforth called “penetrometer units”). The one fruit harder than 5 kg/cm$^2$ was assigned a hardness of 5.

Appendix S2: Additional details about study area, Buxa Tiger Reserve:
Buxa Tiger Reserve (henceforth Buxa) is located in the northern region of the Indian state of West Bengal (26°30’- 23°50 N and 89°25’- 89°55’ E, covering 761 km$^2$). The reserve and surrounding patches contain some 352 species of trees (Das 2000) and are a mosaic of tropical deciduous and evergreen forests, grasslands, dry thorn forests, and degraded forests, all of which constitute elephant habitat. The rivers running through the region also create several flood plains. The cultivated matrix between the patches features tea and mixed forest plantations, agricultural lands, and settlements.

Appendix S3: Focal Watches:
Focal watches for trees obscured by other vegetation: Frequently the view of a focal tree was obscured by other trees from more than 25 meters’ distance. To view the tree without detection by animals easily frightened by humans, focal watches were conducted from 1-2 “monkey blinds,” which were like green mosquito nets with holes cut in them for binoculars.
**Timing, duration, and sampling strategy for focal watches:** Scheduled focal watches were 1.0-5.2 hours long (mean 2.4) and occurred between 6 AM and 6 PM, roughly evenly distributed throughout the four quarters of the day. Focal watches were broken into five-minute sampling periods. At the beginning of each period, the number of individuals of each frugivorous animal species in the tree was counted. Then, for five minutes, 1-2 individuals whose activities were visible were observed closely. During this observation period, the number of fruits consumed by each individual and, if possible, the treatment of the seeds of the fruit were observed.

**Appendix S4: Camera trapping, fruit counts**

**Selection of sample of *D. indica* trees for camera trapping:** First, individual chalta trees were found using a systematic search on foot and by vehicle in Buxa in November of 2010. We divided Buxa into eight different regions and spent 1-2 days searching each region for chalta trees. Half our time was spent searching for trees on foot and half was spent searching by vehicle; most trees found were near forest roads or trails.

We then randomly selected 60 trees for camera trapping. Trees were initially placed randomly in groups of four for simultaneous camera trapping; trees were then shuffled minimally amongst groups so that a) two trees less than 200 m from each other were not simultaneously trapped and b) all trees in a group could be reached and sampled in one day. We endeavored to rotate amongst the groups, trapping at all the trees in a group at the same time. Twenty trees were monitored from November 2010 to May 2011 (field season 1), twenty from November 2011 to February 2012, and twenty from February 2012 to May 2012 (field season 2). If a tree was made inaccessible due to obstruction by elephants or road blocks, another chalta tree as close as possible to the inaccessible tree was sampled; eight additional trees were sampled for this reason. We camera trapped at one group of trees for 2-3 days before moving to another group, rotating back to each group after 2-2.5 weeks (facilitating the *in situ* fruit fate trials).

**Details of camera trapping methods:** Infrared camera traps (Reconyx pro-hyperfire PC-800) were hidden about 1.3-1.7m high at a location, either on the sampled tree or elsewhere under its canopy, where they were unlikely to be detected by people. It was often necessary to clear some brush and place fruits in front of the trap to ensure a frugivore would trigger the camera. Stage 1
and stage 2 fruits were handled using chalta leaves and placed in front of the camera such that the number of fruits in front of the camera formed a clump similar to those formed by natural fruit fall. In our first season, half of the fruit put in front of the camera were left unmarked to determine whether marking affected fruit removal. In our second season, we used our fruit penetrometer to measure the hardness of fruits placed in front of the camera, leaving some unchecked to determine whether the hole created in the fruit while measuring hardness affected fruit removal. When available, partial fruits and free pulps were also placed in front of the camera. We also noted any indications of potential animal frugivory (footprints, dung, etc.) under the tree canopy as we placed the camera traps and counted fruit.

Appendix S5: Ex situ fruit aging trial
The 110 fruits we collected for ex situ trials were collected from 15 trees not used for camera trapping. We placed these fruits on a building rooftop (safe from elephants) on a bed of soil and dry leaves taken from the forest. The fruits were placed under netting to approximate the dappled sunlight experienced by many fruits on the dry season forest floor; however, the moisture content of the soil was likely less than that in a well shaded part of the forest. Fruits were checked every 1-2 days to note progression from stage 1 to stage 2 or from stage 2 to rotting. Stage 2 fruits were again distinguished from rotten fruits by their smell; the latter were opened to confirm rotting.

Results
Appendix S6: Camera trap and marked fruit data
While camera trapping we marked 1-356 fruit under each tree. We monitored 22,290 fruit-days, of which 1216 fruit-days resulted in disappearance of a fruit. Combining this data with our camera trap data, a few assumptions allow us to estimate the amount of marked fruit removed by the three frugivore groups. We assume that a) emptied fruits were the work of macaques and terrestrial rodents; b) terrestrial rodents were not capable of moving stage 1 fruits; c) when elephants or bovids left dung or fresh footprints around the tree they also consumed any missing chalta fruit, even if they failed to trip the camera trap; and d) otherwise, the animal species that triggered the camera were responsible for all the fruit that went missing in a day around a tree. In this case, 19.5% of the stage 1 fruits’ and 6.2% of the stage 2 fruits’ fates are still unaccounted for, as the fruits went missing without any animal triggering the camera trap or leaving any other
sign. Of the remaining, elephants were associated with the disappearance of 72.6% of stage 1 fruit and 10.6% of stage 2 fruit; bovids with 17.3% and 12.6%, respectfully; and small mammals with 10.0% and 76.8%. These estimates are more circumstantial than those obtained from the fruits removed from the camera traps and, perhaps as a result, paint a picture where elephants eat more stage 2 fruits and small animals more stage 1 fruits than is actually the case. Nonetheless, they indicate that the trend observed from the camera traps was probably not noticeably biased, with larger animals consuming hard stage 1 fruits and the smaller animals consuming the fruits that were left behind long enough to soften to stage 2.

Additionally, having triggered the camera, bovids were less likely than elephants to remove stage 1 fruits in front of the camera. Elephants removed at least one stage 1 fruit from the camera on 42 of 49 trigger events, while bovids removed at least one stage 1 fruit from the camera on only 16 of 28 trigger events (Fisher’s test, P=0.0063). In many cases bovids were photographed examining or attempting to eat the stage 1 fruit, but they were unable to, apparently because of the size and hardness of the chalta. On a couple occasions, an elephant later appeared and ate the fruit left by bovids. Very large adult bovids consumed fruits smaller individuals could not. Frugivores exhibited no preference in their removal of marked and unmarked fruit in front of the camera (Fisher’s test, P=0.4679).

**Appendix S7: Fruit penetrometer and hardness of fruits**

Frugivores removed a significantly larger proportion of fruits that were not tested for hardness than those that were tested (Fisher’s test, P=0.010). There is no readily apparent biological explanation for this; holes made by termites or other insects were common in fruits we did not test for hardness, so the appearance of a hole, if even noticeable to frugivores, was not unusual. Another possibility is that the fruit penetrometer changed the smell of the chalta fruits. While possible, it is unlikely; the penetrometer was used only on fruit and kept clean. We believe this probably happened by chance, and that since we randomly tested fruits for hardness this did not have an effect on our other results. Still, we suggest vigilance if this method is replicated.

**Appendix S8: Germination trial details:**
Both stage 1 and stage 2 seeds were planted in December and January, but only began germinating in May. Stage 1 fruit seeds took an average of 137.9 days (sd=8.12, range=122-186) to germinate, while stage 2 fruit seeds required an average of 136.5 days to germinate (sd=6.9, range=121-154)

Reference

Office of the Field Director, Buxa Tiger Reserve, Alipurduar.
CHAPTER 2:

Asian elephants are major frugivores of two tree species with easily edible fruit

AUTHORS: Nitin Sekar, Raman Sukumar.

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Abstract:
Large animal species are generally prone to local extirpation and extinction. Ecologists cannot predict the effects of such losses on ecosystems, even for conspicuous megaherbivores. Although megaherbivores are thought to be potent seed dispersers, few studies have compared the quantity and quality of seed dispersal by megaherbivores versus alternative frugivores in the wild, particularly for plant species with fruit that can be easily consumed by many frugivorous species. Working in a disturbed tropical moist forest in India, we examine the hypothesis that megaherbivores can be a major frugivore (removing more than 5% of fruits taken by animals) of two tree species with easily edible, mammal-dispersed fruit. We quantify the relative fruit removal rates of Artocarpus chaplasha and Careya arborea by Asian elephants (Elephas maximus) and alternative dispersers. Using focal watches and camera trapping, we find that elephants remove more fruit than most smaller and typically more abundant animal species, proving to be amongst the top three frugivores for both tree species. This suggests that megaherbivores may be key dispersers for a larger set of mammal-dispersed fruiting species than previously demonstrated. Furthermore, seed transects under A. chaplasha show that arboreal frugivores spit, throw, or drop seeds only a short distance from the parental tree, underscoring the qualitative importance of elephants as dispersers for this tree species. Since hunting of smaller frugivores is common in the region, elephants may be particularly important for the functional ecology of the disturbed forests they still inhabit across tropical Asia.

Keywords: Artocarpus chaplasha, Buxa Tiger Reserve, Careya arborea, disturbed ecosystems, frugivory, functional ecology, megafaunal fruit, seed dispersal.

Due in part to their lower population densities, low rates of reproduction, and the attention they attract from human hunters, larger animal species are generally more prone to local extirpation and extinction (Cardillo et al. 2005, Peres and Palcios 2007). Despite the growing evidence that the largest animal species in an ecosystem play unique functional roles (e.g., Owen-Smith 1988, Skarpe et al. 2004, Hansen and Galetti 2009), we cannot yet fully understand how their extirpation affects biodiversity and ecosystem function (Corlett 2013). This holds true even for the largest terrestrial animal species, megaherbivores—species weighing over 1000 kg, such as elephants and rhinoceroses (Owen-Smith 1988)—which receive substantial attention due to their charisma and/or cultural significance. Since their size gives megaherbivores
unusual ecological properties, such as the capacity for individuals to consume large amounts of food (Sukumar 2003, Dinerstein 2003), change the physical structure of their habitat (Skarpe et al. 2004), and move over large ranges (Sukumar 2003, Campos-Arceiz et al. 2008, Blake et al. 2009), theory suggests that the extirpation of megaherbivores would have notable effects on ecosystem processes. This may be especially true in systems where medium-sized species are also experiencing population declines (e.g., Blake et al. 2009). Research on whether the loss of megaherbivores leads to expected ecological effects allows us to strengthen our understanding of the resilience of natural systems in the face of modern ecological changes.

The role of megaherbivores in seed dispersal may be important for maintaining biodiversity (Campos-Arceiz and Blake 2011). Fruit make up a substantial part of the diet of some megaherbivore species (Campos-Arceiz and Blake 2011), and mammals such as elephants and rhinos can swallow and defecate even very large seeds whole (Chapman et al. 1992, Campos-Arceiz and Blake 2011). African and Asian elephants also tend to move over larger distances than most other frugivorous species, meaning they may be particularly useful for long-distance seed dispersal (Sukumar 2003, Campos-Arceiz et al. 2008, Blake et al. 2009). Such long-distance movement of seeds may be crucial in the increasingly fragmented natural habitat mosaics of the tropics (Kitamura et al. 2005).

While the available evidence for the functional uniqueness of megafauna as seed dispersers is strongly suggestive (e.g., Tchamba and Seme 1993, White et al. 1993, Dinerstein 2003, Blake et al. 2009), empirical data on the relative importance of megafauna as seed dispersers in natural settings is incomplete (Hawthorne and Parren 2000, Campos-Arceiz and Blake 2011). Megaherbivores’ unusual characteristics do not automatically make them functionally irreplaceable. One of the first steps in gauging the comparative dispersal effectiveness of various animal species is to measure the proportion of available fruit or seeds that is reliably handled by different frugivores (Jordano and Schupp 2000, Dennis and Westcott 2006). There are only a few studies that report the proportion of fruits that are removed by megaherbivores compared to other frugivores in the wild (Cochrane 2003, Sekar and Sukumar 2013). Such studies are necessary since evidence (e.g., Jansen et al. 2012) has emerged that our intuition about what seeds require megaherbivores for dispersal may be too simplistic. The studies on relative fruit removal that do exist have tended to focus on peculiar fruit, such as *Balanites wilsoniana*, which is too toxic for most species smaller than elephants to eat (Cochrane
2003), or *Dillenia indica*, which starts off too hard for most frugivores to consume (Sekar and Sukumar 2013). While such species illustrate the possible evolutionary advantages of dispersal by the largest frugivores, they are only part of the broader swathe of large, mammal-dispersed fruit for which megaherbivores may be particularly important dispersers. Many if not most of the fruits purportedly dispersed by megafauna are either smaller or softer and non-toxic (Janzen and Martin 1982, Kitamura et al. 2002); these fruit are accessible not only to megaherbivores but to smaller animals as well (Corlett 1998, Kitamura et al. 2002). Since these smaller animals are often arboreal and typically far more numerous than elephants and other megaherbivores, they may be able to consume most of the available fruit before megaherbivores even have a chance.

Are megaherbivores competitive enough as frugivores of widely edible fruits to be important for their dispersal? Or are megaherbivores solely important for the dispersal of more specialized species such as *D. indica* or *B. wilsoniana*? Despite the relatively low abundances of megaherbivores and their limited access to fruits in the canopy, the potentially unique advantages provided to mammal-dispersed plant species by megaherbivore dispersal may have selected for plants with characteristics that facilitate substantial (though non-exclusive) megaherbivore frugivory. In this study, we examine the hypothesis that megaherbivores are major frugivores of plant species with easily edible, mammal-dispersed fruits in their ecosystems. Since there is no straightforward link between the quantity of fruit removed by a species and its importance as a disperser (Jordano and Schupp 2000), we arbitrarily define a major frugivore as an animal species that is amongst the top five consumers of fruit and that removes at least 5% of the fruit handled by frugivores over one or multiple fruiting seasons. We assess the relative importance of Asian elephants in the frugivory of two tree species common in South Asian tropical forests, *Artocarpus chaplasha* and *Careya arborea*. *A. chaplasha* is a soft-fruited, wild relative of the jackfruit; *C. arborea* have smaller fruit resembling the domestic pear in hardness. In order to understand the relative importance of elephants and other frugivores as fruit removers and potential seed dispersers, we conducted (a) focal watches of frugivory in *Artocarpus chaplasha* and arboreal camera trapping of *Careya arborea* fruit to learn what percent of fruit are removed by which arboreal frugivores; and (b) camera trapping of fallen fruit to identify the proportion of these fruit removed by elephants and other frugivores. In addition, we also conducted seed transects to gauge how far seeds spit or thrown by arboreal frugivores were deposited from the tree crown. In sum, our research assesses whether elephants consume enough of the seeds of
species with easily edible fruit to be major players in their routine dispersal, even though such fruit are accessible to smaller, typically more abundant species. Such inquiry moves us one step closer to understanding how the loss of megaherbivores affects seed dispersal and ecosystem processes more generally.

METHODS

STUDY SPECIES—We selected two fruit species that were locally reported to be eaten by elephants and other mammals: Artocarpus chaplasha and Careya arborea. Both species were reported to fruit early in the monsoon season.

Artocarpus chaplasha (known in Nepali as the lator tree) is a large evergreen species in the Moraceae family ranging from the sub-Himalayan tracts of Nepal east through Myanmar and in the Andaman and Nicobar Islands (Sahni 1998). The dispersal of the lator’s 1.5cm seeds from its jackfruit-like fruit is not well-documented. Datta and Rawat (2008) write that lator is dispersed by hornbills and squirrels in Arunachal Pradesh, India, though the latter are typically seed predators. Sahni (1998) suggests birds and monkeys disperse the seeds.

Our second study species is Careya arborea (family Lecythidaceae), known as the kumbhi tree (Hindi, Bengali). The kumbhi is a deciduous tree ranging over much of the subcontinent with fruit resembling pears in hardness and 1.5-2cm seeds (Macnae and Fosberg 1981, Mabberley 1997). Sundarapandian et al. (2005) describes the kumbhi’s seeds as animal-dispersed, but without noting the potential dispersers. For measurements and further description of the study species, see Appendix S1.

STUDY AREA: BUXA TIGER RESERVE—Research was conducted from June-August of 2010-2012 in Buxa Tiger Reserve (henceforth Buxa), located in the northern part of the Indian state of West Bengal. The 761 km² reserve is situated 26°30’- 23°50’ N and 89°25’- 89°55’ E, mostly between 80-200 m asl. With an average annual rainfall of c. 4500 mm, the reserve is predominantly a tropical moist forest habitat (Sukumar et al. 2003). Lator trees are typically found in clumps in the southern, wetter portion of the reserve as part of the closed canopy. Kumbhi trees are scattered throughout Buxa but were more often found where the canopy was not entirely closed, such as alongside seasonal rivers and areas and former plantations.
Sukumar et al. (2003) and the 2010 Forest Department census estimated there to be 217 and 228 elephants, respectively, in Buxa (S. P. Chowdhury, pers. comm). Various other frugivorous mammal species inhabit Buxa, including chital deer (*Axis axis*), gaur (*Bos gaurus*), Himalayan crestless porcupines (*Hystrix brachyura*), Rhesus macaques (*Macaca mulatta*), common palm civets (*Paradoxurus hermaphroditus*), Malayan giant squirrel (*Ratufa bicolour*), sambar (*Rusa unicolor*), and wild boar (*Sus scrofa*). Domestic buffalo (*Bubalus bubalis*) and domestic cattle (*Bos primigenius*) are also often found in substantial numbers, sometimes penetrating deep into the reserve. Fruit bats have not been observed in Buxa for many years (Sekar pers. observation, N. P. Sharma, pers. comm.). Conspicuous frugivorous bird species in Buxa include the rose-ringed parakeet (*Psittacula krameri*), Oriental pied hornbill (*Anthracoceros albirostris*), and great hornbills (*Buceros bicornis*).

**Focal watches (lator)**—To determine whether elephants are major frugivores of the fruit of lator and kumbhi, the relative proportion of fruit consumed by both arboreal and terrestrial frugivores must be measured. Focal watches (n=39 at 19 trees, totaling 104 hours) were conducted to identify diurnal arboreal frugivores of the lator tree and (a) quantify the relative consumption of fruits of various arboreal species and (b) compare the proportion of fruit removed by arboreal frugivores to the proportion that fell to the ground. Focal watches covered the period from 5 AM to 7 PM about evenly. Methods followed Sekar and Sukumar (2013), though observations were always conducted from a vehicle due to safety concerns (see Appendix S2).

To estimate relative fruit removal rates by frugivores, focal watches were broken into five-minute sampling periods. At the beginning of each period, the number of individuals of each frugivorous animal species in the tree was counted. Then, one focal individual of each species whose activities were visible was observed for five minutes; there may have been bias towards moving (more detectable) individuals. The number of fruits consumed by each focal individual and the treatment of the seeds of the fruit were observed whenever possible.

We observed that individuals of a species tended towards different activities (e.g., eating versus resting) based on the time of day that the species visited the tree. We therefore estimated the number of fruits consumed by a group of frugivores of a given species X during a 5-minute period by multiplying the number of individuals of species X in the focal tree during that period
by the average number of fruits eaten per 5-minute interval by all the focal individuals from that
group over the course of that group’s visit to the focal tree. A visit was constituted by the
continuous occupation of a focal tree by individuals of species X with a gap of less than 10
minutes. Ultimately the sum of all fruits estimated to have been removed by species X over the
course of the focal watches was divided by the number of hours of focal watches (104) and
multiplied by 14 to provide an estimate of the average number of fruits removed by this species
from a typical lator tree each day (all observed frugivores were diurnal). Using each 5-minute
sampling period as the unit, a bias-corrected and accelerated confidence interval was constructed
for each species’ daily fruit removal estimate using nonparametric bootstrapping from the boot
package in R (Davison and Hinkley 1997, R Core Team 2013).

Similarly, fruit fall rates were estimated by noting the number of fruits seen or heard to
fall from the focal tree during each focal watch period. A daily fruit fall rate was calculated as
the sum of the expected diurnal fruit fall and nocturnal fruit fall. Diurnal fruit fall was estimated
using all the data from the focal watches; nocturnal fruit fall (which assumed no nighttime
frugivore activity) was calculated by excluding the data when animals were in the focal tree. For
both estimates, confidence intervals were calculated using bootstrapping as above.

ARBOREAL CAMERA TRAPPING (KUMBHI)—Focal watches were not possible with kumbhi trees
(see Appendix S2). In order to measure relative arboreal fruit removal and fruit fall rates,
Reconyx camera traps were used to monitor 63 fruit in the canopies of 8 trees; each tree hosted a
camera trap for 6-7 days. More data could not be collected due to time limitations and the risks
of climbing the kumbhi trees when they were wet. The ratio of the number of fruit that fell to the
ground to the number that were removed by arboreal frugivores give us an estimate of the
proportion of fruits that become available to elephants and other terrestrial dispersers.

TERRESTRIAL CAMERA TRAPPING AND FRUIT COUNTS—The next step in gauging whether
elephants are major dispersers of lator and kumbhi was to measure the proportion of fallen fruit
removed by each terrestrial frugivore species. Camera trapping and counts of fruits on the
ground were conducted to identify the terrestrial frugivores of both lator and kumbhi fruits
(Prasad et al. 2010, Sekar and Sukumar 2013). Individual trees were found during searches in
June and November of 2010. Four trees at a time were selected randomly for camera trapping; a
nearby tree was chosen to substitute for randomly chosen trees that had less than half a fruit on the ground. Trees too close to villages or made inaccessible by swollen rivers were excluded. Over two seasons, camera trapping was conducted at 37 lator and 14 kumbhi trees.

At each tree, fruits and partial fruits were counted separately and marked by making 3 holes in a fruit with a sharp piece of bamboo. Rotten fruit were counted when time permitted. Between 0.5 and 5.5 lator fruit (mean=2.4 fruit, with all partial fruits counted as 0.5 fruit) and between 1 and 10 kumbhi fruit (mean=4.5 fruit) were placed in front of the camera trap such that they resembled the number of fruit found naturally clumped together under the tree. During the first season, we subjectively noted when lator fruit we had placed in front of the camera trap appeared to have spoiled, either by rotting or being immersed in mud from the monsoon; for kumbhi fruit, proportion of fruits rotting was not easy to observe or quantify.

We estimated the relative amount of fruit taken by each frugivore species by dividing the total number of fruit each frugivore species removed from the cameras by the total number of fruit-days monitored. This calculation provided the average proportion of fruit removed from the ground per day by each animal species (Sekar and Sukumar 2013). We again used nonparametric bootstrapping to estimate confidence intervals for these estimates.

Our experience suggested that elephants may be more likely to visit a tree when there were more fruit on the ground; we used the Mann-Whitney Test in R to compare the median numbers of marked fruit available when different frugivores triggered the trap to attain evidence of whether such a bias may be occurring (for more, see Appendix S3).

SEED TRANSECTS (FOR LATOR)—While our hypothesis deals with the quantity of fruit removed by elephants and other frugivores, information on the quality of dispersal of seeds spat or dropped (i.e., discarded) by arboreal frugivores further contextualize our findings on the relative importance of megaherbivores as potential dispersers of large but easily edible fruits. Seed transects were conducted from the base of lator trees to estimate the distances to which arboreal frugivores discarded lator seeds (McConkey and Brockelman 2011), allowing a cursory comparison between this type of seed dispersal and the endozoochory that may be provided by larger, terrestrial dispersers. We found two isolated lator trees and one row of seven lator trees running north to south in the multiple use zone in Buxa. Four two-meter wide transects were constructed from each tree, with transects extending 40 m north, south, east, and west from the
base of the tree (for the group of trees, a transect was constructed north from the northernmost tree, east from the central tree, etc.). Each transect was divided into eight 5-m segments. Transects were walked daily for eight days, and the number of loose seeds and seeds attached to fruit parts were counted; feces with seeds in them were also noted. Seed counts were used to calculate the number of seeds per unit area for concentric circles around the tree. A mixed effects model with random effects for each transect sampled and the day of sampling was constructed to predict the proportion of dispersed seeds (seed densities) based on distance from the base of the tree; the observed seed densities were modeled as following a log-normal distribution. JAGS 3.3 (Plummer 2003) was used to fit the Bayesian model and the R2jags package (Su and Yajima 2012) was used to call JAGS from R (see Appendix S4).

RESULTS
FOCAL WATCHES (LATOR)—Over the 104 hours of focal watches conducted, one species, the Rhesus macaque, dominated the removal of fruit from the canopy of A. chaplasha. Fig. 1 shows that macaques removed about 62.0 fruit per day (assuming no activity at night) per tree, about 9 times more than the fruit removed by the rose-ringed parakeet (and another unidentified bird species) and more than twice as much fruit as fell from the canopy. Macaques frequently roosted in lator trees overnight; macaques appeared to monitor the fruit in some trees until they were ripe and to remove them before other frugivores (such as Malayan giant squirrels) could reach them.

Rose-ringed parakeets were the other main species observed consuming lator fruit. They were observed toward the end of both fruiting seasons, presumably when the fruits were softest. One other bird species—possibly the scarlet minivet, Pericrocotus ethologus—made a brief (~5 minute) appearance to consume some fruit during one focal watch towards the end of the fruiting season, indicating that our focal watches have not exhaustively identified the minor arboreal frugivores of A. chaplasha. Collectively, birds were estimated to remove 7.0 fruit per day. No other species were seen eating lator fruit, even early in the morning (5 AM onwards) or late in the evening (up to 7:15 PM).

While the parakeets and other birds clearly appeared to consume the pulp and discard the seeds of lator fruit one-by-one, macaque treatment of seeds was more complicated. Macaques appeared to discard the vast majority of lator seeds, usually close to where they plucked the fruit but sometimes after having moved to a nearby tree. Four of the focal macaques (in 5.6% of scans
FIGURE 1: Rates of fruit removal and fruit fall from lator trees, estimated using data from focal watches. The standard error bars shown were constructed using nonparametric bootstrapping. Rhesus macaques remove the majority of fruit from the canopy; about a ninth as much is consumed by birds, especially the rose-ringed parakeet, and about half as many fruits fall to the ground for terrestrial frugivores. Removal by macaques remains mostly steady between years, whereas a substantial increase in removal by birds and the amount of fruit fall was observed in 2012, suggesting interannual variation in fruit production or frugivore activity. Note that these rates mostly apply to trees that have large numbers of ripe fruit in the canopy. Rates of fruit removal and fruit fall are lower when there are few ripe fruit in the canopy, and when most fruit have been removed (see Appendix S4).
in which macaque handling of fruit was observable) appeared to consume the fruit without discarding the seeds; the monkeys may have chewed the seeds or swallowed them whole. The focal macaques that did not discard the seeds were all adult individuals; at least two were large adult males.

By jumping on and shaking branches, and by discarding fruit that was not yet ripe, macaques appeared to promote fruit fall while the fruit were not yet too soft to survive the descent. We found that fruit fell at a rate of about 1.64 fruit per hour per tree (our calculated diurnal rate, effective for 14 hours a day), but once we excluded the times when animals were in the canopy, the data suggested a fruit fall rate of just 0.46 fruit per hour per tree (the nocturnal rate, which assumed minimal animal activity at night). Overall, we estimated that some 27.6 lator fruit were falling from the crown per day.

**Arboreal Camera Trapping (Kumbhi)**—Of the 63 kumbhi fruit monitored in 8 trees for about a week each (408 fruit-days), 26 fruit fell and 4 were removed by an apparent frugivore (the Malayan giant squirrel). A common palm civet and an unknown animal were also caught on camera in the kumbhi canopy, but they did not remove any of the monitored fruit. These limited data suggest that arboreal frugivory of kumbhi fruit does occur, but that most fruit likely fall to the ground. In one instance, terrestrial camera trap photos suggested that an elephant may have shaken the tree to induce fruit fall.

**Terrestrial Camera Trap and Marked Fruit Data**—Camera traps monitored 37 lator trees, 127 tree-days and 307 fruit-days over the fruiting seasons in 2010 and 2011. Over this time, 78.5 lator fruits were removed from the view of the camera traps (all partial fruit were considered 0.5 fruits): 42.0% by elephants, 38.5% by Rhesus macaques, 10.2% by domestic bovids (buffalo and cattle), 5.7% by wild boar, 1.9% by common palm civets, and 1.3% by porcupines (see Fig. 2a). Numerous other species, particularly small rodents and mongooses, were caught by the camera multiple times; sambar deer, which were usually caught on camera ignoring the fruit, appeared to nibble at a fruit on one occasion. Lator fruit was often found splattered on the ground or in pieces, and seeds were accessible to rodents and perhaps dispersal by water; removal by these vectors was not quantified. Over the monitored period, 24.6% of monitored fruit rotted and 75.4% were removed by frugivores (N=71).
FIGURE 2: a) The proportion of lator and kumbhi fruit removed by each frugivore per day from the forest floor. Estimates were calculated by tallying all the fruit removed from camera traps by a frugivore group during the 2010-11 fruiting seasons and dividing that by the number of fruit-days monitored. Error bars indicate the standard errors, which were calculated using nonparametric bootstrapping; standard errors are large because fruit removal was a rare event. Wild boar, porcupines, and civets removed each fruit of each species from the camera traps only 1-2 times. b) The number of marked lator fruits that went missing from under a tree when a given frugivore triggered the camera trap at that tree. It is speculative to suggest that all the fruit that disappeared were removed by the animal triggering the trap—note that sambhar deer were
never caught eating more than a tiny portion of a lator fruit on camera, and even when no animal triggered the trap, many fruit often disappeared. However, it is clear that elephants, which are known lator consumers, are associated with larger disappearances of fruit than the other frugivores.
Between 0.5 and 66 lator fruits were marked underneath each tree on a given day (mean=10.5 fruit, sd=10.4, n=127). We found an average of 3.5 rotten fruit (sd=7.0, max=41, n=36) and an average of 2.65 new fruit under each tree each day (sd=3.26, max=18, mode=0, n=126) (see Appendix S5 on why this fruit fall rate calculation differs from that made during focal watches). Note that since most trees were visited multiple times, these do not constitute independent samples. As many as 54 fruit went missing over the course of any one day. We calculated the number of marked fruit to go missing when a frugivore of a given species triggered the trap (see Fig. 2b); elephants were associated with the disappearance of large amounts of fruit.

The number of fruit marked under the tree was greater when elephants were caught on camera than when they were not (W=1081, p=0.013, N=117), and the number of marked fruits on the ground was greater when elephants triggered the trap than when macaques did so (W=168.5, p=0.026, N=31). For how this affects our calculations above, see Appendix S3.

Due to the scarcity of accessible, fruiting kumbhi trees, camera traps monitored only 63 tree-days and 283 fruit-days at 14 trees over two fruiting seasons. Over this time, 31.5 fruit were removed from the camera traps, of which 60.3% were removed by domestic bovids (cattle), 22.2% by elephants, 9.5% by wild boar, 3.2% by civets, 3.2% by porcupines, and 1.6% by macaques (see Fig. 2a). Kumbhi fruit were also found floating in monsoon flood water, suggesting dispersal can be aided by the monsoons. Wild boar and macaques appeared to chew the fruit and leave the remnants there; they and the civet caught on camera left at least some of the seeds from the fruit they consumed. While we were not able to quantify the proportion of fruit that rotted, we observed dramatic variation among kumbhi trees, with some (on trails frequented by bovids) having not a rotten fruit beneath them, and others with hundreds.

Between 1 and 234 fruit were marked under each kumbhi tree we visited (mean=32.0, sd=43.3, n=63). Excluding one outlier (628), an average of 5.9 rotten fruit (sd=13.2, max=45, min=0, n=25) were found under each kumbhi tree a day. These averages include multiple counts from the same trees.

SEED TRANSECTS—The vast majority (99.7%) of seeds found on our 40m seed transects were calculated to be within the first 20 meters of the base of the tree. Fig. 3A shows the mixed effects
FIGURE 3: (a) The predicted lognormal densities of lator seeds dispersed by spitting, dropping, or throwing along each of the 12 individual transects from the study. The median of the posterior distribution of the population average (typical) lognormal density is also shown. Despite notable variation amongst the transects, long-distance dispersal by spitting, dropping, or throwing appears to be unlikely. (b) The probability that a seed will be dispersed x meters from the tree, predicted using a survivor function at 10m increments for each of the 12 transects in the study. The black horizontal line segments indicate the point estimates, while the 95% credible confidence intervals are shown. Probability is shown on a log scale. (Figure by Jack Weiss).
lognormal distributions fit to the 12 seed transects. As indicated in Fig. 3B, the probability of a seed being spit or thrown more than 100m from the tree base on any of the transects is less than 1 in a million. Given the large volume of seeds discarded by macaques, this non-routine, medium-distance dispersal may still affect a substantial number of lator seeds. In addition, four macaque feces containing a total of 12 lator seeds were discovered during transects.

**DISCUSSION**

*Elephas maximus* is a major frugivore even for the soft and easily edible fruits of *Artocarpus chaplasha* and *Careya arborea* (see Fig. 4). Excluding fruit that rots, elephants eat around 9.7% of the lator fruit and about 18.4% of kumbhi fruit removed by frugivores. This makes elephants one of the three most substantial frugivores (and potential dispersers) of each of these species in Buxa. Our field study provides empirical evidence that Asian elephants compete well enough with smaller frugivores to be quantitatively valuable for the dispersal of species not specialized for megaherbivore frugivory, particularly in today’s disturbed ecosystems.

As expected, elephants did not exhibit the same dominance as consumers of lator or kumbhi as they had among consumers of species previously studied. Asian elephants removed 63.3% of the *Dillenia indica* fruit taken from camera traps (Sekar and Sukumar 2013); African savanna elephants (*Loxodonta africana*) removed some 26.3% of the potentially toxic *Balanites wilsoniana* fruit available (Cochrane 2003). Our findings are in keeping with Kitamura et al.’s (2002) observation that while large-seeded fruits may have few dispersers, soft fruit with medium or small seeds are widely consumed, regardless of fruit size. Yet despite the greater accessibility of lator and kumbhi to smaller, typically more abundant frugivores, elephants still removed enough of the available fruit to be major contributors to these species’ routine dispersal.

A prominent role for megaherbivores in the dispersal of a widely edible fruit is made possible by several factors. First, a tree species’ ecology may ensure that enough fruits fall to the ground intact to enable dispersal by large terrestrial mammals. Both lator and kumbhi trees produce fruit with seeds embedded in the pulp of fruit too large to be readily manipulated by birds. Though macaques could handle lator fruit, they still induced substantial fruit fall while fruits were still firm and dropped partially eaten fruits, facilitating terrestrial frugivory (as found in other systems, e.g. Prasad and Sukumar 2010). Secondly, our results indicate that, despite their low abundances, megaherbivores may be adapted to successfully compete for fallen fruit.
FIGURE 4: A summary of our findings on the frugivory of lator (Artocarpus chaplasha, red arrows on left) and kumbhi (Careya arborea, green arrows on right) in Buxa Tiger Reserve. The numbers indicate the proportion of the fruit from the canopy that follow each path. Dotted and dashed lines indicate preliminary assessments made on very limited data; questions marks indicate links for which we have anecdotal evidence but no measurements. For lator, Rhesus macaques are the main consumer of fruits, especially in the canopy. For kumbhi, a tree largely found in plantations and away from the late-successional core area, domestic bovids removed the most fruit; due to lack of data, lator’s rate of fruit rot was used. Elephants are amongst the top three frugivores for both fruits in quantity, but the quality of their dispersal may surpass bovids and macaques, particularly since the latter discards so many seeds under the canopy of the parent tree. Malay giant squirrels, rose-ringed parakeets (photo credit: http://www.flickr.com), wild boar, common palm civets, and Himalayan crestless porcupines proved to be more minor frugivores of lator and kumbhi.
Elephants’ wide-ranging habits, likely combined with their memory of the location of food sources, and large appetites may help them compensate for their low abundances (Campos-Arceiz and Blake 2011). Cochrane (2003), for instance, found that elephants visited 46% of *B. wilsoniana* trees in time to consume some of their fruit before their seeds were destroyed by bush pigs. We also found that the median number of lator fruit available was higher when elephants visited trees than when they did not, suggesting that elephants may be able to sniff out trees at the key moments when many fruit are available for consumption. Finally, the frugivore community of Buxa has likely been affected by poaching and other disturbances. Despite the numerous animal species that found lator and kumbhi fruit palatable, most frugivores were only captured removing fruit on camera 1-3 times. Rotting fruit were a regular occurrence, suggesting that Buxa’s frugivore community’s ability to absorb fruit was saturated. The Asian elephant’s cultural status in India (Sukumar 2003) may protect it somewhat from the hunting that locals claim has decimated populations of flying foxes, wild boar, Himalayan crestless porcupines, and other frugivores, accentuating the relative importance of elephants as seed dispersers in Buxa. Since disturbed forests like Buxa are the norm across elephant habitats in south and southeast Asia (Corlett 2009), our results may indicate that megaherbivores are even more quantitatively important as dispersers in today’s forests than previously.

This quantitative importance of Asian elephants as dispersers of lator and kumbhi is compounded by their likely qualitative superiority. Our focal watch data indicate that a large majority of lator seeds handled by macaques and birds are discarded instead of swallowed, and our seed transects indicate that less than one in a million discarded seeds is taken more than 100m. Since macaques handle such tremendous volumes of fruit, even occasional dispersal due to postponed spitting (Corlett and Lucas 1990) or endozoochory by larger individuals (Stevenson et al. 2005)—both of which we documented here—is likely to be ecologically consequential. Still, macaque and elephant dispersal of lator and kumbhi seeds are likely to complement each other spatially, much as found for *Prunus javanica* dispersal by gibbons and macaques (McConkey and Brockelman 2011). Of the other frugivores documented in our study, wild pigs, Himalayan crestless porcupines, and giant squirrels are more often described as seed predators than as dispersers (Kitamura et al. 2004, Kitamura et al. 2006, Kitamura et al. 2007, Corlett 2007). Further work on macaques, civets, wild boar, and domestic bovids will help us better understand the extent to which these alternative dispersers may be able to fill in for
megaherbivores as dispersers. Since domestic bovids are terrestrial, large, likely to swallow seeds, move over substantial areas daily, and are omnipresent in South Asia, their ability to compensate for elephants as dispersers requires direct examination.

CONCLUSION—While our study has notable limitations (see Appendix S6), we provide empirical substantiation for the claim that megaherbivores play a crucial functional role as tropical seed dispersers of species with easily edible fruit. Prior research has classified such large, soft fruits as reliant on megafauna for dispersal (Janzen and Martin 1982, Guimaraes et al. 2008, Blake et al. 2009); demonstrated that wild megaherbivore dung contains their seeds (Tchamba and Seme 1993, Dinerstein 2003); and described the qualitative advantages of megaherbivore seed dispersal (Campos-Arceiz and Blake 2011). Our research acts as a proof of concept, demonstrating that megaherbivores can competitively remove enough such fruit to be considered key dispersers, especially in a disturbed forest system. We also find that smaller species may complement the role of elephants, and that, in Buxa and perhaps many other disturbed forests across South Asia, disturbance-resilient primates and domestic bovids should be examined as likely potential functional replacements for megaherbivores as seed dispersers.

Acknowledgments

We thank the West Bengal Forest Department for permissions to carry out this research in Buxa Tiger Reserve and for their support in the field. Dr. Jack M. Weiss contributed the nonlinear mixed effects model for the seed transects. Dr. Henry Horn provided useful comments. Dr. Andrew Dobson, Dr. Soumya Prasad, Dr. Ahimsa Campos-Arceiz, Dr. Kim McConkey, Dr. Andre Pittet, Dr. Dan Rubenstein, and Dr. David Wilcove provided support and input on the methods. Mr. Netra Prasad Sharma and Mr. Lachu Tim Sina served crucially as field assistants and local guides. N.S. is a National Science Foundation Graduate Research Fellow. This research also received support from the Denver Zoological Foundation, Inc, and the World Wildlife Fund’s Asian Rhino and Elephant Action Strategy Program.

Literature Cited


Appendix S1: Further description of the tree study species
The lator tree (*Artocarpus chaplasha*) is a congener of the jackfruit (*Artocarpus heterophylla*) and breadfruit (*Artocarpus altilis*); its fruit are smaller than the domestic jackfruit, with orange, sour pulp and seeds around 1.5 cm long, but otherwise superficially similar (Sahni 1998). We were informed that local people seldom eat the lator fruit but often cook and eat its seeds (N. P. Sharma, pers. comm., L. Tim Sina, pers. comm.).

Lator fruit were collected by climbing several trees and felling firm, almost ripe fruit. Lator removed from 12 trees averaged 466g in mass (sd=106.3g, range=101-1083g, n=343 fruit); 9.6 cm in length top to bottom (sd=1.5cm, range=5.4-15.0cm, n=259 fruit); and 9.3 cm in width (sd=1.3cm, range=5.7-12.9cm, n=259 fruit). For the 80 fruits we opened, we found an average of 50.9 lator seeds per fruit (sd=25.6, range=8-127 seeds).

The kumbhi tree is known as the slow match tree in English. Campos-Arceiz et al. (2008b), working in Myanmar, confirms that camp elephants consume the fruit, as well as bark and twigs, of the tree. Mabberley (1997) notes that *C. arborea*’s seeds are edible by people as well.

Kumbhi fruit (removed from 11 trees) averaged 112.8g in mass (sd=59.5g, range=29-741g, n=401 fruit); 6.8cm in length (sd=1.1cm, range=3.7-12.6cm, n=401 fruit); and 5.7cm in width (sd=8.5cm, range=3.7-12.0cm, n=401 fruit). Kumbhi fruits also varied dramatically in number of seeds, with anywhere from 0 to 42 seeds (mean=6.0 seeds, sd=6.0 seeds, n=116 fruit).

Appendix S2: Safety concerns during focal watches
Focal watches for lator were conducted from a vehicle instead of the ground, as in Sekar and Sukumar (2013), because the present study was conducted during the monsoon. Poor visibility (due to vegetation) and audibility (due to insects) made it too risky to sit on the ground away from the vehicle, as the sudden appearance of elephants could be life-threatening. During focal watches, the vehicle was typically covered by green netting to avoid disturbing any frugivores, especially when the vehicle was parked less than 35m from the trunk of the tree.
For similar reasons, focal watches could not be conducted from the ground for kumbhi trees. Kumbhi trees are far shorter than lator trees, so frugivores in the tree would be more wary of observers in a vehicle, which would typically be closer to them.

**Appendix S3: Bias in camera trap estimation of proportion of fruit removed by terrestrial frugivores:**

Camera trapping was used to determine the proportion of fruit consumed by different terrestrial frugivores. Since clumps of fruit were usually less than 5 in nature for lator, we never put more than 5.5 lator fruit in front of a camera trap at a time; in fact, clumps in front of the camera trap never exceeded by more than one the largest clump found under the tree being camera trapped. Otherwise, we were afraid that we may systematically attract frugivores that sought out unnaturally large clumps of fruit.

The problem with this is that the variation in the proportion of fruit removed from the camera trap could not capture the variation in the number of fruits removed from under the tree. Camera traps had between 0.5 and 5.5 fruit in front of them—the maximum was 11 times the minimum. Whereas there were between 0.5 and 66 fruit under a tree at any one time—the maximum is 132 times the minimum.

This is not a problem as long as a frugivore species’ probability of visiting a tree does not vary with the number of fruit available under the tree. But what if a megaherbivore frugivore is more likely to visit a tree if there are lots of yummy fruits on the ground, and megaherbivores systematically removes a higher proportion of the available fruit than the other frugivores? In such a case, camera traps may underestimate the difference in the proportion of fruits removed by the megaherbivore and smaller frugivores.

The paper presents some evidence that this happened with lator fruit (due to small sample sizes, we would be unlikely to detect such an effect for kumbhi). The median number of marked fruit on the ground was greater when elephants triggered the camera trap than when elephants did not trigger the trap ($W=1081$, $p=0.013$, $N=117$) or than when macaques triggered the trap ($W=168.5$, $p=0.026$, $N=31$). This suggests that elephants were more likely to be attracted to a lator tree when fruit were available for consumption, perhaps due to the smell of the fallen fruit. Furthermore, Figure 2B in the main text shows that the absolute numbers of marked lator fruit to
go missing when elephants triggered the camera trap far exceeded the numbers to go missing when macaques triggered the trap, though the median number of fruits to go missing for elephants is only about two times that of macaques’. While this evidence is not conclusive, it suggests that our methods may conservatively estimate the relative importance of elephants as terrestrial frugivores of lator as shown in Figure 2A.

A test of whether marking the fruits caused bias found no result. No statistically significant difference was found between the proportion of marked and unmarked lator fruit removed from the camera trap on days when fruit were removed (Fisher’s exact test, p=0.45, n=31). Similarly, there was no difference in the removal of marked or unmarked kumbhi fruit (Fisher’s exact test, p=0.16, n=36).

**Appendix S4: Fitting a nonlinear mixed effects model to transects**

Our objective was to develop a model that described how the proportion of seeds dispersed by spitting, throwing, or dropping by macaques and other arboreal frugivores (hereforth “discarded seeds” or “seeds”) varied with distance from the base of the tree. Seed transect data was used to estimate how far spit and dropped seeds were dispersed by arboreal frugivores. Since the 40-m by 2m transects sampled smaller and smaller proportions of the areas examined (e.g., the first 5m by 2m section covered a larger proportion of the smaller circle wedge it sampled than the last 5m by 2m section), the number of seeds found in each segment of the transect was weighted by the inverse of the proportion of the wedge-shaped area being sampled by that transect segment. These weighted seeds were then plotted against the distance of the mid-point of each transect from the base of the tree. We observed that the distribution of seeds from the base of the tree resembled a log-normal distribution, which has been used to describe seed shadows previously (Russo 2006). However, our sampling strategy necessitated that we account for lack of independence in our seed transect data. We sampled repeatedly from the same 12 transects for 8 days in a row, much as done by McConkey and Brockelman (2011). Furthermore, the 12 transects came from 3 trees or groups of trees. This means that one may expect both spatial correlation amongst transects from the same tree and correlation amongst distributions of discarded seeds taken from the same transect on different days.
In order to account for this structure and lack of independence, Dr. Jack Weiss helped us construct a model that used random effects to link observations from the same transect and transects from the same tree. It took the following form:

\[ y_{ij} = \text{dlnorm}(x_{ij}, a_{jk}, b_j) + \epsilon_{ij} \]

\[ = \frac{1}{\sqrt{2\pi b_j x_{ij}}} \exp \left( -\frac{(\log x_{ij} - a_{jk})^2}{2b_j^2} \right) + \epsilon_{ij} \]  

(1)

where

\[ a_{jk} = \mu_a + v_{0j} + v_{1k} \]
\[ \log b_j = \mu_{\log b} + u_{0j} \]
\[ v_{0j} \sim \text{Normal}(0, \sigma_{a1}) \]
\[ v_{1k} \sim \text{Normal}(0, \sigma_{a2}) \]
\[ u_{0j} \sim \text{Normal}(0, \sigma_{b1}) \]
\[ \epsilon_{ij} \sim \text{Normal}(0, \sigma_y) \]

In which \( a_{jk} \) and \( b_j \) are the mean and standard deviation of the log distances. Here \( j \) denotes an individual temporal transect (level 2), \( j = 1 \) to 96, while \( k \) is the spatial transect (level 3), \( k = 1 \) to 12. \( v_{0j}, v_{1k}, \) and \( u_{0j} \) are random effects, and \( \epsilon_{ij} \) is the error term. Because standard deviations are non-negative the \( b_j \) are assumed to be drawn from a lognormal distribution.

These models could be successfully parameterized using the nlme or lme4 packages of R; nonlinear mixed effects models can be difficult to estimate using a frequentist perspective. Dr. Weiss thus switched to a Bayesian approach, using Markov chain Monte Carlo simulations to obtain samples from each parameter’s posterior distribution. He used JAGS 3.3 (Plummer 2003) to fit the Bayesian model and the R2jags package (Su and Yajima 2012) to call JAGS from R. It took 60,000 iterations to obtain well-behaved solutions. The Rhat values on the final run were all less than 1.1, indicating good mixing of the chains, and the effective sample sizes (n.eff) were all fairly large. Two models were fit: one that included the random transect random effects \( v_{1k} \) (a three-level model) and one that did not (a two-level model). The three-level model addresses the repeated measures aspect of the data while the two-level model ignores it. Using DIC we find the three-level model to be preferable to the two-level model.
Table S1 lists the point estimates (medians of posterior distributions) and 95% credible intervals for the major parameters in these two models. $\mu_b$ is the exponential of the posterior distribution of $\mu_{\text{log} b}$.

**Table S1: Percentiles of the posterior distributions of the nonlinear mixed effects model parameters as estimated by MCMC sampling.**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Percentiles of posterior distributions</th>
<th>Two-level model</th>
<th>Three-level model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50%</td>
<td>2.5%</td>
<td>97.5%</td>
</tr>
<tr>
<td>$\mu_b$</td>
<td>0.4648</td>
<td>0.4432</td>
<td>0.4878</td>
</tr>
<tr>
<td>$\mu_a$</td>
<td>1.8528</td>
<td>1.8051</td>
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</tr>
<tr>
<td>$\sigma_{a1}$</td>
<td>0.2302</td>
<td>0.1988</td>
<td>0.2694</td>
</tr>
<tr>
<td>$\sigma_{a2}$</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>$\sigma_{b1}$</td>
<td>0.1926</td>
<td>0.1535</td>
<td>0.2392</td>
</tr>
<tr>
<td>$\sigma_y$</td>
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<td>0.0090</td>
<td>0.0101</td>
</tr>
<tr>
<td>DIC</td>
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<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

The point estimates of the two lognormal parameters are nearly identical under the two models. The primary difference is that the 95% credible interval for the mean parameter, $\mu_a$, from the three-level model is wider than the comparable 95% credible interval from the two-level model. This is to be expected given that the three-level model accounts for the lack of independence of measurements made on the same transects obtained repeatedly over time. Fig. S1 shows point and interval estimates of the lognormal density from the three-level model for the typical (population average) temporal transect obtained by setting the random effects to zero. Figure 3a in the text portrays the same model, but shows the predicted densities for the 12
**Fig. S1** Point estimates (medians of the posterior distributions) and 95% credible bands for the lognormal density of seed dispersal on the typical temporal transect.
Fig. S2  Predicted lognormal density superimposed on the empirical density for 16 selected (temporal) transects. In each curve point estimates of the lognormal parameters are the medians of their posterior distributions. The temporal transect curve estimate includes predictions of all three random effects. The spatial transect curve estimate includes predictions of the level-3 (spatial transect level) random effects but both level-2 random effects are set equal to zero. In the population-average transect curve estimate all of the random effects are set equal to zero.

transects instead of the 95% confidence intervals. Both figures indicate that the proportion of seeds dispersed beyond 40 meters will be quite small. Figure 3b in the text indicates that the probability of dispersal of discarded seeds beyond 100m is less than 1 in a million.

As a check on the fit of the model, Dr. Weiss constructed Fig. S2, which displays the predicted lognormal densities superimposed on top of the empirical densities for selected temporal transects. The population-average curve is the typical curve obtained by setting all three random effects equal to zero. The spatial transect curve adds to the parameter of the population-average curve predictions of the level-3 random effects ($v_{1k}$). The temporal transect curve includes predictions of the level-2 and level-3 random effects. The spatial transect curves are random deviations about the population-average curve. The temporal transect curves are random deviations about their corresponding spatial transect curves. The figure demonstrates the adequacy of our model in describing dispersal of discarded seeds of *Artocarpus chaplasha*.

Appendix S5: Inconsistency in fruit fall rate estimations

There is a large difference in how many fruit we observed falling from trees during focal watches (we calculated about 28 a day) and how many newly fallen fruit we observed on the ground (an average of 2.7 daily). This difference may be attributed mainly to how the trees for focal watches and the trees for camera trapping were selected—namely, we were biased in favor of trees with more fruit in their canopy for focal watches, but not for camera trapping.

Fruiting lator trees seem to go through a (first) long stage when the fruit in the canopy are green and unripe, but a few fruit have ripened; then a (middle) stage of relatively rapid ripening, when many of the fruit are becoming attractive to frugivores and fall more rapidly; and then a long tail stage when the few remaining fruit ripen and fall. For camera trapping, trees were
chosen essentially randomly from amongst lator trees identified during searches conducted prior to camera trapping; trees could be in any of these stages. We adhered to this method so long as even half a lator fruit was available on the ground under the canopy of the selected tree; if not, the nearest available lator tree was then examined, and so on until a tree with fruit on the ground was found.

In contrast, for focal watches, trees were mostly selected opportunistically such that they were en route to or near trees where camera trapping was being conducted, though we stratified to ensure that trees from all parts of the reserve were sampled at all periods of the day. Since it was difficult to observe frugivore treatment of fruit if the fruits were not visible from whatever vantage point was available from our vehicle, we chose mostly middle-stage lator trees with a substantial number of ripe fruit visible in the canopy—we believe this led to a bias in the observed fruit fall rate.

We have some evidence that these biases explain the discrepancy. At the beginning and end of each focal watch or camera trapping session, the number of fruits visible in the canopy was counted using binoculars and the approximate percent of the canopy visible was estimated visually. Counts at the same tree on the same day were found to vary considerably based on lighting, weather, and the ripeness of the fruit; thus, they were not used to calculate fruit fall rates. However, since the same approach was used for both focal watch trees and camera trap trees, this gives us an opportunity to compare the approximate number of fruit in each.

A Mann-Whitney test in R (R Core Team 2012) was used to compare the estimated number of fruit in the canopies of focal trees and camera trap trees. The median estimate for the number of lator fruit in the canopy of focal trees was 215 fruit (mean=327.2, sd=335.0, range=10-1316.7, n=39). We estimated that a median of 62.5 fruit (mean=149.1, sd=256.4, range=0-1492, n=59) were in the canopy of the trees under which we conducted camera trapping. The number of fruit in the canopy of focal watch trees was significantly greater than the number in camera trap trees (W=1652, p<0.001).

In addition, there may have been temporal variation in fruiting loads that contributed to this result, since camera trapping was conducted 2010-2011 and focal watches from 2011-2012. As Figure 1 shows, we also found a substantially larger fruit fall rate in 2012 (36.55 fruit/day) than in 2011 (14.67 fruit/day); the same is true for bird frugivory. There were more fruit in the canopies of the focal watch trees in 2012 (mean=362.5, sd=319.9, median=275) than in 2011.
(mean=299.9, sd=351.1, median=151.3). Though they were not significantly different statistically (W=220.5, p=0.175), it is possible that greater fruit availability in 2012 saturated the macaque population’s appetite, allowing for greater fruitfall in 2012 than 2011.

There are other possibilities, too. Perhaps we overestimated fruit fall during focal watches because we mistook other falling objects in the windy jungle to be fruit; even just a handful of such mistakes could propagate through our estimate. When macaques knocked down fruits, it is possible that their companions often removed those fruit from the ground soon afterwards such that they would not be available to count when we came to check the camera trap. Still, the bias in the number of fruit available in the canopy is, in our opinion, likely the best explanation for the discrepancy in fruit fall rate.

What does this bias mean for our findings? Since estimating the relative proportion of fruits experiencing each fate is our central objective, the question is whether proportions of fruit removed by different frugivores vary based on the number of fruit available. Focal watches occurred when most fruit were in play for frugivory—did camera trapping fail to capture the main dynamics of fruit removal by including too many trees with few ripe fruit? If anything, our findings (Appendix S3) suggest that elephants may be more likely to visit a tree with lots of fruit available on the ground, which would mean our estimate of the proportion of fruit removed from the ground by elephants is an underestimate.

Appendix S6: Limitations
Precise estimates of frugivory were difficult to acquire due to the short fruiting seasons and difficult field conditions. Camera trapping offered small sample sizes. Counting the number of macaques in a focal tree at any given moment was challenging, and observing how a randomly chosen individual handled fruit was often not possible. Availability, accessibility, time constraints, and safety concerns limited our understanding of the kumbhi’s ecology. Nocturnal focal watches (though not likely important for lator) were not permitted. We were also unable to account for dispersal by the smallest animal vectors (e.g., rodents moving loose lator seeds) or water. It would be useful to have data on whether the trends we have described here hold for other large-fruited species, other forests, and even other years. Since the lator has persisted in the Andaman and Nicobar Islands without native megaherbivores, more research on such alternative dispersal mechanisms (or possible evolution of lator) there would also be useful. Finally, fruit
removal does not necessarily translate into seed dispersal; the quantity of seeds removed by elephants means that the quality of their seed dispersal must be assessed and compared to that conducted by other species (Chapman 1995, Wang and Smith 2002).

Relatedly, since we focus on two tree species in this paper, we provide no insight as to how many fruiting species are likely to be partly reliant on elephants for dispersal. Kitamura et al. (2002) and Campos-Arceiz and Blake (2011) argue that relatively few species in tropical Asia are even eaten by elephants. The relationships we describe here may hold for smaller number of Asian plant species, but be more common in other regions of the world.

Cited references
CHAPTER 3:

In the Elephant’s Seed Shadow: the prospects of domestic bovids as replacement dispersers of three tropical Asian trees

AUTHORS: Nitin Sekar, Chia-Lo Lee, Raman Sukumar.

STATUS: Submitted to Ecology (August 2014).
Abstract
As populations of the world’s largest animal species decline, it is unclear how ecosystems will react to their local extirpation. Due to the unique ecological characteristics of megaherbivores such as elephants, seed dispersal is one ecosystem process that may be affected as populations of large animals are decimated. In typically disturbed South Asian ecosystems, domestic bovids (cattle, Bos primigenius, and buffalo, Bubalus bubalis) may often be the species most available to replace Asian elephants (Elephas maximus) as endozoochorous dispersers of mammal-dispersed fruit species. We use feeding trials, germination trials, and movement data from the tropical moist forests of Buxa Tiger Reserve (India) to examine whether domestic bovids are viable replacements for elephants in the dispersal of three species: Dillenia indica, Artocarpus chaplasha, and Careya arborea. We find that a) once consumed, seeds are between 1.96 (C. arborea) and 15.9 (D. indica) times more likely to pass undigested into elephant dung than domestic bovid dung; and b) more seeds from elephant dung germinated than seeds taken from bovid dung for all plant species, with D. indica seeds 52.7% more likely to germinate if from elephant dung. Furthermore, since wild elephants have less constrained movements than even free-roaming domestic bovids, we calculate that maximum dispersal by elephants is between 9.54 and 11.2 times farther than that of domestic bovids, with about 20% of elephant-dispersed seeds being moved farther than the maximum distance seeds are moved by bovids. Our findings suggest that, while bovids are able to disperse viable seeds for some fruiting species, domestic bovids will be unable to routinely emulate the reliable, long-distance dispersal of seeds executed by elephants in this tropical moist forest. The functional loss of elephants and other wild dispersers may result in the decline of various mammal-dispersed fruiting species, particularly since such species may be dispersal limited due to the challenges posed by overhunting, habitat fragmentation and climate change.
Keywords: Artocarpus chaplasha, Asian elephant (Elephas maximus), Careya arborea, Dillenia indica, domestic buffalo, domestic cattle, functional compensation, seed dispersal.

Introduction
In the ongoing, human-induced global extinction event (Ebenman and Jonsson 2005, Barnosky et al. 2011), large animals are particularly likely to be extirpated both locally and globally (Cardillo et al. 2005, Duffy et al. 2009). While the loss of large charismatic animals is
certainly of social and cultural concern, the extent to which ecosystem processes and functions will be affected by such extirpations is unclear. There is increasing evidence that the largest species in an ecosystem fulfill roles that sympatric species cannot (Skarpe et al. 2004, Hansen and Galetti 2009); in particular, megaherbivores (animals over 1000 kg) are thought to form unique functional groups (Owen-Smith 1988, Campos-Arceiz and Blake 2011, Asner and Levick 2012). A better understanding of the role of large animals in ecological processes may help us understand how ecosystems will change due to the loss of these functional groups, shaping our conservation priorities.

One ecological process that may be affected by the loss of large animals is animal-mediated seed dispersal (Campos-Arceiz and Blake 2011, McConkey et al. 2012). By attracting animals to consume their fruit and remove their seeds, many species of plants are able to move their offspring to favorable locations and remote patches far from the parent, promoting survival of the plant species, community-level diversity, and adaptation of plant populations in the face of climate variability and other perturbations (Wang and Smith 2002, McConkey et al. 2012). While animal-mediated dispersal can involve a range of partners spanning from ants to birds to deer, some fruiting species seem to depend on megaherbivores. Fruits form a major part of the diets of the African forest elephant (*Loxodonta africana cyclotis*) and the one-horned rhinoceros (*Rhinoceros unicornis*) (Tchamba and Seme 1993, Dinerstein and Wemmer 1988). Elephants and other megaherbivores are able to swallow very large seeds without damaging them (Chapman et al. 1992, Campos-Arceiz and Blake 2011), giving trees an opportunity to produce seeds with larger energy reserves that are less sensitive to environmental stresses (Yumoto et al. 1995, Muller-Landau 2010). Studies of African forest elephants and Asian elephants (*Elephas maximus*) have shown them capable of moving seeds far from adult conspecifics, protecting them from Janzen-Connell distance-dependent effects (Campos-Arceiz et al. 2008, Blake et al. 2009). Once consumed and defecated, seeds found in megaherbivore dung sometimes germinate better than seeds taken directly from fruit (Theuerkauf et al. 2000, Chapman et al. 1992, Dinerstein et al. 2003). As such, a variety of plant species are believed to rely heavily on megaherbivores for dispersal (Campos-Arceiz and Blake 2011).

The question then is whether the extirpation of megaherbivores would result in the reduced ability of mammal-dispersed plants to persist. Plant species are rarely dispersed solely by megaherbivores or any other one group, as attracting multiple dispersers insures fruiting
species against the loss of any one disperser (Corlett 1998, Hawthorne and Parren 2000, Kitamura et al. 2007). Thus, addressing this question requires direct comparison between megaherbivore dispersers and their most likely replacements. Alternative dispersers, for instance, may drop seeds instead of ingesting them, or they may digest most of the seeds they consume. Comparisons between megaherbivores and alternative dispersers are scarce: Campos-Arceiz et al. (2012) found that Malayan tapirs digested more seeds than Asian elephants, and Blake et al. (2009) showed that the maximum displacement of seeds moved by African forest elephants surpassed the home range sizes of other dispersal agents in the Congo. Few if any studies have empirically compared megaherbivores’ seed dispersal ability with that of their most likely replacements: domestic cattle and domestic buffaloes.

Across the tropical world, domestic bovids are arguably inheriting ecosystems from megaherbivores and wild ungulates. They are an undeniable ecological force, supplanting or supplementing wildlife from South America (Seidl et al. 2001, Palmeira et al. 2008) to Africa (Fritz et al. 1996, Hibert et al. 2010) to south Asia (Dinerstein 1979). In India, home to the world’s largest populations of domestic cattle (Bos primigenius) and domestic buffaloes (Bubalus bubalis) (Chabbra et al. 2009), the influence of domestic bovids in protected areas is well-documented (Venkataswaran and Parthasarathy 2003, Johnsingh and Negi 2003, Mishra et al. 2004, Madhusudan 2004, Shahabuddin and Kumar 2007). In Buxa Tiger Reserve in India, we found that domestic cattle and buffaloes (along with Rhesus macaques) are the most likely alternative frugivores to elephants (Sekar and Sukumar 2013, Sekar and Sukumar in review), a finding that likely applies to other protected areas—and certainly to unprotected areas—across the region. Given the ubiquity of cattle in the globe’s tropical landscapes, the idea that domestic animals may provide an effective ecological surrogate for wild megafaunal dispersers—first suggested by Janzen and Martin (1982) when proposing the concept of megafaunal fruit—should be more adequately examined.

In this study, we directly compare the disperser qualities of a megaherbivore—the Asian elephant (Elephas maximus)—to that of domestic cattle and domestic buffaloes. We do so for three fruiting species with varied natural histories: the chalta tree (Dillenia indica), the lator tree (Artocarpus chaplasha), and the kumbhi tree (Careya arborea). For each species’ fruit, we estimate the proportion of seeds consumed by elephants, cattle, and buffaloes that pass undigested into these animals’ feces. We plant the surviving seeds to see what proportion
germinate. We also combine data on the amount of time seeds are retained in each animal species’ gut with movement data to estimate how far elephants and bovids are likely to disperse seeds from their point of consumption. Overall, our study examines whether the local loss of elephants also means reduced dispersal—and, potentially, reduced probability of survival—for various mammal-dispersed fruiting species in South Asia’s cattle- and buffalo-dominated landscapes.

**Methods**

**Study species**

We fed the fruit of three species to elephants, buffaloes, and cattle: *Dillenia indica*, *Artocarpus chaplasha*, and *Careya arborea*. Despite all being mammal-dispersed, the three species represent somewhat different natural histories. *D. indica*, known in Bengali as the chalta tree, is an evergreen member of the Dilleniaceae family endemic to Asia (Abdille et al. 2005, Campos-Arceiz et al. 2012); its range coincides with that of the Asian elephant (Sukumar 2003). The chalta is known to fruit in the dry season, though in some places fruiting extends into the monsoon; the chalta’s fruit averages 427.6g and 9.8cm in diameter, and has an average of 103.1 six-millimeter seeds embedded in a pulpy mass in the center of the otherwise hard fruit (Sekar and Sukumar 2013). The hardness of the fruit appears to act initially as a barrier against consumption by smaller frugivores, and both tapirs and smaller domestic bovids have been shown to struggle to eat chalta fruit (Campos-Arceiz et al. 2012, Sekar and Sukumar 2013). As such, the chalta may be one of the best-documented Asian megafaunal fruits: in Buxa Tiger Reserve, 63.3% of fruit removed from camera traps were taken by Asian elephants; gaur and domestic bovids removed 20.9% of chalta fruit; and 78% of elephant dung piles opened during the chalta’s fruiting season contained chalta seeds (Sekar and Sukumar 2013).

In contrast, *A. chaplasha* and *C. arborea* are monsoon-fruiting species whose softer fruit are accessible to macaques and a slew of smaller-bodied animals (Sekar and Sukumar in review). *A. chaplasha*, known in Nepali as the lator tree, is a large evergreen species of the Moraceae family and a relative of the jackfruit (*Artocarpus heterophylla*) (Sahni 1998). The fruit are about 466g in mass and 9.3cm in diameter; like the jackfruit, each of its 1.5cm seeds (averaging 51 per fruit) are individually covered in edible pulp. *Careya arborea*, or kumbhi in Nepali, has smaller fruit (averaging 112.8g, 9.6cm in length) about the same hardness as a pear. Its seeds, also 1.5cm
in length, number about 6 per fruit, but this varies widely amongst fruits (Sekar and Sukumar in review). The kumbhi’s seeds are less embedded in the fruit’s pulp than those of lator and chalta fruit. A camera trap study showed elephants and domestic bovids to be two of the three primary seed-ingesting frugivores of the lator and kumbhi fruit, making these animals likely dispersers of lator and kumbhi seeds (Sekar and Sukumar in review).

Study area

Buxa Tiger Reserve (henceforth Buxa) is located in the northern region of the Indian state of West Bengal (26°30’–23°50’ N and 89°25’–89°55’ E, covering 761 km²). Buxa has an average annual rainfall of c.4500 mm, and is predominantly a tropical moist forest habitat (Sukumar et al. 2003, Sekar and Sukumar 2013). A core area consisting of mostly native vegetation is surrounded by various types of plantation and degraded forest. Careya arborea is mostly found in the disturbed areas, A. chaplasha mostly in low-lying parts of the core area, and D. indica is scattered throughout.

In 2003, elephant density in the region was estimated to be 0.31 per square kilometer, or about 217 elephants throughout Buxa (Sukumar et al. 2003). Buxa’s Forest Department keeps a number of elephants captive in villages across the reserve, mostly for the purpose of patrolling the forests. In addition, these captive elephants are taken to collect food from nearby villages every 2-3 days. As the elephants had all been exposed to the fruit of our study species, they were ideally suited to our feeding trials.

Domestic buffalo (Bubalus bubalis) and cattle (Bos primigenius) penetrate deep into Buxa, typically returning to villages in and near the reserve to sleep. Some groups live in the forest and only return to villages for salt and other specific nutrients, and others are effectively feral. We conducted feeding trials with and collected movement data from free-range domestic cattle and buffaloes that had access to wild fruits in the forest.

Feeding trials

Feeding trials with elephants, domestic cattle (hereafter, cattle), and domestic buffaloes (hereafter, buffaloes) were conducted to estimate the gut passage proportions (GPPs), gut retention times (GRTs), and germination rates of study species seeds consumed by these dispersers. Trials were conducted over three fruiting seasons (2010-2) for lator fruits and in 2012
for chalta and kumbhi fruits. Fruit for trials conducted in the same year were drawn from the same set of trees, but for logistical reasons trials for the different animal species could not always be conducted simultaneously. Each animal was offered fruits until an hour had passed or the fruit supply had been exhausted.

Calculations of gut retention times—the amount of time required for seeds to be defecated after initial consumption—required that we note when each animal defecated and count the number of seeds in their dung. Defecation times of each animal were monitored hourly from 4 AM to 12 AM; when feasible, camera traps were used the remaining hours. This allowed us to estimate defecation times within 2 hours. We monitored each elephant’s dung until seeds had not been detected for at least 36 hours (Campos-Arceiz et al. 2008); since ruminant digestive systems are thought to behave differently (Claus et al. 2003), we monitored bovid dung until seeds had not been detected for at least three days, on some occasions checking for up to a week. For more information on the feeding trials, see Supplement A. For visualization of gut retention times, we used the vioplot package in R (R Core Team 2012).

Estimation of gut passage proportions

Calculation of gut passage proportions (GPP) required estimations of the number of seeds ingested by each individual elephant and bovid. To make these estimates for the indehiscent fruit of our study species, we measured the mass and number of seeds in fruit of each species (for chalta: N=133 fruit from 42 trees; for lator, 73 fruit from 11 trees; and for kumbhi, 115 fruit from 11 trees), and calculated a linear regression with mass as a predictor for seed number (glm method, R Core Team 2012). For all three fruit species, mass was a significant predictor of seed number; for lator fruit, the source tree was also a significant predictor of seed number. Fruits were numbered and weighed before they were fed to elephants and bovids, and the regression equations were used to estimate the number of seeds in each fruit fed to each animal (following Campos-Arceiz et al. 2012).

In the 2010 and 2011 lator feeding trials, fruits were weighed before the feedings but individual fruits were not tracked. To estimate gut passage rates for these trials, we took the average mass of the fruits used for the feeding trials each year and estimated the number of seeds in a typical fruit using the seed number v. mass equation from 2012. We then multiplied this number by the number of fruits consumed by each individual animal, subtracting the number of
seeds dropped by that individual; this provided an estimate of the number of seeds ingested by that individual.

The GPPs of elephants and bovids were compared using one-sided t-tests in R since we predicted greater gut passage for elephants.

*Germination trials*

Seeds from the feeding trials were planted in individual pots in an outdoor nursery in Buxa to determine whether germination rates of seeds from elephant dung, bovid dung, and directly from fruit varied, as well as whether gut retention time (GRT) significantly affected germination probability. We also examined whether the time until germination was affected by defecation by a disperser, controlling for how late in the season each seed was planted. Up to 30 seeds from each dung pile were planted in the nursery. For our control, we planted 300 seeds from 30 chalta fruit from 10 trees, 640 seeds from 60 lator fruit from 8 trees, and 504 seeds from 93 kumbhi fruit from 7 trees. The source trees for the control seeds were also the source of fruit used for the feeding trials.

The nursery was watered 2-3 times a week in the absence of rain, and seeds of a given species were monitored every 2-3 days for germination until a month after the last seed had germinated.

For analysis, we created logit-linked linear mixed-effects models from the lme4 package (R Core Team 2012), coding the animal species that defecated the seeds as factors and the individual animal as random intercepts (all seeds unfed to animals were necessarily assigned a single random intercept, ultimately calculated to be approximately 0). Since lator germination trials were conducted over two years, we controlled for the year of the feeding trial. Similarly, in order to understand whether seeds were less likely to germinate if they spent more time in the digestive tract of the prospective disperser, we fit a logit-link mixed effects model to the data from each disperser species separately in R, with gut retention time as a predictor, individual animals as random effects, and germination (a binary variable) the response. Finally, we analyzed whether consumption and defecation by any of the animal species affected the time taken between planting and germination using yet another mixed-effects model with a Gaussian link. Ordinary least squares random effects models with Gaussian links were also used to interpret results from logit-link models.
**Movement Data**

In order to estimate how far seeds defecated by elephants and bovids were likely to be displaced from their parent trees, we used movement data from elephants, buffaloes, and cattle.

**Elephants**

Of four elephants in Buxa Tiger Reserve fitted with GPS collars in February 2005 as part of a broader study of elephant ecology (Sukumar et al. 2003; Venkataraman et al. 2005), one male elephant tracked from March to November of 2005 and one female from March to December 2005 provided data at sufficiently short time increments for the purposes of our modeling. The male elephant was a solitary adult bull while the female was an adult cow in a family unit of five individuals; the movement of the latter thus represents that of the entire family.

GPS transmitters typically recorded a location every 8 hours, but gaps of several days exist in the data when environmental conditions were presumably unfavorable for telemetry. Each signal was associated with a point, which had a location and a time. These points were used to create two matrices: one that contained the displacement between each pair of points (calculated using Hawth’s Tool on ARC GIS), and one that contained the time elapsed between each pair of points (calculated using Excel). The corresponding columns of the two matrices formed a single displacement versus time curve, with each curve originating from a different starting point. Each starting point signified a potential place of consumption of a fruit, and the displacement versus time curve could be used with gut retention time to calculate how far from this point of origin the seeds of that fruit may be deposited.

**Bovids**

We collected bovid movement data by using a handheld GPS and following a particular cow or buffalo from sunrise to sunset for periods of 5-10 days. Bovids did not generally move at night and stayed with their companions or herds, making them easy to locate in the mornings. Cattle from five herds were followed for a total of six periods from February 2011 to August 2012. Buffaloes from four herds were followed for a total of four periods from November 2011 to August 2012. The five cattle herds were selected such that they came from different parts of
Buxa. Three buffalo herds originated from the same village (Rajabhatkhawa); the fourth was a semi-feral herd living in the core area of the reserve. Aside from this last herd, all were accustomed to people and easy to follow; they were sometimes accompanied by a cowherd, and their movements were not likely to be unnaturally affected by our presence. Bovid movement data was analyzed using the same ARCGIS tools and techniques as elephant movement data.

Seed displacement simulation

We combined the gut retention time data and movement data to simulate dispersal kernels for 30,000 seeds defecated by elephants, domestic buffaloes, and cattle, using an approach similar to Holbrook and Smith (2000), Campos-Arceiz et al. (2008), and Lenz et al. (2011).

For each seed in our model, we needed to a) assign a gut retention time so that we may b) estimate a dispersal distance for the seed using the movement data. Gut retention times needed to be assigned in accordance with the distributions of GRTs for each disperser-plant combination. We thus constructed average gut retention curves for every animal-plant combination in the study. To do so, we controlled for variation in the number of seeds consumed by different individuals of the same animal species: we divided the number of seeds recovered from each dung pile by the estimated number of seeds ingested by the individual that produced that dung. We then combined all gut retention time data for each animal-plant combination. To ease interpretation, the resulting values were divided by the number of individuals of that animal species that had participated in feeding trials for the given fruit species. The result was a distribution of the average proportion of ingested seeds one could expect to find defecated at a given time for each of the nine animal-plant combinations. For each animal-plant combination, “seeds” were sampled from this proportion of ingested seeds defecated v. gut-retention time distribution 30,000 times, providing a vector of simulated gut retention times.

Then we used these GRTs to estimate a dispersal distance for each seed. For each simulated time, a displacement curve was randomly selected with replacement from those available for the animal species at hand (see Movement Data section), and the distance corresponding to the simulated time on that curve was taken as the simulated displacement of the seed from the point of fruit consumption. Linear, constant-velocity trajectories were assumed between points defined on the displacement v. time curves. Since bovids seldom, if ever,
consumed fruit during the night, only displacement curves beginning during the day were used for cattle and buffaloes. Density histograms of the distribution of seed displacements for each animal-plant combination were created using R (R Core Team 2012). For more detail on the model, please see Appendix B.

**Results**

*Fruit consumption and gut passage proportions*

Individuals of each animal species varied dramatically in their interest in different fruit species (see Table 1). In captive elephant trials, for instance, one individual ate over seven times as many chalta fruits as the least interested individual; on several occasions, we ran out of fruit to feed the elephant before the hour elapsed. Bovids, on the other hand, labored to consume the chalta fruit.

Estimated gut passage proportions suggest that elephants can be effective dispersers of the seeds of all three fruits (Table 1). For all three fruit species, each and every elephant passed at least 20% of seeds consumed. Elephant GPPs were highest for the softest fruit (lator) and lowest for the hardest fruit (chalta), suggesting the chewing required for harder fruits led to more seed destruction. Bovid GPPs showed more variation among fruit species and individuals. Bovids had very low GPPs for chalta, with a maximum of 6.5% and many individuals defecating few or no seeds. Buffaloes performed poorly as potential dispersers for lator (though note sample size, n=3). For cattle, the story for lator is different: GPPs ranged from 0 to 94.6%, indicating that bovids may sometimes disperse lator seeds effectively. Buffaloes and cattle both passed moderate proportions of the kumbhi seeds they ingested, with the bovids’ maximum GPP resembling the minimum GPP of the elephants.

Lumping cattle and buffaloes together, elephant GPPs were significantly greater than bovid GPPs for all three fruits species’ seeds (chalta: t=7.61, df=3.15, p<0.01; lator: t=3.15, df=11.53, p<0.01; kumbhi: t=3.04, df=7.00, p<0.01), but elephant GPPs were not significantly greater than those of buffaloes alone for kumbhi (t=1.79, df=2.67, p=0.091), perhaps due to small sample sizes.

*Gut retention times*
Average gut retention times of bovids were greater than those of elephants, but elephants seem to generally have maximum GRTs between those of buffaloes and cattle (Table 1). Figure S1 (in supplement) displays plots of the GRT distribution for each individual from the feeding trials, showing that elephants generally passed far more seeds than bovids, and that most of those seeds happened to emerge earlier, down-weighting the mean. Figure 1 controls for the fact that individual elephants can eat more fruit than individual bovids; to compare different dispersers, it is instructive to see how they would handle the same number of seeds. Bovids, particularly buffaloes, had more uniform seed defecation times; for most individuals, the distributions seem to show the sporadic escape of a seed from ruminant mastication. In any case, GRTs mediate seed displacement through animal movement (see below). For all species, older and larger individuals appeared to have greater GPPs and GRTs, respectively, but the paucity of age and size data precludes strong conclusions.

Germination trials

Overall, seeds defecated by elephants germinated at least as well as seeds taken directly from fruit, whereas seeds from bovid dung varied between species and year, sometimes germinating as well as elephant-defecated seeds (see Figure 2). The result is most striking for chalta seeds, which were 52.7% more likely to germinate if taken from elephant dung than bovid dung. Our logit-linked mixed-effects model found that chalta seeds from both buffaloes (N=25, z=-2.59, p<0.01) and cattle (N=18, z=2.06, p<0.05) had significantly lower germination rates than seeds taken directly from chalta fruit (N=300), and that kumbhi seeds defecated by buffaloes (N=29, z=-2.58, p<0.01) were significantly less likely to germinate than kumbhi seeds taken directly from fruits (N=504). Though Figure 2 suggests that germination was higher for lator seeds defecated by elephants than those defecated by bovids, our tests found none of the dispersers defecated lator seeds that were significantly more or less likely to germinate than the control (all lator seeds, N=1974); the year of the trial, however, did produce a statistically significant effect on lator germination rates. The fact that cow-defecated lator seeds germinated so much better in 2011 than 2012 could be due to environmental factors or could indicate that there is variation in the effects that different individual bovids have on seeds.

The effects of gut retention time on seed germination probability were not consistent across plant study species. GRT failed to predict germination probability of chalta seeds
Table 1: Results from the feeding trials in which elephants, buffaloes, and cattle were fed the fruit of Dillenia indica (chalta), Artocarpus chaplasha (lator), and Careya arborea (kumbhi). Standard deviations are in parentheses. Despite small sample sizes, differences amongst the species are apparent, particularly with regards to gut passage proportions. On average, elephants pass between 1.96 times (kumbhi) and 15.9 times (chalta) as many seeds without destroying them as do bovids. Though bovids have greater average gut retention times in several cases, maximum GRT are comparable amongst the species.

<table>
<thead>
<tr>
<th>Animal</th>
<th>No. Trials</th>
<th>Average no. per individual</th>
<th>Range</th>
<th>Average</th>
<th>Min.</th>
<th>Max.</th>
<th>Total seeds</th>
<th>Avg GRT by seed</th>
<th>Avg. avg. GRT by ind.</th>
<th>Avg. max GRT</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Chalta</strong></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Elephants</td>
<td>4</td>
<td>30.5 (22.8)</td>
<td>7-52</td>
<td>0.398 (0.100)</td>
<td>0.299</td>
<td>0.536</td>
<td>6021</td>
<td>31.1 (10.0)</td>
<td>29.2 (8.1)</td>
<td>71.4 (18.0)</td>
<td>87.1</td>
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<td>12.5 (4.4)</td>
<td>6-15</td>
<td>0.005 (0.003)</td>
<td>0</td>
<td>0.007</td>
<td>25</td>
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<td>60.4 (13.8)</td>
<td>93.6 (5.8)</td>
<td>99.3</td>
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<tr>
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<td>0.001</td>
<td>0.065</td>
<td>18</td>
<td>44.8 (15.0)</td>
<td>40.7 (10.1)</td>
<td>52.5 (21.4)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elephants</td>
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<td>23.3 (14.3)</td>
<td>6-37</td>
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<td>0.036</td>
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<tr>
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<td></td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
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<td>0.343</td>
<td>55</td>
<td>39.3 (17.1)</td>
<td>39.1 (0.18)</td>
<td>64.9 (23.3)</td>
<td>81.4</td>
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</table>

* for GRT estimates of mean of means and mean of maximums, individuals who had not passed any seeds were excluded.
Figure 1: Relative average estimated gut passage proportions and gut retention times of 10,000 seeds consumed by elephants (E), buffaloes (B), and cattle (c), allowing a direct comparison of how the different dispersers would deal with the same number of seeds as a species. The figure displays the average GRT data normalized by the estimated number of seeds consumed by each individual. Violins’ scaling parameters are set based on GPP, giving some visual representation of the differences in the proportion of consumed seeds being defecated by each disperser. On average, elephants defecate a much higher proportion of chalta and lator seeds than buffaloes or cattle, and somewhat more kumbhi. While elephants’ maximum gut retention times (hours since feeding) are not much less than that of buffaloes, elephants dump the bulk of the seeds before 50 hours, and the bovids appear to have a more uniform distribution of gut retention times.
Figure 2: Germination rates from feeding trials with all three study species, including two trials for lator (Artocarpus chaplasha). Standard error bars shown here are estimated assuming a binomial distribution. The number on each bar indicates the number of individual animals from whose dung seeds were used. The data suggest that seeds recovered from elephant dung perform at least as well as seeds taken directly from fruit and generally better than seeds taken from bovid dung. Seeds defecated by buffaloes never do as well as seeds defecated by elephants, but the results from the kumbhi germination trial and the different results between the two lator feeding trials indicate that, under some circumstances, seeds defecated by cattle may germinate at similar rates to elephant-defecated seeds. Overall, seeds defecated by elephants germinate more reliably than seeds defecated by bovids.
defecated by any of the disperser species. Elephant GRT predicted a reduction in germination probability for lator seeds \( (N=1031, z=-4.329, p<0.0001) \); for every additional hour in an elephant’s body, the odds ratio of germination reduced 2%. According to the OLS-approximation, this is the equivalent of an average decrease in germination probability of about 0.4% per hour. Cattle GRT predicted a reduction in germination probability for kumbhi \( (N=55, z=-2.128, p<0.05) \); for every hour a kumbhi seed spent in a cow’s gut, the OLS-approximation predicted a 0.7% reduction in germination probability. Otherwise, GRT was not found to have an effect on germination, perhaps due to small sample sizes for several bovid-fruit combinations.

We also found that chalta seeds defecated by elephants \( (N=1430, t=-9.16, p<0.0001) \) and by buffaloes \( (N=25, t=-2.90, p<0.01) \) tended to germinate 4.9 and 5.5 days earlier, respectively, than seeds taken directly from fruit \( (N=300) \), controlling for the date of planting. Ingestion by cows led to a 6.5-day increase in germination time for kumbhi seeds \( (N=55, t=3.206, p<0.01) \) compared to controls \( (N=504) \).

Movement patterns

Data from two elephants over 9 months allowed construction of 838 displacement curves (i.e., displacement versus time curves), and nearly all of these curves allowed us to calculate seed displacement for the maximum gut retention time found for elephants (135.1 hrs). In contrast, data from four buffaloes (from different herds) allowed us to construct only 46 displacement curves (from 4 periods spaced over 8 months); of these 46 curves, only 11 surpassed the maximum gut retention time of buffaloes (175.3 hrs). Finally for cattle, data on 5 cattle herds from 6 periods spaced over 18 months afforded us 54 displacement curves of which 20 surpassed cattle’s maximum gut retention time (132.1 hrs).

Elephants moved farther on average than bovids, and after about 80 hours the mean elephant displacement was greater than the maximum displacement found for bovids. Most striking is that elephants sometimes moved on a different order of magnitude than the domestic bovids, going over 50 kilometers in 100 hours (see Figure 3). Domestic bovids were not found to move over 5 kilometers from the point of origin in that time, with buffaloes moving slightly greater distances than domestic cattle. With a few exceptions, domestic bovids tended to return to a sleeping spot near their owner’s village on an almost nightly basis. The feral buffaloes (who were followed in April, the dry season) moved shorter distances than the still-domestic herds,
Figure 3: Mean and standard deviation of displacement over time for the three animal dispersers, using GPS-transmitter data for elephants (N=2) and hand-held GPS data from buffaloes (N=4) and cattle (N=5) in Buxa Tiger Reserve. Data cover multiple seasons for all three species, but for bovids data are restricted to periods of 10 days or less continuously. Starting points for displacement curves are at least 8 hours apart to reduce autocorrelation, and curves begin at different points in the day. The nearest fifth of the data are used to construct mean and standard deviation lines using the bandplot function from the gplots package in R (R Core Team 2012). The movement of both buffaloes and cattle appear constrained, with herds moving no more than 5 km over the course of five days. Elephants may stay in one area for a long period of time, or may move over 50 km in several days (for graph of raw data, see supplement). The mean and standard deviation of displacement increases steadily over time for elephants, while those of the bovids stay relatively constant. This may have implications for seed dispersal.
perhaps because they did not need to return to their owner’s area (in one case, the feral herd was only located 8 hours after sunrise; unusual movement may have been missed). In addition, we found that the bovids tended to visit the same areas several days in a row, only slowly shifting to new foraging areas over the course of weeks. This means that a seed ingested at time 0 and defecated at time 24 hrs or 48 hrs may end up very close to where it was originally picked up by the bovid. This back-and-forth behavior is also why the mean displacement of buffaloes and cattle oscillates over time. In contrast, elephants exhibit a wide variety of movement behaviors—sometimes, they stay quite close to the point of origin for many days. On other occasions, they move ten kilometers in a day. The data suggest that domestic bovids are not likely to emulate the movement patterns of elephants. Our data on domestic bovid movement is limited and thus may not capture less frequent long-distance movement by cattle and buffaloes; however, what we know about the oscillatory movements of domestic bovids suggest that such movements are probably significantly less likely for bovids than for elephants.

Seed dispersal simulations

As foreshadowed by the movement data, simulations show elephants to be capable of moving seeds much farther than domestic bovids (see Figure 4). The maximum seed displacement by an elephant was between 46 and 54 km for the three plant species, compared to about 4.9 km for bovids (see Table 2). Although mean seed dispersal distances were not so dramatically different (about 3.5 km for elephants compared to about 1.3 km for cattle and around 2 km for buffaloes), some 20% of seeds dispersed by elephants are expected to go farther than the maximum distance seeds are taken by bovids. The oscillations seen in the bovid movement data seem to persist into the bovids’ seed shadows, presumably a result of the cattle’s and buffaloes’ tendency to spend their nights in a single location and their days ranging in the same area for many consecutive days.

Discussion

Elephants are markedly more effective than domestic bovids as dispersers of Buxa’s large-fruited tree species. The results are stark for Dillenia indica, which appears to be a true megafaunal fruit. In addition to being primarily eaten by elephants in the wild (Sekar and Sukumar 2013), chalta seeds were at least 15.9 times more likely to survive elephant gut passage
Figure 4: Log base-10 seed shadows of elephants, buffaloes, and cattle for all three plant study species. The curves were constructed by running a dispersal simulation based on gut retention time and movement data 30,000 times for each animal-plant combination, and then multiplying each density curve by the pertinent average gut passage proportion. Despite reasonably similar gut retention times amongst the disperser species, elephants’ ranging behavior makes much longer distance dispersal possible. The long tail of the elephant’s seed shadow suggests even routine dispersal by elephants may result in greater dispersal distances than the routine dispersal by bovids documented here.
Table 2: Summary of seed shadow simulation results, showing how elephants may disperse about 20% of seeds farther than the seed farthest-dispersed by bovids. Maximum dispersal by elephants is between 9.54 and 11.2 as far as maximum dispersal by bovids. This data likely does a better job of capturing infrequent long-distance movements by elephants than by bovids, but the latter is probably quite rare, happening most often due to sale or theft of a cow or buffalo. Differences in elephant gut retention times for the three plant species lead to only small differences in the distance dispersed.

<table>
<thead>
<tr>
<th>Fruit species</th>
<th>Animal disperser</th>
<th>Mean seed displacement (m)</th>
<th>SD seed displacement (m)</th>
<th>Max displacement (m)</th>
<th>% Seeds &gt;1 km</th>
<th>% Seeds &gt;2km</th>
<th>% Seeds &gt;5 km</th>
<th>% Seeds &gt;10km</th>
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<tr>
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than bovid gut passage, and 52.7% more likely to germinate if taken from elephant dung than from bovid dung. Our findings from feeding trials of *A. chaplasha* and *C. arborea* indicate that elephants may generally be more effective dispersers than bovids for large-fruited species. Lator seeds were 2.73 times more likely to survive gut passage through elephants than through cattle and 37.3 times more likely to survive passage through elephants than through buffaloes. Kumbhi seeds were 1.96 times and 3.42 times more likely to survive gut passage through elephants than through buffaloes and cattle, respectively. Lator and kumbhi seeds taken from elephant dung germinated as well as seeds taken directly from fruit and better than seeds taken from bovid dung, particularly buffalo dung. Lator seeds were 98.4% and kumbhi seeds were 22.8% more likely to germinate if defecated by elephants than by buffaloes; this may be largely due to physical damage done to seeds by the latter, since bovid GRT did not affect germination. Finally, since wild elephants range widely and, unlike domestic bovids, do not regularly return to a central location, we calculated maximal seed dispersal by elephants to be between 9.54 and 11.2 times as far as maximal dispersal by domestic bovids. Our simulations indicated that about 20% of seeds dispersed by elephants are moved farther than the maximum distance seeds are moved by bovids. Although cattle and buffaloes participate in the dispersal of large-fruited species, our findings suggest that domestic bovids will be unable to routinely emulate the reliable, long-distance dispersal of seeds executed by elephants in Buxa Tiger Reserve.

Elephants’ gut physiology and size (which may be linked—Claus et al. 2003) are most likely what differentiate them functionally as seed dispersers from bovids and other ruminants. The ruminant propensity to chew cud—part of a strategy to maximize extraction of nutrients from their food—is likely responsible for the low proportions of lator and kumbhi seeds surviving cow or buffalo gut passage. Also, the low proportions of chalta seeds surviving bovid gut passage suggests that bovids had to chew down the chalta’s fibrous pulp before swallowing, likely killing most of the seeds; in contrast, elephants’ size allows them to swallow large chunks of chalta fruit without mastication (Sekar and Sukumar 2013), making them capable dispersers of chalta seeds and perhaps other hard-fruited and large-seeded species. Elephants’ size and high-quantity, low-quality digestive strategy can also require them to move great distances in search of resources (Sukumar 2003, Claus et al. 2003, Blake et al. 2009), extending the length of their seed shadows. Notably, elephants’ body mass alone appears to give them an edge as seed dispersers; Campos-Arceiz et al. (2012) found that Malayan tapirs, which like elephants are
hindgut fermenters, passed very small percentages of medium- and large-seeded species, and moved seeds only up to 3.3 km from their point of origin. Overall, our findings support the intuition that species with very different behaviors and physiologies are likely to differ in their functional contribution to ecosystem processes.

Our results also suggest that there is substantial variation in a) how the same plant species is processed by different individuals of the same animal species, and b) how different plant species are processed by the same animal species. For lator seeds, for instance, gut passage proportions for cows ranged from 0 to 94.6%, and for elephants GPP ranged from 20.4 to 99.2%; these differences could be due to individual factors such as age and size (Campos-Arceiz et al. 2008), or even personality. Inexplicably, while kumbhi seed GPP was better in buffaloes than in cattle, gut passage for lator seeds was more likely through cattle than through buffaloes. While greater elephant gut retention time reduced the probability of germination for lator seeds, there was no such effect on chalta or kumbhi seeds.

The solution to understanding this variation may lie in larger sample sizes and repeated trials, which are difficult to execute in the field. Still, the scatter in our results adds to prior research that suggests there is not an easy-to-discern, cross-species relationship between gut retention time and germination probability. Studies have found that some plant species’ seeds experience increased or decreased germination rates due to elephant gut passage compared to seeds taken from fruit (Chapman et al. 1992, Nchanji and Plumptre 2003, Campos-Arceiz et al. 2008, Campos-Arceiz and Blake 2011), while others find a more neutral effect of frugivore ingestion (Kitamura et al. 2007). The reduced germination of lator seeds due to increased elephant GRT, though at odds with our data for chalta and kumbhi, matches Campos-Arceiz et al.’s (2008) findings on how the seeds of Tamarindus indica respond to prolonged elephant gut treatment.

Despite the unexplained variation in our results, our study strongly suggests that a suite of mammal-dispersed fruiting species cannot be as effectively dispersed by domestic bovids as by Asian elephants, especially over longer distances. This would make species like chalta, lator, and kumbhi less competitive and more prone to population decline, particularly if they are dispersal-limited. Given that wild, large-bodied, non-ruminant seed dispersers are in decline in many parts of South America (Peres and Palacios 2007, Terborgh et al. 2008), west Africa
(Wang et al. 2007, Maisels et al. 2013) and southeast Asia (Corlett 2007, Brodie et al. 2009), what do our findings mean for the world’s fruiting plant diversity?

Making such predictions requires further work along several lines of inquiry. Firstly, some megaherbivore-dispersed species may yet turn out to be effectively dispersed by bovids and other ruminants. Researchers have found that cattle can disperse seeds of some plants effectively (Balasubramanian and Bole 1992, Middleton and Mason 1992), and even in Buxa, seeds of some hard-seeded species like *Gmelina arborea* and *Trewia nudiflora* can commonly be found in cow dung (personal observation). Feeding trials with more plant species may produce better generalizations on the types of seeds and fruits megaherbivores handle better than domestic bovids.

Secondly, the scientific community is only starting to explore how smaller mammals may serve as surrogate dispersers of megafaunal fruit. Admittedly, there are several reasons to doubt that smaller mammals could fill in for the likes of elephants. In Buxa, for instance, we previously found that while giant squirrels (*Ratufa bicolor*), common palm civets (*Paradoxurus hermaphroditus*), wild pigs (*Sus scrofa*), and Himalayan crestless porcupines (*Hystrix brachyura*) consumed the fruit of our study species, these animals ate only a small proportion of the fruit available (Sekar and Sukumar 2013, Sekar and Sukumar in review), perhaps because they too have populations suppressed by hunting and habitat loss. This suggests that these species do not consume enough fruit to disperse seeds to the same extent as elephants. Furthermore, giant squirrels, wild pigs, and porcupines have frequently been found to be seed predators instead of dispersers, particularly for larger seeds (Corlett 2007). Species like the Rhesus macaque that do exist in sufficient numbers may not swallow that many seeds, leaving most under the crown (Sekar and Sukumar in review). Finally, such smaller species are probably less likely to take seeds long distances than domestic bovids. Nonetheless, we need system-level assessments of how dispersal changes without megaherbivores to be sure of just how important they are for dispersal. On Barro Colorado Island, Jansen et al. (2012) showed that agoutis (*Dasyprocta punctata*, a large rodent) may have been the main dispersal vector for one so-called megafaunal fruit species all along. Perhaps the combination of occasional dispersal and secondary dispersal by seed predators, short-distance dispersal by macaques, occasional long-distance dispersal by domestic bovids, and limited dispersal by water are enough to maintain populations of species like the chalta, kumbhi, and lator.
Our work provides strong motivation for such system-level analyses of seed dispersal in our changing world. Contrary to the suggestions of Janzen and Martin (1982), we found that domestic bovids cannot be assumed to be ecological equivalents of megaherbivores. Our findings add to the growing body of evidence that, in a world besieged by habitat fragmentation, climate change, and ever-shifting human populations (Corlett 2009, McConkey et al. 2012), native flora would find dispersal more challenging due to the loss of elephants and other large-bodied native fauna (Campos-Arceiz and Blake 2011, McConkey et al. 2012).

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References:


Supporting Information (Ch. 3)

Supplement A: Feeding trials

*Chalta fruit*

The details of feeding trials varied amongst seasons. Four elephants, four buffaloes, and four cattle were used for the chalta feeding trial in 2012. The elephants included one male and three females (aged c.11 to 55 years). The four buffaloes included an 8-year old female, a seven-year-old female, and two four-year-old males. The cattle included two 10-year old females and two 5-year old males; one of the males was said to be of a local Duars breed, whereas the others were of a Bhutanese variety, but no documentation was available. Two other cows and another buffalo were also offered chalta fruit, but refused to eat them. Feeding trials with bovids were conducted between feeding trials for elephants in an effort to control for the time of chalta fruit harvest.

Chalta fruits (both the freshly fallen, hard and older, soft varieties) were collected from under fourteen trees in Buxa. Each fruit was assigned a number and marked by making small holes in the outer layer of the fruit with a sharp stick shortly prior to the feeding trial; the mass of each fruit was recorded. Fruits from the same trees were used for feeding trials of all animals. Prior to the trial, animals were not given access to chalta fruits. Their dung was monitored for chalta seeds until seeds had not been found for 3 days (Campos-Arceiz 2008, Campos-Arceiz et al. 2012); after this we presumed that the animal’s system no longer contained any chalta seeds. Chalta fruits were offered to each animal over the course of an hour, after which animals were not allowed to consume chalta fruits until completion of the trial. Many of the bovids struggled to consume the chalta fruit; two of the cattle and one of the small male buffaloes were unable to eat the harder fruit and ate exclusively the older, softer chalta fruit. The numbers of fruits consumed and rejected were noted; we also tried to count the number of seeds dropped by each animal while feeding, though this was not always possible with the elephants.
Elephants were accompanied during their patrols, baths, and food collection trips to ensure they did not eat any other chalta fruit and to collect dung deposited during outings. Elephants did not share space with other individuals, so there was no risk of confusing the dung of different animals. Bovids were restrained for the duration of the trial by their owners, who similarly restrain their animals at times of illness or pregnancy or to prevent crop raiding, thus also preventing mixing of their dung.

Each dung pile was filtered for seeds by washing it with water using a 2-mm wire mesh; the number of seeds in each pile was then recorded and seeds were stored in labeled envelopes for germination trials (see below). For elephants, dung deposited after the feeding trial was searched for seeds until seeds were not detected for 36 hours; for bovids, dung was examined for seeds until seeds were not detected for at least three days and up to a week.

During the trial, elephants maintained their regular diet of banana plants and leaves, rice, and lentils fed to them by their mahouts, and various other items (bread, sweets, fruits) by villagers. They also opportunistically grazed and browsed vegetation while working in the reserve. Buffalo and cattle were fed hay from rice paddy, corn or wheat meal with salt, and browse harvested from some thirteen tree species in and around the village.

**Lator fruit**

Trials for lator fruit were conducted over three years. In 2010, trials were conducted with two elephants and one cow; in 2011, with one elephant and four cows; and in 2012 with three elephants, three buffaloes, and three cows (including one of the cows from 2011 for a second trial). The elephants included one male (c. 20 years old) and 5 females (aged c. 13-60 years old), including one very old female with few if any remaining teeth. The buffaloes included two young males (c. 4 years old) and a 7-year old female. The cattle included seven female cattle of reproductive age and a male less than five years old; two of the females were considered of the local Duars breed, whereas the other six cattle were said to be Bhutanese breed.

Fruit were drawn from 3, 6, and 11 trees in 2010, 2011, and 2012, respectively. Since whole lator fruit was not easily found on the ground, fruits were often harvested from the canopy. Lator fruit ripened and rotted quite quickly; thus, whichever fruits were ripened were fed to animals on the day of the feeding trial. Thus, fruit allocation to individuals was not random for
lator as it was with the other fruit species. In addition, due to logistical limitations in 2012, bovid feeding trials were begun three weeks before elephant feeding trials for logistical reasons. Since lator seeds are substantially bigger, searches for seeds in elephant and bovid dung was sometimes conducted by hand, though filters were used most of the time. Different plants were harvested from the jungle to feed bovids and elephants during the feeding trials, in keeping with the season. Otherwise, methods were the same as those used for chalta feeding trials.

**Kumbhi**

Feeding trials with kumbhi fruit were conducted in 2012 at the same time as that year’s lator feeding trials. Three female elephants (c. 13–56 years old), three buffaloes (same as for lator), and three female cattle of reproductive age were utilized for the kumbhi feeding trials. Fruit for the kumbhi trials were drawn from 11 trees. Since kumbhi trees generally ran out of fruit before many lator trees’ fruit had reached maturation, some kumbhi fruit had to be refrigerated before the trials, particularly the elephant feeding trials, which were later. Fruit from each tree were essentially randomly allocated amongst elephant, bovid, and control groups. Otherwise, kumbhi feeding trials followed the same methods as those described for lator above.

**Supplement B: Seed displacement simulation**

Beginning with elephants, the gut retention time data from all four individuals were pooled. Seed numbers were weighted based on the number of seeds consumed by that elephant. If, e.g., elephant 1 had eaten 100 seeds, and elephant 2 had eaten 50 seeds, one seed found in elephant 1’s dung would count as one seed in the pooled data, but one seed found in elephant 2’s dung would count as 2 seeds in the pooled data. Our final gut retention curves were calculated based on the proportion of ingested seeds defecated versus time, instead of just the absolute number of seeds defecated versus time.

Using these gut retention curves, we created a cumulative distribution function (CDF) for elephant gut retention times. This CDF was used to assign gut retention times to numbers from 1 to 100. For example, if it took 42.5 hours for an elephant to defecate 50% of the chalta seeds it
would deposit overall, then 42.5 was assigned to the number 50. The maximum gut retention was assigned to the number 100.

Next, 30,000 gut retention times were randomly sampled from these 100 numbers. We then needed to calculate a corresponding displacement value for each of these gut retention times. For each of the 30,000 GRTs, a displacement versus time curve was then randomly selected with replacement from the movement data (see Movement Data—Elephants) until the curve included the randomly selected gut retention time. For instance, if the randomly selected gut retention time was 72 hours, and the displacement versus time curve we selected ran only to 55 hours, another displacement versus time curve was selected.

Then, the displacement corresponding to the selected GRT in the randomly chosen curve was found by assuming the animal moved in a straight line at a constant pace between two available points. In the above example, if movement data points were available at 68 hours and 76 hours on our displacement v. time curve, we assumed that the displacement at 72 hours was the average of the displacements at 68 and 76 hours.

Once 30,000 displacement values were thus generated for elephants, the same procedure was followed for buffaloes and then cattle. The only difference was that no displacement versus time curves that started at night were utilized, since bovids were unlikely to find and consume chalta at night. The displacements were then plotted as dispersal kernels, or seed shadows, for each species.
Supplement C: Additional figures

Figure S1: GRT violin boxplots for (a) chalta, (b) lator, and (c) kumbhi. Each violin illustrates the density of seed GRTs from one individual; solitary points indicate that all seeds had the same GRT. Violin scaling parameters are set based on the total number of seeds defecated by each individual. The plots show the large numbers of seeds defecated by elephants, and the lower number of seeds available from bovid dung. Many bovid GRTs have almost uniform distributions. Though comparable, buffalo maximum GRTs are a little higher than elephants'.
Figure S2: Plot of the raw movement data for elephants and bovids, as well as the mean and standard deviation. The different scale on which elephants move is even more evident by comparing the top plot with the others. Note that elephants begin to move over 50 km in just 72 hours.
CHAPTER 4:

How much seed predation occurs from Asian elephant dung?

AUTHORS: Nitin Sekar, Netra Prasad Sharma, Xingli Giam, Raman Sukumar.

ABSTRACT

Elephants are thought to be effective seed dispersers, but research on whether elephant dung effectively protects seeds from seed predation is lacking. Quantifying rates of seed predation from elephant dung will facilitate comparisons between elephants and alternative dispersers, helping us understand the functional role of megaherbivores in ecosystems. We conducted an experiment to quantify the predation of *Dillenia indica* seeds from elephant dung in Buxa Reserve, India from December 2012 to April 2013. Using dung boluses from the same dung pile, we compare the number of seeds in boluses that are a) opened immediately upon detection (control boluses), b) made available only to insect seed predators for 1-4 months, and c) made available to all seed predators and secondary dispersers for 1-4 months. We found seed predation by insects is responsible for the loss of about 82% of chalta seeds over the course of the study. Exposure to larger seed predators and secondary dispersers led to negligible additional loss of seeds from dung boluses. Evidence suggests that boluses deposited by elephants in the colder months may be less susceptible to seed predation than dung deposited in the spring. Insects are likely the main predator of seeds in elephant dung.

**Keywords:** Asian elephant (*Elephas maximus*), Buxa Tiger Reserve, *Dillenia indica*, dispersal ecology, elephant dung, post-dispersal seed predation.

INTRODUCTION

Seed dispersal is widely recognized as a crucial ecological process underpinning plant diversity (Wang and Smith 2002, McConkey et al. 2012), and the deterioration of populations of animal dispersers is seen as a threat to biodiversity (Babweteera and Brown 2009, Campos-Arceiz and Blake 2011). The concern is acute for fruit species dispersed by large-bodied animals (Terborgh et al. 2008, Hansen and Galetti 2009), which are becoming increasingly rare in ecosystems across the world (Cardillo et al. 2005). Many researchers believe that large-bodied animals may be particularly important dispersers due to the volume of fruits eaten and seeds dispersed (Tchamba and Seme 1993, Dinerstein 2003, Blake et al. 2012), the size of seeds that larger animals can swallow (Chapman et al. 1992, Campos-Arceiz and Blake 2011), and the distances that larger animals can disperse seeds (Fragoso et al. 2003, Campos-Arceiz et al. 2008, Blake et al. 2009). In some cases, seeds even germinate better in dung than they do if taken
directly from fruit, perhaps due to scarification during gut passage (Chapman et al. 1992, Theuerkauf et al. 2000, Dinerstein 2003).

However, the celebration of large-bodied animals’ ability to disperse seeds is premised on the assumption that, after dispersal, the probability of seed survival to germination and establishment is sufficiently high (e.g., Janzen and Martin 1982). Research has shown that dispersal of seeds is just the first part of the story—after dispersal, seeds may yet again face seed predators that could cut short their journey to maturity (Wang and Smith 2002). Post-dispersal seed predation has been documented from the feces of numerous large-bodied frugivores, including gibbons (McConkey 2005a, McConkey 2005b), howler monkeys (Andresen 1999, Andresen 2002), chimpanzees (Balcomb and Chapman 2003), and horses (Janzen 1982). Though it is a common phenomenon, most assessments of species’ dispersal effectiveness have neglected post-dispersal predation (Blake et al. 2009, Campos-Arceiz et al. 2012), which may be expected to vary substantially amongst dung of different disperser species.

Evidence suggests that both Asian and African elephants are likely to be effective dispersers due to their diet, digestive physiology, and ranging habits (Campos-Arceiz and Blake 2011). However, elephants also produce some of the most visually conspicuous fecal matter in the terrestrial world. The smell of elephant dung can also be quite strong even to humans; for seed predators, elephant dung may serve as advertisements for a seedy meal. While early commentators suggested that high dung mass to seed mass ratio should protect seeds (Janzen 1982), there have been few efforts to measure levels of seed predation from elephant dung. Cochrane (2003) studied African elephant (Loxodonta africana) dispersal of Balanites wilsoniana and projected that bush pigs (Potamochoerus porcus) may visit all elephant dung piles and consume about half of elephant-dispersed Balanites seeds prior to germination. In the Republic of Congo, sitatungas (Tragelaphus spekii) and red river hogs (Potamochoerus porcus) were observed spending 20% and 33% of their feeding time, respectively, consuming Panda oleosa nuts and other seeds from elephant dung (Magliocca et al. 2003). In South Africa, the savanna tree squirrel (Paraxerus cepapi) removed and sometimes predated upon marula (Sclerocarya birrea) stones from elephant dung (Midgley et al. 2012). Collectively, research indicates that post-dispersal seed predation from elephant dung is pervasive but fails to sufficiently document seed predation or provide estimates of the probability of seed survival post-defecation.
We attempt here to advance the general understanding of seed predation from elephant dung. In the course of conducting other elephant-related studies, we observed that elephant dung in tropical moist forests of Buxa Reserve, India was often pulled apart and scattered (presumably by rodents) or infested with ants or termites, even during the dry season (November-March). Since elephants are known to disperse *Dillenia indica* seeds (Sekar and Sukumar 2013), and since *D. indica* seeds typically germinate in May just prior to the monsoon (Sekar et al. in review), *D. indica* seeds in elephant dung could be vulnerable to seed predation over a prolonged period of time. The ubiquity of insects and rodents (Peres 2000, Stoner et al. 2007) makes them potentially more formidable seed predators than wild swine.

We executed an experiment in which boluses from the same elephant dung pile were assigned to three treatments: (1) the bolus was excavated upon discovery and seeds counted (control); (2) the bolus was placed near its place of discovery and left open to all seed predators and secondary dispersers; and (3) the bolus was placed near the point of discovery, but was only accessible to insects, and secondary dispersal was not possible. Comparisons amongst these treatments allowed us to discern the relative importance of seed predation by insects compared to other post-dispersal processes and estimate what proportion of seeds were likely to survive seed predation after dispersal by an elephant. Although our study is an exploratory study, our findings suggest that post-dispersal seed predation plays a major role in mediating the success of elephants as seed dispersers in a tropical moist forest habitat.

**METHODS**

**Study area and study species**

Our experimental approach is possible because of the strong relationship between Asian elephants (*Elephas maximus*) and the chalta tree (*Dillenia indica*) in Buxa Tiger Reserve. Buxa Tiger Reserve (henceforth Buxa) is located in the northern region of the Indian state of West Bengal (26°30’- 23°50’ N and 89°25’- 89°55’ E, covering 761 km²). Buxa has an average annual rainfall of c.4500 mm, and is predominantly a tropical moist forest habitat (Sukumar et al. 2003, Sekar and Sukumar 2013). Chalta trees are found throughout the reserve.

Chalta trees produce what are described as megafaunal fruits. Although the chalta’s 6 mm seeds are smaller than those of the stereotypical megafaunal fruit, the fruits are hard and initially difficult for small frugivores to consume; elephants are estimated to consume nearly 60% of fruit.
produced by the chalta trees in Buxa (Sekar and Sukumar 2013). Furthermore, the proportion of consumed chalta seeds that make it into elephant dung is almost 16 times greater than the proportion that makes it into dung of the next most common frugivore (domestic cattle/buffaloes), and more than 80% of chalta seeds taken from elephant dung germinate (Sekar et al. in review). Finally, 78% of elephant dung piles opened during the chalta’s fruiting season had chalta seeds in them (Sekar and Sukumar 2013). While the chalta tree fruits throughout the dry season, seeds only germinate beginning in late May just before the onset of the rainy season.

**Seed predation experiment**

We executed a field experiment from December 2012 through April 2013 in Buxa to quantify the proportion of chalta seeds lost to seed predation from elephant dung before germination was possible. From December through March, we located elephant dung piles with 3 or more boluses (presumably from the same elephant at the same time). Each bolus was weighed and then placed randomly into one of three treatments: “extract”, “insects only”, or “all seed removers”. Boluses in the control, or “extract”, treatment were opened immediately, and the number of chalta seeds was counted. Since the numbers of seeds in different boluses from the same dung pile are likely to be correlated, the “extract” boluses served as our reference of the original number of seeds per unit mass in the boluses from that dung pile.

Boluses in the experimental “insects only” treatment were placed inside a 2-mm mesh box closed on all six sides and placed near where the dung pile was initially found (though dung was often moved farther from the road and mesh boxes sometimes covered with leaves to prevent detection by people). The boxes, resembling those in Estrada and Coates-Estrada (1991), ensured that no whole chalta seeds (~4mm x 6 mm) could be removed from the site without removal of the box, and that only relatively small insects could enter. Thus, any seed disappearance from the dung in the boxes had to be due to in situ seed predation by insects or other small organisms, and not due to secondary dispersal or predation by rodents.

Boluses in the “all seed removers” treatment were placed near those in the insect treatment in the same form as they were found. Thus, seeds in these boluses were susceptible to seed predation by insects, seed predation by rodents and other larger animals, and secondary seed dispersal. Comparison between the two experimental treatments would thus allow us to gauge the relative importance of predation by insects to other fates (allowing for certain assumptions).
The major advantage of our approach is that the experimental boluses maintained their original shape, structure, and distribution of chalta seeds; all these factors may contribute to the detection and accessibility of embedded seeds by seed predators.

The experimental boluses remained in the field until April, when widespread brush fires in Buxa forced us to end the experiment in order to maintain adequate sample sizes. Some “insect” treatment boluses were apparently stolen by people (presumably for the wire mesh box). All remaining boluses were collected between April 1 and April 22. The stage of each bolus and presence of potential seed predators or secondary dispersers were noted. Each bolus and any surrounding pieces of dung were taken and searched for seeds.

Analysis

In order to estimate the effect of exposure to seed predation on the number of seeds per bolus, we constructed a suite of candidate generalized linear (fixed-effects) models (GLMs) in R (R Core Team 2012). The response variable, number of seeds per bolus, was modelled as having a Poisson distribution. Each model used dung pile as a fixed effect since our questions deal entirely with intra-dung pile predictors and variation. The mass of each bolus was used as a control. There were three key predictor variables. First was the number of days the bolus was left in the forest after discovery; it was expected that the longer a bolus was exposed to seed predation, the greater the probability a seed would likely be removed. The last two predictors were dummy variables for the “insects only” treatment and the “all seed removers” (ASR) treatment. Since all the experimental boluses were accessible to insects, they all received a value of 1 for the “insects” dummy. Then, only experimental boluses placed in the forest without a box received a 1 for the ASR dummy. The “insects” dummy thus measured seed removal by insect seed predators, whereas the ASR dummy measured the additional removal of seeds by secondary seed dispersers and larger seed predators. The nested structure of our model assumes an additive relationship that will be further discussed below.

We analyzed the GLMs in a multimodel inference framework (Burnham & Anderson 2002). The best-supported models were chosen using small-sample Akaike Information Criterion ($\text{AIC}_c$). Boluses that had been burned to ashes were excluded, as were the first four dung piles in which no seeds were found (since they likely pre-dated widespread chalta consumption by elephants that season).
Camera traps

In order to identify the likely seed predators, camera traps were opportunistically deployed to monitor dung piles in the 2010-11 and 2011-12 chalta fruiting seasons. Dung piles were typically moved for these exercises so that the camera traps could be placed out of the line of sight of people on nearby paths or roads. Additionally, three camera traps were rotated amongst the dung piles used for the seed predation experiment for approximately two-week periods in 2012-13. While the specific removal of seeds was not visible on camera, the traps gave a general idea of the animals visiting and utilizing elephant dung piles in Buxa.

RESULTS

We originally collected 344 boluses from 65 elephant dung piles in Buxa, of which 52 dung piles with 257 boluses remained for analysis; 22 boluses were excluded since they were too early in the season to contain seeds, 58 boluses were excluded due to destruction by fire, and 7 were taken by people. Of the remaining boluses, 89 were “extract” treatment boluses (mean mass=832.3g, sd=488.9g), of which 72 were found to have chalta seeds (mean=13.7 seeds, sd=22.4, min=0, max=122). There were 80 “insect only” treatment boluses (mean mass=866.1g, sd=415.8) which were left in the forest for an average of 66.3 days (sd=20.5). Of these, 40 were found to have seeds remaining after treatment (mean=2.65 seeds, sd=5.85, median=0.5, max=36). Finally, there were 88 “all seed remover” treatment boluses (mean mass=820.3, sd=502.2) which were left in the forest for an average of 66.4 days (sd=22.2). Of these, 42 boluses had seeds remaining post treatment (mean=2.26 seeds, sd=4.06, median=0, max=20) (see Figure 1).

Seed predation experiment

We constructed seven models to estimate seed predation rates in our experimental boluses (see Table 1). Our best model (model number 5) indicated that insects are the major predators of chalta seeds dispersed by elephants, and contradicted two of our prior expectations. Firstly, inclusion of a term for the all seed removers (ASR) dummy variable did not improve the model (shown as model number 7), suggesting that exposing boluses to larger seed predators and secondary seed dispersers had a negligible effect on the number of seeds in boluses. Secondly,
Figure 1: Frequency of seed counts per bolus for each of the three treatments on a log_{10}-transformed scale (one was added to each bolus to allow transformation, and the axis has been adjusted accordingly). Boluses that we immediately extracted often had more than 40 seeds each, and only about 20% of boluses lacked seeds. In contrast, the experimental boluses made available to dispersers never had more than 40 seeds a piece, with over 50% of boluses having no chahta seeds at all. Boluses open to secondary dispersers and large seed predators had somewhat fewer seeds remaining than boluses only open to insects.
Table 1: Seven models to estimate how seed predation affects the number of seeds surviving seed predation and/or secondary dispersal. Model 5 was our best model, indicating that exposure of elephant dung to insects was the primary cause of seed loss. Contrary to expectations, dung boluses exposed to potential predation in the field longer lost fewer seeds, likely because dung piles left for longer periods were returned to the field in the cold months of winter, when invertebrate activity may be less. Dung freshly deposited in March or April may be easier for insects to find or penetrate. At bottom of table, \( k \): number of model parameters; QAIC\(_c\): quasi-Akaike’s Information Criterion corrected for small sample size (Zuur et al. 2009); wQAIC: QAIC\(_c\) weights representing the probability that a given model is the best in the candidate model set. \( \% \text{DE} \): percent deviance explained, which represents the percent of deviance explained by a given model compared to the “null” model with control fixed effects predictors “mass” and “dung pile ID”.

<table>
<thead>
<tr>
<th>Dependent variable is log(no. seeds)</th>
<th>(1)</th>
<th>(2)</th>
<th>(3)</th>
<th>(4)</th>
<th>(5)</th>
<th>(6)</th>
<th>(7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.86**** (0.091)</td>
<td>4.59**** (0.088)</td>
<td>4.05**** (0.088)</td>
<td>4.59**** (0.088)</td>
<td>4.54**** (0.089)</td>
<td>4.62**** (0.087)</td>
<td>4.54**** (0.089)</td>
</tr>
<tr>
<td>Mass in grams (scaled)</td>
<td>0.029 (0.038)</td>
<td>0.221**** (0.049)</td>
<td>0.203**** (0.046)</td>
<td>0.237**** (0.050)</td>
<td>0.241**** (0.050)</td>
<td>0.209**** (0.048)</td>
<td>0.259**** (0.051)</td>
</tr>
<tr>
<td>Insect only Treatment Dummy</td>
<td>-1.79**** (0.059)</td>
<td>-1.71**** (0.076)</td>
<td>-2.65**** (0.212)</td>
<td>-2.57**** (0.217)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All Seed Removers Treatment Dummy</td>
<td>-1.38**** (0.078)</td>
<td>-0.18**** (0.101)</td>
<td>-0.444**** (0.094)</td>
<td>-0.186* (0.102)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>#Days Left in forest</td>
<td>0.0125**** (0.105)</td>
<td>-0.021**** (0.001)</td>
<td>0.013**** (0.003)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dung pile ID</td>
<td>Fixed effect</td>
<td>Fixed effect</td>
<td>Fixed effect</td>
<td>Fixed effect</td>
<td>Fixed effect</td>
<td>Fixed effect</td>
<td>Fixed effect</td>
</tr>
<tr>
<td>k</td>
<td>53</td>
<td>54</td>
<td>54</td>
<td>55</td>
<td>55</td>
<td>55</td>
<td>56</td>
</tr>
<tr>
<td>QAIC(_c)</td>
<td>912.1</td>
<td>531.0</td>
<td>770.5</td>
<td>533.2</td>
<td>528.0</td>
<td>578.2</td>
<td>530.1</td>
</tr>
<tr>
<td>wQAIC(_c)</td>
<td>&lt;0.001</td>
<td>0.132</td>
<td>&lt;0.001</td>
<td>0.045</td>
<td>0.614</td>
<td>&lt;0.001</td>
<td>0.210</td>
</tr>
<tr>
<td>% DE</td>
<td>-</td>
<td>64.8</td>
<td>24.4</td>
<td>65.0</td>
<td>65.9</td>
<td>57.4</td>
<td>66.1</td>
</tr>
</tbody>
</table>

* \( p<0.1; \) ** \( p<0.05; \) *** \( p<0.01; \) **** \( p<0.001 \)
we found that leaving a bolus in the forest for longer corresponded with an increase in the number of seeds expected to be found in the forest. This finding must be considered in the context of our research design; all control boluses were left in the forest for 0 days, and treatment boluses (all of which were exposed to insect seed predation, and some to ASR) were left in the forest for between 26 and 102 days. Thus all treatment boluses were found to have fewer seeds than control boluses, as the former were exposed to insects—but boluses that were left for shorter periods of time were found to lose fewer seeds to predation. This counterintuitive result may be because our “days” variable was correlated with time of year: boluses left for shorter periods of time were deposited later in our study period, during the warmer and slightly wetter month of March. Thus, the proper interpretation of the model may be that insects were the main seed predators of chalta seeds from elephant dung, but elephant dung deposited in the drier, colder winter months experienced less seed predation than dung deposited later.

Our best model suggests that dung boluses deposited at the beginning of our dung collection period (in late December) lost about 74.7% of chalta seeds to seed predators by collection in April; boluses deposited in the middle of the period (mid-February) lost about 84.3% of their seeds; and boluses deposited at the end of the period (the end of March) lost about 90.2% of their seeds. If our interpretation of the “days” coefficient is correct—and that dung deposited in warmer months are more susceptible to attack—then elephant dung deposited in mid-late April (when “days” would be close to 0) would lose around 92.9% of their seeds to insect seed predators.

**Camera trapping**

Cameras monitored 32 dung piles for a total of 264 days (dung-pile days). While a large set of animals were observed moving past or around the dung, there were three groups of clear relevance to our study: insects, mammals that dug through the dung, and insectivorous and granivorous birds. Insects were visible in camera trap photos of only 5 dung piles, but termites were observed on 69.0% of boluses removed at the end of the experiment. Dung beetles were occasionally observed, but were not seen substantially dismantling dung. Rodents—species of rats and mice, mostly resembling house rats (*Rattus rattus*) and Himalayan rats (*Rattus nitidus*)—were photographed excavating 16 of the 32 dung piles monitored. Notably, they appeared to be able to fully deconstruct elephant boluses, exposing their internal contents.
(Figure 2). Indian barking deer (*Muntiacus muntjak*) twice excavated elephant dung, suggesting that (as in Africa) larger herbivores also use dung as a source of food. Finally, 11 species of birds—most frequently the red jungle fowl (*Gallus gallus*—photographed with 14 of 32 piles), but also the white-rumped shama (*Copsychus malabaricus*), emerald dove (*Chalcophaps indica*), peafowl (*Pavo cristatus*), white-tailed robin (*Myiomele leucura*), Indian pita (*Pitta brachyura*), snowy-browed flycatcher (*Ficedula hyperythra*), Siberian rubythroat (*Luscinia calliope*), grey-backed shrike (*Lanius tephronotus*), rufous-bellied niltava (*Niltava sundara*), and orange-headed thrush (*Zoothera citrine*)—were photographed on and around 25 of the 32 monitored dung piles. Birds were likely feeding on insects from the boluses; only jungle fowl ever majorly changed the structure of boluses, spreading the fibers much like the rats.

**DISCUSSION**

The high prevalence of chalta seeds in elephant dung confirms that elephants are frequent dispersers of *Dillenia indica’s* seeds. However, this study indicates that post-dispersal seed predation must be considered when measuring the effectiveness of elephants as seed dispersers. Around 84% of seeds were removed from elephant dung piles, with predation rates going as high as 93% for dung deposited late in the chalta’s fruiting season. This high post-dispersal mortality rate of seeds is not unusual. Seed predators in Central Borneo were found to destroy 88.3% of seeds dispersed by gibbons over 4-11 months (McConkey 2005a). Janzen (1982) found that 95.4% of Guanacaste seeds mixed in 8L of horse manure were removed by rodents in 10 nights, and Chapman (1989) found that 51.8% of seeds dispersed by primates in Santa Rosa National Park, Costa Rica, were removed from dung within five days. Estrada and Coates-Estrada (1991) found that rodents destroyed an average of 59% of the seeds per species dispersed by howler monkeys in Mexico in just 24 hours.

In contrast, it was insects—not rodents—that were the most formidable seed predator for seeds buried in elephant dung in Buxa, perhaps because recovering seeds from elephant dung as opposed to primate feces requires more work for rodents, as suggested by Janzen (1982). Understanding the factors that make dung piles more detectable and accessible to insects could thus help us predict the conditions that facilitate seed survival. The factors that determine insect predation of seeds may differ from those determining rodent predation of seeds. For instance, the density of dung clumps increased seed detection by rodents, but not by dung beetles in Central
Figure 2: Some of the visitors to elephant dung piles. The top row of pictures shows how rats can disassemble elephant dung from the form on the top left to the form on the top right, presumably in search of seeds, insects, and other food. The bottom row shows some of the serial visitors to elephant dung piles captured on camera: barking deer (Muntiacus muntjak), Siberian rubythroats (Luscinia calliope), jungle fowl (Gallus gallus), and white-rumped shamas (Copsychus malabricus). Jungle fowl visited nearly half the dung piles (14 of 32), and both barking deer and jungle fowl were found to be capable of substantially changing the structure of dung piles, much like the rats.
Amazonia (Andresen 2002). The fact that our model found more recently deposited dung to lose more of their seeds suggests that the seasonality of deposition matters; perhaps newly deposited dung piles smell more strongly or are softer and easier to penetrate, making them more susceptible to attack by insects, which are more active and abundant in the warmer spring months. If further research confirms this hypothesis, it could explain how seeds dispersed by large animals in the winter months survive the lengthy period until they germinate in the spring.

That non-insect seed predators and secondary seed dispersers had no net effect on the number of seeds in dung boluses was surprising given the various vertebrate species that we found to visit elephant dung. Since rodents excavated the dung, and are known seed predators of the chalta (Sekar and Sukumar 2013), one might expect that dung boluses in the “all seed removers” treatment would have fewer seeds than those exposed only to insects. Perhaps rodents did not open enough of the ASR treatment boluses. Even if rodents do consume seeds they find during excavation of elephant dung, perhaps rodents, barking deer, jungle fowl, and other animals sometimes serve unwittingly as seed rescuers by scattering the fibers of the bolus, reducing the probability that individual chalta seeds are consumed by termites and other seed predators. Seed predators often inadvertently become secondary dispersers (Dennis and Westcott 2006, Jansen et al. 2012). Rodents searching through elephant dung may have provided the selective force that has kept chalta seeds so small, even though megaherbivore-dispersed seeds, in theory, may benefit from being larger (Janzen and Martin 1982). Furthermore, insectivorous birds like the jungle fowl may rescue seeds by exerting some top-down control on insects that would otherwise destroy all the available seeds. As such, our dummy variable for “all seed removers,” which implicitly assumes that all larger dung visitors exert the same (either positive or negative) influence on seeds per dung bolus, may obscure a range of interactions that differ in their respective effects on the probability of seed survival, but that in net have no significant effect.

If further study confirms the high rate of chalta seed predation from elephant dung, is it still reasonable to consider elephants the primary disperser for Dillenia indica? The likely answer, at least in tropical moist forests such as Buxa, is yes. Elephants consume a much larger absolute number of fruit than the nearest alternatives, and pass a much higher proportion in their feces (Sekar and Sukumar 2013, Sekar et al. unpublished). Termites attack the dung of other animals, including domestic cattle, in addition to that of elephants (Freymann et al. 2008, He et al. 2013). Moreover, seed survival in elephant dung was not negligible in our study. Using the “extract”
boluses for comparison, about 59.0% of boluses with chalta seeds left in the open had at least one surviving chalta seed in them at the end of treatment (though this number may be lower by the time of germination a month later). In fact, reducing the number of chalta seeds per dung pile may improve the overall chances of recruitment post-germination by decreasing intraspecific competition or infection (Howe 1989, Harms et al. 2000). Finally, the number of dung piles followed in this study was modest. Based on experience from chalta feeding trials with captive elephants (Sekar et al. in review), 52 dung piles amount to the quantity of dung defecated by one elephant in 3–7 days. Since chalta trees in Buxa bear fruit over a period of four months, the number of chalta seeds surviving post-dispersal predation in absolute terms is still likely to be substantial.

In any case, our study confirms prior research suggesting that seed survival post-dispersal is a community affair (McConkey 2005a, Visser et al. 2011)—even elephants cannot fully rescue seeds from predation. The populations and interactions of other species—especially insects, but also perhaps their predators and rodents (DeMattia et al. 2004)—ultimately mediate elephants’ success as dispersers. As such, the effects that anthropogenic forces have on the populations of seed predators, seed rescuers, and secondary dispersers will also affect the nature of tropical forests (DeMattia et al. 2004, Terborgh et al. 2008).

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CHAPTER 5:

More than Just Charisma? Asian elephants are not easily replaceable as dispersers of large-fruited trees

AUTHORS: Nitin Sekar, Chia-Lo Lee, Raman Sukumar.

STATUS: In preparation for submission to PNAS
Abstract:

While the threat of global extinction motivates many conservation efforts, even the local extirpation of functionally non-redundant species could have undesirable effects on ecological processes and services. Yet ecologists have seldom been able to measure or predict the functional consequences of losing a species, even for the largest and most charismatic (and often extinction-prone) animals. In this study, we endeavor to measure the Asian elephant’s contribution to the dispersal of three large-fruit species in a typically disturbed Indian forest, as well as predict the extent to which alternative dispersers will be likely to compensate for elephants if they are lost. Our empirical probability model indicates that the loss of elephants would result in a reduction of about 26% (Artocarpus chaplasha), 42% (Careya arborea), and 66% (Dillenia indica) in the number of seeds dispersed of each plant species (in the absence of compensation by other seed dispersers). Median dispersal distance is reduced by an order of magnitude for A. chaplasha. In compensation scenarios, other frugivores could ameliorate these reductions in dispersal, making them as low as 6% if species such as gaur persist. Thus while elephants appear to be non-redundant as seed dispersers, their importance is dramatically amplified by the overall reduction of other disperser species throughout tropical Asia.

Keywords: Asian elephant (Elephas maximus), domestic cattle, domestic buffalo, ecological redundancy, ecosystem processes, extirpation, functional compensation, gaur (Bos gaurus) Rhesus macaques (Macaca mulatta), seed dispersal

Introduction

The global extinction crisis motivates conservation efforts to save species threatened by forces such as habitat loss, overhunting, and climate change (Brook et al. 2008). The existential threat of global extinction elicits and requires special attention. Yet for those concerned with the integrity of ecological processes and services, even the local extirpation of functionally essential species is a major concern. A better understanding of if, when, and how the local extirpation of a species affects ecosystem processes and services is key to developing a functionally oriented conservation paradigm (Tilman et al. 1997, Loreau et al. 2001, Dobson 2005).

While the ecology and conservation literature has long invoked the functional importance of individual species and biodiversity generally (Paine 1966, Power et al. 1966, Dobson 2005), conservation science has only occasionally been able to quantify or predict the functional effects.
of the local disappearance of a given species or guild (Solan et al. 2004, Terborgh and Estes 2010, Pattemore and Wilcove 2011). This is true even for large-bodied, charismatic animals that otherwise receive a great deal of cultural and conservation attention. Since larger animal species are disproportionately prone to extinction (Cardillo et al. 2005), their relative importance in sustaining ecological processes is immediately pertinent information (Dobson et al. 2006). Understanding the functional role of large-bodied species can be challenging for a variety of reasons (Terborgh 1988), but one key hurdle is assessing how the reaction of the remaining species in a community or ecosystem may mitigate the functional consequences of a single species’ extirpation; community-level assessment is key for identifying functional redundancy or compensatory mechanisms (Naeem et al. 2009). Without the data required to explore the possibility of compensation, much of the literature on the functional ecology of large-bodied and extinction-prone species cannot be used to make specific predictions about what may change due to extinction.

Our understanding of the functional ecology of megaherbivores as seed dispersers is a case in point. The dispersal of seeds from parent plants to sites where germination and establishment are more likely underpins the survival of most plant populations (Nathan and Muller-Landau 2000, Wang and Smith 2002). Observations and theory suggest that frugivorous megaherbivores—animals weighing over 1000 kg—should be functionally unique as seed dispersers (Janzen and Martin 1982, Naeem et al. 2009). African forest elephants and one-horned rhinos can eat tremendous amounts of fruit (Tchamba and Seme 1993, White et al. 1993, Dinerstein 2003). Asian and African elephants are known to travel long distances over short periods of time, allowing them to move seeds well beyond many distance- and density-dependent sources of mortality (Campos-Arceiz et al. 2008, Blake et al. 2009), helping plant populations shift as conditions change (Corlett 2009). Finally, seeds are believed to generally have high probabilities of surviving the megaherbivore gut and germinating in their dung (Nchanji and Plumptre 2003, White et al. 1993, Dinerstein 2003). As a result, researchers have surmised that, without megaherbivores, a whole guild of large-fruited or large-seeded species are likely to face dispersal limitation (Campos-Arceiz and Blake 2011). Such species may then be out-competed by smaller-seeded or abiotically dispersed vegetation, changing the character of forests, affecting other frugivores, and adding to the deterioration of biodiversity and any attendant ecological functions (Blake et al. 2009, Corlett 2009, McConkey et al. 2012).
However, showing that megaherbivores defecate large amounts of viable seeds is not enough information to understand their relative importance as seed dispersers, or how ecosystems may respond to their disappearance. Instead, a community-level analysis is necessary to understand how megaherbivores compare to other frugivores (Jordano and Schupp 2000), and whether smaller species can compensate for megaherbivores in their absence. A quantitative, empirical, mechanistic evaluation can help us measure the relative importance of a species for an ecosystem process, allowing us to predict how the ecosystem may change in that species’ absence.

In this study, we present an empirical probability model of the routine dispersal of the seeds of three large-fruited tree species in northeast India. Previous research in Buxa Tiger Reserve (Sekar and Sukumar 2013, Sekar and Sukumar in review, Sekar et al. in review) indicate that Asian elephants (Elephas maximus), domestic bovids (Bos primigenius and Bubalus bubalis) and Rhesus macaques (Macaca mulatta) are the most quantitatively important frugivores for the chalta tree (Dillenia indica), kumbhi tree (Careya arborea), and lator tree (Artocarpus chaplasha). Prior work also indicates that the gaur (Bos gaurus), wild pig (Sus scrofa), common palm civet (Paradoxurus hermaphroditus), Himalayan crestless porcupine (Hystrix brachyura), Malayan giant squirrel (Ratufa bicolor), rose-ringed parakeet (Psittacula krameri), and rat and small squirrel species were the minor frugivores of these tree species in Buxa. We combine empirical data on these animals’ frugivory rates, seed handling processes, and movement data from the literature to address two questions.

A. What percent of successfully dispersed seeds (SDS) are dispersed by Asian elephants compared to other frugivores? We define successfully dispersed seeds as seeds that survive the Janzen-Connell effect, the effects of disperser-specific gut passage, and intra-feces intra-specific competition.

B. If elephants were to be extirpated in this region, how would this change the quantity and distance of seeds dispersed? We explore three scenarios for the fruit that would have been eaten by elephants. The first is a proportional compensation model which presumes a healthy frugivore community after elephant extirpation. Here, the remaining terrestrial frugivores eat both the fruits they would normally eat and a proportion of the fruits formerly eaten by elephants based on the proportion of fruits they currently consume (Sekar and Sukumar 2013, Sekar and Sukumar in review);
this scenario, no additional fruits rot without elephants. In the second scenario, all fruits that would have been eaten by elephants are eaten by domestic bovids, whose population and range in Buxa may be growing. This scenario assumes that other wild dispersers continue to remove the same amount of fruit as before, but are unable to compensate for elephants; here, too, no additional fruits rot. Finally, we calculate the likely effects on dispersal if there is no compensatory frugivory in the absence of elephants, and all fruits formerly eaten by elephants rot.

Overall, we provide the most comprehensive, quantitative estimate of the relative importance of a megaherbivore in seed dispersal that we know of, allowing us to make basic predictions on how seed dispersal may change without the Asian elephant. Our community-level model gauging the functional contribution of elephants to seed dispersal adds to our understanding of the changes that occur through local extirpation of a large-bodied species.

Results

Relative importance of elephants for successful seed dispersal

Elephants are one of the top two dispersers of successfully dispersed seeds for each of the three tree species in Buxa, dispersing more chalta SDS than any other animal (Figure 1). In our best estimate model, we find that elephants disperse 28% (SE=0.9%) of lator SDS, 33% (SE=1.8%) of kumbhi SDS, and almost 67% (SE=0.8%) of chalta SDS (Table 1).

Janzen-Connell processes have a substantial effect on how many seeds initially dispersed by macaques, giant squirrels, and rose-ringed parakeets and other birds survive, while intra-dung competition heavily affects the survival of seeds dispersed by elephants, gaur, and domestic bovids (Figure 1). Macaques disperse about 83% of initially dispersed lator seeds, mostly through spitting or dropping of seeds while feeding. Since so many seeds remain close to the parent tree and are subject to distance-dependent mortality, macaques ultimately disperse about 56.9% of successfully dispersed lator seeds. While elephants disperse 83% of initially dispersed chalta seeds, allowing only one seed to survive per dung pile means that elephants ultimately disperse just 66.9% of chalta SDS. Intra-dung competition is shown to have less effect on chalta and lator seeds defecated by domestic bovids since few seeds survive in each dung pile—but such competition has more of an effect on bovid-defecated kumbhi seeds. Domestic bovids
Figure 1: Bar plots showing the relative number of initially dispersed seeds by each disperser species, as well as the number of seeds that survive Janzen-Connell effects, germinate after dispersal, and survive conspecific intra-dung competition. Bars show the average number of seeds from 100 iterations of the model, and error bars illustrate the standard error.

a) For the chalta tree, elephants disperse the most seeds initially, and most of these seeds are untouched by distance-dependent mortality, i.e. Janzen-Connell effects. Germination rates for elephant-defecated chalta seeds are also high. However, since tens to hundreds of chalta seeds may share a single dung pile and only one is likely to win out, intra-dung competition reduces the number of surviving seeds by around 90%. Seeds dispersed by gaur similarly face substantial intra-dung competition; macaques face less.

b) For kumbhi, domestic bovids disperse the most seeds initially, despite having lower gut passage proportions than elephants. However, since the same cattle visit fruiting kumbhi trees over and over again, they tend to have
more kumbhi seeds per dung pile than elephants (see SI); this increases intra-dung competition.

c) Finally, for lator, initial dispersal is dominated by macaques, which disperse nearly ten times as many seeds as the closest competitor. Janzen-Connell effects dramatically reduce survival of most of these seeds since they are dropped under or near the canopy of the parent tree; the same happens for seeds dispersed by rose-ringed parakeets and other birds. Still, macaques ultimately prove to have dispersed the most successfully dispersed lator seeds, with elephants a distant second.
Table 1: The percentage of “successfully dispersed” seeds (SDS) dispersed by each frugivore. Our best estimate model is itself conservative with regards to the likely importance of elephants, making assumptions that were difficult to test in the field. For instance, the best estimate model assumes that species such as wild macaques and gaur will defecate the same proportion of ingested seeds as elephants. The “most conservative” and “generous” models use parameter estimates that are plausible but less likely to hold. While we vary up to eight parameters amongst the three model types, most of the differences in estimates are driven by our estimates of gut passage proportions for macaques and gaur (chalta), the strength of the Janzen-Connell effect (kumbhi, lator), the proportion of fallen fruits that rot (kumbhi, lator), and the number of seeds that survive per dung pile for gaur and elephants (all). Overall, our best estimates suggest elephants may be responsible for around one-third of successfully dispersed lator and kumbhi seeds, and closer to two-thirds of chalta seeds.

<table>
<thead>
<tr>
<th>Animal species</th>
<th>Chalta</th>
<th></th>
<th>Kumbhi</th>
<th></th>
<th>Lator</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Best Estimate</td>
<td></td>
<td>Most Conservative Model</td>
<td></td>
<td>Generous Model</td>
<td></td>
</tr>
<tr>
<td>Elephant</td>
<td>66.9 (0.8)</td>
<td></td>
<td>63.9 (1.1)</td>
<td></td>
<td>93.6 (0.2)</td>
<td></td>
</tr>
<tr>
<td>Gaur</td>
<td>6.3 (0.4)</td>
<td></td>
<td>6.7 (0.4)</td>
<td></td>
<td>1.7 (0.1)</td>
<td></td>
</tr>
<tr>
<td>Domestic Bovids</td>
<td>2.7 (0.2)</td>
<td></td>
<td>3.1 (0.2)</td>
<td></td>
<td>2.4 (0.1)</td>
<td></td>
</tr>
<tr>
<td>Wild pig</td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
</tr>
<tr>
<td>Macaques</td>
<td>22.0 (0.8)</td>
<td></td>
<td>23.7 (0.09)</td>
<td></td>
<td>0.8 (0.06)</td>
<td></td>
</tr>
<tr>
<td>Civet</td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
</tr>
<tr>
<td>Porcupine</td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
</tr>
<tr>
<td>Giant Squirrel</td>
<td>0.49 (0.04)</td>
<td></td>
<td>0.74 (0.05)</td>
<td></td>
<td>0.4 (0.04)</td>
<td></td>
</tr>
<tr>
<td>Small rodents</td>
<td>1.6 (0.09)</td>
<td></td>
<td>1.9 (0.12)</td>
<td></td>
<td>1.1 (0.07)</td>
<td></td>
</tr>
<tr>
<td>Parakeets, other birds</td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
<td>___</td>
<td></td>
</tr>
</tbody>
</table>
initially disperse 22% more kumbhi seeds than elephants, but bovids ultimately disperse nearly the same number of kumbhi seeds as elephants due to intra-dung competition.

*Robustness checks*

While our main model was itself conservative with respect to the relative importance of elephants as dispersers, as a robustness check we ran our model with a set of “most conservative” parameter values that were plausible but likely underestimated the relative quantitative importance of elephants as seed dispersers. We similarly re-ran our model with a “generous” set of parameter values that, while reasonable, may over-estimate the quantitative role of elephants as dispersers. We varied between five (chalta) and eight (kumbhi) parameters for these checks (see Methods). In our most conservative models, allowing a weaker Janzen-Connell effect and increasing the proportion of kumbhi and lator fruits that rot on the ground make macaques and other arboreal frugivores relatively more important as dispersers; for kumbhi, we also allow arboreal frugivores to remove twice as many fruits as was observed since we had limited empirical data (Sekar and Sukumar in review). This scenario made giant squirrels and macaques more important than terrestrial dispersers for kumbhi. In our generous model, allowing for lower GPPs for gaur and macaques and allowing two seeds to survive per dung pile for elephants and gaur (due to wider spatial distribution of a dung pile) promote the relative success of elephants as dispersers. In our most conservative models, elephants disperse no less than 17% of successfully dispersed seeds (for kumbhi) and continue to disperse over 60% of successfully dispersed chalta seeds. If gaur and macaques destroy as high a proportion of chalta seeds as domestic bovids—as stipulated in the generous model—elephants may be responsible for 94% of successfully dispersed chalta seeds in our study system.

*Potential compensatory seed dispersal in the absence of elephants*

In the absence of elephants, the remaining dispersers are not able to fully compensate for elephants’ contribution to the seed shadows (here, the spatial distribution of successfully dispersed seeds) of the three tree study species. For all three tree species, segments of the elephant’s seed shadow do not overlap with any other disperser’s, illustrating their unique,
complementary contribution to seed dispersal (Figure 2). Elephants take seeds an order of magnitude farther than domestic bovids and almost four times farther than gaur.

Table 2 shows how the number of seeds dispersed and distance of seed dispersal change for each of the three fruit species under the three compensation scenarios. As we assume that gaur and macaques are able to pass a similar proportion of chalta seeds to elephants without digesting them, the overall reduction of seeds dispersed in a proportional compensation scenario is 6%. In the scenario that only domestic bovids are able to absorb the chalta fruits left unconsumed by elephants, there is a 53.5% reduction in successfully dispersed seeds driven by domestic bovids’ poor gut passage proportions. Without elephants, the median dispersal distance falls 54-66%.

For kumbhi, since domestic bovids are already the main consumer of fruit, the proportional and domestic bovid compensation scenarios are fairly similar. About 25-30% fewer seeds are successfully dispersed without elephants, and median seed dispersal distance falls by about 33%.

About 9-15% fewer lator seeds are likely to be successfully dispersed in the absence of elephants; since elephants disperse a smaller proportion of successfully dispersed seeds, the quantitative effect of their absence is reduced. However, the median dispersal distance drops by an order of magnitude without elephants, from 210m to about 20m; this means that the size of the possible area to which the median lator seed may arrive is one-one-hundredth of that accessible in the presence of elephants.

**Discussion**

Our empirical probability model indicates that elephants form a quantitatively and qualitatively integral part of the seed shadows of *Dillenia indica*, *Careya arborea*, and *Artocarpus chaplasha*. Even when we attempt to account for the likelihood that most seeds in the same dung pile will not survive, elephants still prove to be disproportionately intrepid vessels of dispersal due to their high gut passage proportions. The megaherbivores eat only some 9.7% and 18.4% of frugivore-consumed lator and kumbhi fruit, respectively (Sekar and Sukumar in review), but they disperse 28% of lator SDS and 33% of kumbhi SDS. Camera trap data suggest that elephants also consume about 65% of fallen chalta fruits (Sekar and Sukumar 2013), and are responsible for dispersing almost 67% of successfully dispersed chalta seeds.
Figure 2: The seed shadows for successfully dispersed chalta, kumbhi, and lator seeds with and without elephants on a log-log scale. Note that each 10-m bin looks thinner as distance increases. The dotted and solid lines show how the median and mean distances of dispersal, respectively, change in the different scenarios. For all three tree species, the unique role elephants play in long-distance dispersal is evident; domestic bovids do not take seeds over 5 kilometers, and gaur hardly surpass 10 kilometers, but elephants take seeds up to 40-50 kilometers. In contrast, the redundancy in short-distance dispersal is also evident, with macaques, giant squirrels,
rodents, parakeets, and other species all dispersing some seeds close to the parent tree, though macaques are quantitatively the most important. The differences between the macaque’s seed shadows for chalta compared to lator and kumbhi reflect how the larger seed sizes of the latter may affect the probability of ingestion and dispersal by medium-sized frugivores. Elephants are the most quantitatively important for chalta seeds.
Table 2: Results of the compensation models, showing how the number and distance of seeds dispersed may change without elephants. “Available seeds” means all the seeds in the system per iteration, or the number of fruits x seeds/fruit. We use per mille of available seeds so that the denominator remains constant amongst models, facilitating comparison. The number of seeds dispersed falls more than 9% without elephants in all cases except in the chalta proportional compensation model, where gaur and macaques are simulated as ingesting all the seeds they handle and having the same gut passage proportion as elephants. The median distance of dispersal falls considerably without elephants, particularly for lator seeds, for which the decline is an order of magnitude.

<table>
<thead>
<tr>
<th>Fruit species</th>
<th>Model type</th>
<th>Per mille (%) of available seeds dispersed by species (with standard errors)</th>
<th>Model summaries</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Elephant</td>
<td>Gaur</td>
</tr>
<tr>
<td>Chalta</td>
<td>With elephants</td>
<td>17.3 (0.277)</td>
<td>1.61 (0.097)</td>
</tr>
<tr>
<td></td>
<td>Proportional compensation</td>
<td>______</td>
<td>4.55 (0.157)</td>
</tr>
<tr>
<td></td>
<td>Compensation by domestic bovids</td>
<td>______</td>
<td>1.8 (0.112)</td>
</tr>
<tr>
<td></td>
<td>No compensation</td>
<td>______</td>
<td>1.67 (0.112)</td>
</tr>
<tr>
<td>Kumbhi</td>
<td>With elephants</td>
<td>30.3 (2.00)</td>
<td>______</td>
</tr>
<tr>
<td></td>
<td>Proportional compensation</td>
<td>______</td>
<td>______</td>
</tr>
<tr>
<td></td>
<td>Compensation by domestic bovids</td>
<td>______</td>
<td>______</td>
</tr>
<tr>
<td></td>
<td>No compensation</td>
<td>______</td>
<td>______</td>
</tr>
<tr>
<td>Lator</td>
<td>With elephants</td>
<td>8.71 (0.273)</td>
<td>______</td>
</tr>
<tr>
<td></td>
<td>Proportional compensation</td>
<td>______</td>
<td>______</td>
</tr>
<tr>
<td></td>
<td>Compensation by domestic bovids</td>
<td>______</td>
<td>______</td>
</tr>
<tr>
<td></td>
<td>No compensation</td>
<td>______</td>
<td>______</td>
</tr>
</tbody>
</table>
In the field, it was found that fruits of all three species rotted commonly (Sekar and Sukumar 2013, Sekar and Sukumar in press), suggesting that the frugivore community of Buxa is saturated even though elephants are present; thus, compensatory frugivory in the case of the local extirpation of elephants may not be likely. Yet even if all the fruits eaten by elephants are consumed by other species, the character of the tree species’ overall seed shadows will change—median seed dispersal distances decrease, and the overall number of seeds successfully dispersed will decrease by as much as 54%. Given the remaining challenges faced by successfully dispersed seeds trying to establish as seedlings, such a reduction in dispersal could be consequential. The magnitude of this decrease in dispersal depends on both the characteristics of the fruit and the alternative dispersers. The small seed size of the chalta makes it plausible that smaller animals like the Rhesus macaque can swallow and defecate the seed whole, facilitating dispersal distances over a kilometer. The chalta also is consumed by gaur, a far-traveling giant that can surpass 1000kg (Clauss et al. 2003); thus, the loss of one megaherbivore, the elephant, can be best mitigated by the frugivory of another megaherbivore. In contrast, kumbhi and lator trees produce 1.5cm seeds which are only occasionally swallowed by macaques; in the field, even civets and wild pigs were found to leave kumbhi seeds behind after feeding (Sekar and Sukumar in review). All this supports the theory that larger frugivores—like elephants—become more important for long-distance dispersal of larger seeded species (Yumoto 1995, Blake et al. 2009), even when they remove a relatively small amount of the species’ fruit.

The shortcomings of domestic bovids as replacement dispersers for elephants underscores that body size is most useful if it enables high gut passage proportions. Cattle and buffaloes, like tapirs (Campos-Arceiz et al. 2012), do not pass a high enough proportion of ingested seeds of the researched species to supplant elephants. To the extent that gaur and macaques mitigate the loss of elephants in the proportionate compensation model, it is because we assume them to have high, elephant-like gut passage proportions (see Methods/SI). The gaur is rare in that it is both a megaherbivore and a ruminant; its properties as a seed disperser deserve further exploration.

Elephants also differ notably from domestic bovids in their ranging tendencies, allowing the megaherbivores to disperse seeds up to 10 times as far (Sekar et al. unpublished). The dramatic decline in median seed dispersal distance for the three tree study species is particularly consequential in the disturbed landscape of Buxa Tiger Reserve, where work by Sukumar et al. (2003) showed that chalta, kumbhi, and lator trees make up only 0.2%, 0.2%, and 0.02% of adult
trees over 1 cm in width, respectively. In order to compete for patches in the abandoned plantations and forest fragments characteristic of South Asia, greater dispersal distances are key.

The notable seed mortality occurring due to intra-dung, intraspecific competition highlights the benefits plants may accrue from distributing a given number of seeds across as many dung piles and feces as possible (Howe 1985)—this means getting fruits to different individuals at different times, even if the dispersers are the same species. The high number of kumbhi seeds per cow dung pile we found (and used to inform this model, see SI) were likely a consequence of the same individual cattle visiting the same areas day after day (Sekar et al. unpublished), gradually accumulating seeds in their system. This was not ideal from the kumbhi’s perspective. In contrast, the chalta tree spreads its fruiting season out over many months (Sekar and Sukumar 2013), and the movement data indicates that elephants likely have less regular routes than domestic bovids (Sekar et al. in review), potentially making intra-dung competition less that it would otherwise be. As a result, the effects of intra-dung competition in elephants do not negate their role as dispersers.

So what do our findings mean for other fruiting species? Our data suggest a dualistic role for elephants as dispersers. For less accessible megafaunal fruits like the chalta, elephants tend to be quantitatively important as dispersers: small animal species simply cannot process as much fruit, and other large animal species (who can move seeds large distances) tend to be too rare to pick up the slack left by elephants. For more widely accessible fruits like the lator, elephants turn out to be more qualitatively important: most of the seeds handled by smaller frugivores tend to be deposited near the parent tree, and the small proportion of seeds dispersed by elephants dramatically increase the median dispersal distance. Since our three tree study species have small- or medium-sized seeds, this duality may apply to a large number of other plants; further work on species ranging from the wild mango (*Mangifera indica*) to wild figs (*Ficus* spp) may confirm that the dispersal of other fruiting species would suffer either quantitatively or qualitatively without megaherbivore dispersers. On the other hand, our specific findings may not fully apply even to our three tree study species in a totally in-tact frugivore community. For trees in forests with healthy populations of civets, fruit bats, macaques, porcupines, wild pigs, sloth bears, and other frugivores all ingesting or moving seeds, assuming reasonably high GPPs, elephants may not be quite so quantitatively crucial; their particular functional importance may be a consequence of the disturbed context in which we worked.
Yet since such disturbed forests with low densities of large- and medium-bodied species are now the norm in tropical Asia (Corlett 2007, McConkey et al. 2012), the broader consequences of losing elephants in already-defaunated ecosystems should be considered. Would the tree composition of tropical Asian forests come to look much different without elephants available to disperse seeds? Work in the Neotropics has shown how the loss of medium-sized dispersers (Terborgh et al. 2008) and the region’s megafauna (Guimaraes et al. 2008) have likely changed species distribution and the composition of forests. Our work suggests that, unlike the livestock believed to have replaced gomphotheres in Costa Rica (Janzen 1981, Janzen and Martin 1982), domestic buffalo and cattle are a poor substitute for elephants. Still, there are also many reasons to suspect that the loss of elephants would not result in unrecognizable ecosystems. First, observers have noted that mammal-dispersed fruiting species are not dominant in many Asian ecosystems, a contrast to tropical Africa (Campos-Arceiz and Blake 2011); this could mean that fewer species are dispersed by elephants (as suggested by Kitamura et al. 2002 and Kitamura et al. 2007), though it could also mean that reductions in successful dispersal of fruiting trees due to elephant extirpation could have sizeable effects on smaller animals that seem to rely on fruit, as Rhesus macaques seem to rely on lator (Sekar and Sukumar in review).

Secondly, fruits may undergo rapid selection to become more palatable and disperse-able by smaller creatures. *Dillenia indica*, for instance, may become softer so that macaques and civets can disperse its 6-mm seeds (Sekar and Sukumar 2013); *Artocarpus chaplasha* has apparently already found a way to survive in the Andaman Islands without endemic elephants (Sahni 1998). In Brazil, researchers showed that the loss of toucans led to the swift evolution of smaller seeds (Galetti et al. 2013), an adaptive trajectory that may be within the reach of many fruiting species, though smaller seeds are often less likely to survive (Howe and Miriti 2004). Additionally, occasional dispersal by small rodents (e.g., Jansen et al. 2012) and dispersal by water, which we did not explicitly quantify for kumbhi or lator, may ameliorate the effects of the loss of elephants. While our work confirms that elephants can play a unique role as a disperser, the dynamic adaptability of forests means we cannot yet surmise the broader consequences of elephant extirpation.

Still, two broader theories gain currency from our study. First, the loss of megaherbivores is likely to add to the dynamics of global change; such extirpations may exacerbate stresses occurring due to climate change and habitat destruction, making our world’s ecosystems less
recognizable and less rich (Campos-Arceiz and Blake 2011, McConkey et al 2012). Secondly, the largest species in an ecosystem do appear to have ecological properties that other species do not have—in this case, high gut passage proportions and large range sizes. Thus ecosystems may not be able to compensate for their loss using their other players (Owen-Smith 1988, Hansen and Galetti 2009). Elephants have been shown to create habitat for smaller animals by damaging trees (Pringle 2008) and simply by defecating (Campos Arceiz 2009). Owen-Smith (1988) writes that megaherbivores help keep the savannas lush by serving as a drip-fertilization system, maintaining or even boosting nutrient levels at precipitation levels from 700 to 1200 mm a year. The largest species in other systems perform uniquely in functions ranging from bioturbation (Solan et al. 2004) to disease dilution (Ostfeld and LoGiudice 2003). The large-bodied animals in an ecosystem may be not only charismatic but highly functional, and our study provides considerable evidence that their role in maintaining ecological processes should be considered in our conservation calculus.

**Methods**

*Study species and study area*

We try here to quantify the role of elephants in dispersing the seeds of three species: *Dillenia indica* (the chalta tree), *Careya arborea* (the kumbhi tree), and *Artocarpus chaplasha* (the lator tree) in Buxa Tiger Reserve in northern West Bengal, India. Buxa is composed of tropical and subtropical moist forests and plantations. The chalta tree fruits in the dry season (December-May) in Buxa; its fruits are hard and weigh about half a kilogram, with about 103 6mm seeds per fruit. The kumbhi and lator trees fruit in the monsoon, with the kumbhi possessing smaller fruit with an average of six 1.5cm seeds per fruit. The lator’s fruit, which resembles that of the jackfruit (*Artocarpus heterophylla*) average about 466 g, and have seeds resembling the kumbhi’s in size. For more information on the study site and species, please see (Sekar and Sukumar 2013, Sekar and Sukumar in review, Sekar et al. in review).

*The empirical probability model*

Our model proceeds in four parts (See *Figure 3*). Beginning with an arbitrary number of fruit, the first section of the model allocates a proportion of the fruit available to each frugivore species based on empirical observations, primarily from focal watches and camera traps (Sekar...
Figure 3: A summary of the empirical probability model used. Each arrow in the left part of the figure indicates a probability calculated from empirical studies or the literature (see SI). Arboreal frugivores (mostly macaques) remove some fruits, while the rest go to the ground. While some fallen fruit rot, the rest are allocated amongst terrestrial frugivores. Frugivores that drop seeds are modeled as doing so, while those that ingest the seeds are modeled to digest a proportion of them and pass the rest into their dung. Then, since each surviving seed is associated with a disperser species, dispersal distance, and (if defecated) gut retention time, a probability of post-dispersal survival can be calculated and used to translate initially dispersed seeds to successfully dispersed seeds, as described in right part of figure.
and Sukumar 2013, Sekar and Sukumar in press). In essence, we use the proportions of fruit that meet each fate (removal by a specific frugivore in the canopy, fruit fall, or removal by a terrestrial frugivore) in bootstrapped samples of our data to determine what proportion of fruit will be removed by each frugivore for every iteration of the model. A certain proportion of fruit is also set to rot based on field data, with the precise rotting rate for each iteration of the model being sampled from a binomial distribution defined by the number of fruits whose fate was observed.

Once all the fruits are allocated to a frugivore (or rotting), the second part of the model emulates seed handling by each disperser. For elephants and bovids, data from feeding trials is used to determine the proportion of seeds that survive gut passage (gut passage proportion, or GPP) (Sekar et al. unpublished); for Rhesus macaques, we use observations from focal watches and seed transects (Sekar and Sukumar in press) to estimate the probability of seed swallowing versus dropping, and data from feeding trials of Japanese macaques (Tsuji et al. 2010) to estimate GPP. The GPPs vary each iteration of the model based on the variation in the data. We make conservative assumptions about how many seeds survive ingestion by the remaining dispersers, allowing for a conservative estimate of the relative importance of elephants as dispersers.

Next, each surviving seed is assigned a distance of dispersal. Seeds spit or dropped near the parent tree are assigned a distance based on the distribution of distances from seed transects conducted under lator trees (Sekar and Sukumar unpublished, McConkey and Brockelman 2011). Seeds ingested by elephants, domestic bovids, and macaques are assigned a gut retention time (GRT) based on the distribution of GRTs found during feeding trials (Sekar et al. in review) or the literature (Tsuji et al. 2010). Movement data on elephants, domestic bovids, and wild Rhesus macaques are then used with the GRT to estimate how far each seed is dispersed from the parent tree, as done in Sekar et al. (unpublished), Campos-Arceiz et al. (2008), and Lenz et al. (2011). For the remaining, minor dispersers (except gaur, Bos gaurus) we assume seeds are uniformly distributed over a distance determined by the literature on their territory size. A rudimentary model of gaur movement was developed based on Conry (1989), which provides data on how far gaur moved between consecutive daily locations.

The final part of the model calculates the probability of post-dispersal fatality of seeds due to several dispersal-related processes, translating initially dispersed seeds to successfully
dispersed seeds. A probability of a seed’s survival of Janzen-Connell processes is simulated using the empirically derived model from Swamy et al. (2011), in which the probability of seeds surviving to adulthood is a function of distance from a conspecific tree (in the model, the parent tree). We then use the disperser-specific germination rates of chalta, kumbhi, and lator seeds from our feeding trials to estimate the probability of germination for the remaining seeds (Sekar et al. unpublished). Since elephant-defecated seeds germinated at least as well as seeds directly from fruit for all three species, we use the germination rates of seeds from elephant dung for seeds passed by dispersers for which we lack data. Finally, we attempt to account for the fact that only a limited number of seeds (typically one) in a single fecal mass is likely to ultimately establish due to intraspecific competition. In order to determine the probability that a seed in the model (a “focal seed”) will be the one to survive intra-dung competition, we model the likely number of seeds to be found in each dung pile along with that focal seed. To do so, we approximate the number of seeds to be consumed and defecated by a wild disperser. First, we sample from the numbers of marked fruit to go missing when a disperser triggered a camera trap (see Sekar and Sukumar 2013). If, for instance, 15 fruits went missing one day when an elephant triggered the camera, we assume all the fruits were eaten by one elephant. Then, using the focal seed’s gut retention time, we calculate the approximate proportion of consumed seeds likely to be in the same dung pile as the focal seed based on data from the feeding trials. Since the same elephant may have eaten fruit on multiple occasions, we then add additional seeds based on one or two randomly timed additional feedings. For chalta, we were able to approximate the number of additional feedings each elephant was likely to partake in using data on the number of chalta seeds per wild elephant dung pile (Sekar and Sukumar 2013).

As a robustness check, we vary up to eight parameters in our model to create a “most conservative” and “generous” model with regards to the relative importance of elephants for the dispersal of each tree species. We altered the proportion of fruits taken by arboreal frugivores (kumbhi), proportion of seeds swallowed by macaques (kumbhi, lator), proportion of fruit rotting (kumbhi, lator), strength of the Janzen-Connell effect (all species), expected number of elephants per tree visit (kumbhi, lator), the number of seeds surviving per dung pile for large frugivores (all species), macaque gut passage proportions (all species), gaur gut passage proportion (chalata), and the probability of bovids eating fruit multiple times within gut retention time (kumbhi) For more information, see SI.
Modeling compensatory seed dispersal in the absence of elephants

We changed only one set of parameters for the compensation models. In order to model proportional compensation, we divided up the fruits originally allocated to elephants to each of the other terrestrial frugivores based on the proportion of the remaining removed fruits that they consumed. In the case of the domestic bovid compensation model, all fruits initially allocated to elephants were allocated to the domestic bovids. In these two models, there was effectively no change in the amount of fruit that was modelled as rotting.

In the final model with no compensation, all the fruit that had been allocated to elephants was effectively set to rot.

Acknowledgments

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References


Sekar, N., Lee, C., & Sukumar, R. (in review). In the Elephant’s Seed Shadow: the prospects of domestic bovids as replacement dispersers of three tropical Asian trees.


Section 1: Equations, principles, and assumptions underlying the empirical probability model

Each iteration of the model represents the fate of 100-300 fruits’ seeds over the course of one fruiting season. The model essentially goes through four parts. Here we will cover the main variables and parameters for each part and explain how they were calculated or derived.

Part 1: Allocating fruit

First, fruit in the tree is allocated to the dispersers, or to rot.

Arboreal species (sp) are allocated fruit as follows...

\[ f_{sp-arb} = a_{sp} \times F \]  

(Eq 1)

Terrestrial species (sp) are then allocated fruit as follows...

\[ f_{sp-terr} = a_g \times F \times (1 - R) \times g_{sp} \]  

(Eq 2)

\[ f_{sp} = f_{sp-arb} + f_{sp-terr} \]  

(Eq 3)

Table S1: Parameters and justifications for parameter choice for the fruit allocation part of the empirical probability model.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>MEANING</th>
<th>ESTIMATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>( F )</td>
<td>The number of fruit whose fate is being estimated.</td>
<td>Arbitrary</td>
</tr>
<tr>
<td>( f_{sp} )</td>
<td>Number of fruit consumed by species ( sp ) over an iteration of the model; it is the sum of the number of fruits taken by that species arboreally and terrestrially.</td>
<td>See equation 3 above.</td>
</tr>
<tr>
<td>( a_{sp} )</td>
<td>The proportion of fruit available in the canopy being removed by arboreal species ( sp ) (macaques, giant squirrels, Chalta: Focal watches and the ratio of “split” fruit (excavated by frugivores) to total fallen fruit per day (Sekar and Sukumar 2013). For each iteration, the ratio is calculated by creating a bootstrap sample of the number of</td>
<td></td>
</tr>
</tbody>
</table>
rose-ringed parakeets and other birds) split fruit and fallen fruit, and dividing the former by the sum of the two.

| **Kumbhi:** Arboreal camera trapping—proportion of monitored fruits removed by Malayan giant squirrel (Sekar and Sukumar unpublished). For each iteration, $a_{sp}$ was sampled from a binomial distribution centered around 0.133, with SE determined using $n=30$. We randomly divided $a_{sp}$ amongst macaques and giant squirrels; the former had not been caught on arboreal camera traps, but had been seen in kumbhi trees and caught on terrestrial cameras. Since macaques are likely to be better dispersers than giant squirrels (e.g. Kitamura et al. 2004), assuming macaques disperse kumbhi seeds allows for a conservative estimation of the relative importance of elephants.

| **Lator:** Focal watches—estimated proportion of fruit removed by Rhesus macaques and birds, as opposed to allowed to fall to ground. The proportion is calculated using a bootstrapped sample of 5-minute intervals from all the focal watches, from which we determine the number of fruit consumed per day, as in Sekar and Sukumar (in review). We then do a similar operation using the fruit fall data, and divide the average number of fruit removed by species $sp$ per day by the sum of the fruit removed and dropped.

| $a_g$ | The proportion of fruit available in the canopy that fall to the ground. Converse of above, $a_{sp}$ |

| $R$ | Proportion of fallen fruit that rot before being handled by frugivore. **Chalta:** The fate of several hundred fallen fruit were followed, and the proportion rotting was thus determined (Sekar and Sukumar 2013); a binomial distribution was used to generate variation across iterations.

| **Kumbhi/Lator:** 24.6 of monitored 71 monitored lator fruits rotted instead of being removed (Sekar and Sukumar in review). A binomial distribution was used to generate variation across iterations. Due to lack of data, the same estimate was used for kumbhi, which fruits at the same time as lator trees. |
The proportion of fallen, non-rotten fruit taken by terrestrial disperser *sp* over the course of a season.

Camera trap data allows us to calculate the total fruit removed by frugivore *sp* over 2 years and divide that by the total number of fruit-days available (e.g., 3 fruit in front of a camera for 2 days means 6 fruit-days). This gives us an estimate of the number of fruits species *sp* removed per day.

### Part 2: Seed handling

Now we must emulate seed handling by each species to determine a) what proportion of seeds are ingested versus discarded (spit, dropped, or thrown) immediately, and b) what proportion of ingested seeds will survive.

*How many seeds are discarded instead of ingested?*

Observations from Sekar and Sukumar (2013) make it plausible that few if any chalta seeds are discarded; all chalta seeds are treated as ingested.

For kumbhi and lator, Sekar and Sukumar (in review) indicate that parakeets drop all the seeds they handle, and all the terrestrial dispersers aside from macaques appear to ingest the seeds. That means that deciding how many seeds were ingested was a concern only for macaques and for giant squirrels (and giant squirrels only ate kumbhi fruits).

We assumed that macaques’ handling of kumbhi seeds resembled their handling of lator seeds, since the seeds are very similar in size and kumbhi seeds are even easier to discard. While giant squirrels are generally thought to drop seeds of this size (Kitamura et al. 2004), we also assumed that giant squirrels swallowed the same proportion of kumbhi seeds as macaques did lator seeds, again facilitating a conservative estimate of the relative importance of elephants in distance dispersal.

So…

(Eq 4) \[ se_{sp} = f_{sp} * s_f * (1 - disc_{sp}) \]

(Eq 5) \[ sd_{sp} = f_{sp} * s_f * disc_{sp} \]

… where \( se_{sp} \) is the number of seeds species *sp* ingests, and \( sd_{sp} \) is the number of seeds whose seeds species *sp* discards. \( s_f \) is the average number of seeds per fruit for the given tree species, and \( disc_{sp} \) is the proportion of handled seeds that is discarded (instead of ingested). \( disc_{sp} \) is 0 for all terrestrial dispersers except macaques and giant squirrels, and
\( \text{dis}c_{sp} \) is 1 for birds. For macaques and giant squirrels, \( \text{dis}c_{sp} \) is 0.944 with a standard error of 0.024 (computed assuming a binomial distribution, as \( n=90 \)), based on data presented in Sekar and Sukumar (in review).

**How many of the ingested seeds are defecated?**

Sekar et al. (in review) conduct feeding trials of elephants and domestic bovids, feeding them all three of the fruit study species. This provided gut passage proportions (GPP) for 3 to 8 individuals for each plant-animal combination. Since we had only a few individuals for some of the combinations, we came up with a more mechanistic way of incorporating the variation in GPP than to take the mean. For each GPP calculated for a given species, we allocate a random proportion of the seeds to be funneled through individual animals with that GPP. The number of seeds \( \text{spoop}_{sp} \) that ultimately survive passage through the collective guts of species \( sp \) is calculated as such:

\[
\begin{align*}
\text{spoop}_{sp} &= se_{sp} \left( \sum_{i}^{n} gpp_{i} \times \left( \frac{p_{i}}{\sum_{i}^{n} p_{i}} \right) \right)
\end{align*}
\]

Where \( p_{i} \) are random numbers between 0 and 1 and \( n \) is the number of individuals of species \( sp \) with whom feeding trials of the given fruit were conducted. Given our small sample sizes, this may allow for more variation in \( \text{spoop}_{sp} \) than assuming a normal distribution.

Since we only had chalta/kumbhi/lator \( gpp_{i} \) data for elephants and domestic bovids, we had to make assumptions about the proportion of seeds passed by other species. These estimates were particularly important for Rhesus macaques and gaur, since these species ate significant proportions of available fruit, thus having a substantial influence on the outcomes. The table below describes how we parameterized this critical portion of the model.

How do we justify our choices of GPP? For Rhesus macaques, the data present no clear choice; proper feeding trials have not been conducted with any fruit species. Corlett (2011) notes that macaques do not reliably disperse seeds over 3-5 mm, but Tsuji et al. (2013) found seeds up to 1.7 cm in the feces of Rhesus macaques. In our own field work, lator seeds about 1.5 cm in length were found in macaque feces on several occasions (Sekar and Sukumar in review). During the dry season, we found seeds of *Baccaurea sapida* and what is locally known as “guruga climbers” (Nepali) in macaque feces; both species’ seeds are larger than chalta seeds. However, even though we saw these macaques around chalta trees attempting to eat their fruit, we didn’t
find any chalta seeds in their feces. Thus, while we know that at least some macaques can swallow the chalta’s 6mm seeds and even pass seeds up to 1.5 cm in length, we do not know how often they do so. As noted in Sekar and Sukumar (in review), it appears that the largest macaques (adults, perhaps adult males) commonly swallow lator seeds while the other individuals are more likely to spit them out.

Table S2: Gut passage proportions (GPP) used for each animal x plant combination in model.

<table>
<thead>
<tr>
<th>Animal species</th>
<th>Chalta GPP</th>
<th>Kumbhi GPP</th>
<th>Lator GPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhesus macaques</td>
<td>Used elephant GPPs for chalta</td>
<td>Japanese macaque GPPs for radish seeds (mean length = 4.14 mm), eggplant seeds (3.45 mm), spinach seeds (3.84 mm), and melon seeds (6.24 mm) from Tsuji et al. 2010.</td>
<td>Japanese macaque GPPs for radish seeds (mean length = 4.14 mm), eggplant seeds (3.45 mm), spinach seeds (3.84 mm), and melon seeds (6.24 mm) from Tsuji et al. 2010.</td>
</tr>
<tr>
<td>Gaur</td>
<td>Used elephant GPPs for chalta</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild Pig</td>
<td></td>
<td>Used bovid GPPs for kumbhi</td>
<td>Used bovid GPPs for lator</td>
</tr>
<tr>
<td>Common palm civet</td>
<td></td>
<td>Used elephant GPPs for kumbhi</td>
<td>Used elephant GPPs for lator</td>
</tr>
<tr>
<td>Porcupine</td>
<td></td>
<td>Used bovid GPPs for kumbhi</td>
<td>Used bovid GPPs for lator</td>
</tr>
<tr>
<td>Malayan Giant Squirrel</td>
<td>Used bovid GPPs for chalta</td>
<td>Used bovid GPPs for kumbhi</td>
<td></td>
</tr>
<tr>
<td>Small rodents</td>
<td>Used bovid GPPs for chalta</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Tsuji et al (2010) conducted feeding trials with Japanese macaques, which are somewhat larger than Rhesus macaques, feeding them the seeds of four different species embedded in bananas. The largest seed was 6 mm, and the gut passage proportion for these seeds was 0.47 (0.49 excluding the spat seeds, sd=0.195). We reasoned that this is not significantly different from that Sekar et al. (in review) calculated for elephants (mean 0.40, sd=0.10), and that our personal observations of macaques eating chalta fruit suggested that they destroyed most of the
seeds as they tried to process the gooey pulp. Thus, we assumed that macaques have the same GPPs as elephants for the chalta fruit.

For lator and kumbhi, due to a lack of other options, we used the four average GPPs reported in Tsuji et al. (2010): 0.36, 0.78, 0.24, 0.49. Elephant GPPs for lator’s 1.5 cm seeds seemed implausibly high for macaques given what Corlett (2011) and others have noted. For all three fruits, we believe our estimates of macaque GPP likely estimate them to be more competent endozoochorous dispersers than they likely are.

For gaur, which we only detected eating chalta (Sekar and Sukumar 2013) but not kumbhi or lator (Sekar and Sukumar unpublished), we found no literature to inform our parameterization. Since gaur are bovids, it may be reasonable to use bovid GPPs; however, it is also plausible that gaur’s greater size allow them to swallow larger chunks of chalta fruit without mastication or rumination. We therefore conservatively attribute elephant GPPs to gaur.

Malayan giant squirrels and smaller rodents are well known seed predators of seeds over 1.5 cm in size (Kitamura et al. 2004, Kitamura et al. 2006, Velho et al. 2009), and Sekar and Sukumar (2013) found that rats and smaller squirrels were often eating the seeds of chalta fruit on the spot, leaving just the seed coats. Most likely, all these species destroy all or almost all the chalta seeds they handle. However, giant squirrels are likely big enough to swallow some chalta seeds, and since rats were sometimes seen moving the free pulps of chalta fruit, it is possible that the cache some seeds in a place where they may then germinate. Thus we accord them the same GPPs as bovids as reported in Sekar et al. (in review).

Similarly, for kumbhi and lator seeds, we accord wild pig, Himalayan crestless porcupines, and Malayan giant squirrels the same GPPs as domestic bovids. Since all three of these species are widely regarded to be seed predators (Corlett 2007), allowing them to have such high GPPs results in a conservative estimation of the relative importance of these species. Wild pigs disperse some small seeds, but are generally regarded to be seed predators (Corlett 2007). Porcupines in southeast Asia are documented predating upon Aglaia spectabilis’ 1.8-4.0 cm seeds (Kitamura et al. 2004) and other seeds 1.5-3.3 cm in length (Kitamura et al. 2007), with Himalayan crestless porcupines being one of the primary seed predators of the 2 to 3.5 cm seeds of five tree species in Arunachal Pradesh (Velho et al. 2009). Malayan giant squirrels were found to be predators of two 1.8 cm species (Kitamura et al. 2004, Kitamura et al. 2006). Thus, since domestic bovids have reasonably high GPPs for these fruits (Sekar et al. in review), this again
can be seen as elements of our conservative estimation. In contrast, since civets are known to commonly act as seed dispersers (Corlett 1998, Corlett 2007), and since we found civet scat with intact lator seeds, we attributed to them the same high GPPs of elephants. It should be noted, though, that wild pigs and civets both left at least some kumbhi seeds on site when they ate kumbhi fruit (Sekar and Sukumar in review), suggesting they may many times avoid ingesting the seeds altogether.

**Part 3: Distance of seed dispersal**

In order to help determine post-dispersal seed fate and assess the quality of seed dispersal by different dispersers, we needed to estimate the dispersal distances of each seed in the model. Assigning such dispersal distances took one of five approaches:

*Seeds dropped without ingestion by arboreal dispersers:*

For seeds dropped by macaques, rose-ringed parakeets, or giant squirrels, we used the seed transect data from Sekar and Sukumar (in review) to assign distances of dispersal. In Sekar and Sukumar (in review), a lognormal distribution is fit to dispersal distances; for our model, dispersal distances for dropped seeds are sampled from this distribution and assigned to each seed.

*Seeds ingested by elephants and domestic bovids:*

For seeds ingested by elephants and domestic bovids, we had both movement data and gut retention time data from feeding trials, allowing us to estimate how far seeds were taken. The approach used in this model is identical to that used in Sekar et al. (in review).

*Seeds ingested by Rhesus macaques:*

For seeds ingested by Rhesus macaques, we had movement data which was acquired in the same manner as for domestic bovids in Sekar et al. (in review)—that is, by following wild individuals with a handheld GPS from morning until sunset for multiple ~1-week periods. Feeding trials, however, could not be executed. Thus, we use data from Tsuji et al.’s (2010) study on Japanese macaques to estimate how long chalta, lator, and kumbhi seeds may be retained in the Rhesus macaque gut. Since Japanese macaques are larger than Rhesus macaques,
this should amount to a generous estimate of Rhesus macaque gut retention time and a conservative estimate of the relative importance of elephants in distance dispersal. The greatest gut retention time for a seed in the Tsuji et al. (2010) study was 120 hours for potherb mustard seeds, and the average mean retention time for the five Japanese macaques fed potherb mustard seeds was 42.7 hours. These two numbers were used to define a gamma distribution (which is commonly used to describe gut retention times and other waiting times—Pearson and Dawson 2005, Morales and Carlo 2006) which was then used to describe the gut retention times of Rhesus macaques for all three of our study species. In other words, we sampled from this gamma distribution to allocate gut retention times to seeds ingested and defecated by Rhesus macaques.

*Chalta seeds ingested by gaur:*

Gaur ate chalta seeds, but we had neither gut retention time data nor bovid data. For their gut retention times, we sampled from the domestic bovid gut retention times—however, we also made an adjustment for gours’ greater size. Claus et al. (2007) found that for ruminants, the relationship between mean retention time (y) and body size (x) is \( y = 24.7 \times x^{0.13} \). Using 825 kg as an estimate of the weight of a gaur (Smith and Xie 2008), and 300 kg for the domestic bovids (FAO 1977), we find that the mean retention time for gaur should be about 1.14 times greater than that for cattle. (300 kg is on the smaller size for buffaloes, and we reasoned that the cattle and younger buffaloes would bring down the average weight of the group.) As a result, we multiply all GRTs by 1.14 to determine the gaur’s gut retention time curve.

For the gaur’s movement data, we create a rudimentary model using data from Conry (1989). Conry (1989) reports that gaur move an average of 1.6 km/day but note that they can move 4.2 kilometers in a day as well. We create a gamma distribution of distances with mean 1.6 and max 4.2, and sample from this distribution for each day of gut retention time. If, e.g., a gut retention time is 84 hours, we would sample from the distribution four times and then add the first three numbers and half the fourth number. The result would be the distance of dispersal for the seed with GRT 84 hours.

*Seeds ingested by other dispersers:*

For seeds ingested by small rodents, giant squirrels, porcupines, civets, and wild boars, we lacked both gut retention time and movement data. In addition, the numbers of seeds moved
by these species was relatively low. Thus, we simply assumed that individuals of these species initially dispersed seeds uniformly over their territory. For a conservative estimate of dispersal distances, we took the territory size for each species/group given by the literature. We assumed that territories were square, that each individual animals found the parent tree at the corner of their territory, and that they dispersed seeds along the diagonal of their territory. Thus, if territory size is \( \text{terr} \), then the max dispersal distance (MDD) was calculated as:

\[
MDD = \sqrt{\text{terr} \times \sqrt{2}}
\]  

(Eq 7)

As a result, we used the territory size of the most closely related species of each disperser and calculated the following for maximum dispersal distances:

Table S3: Estimated home range diagonal lengths—and thus maximum dispersal distances—for minor dispersers of our three study species. The sources upon which these estimates are based is also provided.

<table>
<thead>
<tr>
<th>Animal disperser</th>
<th>maximum dispersal distance</th>
<th>source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Malayan giant squirrel, small rodents</td>
<td>217m</td>
<td>Saiful et al. 2001 for <em>Callosciurus caniceps</em></td>
</tr>
<tr>
<td>Himalayan Crestless Porcupine</td>
<td>2036m</td>
<td>Lovari et al. 2013 for <em>Hystrix cristata</em></td>
</tr>
<tr>
<td>common palm civet</td>
<td>2608m</td>
<td>Grassman 1998 for common palm civets</td>
</tr>
<tr>
<td>wild pig</td>
<td>2386m</td>
<td>Genov et al. 2007, <em>Sus scrofa</em> in Italy</td>
</tr>
</tbody>
</table>

Part 4: Post-dispersal processes.

Once all the surviving, initially dispersed seeds have been assigned dispersal distances, we can now start accounting for likely post-dispersal sources of mortality. We look at three such sources of mortality: distance-based mortality (as a function of distance from the parent tree), or Janzen-Connell effects; differential germination rate amongst seeds from different dispersers; and mortality due to intradung, intraspecific competition. Seeds that survive all of these processes are considered “successfully dispersed seeds”, or SDS.
The Janzen-Connell effect:

Swamy et al. (2011) constructed an empirical model of the Janzen-Connell effect based on 15 Neotropical species in Manu National park, Peru. The model estimates the sapling to seed ratio as a function of distance from the nearest large conspecific tree, with distances relativized in terms of the average radius of the tree crown for that species. While it would have been far preferable to find a model based on a south or southeast Asian forest, we could not find such a model.

Using the data from all 15 species, Swamy et al. (2011) found that the following model was the best fit:

(Eq. 8) \[ y = \frac{1}{1 + \left( \frac{x}{b} \right)^a} \]

with \( a = -1.722 \) and \( b = 5.669 \). In this equation, \( y \) is the sapling to seed ratio, and \( x \) is the distance from the nearest conspecific tree. We used \( y \) as the probability that a seed at distance \( x \) from the parent tree would survive Janzen-Connell distance-dependent effects. Since chalta, kumbhi, and lator trees are not very common species in Buxa (Sukumar et al. 2003), chances are good for spit and thrown seeds in particular that the parent tree is the closest available conspecific tree.

For the radii of the three tree species, we used the means from Table S4, which were measured in the field. The trees used were used for camera trapping and focal watches in Sekar and Sukumar (2013) and Sekar and Sukumar (in review).

<table>
<thead>
<tr>
<th>Mean crown radius (m) +/- sd</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chalta</td>
<td>6.5 +/- 1.8</td>
</tr>
<tr>
<td>Kumbhi</td>
<td>3.9 +/- 0.78</td>
</tr>
<tr>
<td>Lator</td>
<td>11.7 +/- 2.0</td>
</tr>
</tbody>
</table>

Differing germination rates:

In Sekar et al. (in review), we show differences in the germination rates of seeds taken from elephant and bovid dung after feeding trials. We use those differing germination rates in the model. Since we averaged the germination rates of cattle and buffaloes, and we averaged germination rates over two years for lator, we here reproduce the table of germination rates that
we utilized for the study. For each iteration of the model, we sampled from the normal distribution described below. For chalta and kumbhi, since we only have one year of germination data, we construct a binomial standard error for the distribution. However, for lator, we have notably differing germination rates from two years, so here we use the standard deviation of the different values. Note that we used elephant germination rates for all species for which we did not have data (i.e., all species aside from the domestic bovids).

Table S5: Germination rates used in model, with standard deviation of the normal distribution used for the model in parentheses.

<table>
<thead>
<tr>
<th>Disperser</th>
<th>Chalta</th>
<th>Kumbhi</th>
<th>Lator</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elephants</td>
<td>0.817 (0.010)</td>
<td>0.805 (0.025)</td>
<td>0.776 (0.162)</td>
</tr>
<tr>
<td>Domestic Bovids</td>
<td>0.535 (0.076)</td>
<td>0.75 (0.047)</td>
<td>0.711 (0.289)</td>
</tr>
</tbody>
</table>

*Intra-dung, intraspecific competition:

While large-bodied species like elephants may serve fruiting species by moving lots of their seeds, seeds found in the same dung pile are not all likely to succeed. If the dung pile is clumped, then at best one of the seeds will ultimately out-compete other seeds to become the reigning sapling and then tree. Thus, understanding how many seeds will be successfully dispersed by different frugivores requires some estimate of how many seeds are likely to be in each dung pile.

For chalta, we collected data from 79 elephant dung piles during the chalta’s fruiting season, 52 of which contained chalta seeds. This gave us an idea of the average probability a seed had of winning over conspecific seeds and being the SDS in the dung pile—that is, the average of the reciprocals of the number of seeds per dung pile was 0.084 (sd=0.125). On average, a chalta seed had an 8.4% chance of being the single seedling to establish in the spot of an elephant dung pile.

However, we did not want to apply this probability across all elephant dungs because seeds that emerge early or late from an elephant are likely to have less other seeds with them, whereas seeds which were retained in the gut (i.e., with a GRT) near the mean would have the
most competition. Since seeds with longer GRTs were also more likely to be taken greater distances, we wanted to model how GRT affected intradung competition.

To do so, we created a sub-model to mechanistically predict the number of seeds in a given elephant or bovid dung pile. While camera trapping for Sekar and Sukumar (2013), we noted how many fruit around the tree disappeared each time an animal tripped the camera trap. While not all those fruit may have been taken by the culprit on camera, since fruit removal was a reasonably rare event in Buxa, we can assume that the species that tripped the camera likely took most of the marked fruit to go missing on most occasions. This gave us an opportunity to estimate of the number of fruits—and thus seeds—likely to be consumed by a wild elephant in a single feeding. So in order to calculate the number of seeds $D_{sp,fs}$ in any given dung pile of disperser species $sp$ for a focal seed $fs$ with a given GRT, we would sample a value $MF$ from the numbers of missing fruit for the given species and do as follows:

$$D_{sp,fs} = \frac{MF}{N} \ast p_{sp,GRT,fs} \tag{Eq. 9}$$

Where $N$ is the average number of individuals of species $sp$ to eat fruit during a visit a fruiting tree, and $p_{sp,GRT}$ is the proportion of consumed seeds to emerge in a dung pile of species $sp$ at the given GRT during feeding trials. For elephants, we arbitrarily assumed $N$ was 1; for gaur, 2; and for domestic bovids, 3 based on their respective body sizes.

Equation 9 assumes that the individual animal from which the focal seed emerged had only one feeding of chalta fruit for days before and after the feeding—an unlikely scenario, given the popularity of chalta fruits with elephants. In fact, when we find the average value for $1/D_{ELE}$ based on equation 9, the value is around 0.207—more than twice as high a probability of survival as that we found in wild elephant dung. So we assume that that the animal carrying the focal seed has an additional feeding of chalta with probability $PROB$ either before or after the consumption of the focal seed, meaning that seeds from this second feeding could have any GRT within the range of GRTs found during feeding trials. Thus the formula below requires two randomly chosen quantities: a probability $q$ of there being a second feeding from a uniform distribution between 0 and 1, and a random GRT called $rGRT$:

$$D_{sp,fs} = \frac{MF_1}{N} \ast p_{sp,GRT,fs} + (q < PROB) \ast \frac{MF_2}{N} \ast p_{sp,rGRT} \tag{Eq. 10}$$
We then solve for PROB such that the average value of $1/D_{sp}$ resembles that found in nature. PROB in the model is currently set at 0.86, meaning that 86% of the time focal seeds find themselves in elephants that have one additional feeding before or after the focal seed was eaten such that seeds from that other feeding may also end up in the same dung pile as the focal seed, but 14% of the time the elephant has no additional feedings that would add more or less seeds to the dung pile containing the focal seed.

While we have dung pile data from wild elephants during the chalta season, we lack analogous data for any other disperser species, and we also lack this data for wild elephants for the other two fruiting species. As a result, PROB is set somewhat arbitrarily in the other cases. We know that domestic bovids do not eat chalta as frequently as elephants, and perhaps since they travel in larger herds the same individual is even less likely to eat multiple chalta within a space of time that would affect focal seeds. Thus, PROB is zero for all frugivores of chalta aside from elephants.

For kumbhi and lator, we arbitrarily set PROB to 0.2 for elephants. Kumbhi and lator trees are less common in Buxa, and they are less frequently visited by elephants (see main text). As such, we think it is less likely than for chalta that the same elephant will have two meals of kumbhi or lator within 5 days, but it probably happens once in awhile. Since domestic bovids eat lator even more occasionally, we set PROB to 0 for them.

However, domestic bovids are the top frugivore of kumbhi (Sekar and Sukumar in review). Furthermore, cattle and buffaloes were shown to visit the same general area for consecutive days, meaning that they are likely to come past an area with kumbhi trees with regularity, despite the rarity of kumbhi trees (Sekar et al. in review). While collecting movement data on bovids, Sekar et al (unpublished) collected 30 dung piles from cattle with kumbhi seeds. The average number of seeds per dung was 8.77 (sd=9.89), and average value of the reciprocal was 0.217, suggesting a kumbhi seed on average had a 21.7% chance of being the SDS in a domestic cow’s dung pile.

While these dung piles were collected from just one herd (and may not be representative), they serve as a valuable bench mark. In our model, we set PROB to 0.8 for cattle eating kumbhi, and we find that the average $1/D_{domestic bovid}$ is 0.43—two times higher than that calculated
from the 30 cow dung piles. Thus, we feel that setting PROB to 0.8 for domestic cattle is conservative and appropriate given our research question.

For macaques, since we lack gut retention time data for our three study species, we used a less mechanistic method to account for intra-dung, intraspecific competition. During lator seed transects and focal watches (Sekar and Sukumar unpublished), we found five macaque feces with between 1 and 7 lator seeds (mean 3.4) per pile. We therefore created a “triangle function” in which macaque seeds as follows:

\[
D_{mac,fs} = \frac{\text{half}_{mac}-|GRT_{fs}-\text{mid}_{mac}|}{\text{half}_{mac}} \times (\text{max}_{sd_{mac}} - \text{min}_{sd_{mac}}) + \text{min}_{sd_{mac}}
\]

\(D\) is the number of seeds in macaque feces for focal seed \(fs\), \(\text{half}_{mac}\) is half the difference between the maximum and minimum GRTs for the Rhesus macaques, \(GRT_{fs}\) is the GRT of focal seed \(fs\), \(\text{mid}_{mac}\) is the GRT halfway between the minimum and maximum GRTs, and \(\text{max}_{sd}\) and \(\text{min}_{sd}\) refer to the maximum and minimum number of seeds found in a single macaque feces—in our model, \(\text{max}_{sd}\) fluctuates randomly between 5 and 7 for each focal seed, and \(\text{min}_{sd}\) is 1.

For gaur, the approach was a hybrid between that taken for elephants/bovids and macaques. Since we used domestic bovid GRTs and elephant GPPs for gaur, we had to make an adjustment as follows:

\[
D_{gaur,fs} = \frac{\text{MF}}{N} \times P_{dom bovid,GRT,fs} \times \frac{\text{half}_{gaur}-|GRT_{fs}-\text{mid}_{gaur}|}{\text{half}_{gaur}} \times (2 \times \frac{\text{GPP}_{ele}}{\text{GPP}_{bov}} - 1)
\]

Here, \(\text{half}_{gaur}\) is half the difference between the minimum and maximum gaur (i.e., domestic bovid) GRT, and \(\text{mid}\) is the GRT value halfway between the minimum and maximum GRT values. (The remaining terms are defined with equation 9).

Finally, for all remaining species for which we assumed uniform distributions of seeds across the diagonal of their territories, we again assumed a triangle function, but this time based on distance. Seeds per pile peaked at 7 for civets (known dispersers) and at 5 for seed predators at the midpoint of their maximum distance of dispersal.
Section 2: Adjustments made for the conservative and generous (i.e., alternative) models

We necessarily made many assumptions in order to make the calculations in the main text. For eleven of those parameters, we made modifications in order to come up with “most conservative” and “generous” estimates of the relative importance of elephants as seed dispersers. To be clear, we believe our best estimate model in itself takes a conservative approach towards estimates presented in the paper. The parameters we altered are in Table S5; some explanation of the changes can be found below.

Table S5: Modifications made to parameters from our best estimate model to our conservative and generous models.

<table>
<thead>
<tr>
<th>Parameter(s)</th>
<th>Tree species applicable</th>
<th>Best estimate model</th>
<th>Most conservative model</th>
<th>Generous model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion fruits taken by arboreal frugivores</td>
<td>kumbhi</td>
<td>0.133 (mean of binomial distribution, n=30)</td>
<td>0.266</td>
<td>0.066</td>
</tr>
<tr>
<td>Proportion of seeds swallowed by macaques and giant squirrels</td>
<td>kumbhi, lator</td>
<td>0.056 +/- 0.023 (std error)</td>
<td>0.1 +/- 0.03 (std error)</td>
<td>0.056 +/- 0.023 (std error)</td>
</tr>
<tr>
<td>Proportion of fallen fruit that rots</td>
<td>kumbhi, lator</td>
<td>0.246</td>
<td>0.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Janzen-Connell parameters</td>
<td>chalta, kumbhi, lator</td>
<td>a = -1.7221, b = 5.6692 in equation 8</td>
<td>a = -3.932276, b = 2.14 in equation 8</td>
<td>a = -5.0552, b = 9.4604 in equation 8</td>
</tr>
<tr>
<td>Number of elephants visiting tree at once (N in equation 9 or 10)</td>
<td>kumbhi, lator</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Max number of seeds surviving per dung pile of megaherbivores</td>
<td>chalta, kumbhi, lator</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>
**PROB for domestic bovids in equation 10**

<table>
<thead>
<tr>
<th></th>
<th>kumbhi</th>
<th>0.8</th>
<th>0.2</th>
<th>0.9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macaque GPPs</td>
<td>chalta</td>
<td>Elephant GPPs</td>
<td>Elephant GPPs</td>
<td>Domestic bovid GPPs</td>
</tr>
<tr>
<td>Macaque GPPs</td>
<td>kumbhi, lator</td>
<td>Tsuji et al. 2010 GPPs for four vegetables eaten by Japanese macaques</td>
<td>Tsuji et al. 2010 GPPs for four vegetables eaten by Japanese macaques</td>
<td>Domestic bovid GPPs</td>
</tr>
<tr>
<td>Gaur GPPs</td>
<td>chalta</td>
<td>Elephant GPPs</td>
<td>Elephant GPPs</td>
<td>Domestic bovid GPPs</td>
</tr>
</tbody>
</table>

*Proportion fruits taken by arboreal frugivores:* while we conducted focal watches for lator and chalta trees, we were not able to do so for kumbhi (see Sekar and Sukumar in review). Instead, we used camera traps in the canopy for a short period of time. To address the possibility that we were off by a factor of two in either direction, we alter this parameter for the alternative models.

*Proportion of seeds swallowed by macaques and giant squirrels:* the estimate we use for this parameter was again derived from focal watches (Sekar and Sukumar in review), and the uncertainty is explained there. It is impossible to know whether a macaque 30 meters up in a tree, partially hidden by leaves is spitting every seed she eats or swallowing some of them. We found that in 5.6% of cases, macaques were clearly swallowing all the seeds (though perhaps after chewing them). Thus we set the parameter as we have, and vary it for the alternative models.

*Proportion of fallen fruit that rots:* in fact, the amount of fruit that rots should be a consequence of the level of terrestrial frugivory, and not predetermined. However, in order to describe the situation we observed in Buxa, we needed to ensure a similar proportion of fruit was taken out of the model by rotting as in nature. While for chalta we systematically followed fruit fates for hundreds of fruits (Sekar and Sukumar 2013), we were not able to do this for kumbhi or lator. We followed a small number of lator fruit fates in front of the camera trap, and use this to inform our rotting rates for both kumbhi and lator. Thus we vary this parameter to what we intuitively believe (after three monsoon seasons in the field) may be the minimum and maximum overall rotting rates.
Janzen-Connell parameters: Dr. Varun Swamy kindly shared the data underpinning the Janzen-Connell equation in Swamy et al. (2011) with us so that we could see how much the parameters changed for the 20 different species for which they collected data. Since no one species had more than about 5 data points for sapling:seed ratio versus distance, we created two subsets of the data: we took the 10 tree species with the highest sapling:seed ratio at 5 crown radius units (CRUs), and deemed these the low-JC effect species. The remaining species were the high-JC effect species. We then repeated Swamy et al. (2011)’s approach, fitting the same models they did and selecting the one with the best AIC. In all cases, the same modified logistic equation ultimately selected by Swamy et al (2011) was the best fit.

Having fit the modified logistic model to the two subsets of Swamy et al. (2011)’s data, we then used the low-JC effect species’ model parameters for the “most conservative” alternative model, and the high-JC effect species’ model parameters for the “generous” model alternative, since a higher Janzen-Connell effect would further increase the relative importance of endozoochorous dispersers like elephants. We did slightly modify the b-parameter for the low-JC effect species such that predicted seed mortality would not be lower than that for the best-estimate model at any point, as the best-fit parameters for the low-JC effect species involved high mortality near the base of the parent tree, which is where most arboreal frugivores dispensed their seeds.

Max number of seeds surviving per dung pile of large frugivores: One of the points of emphasis of our model is that we attempt to account for the likely mortality of almost all the seeds sharing a single feces. But how many seeds from a single dung pile can eventually become full-grown trees? We have no empirical data to answer this question, and in general it does not appear that the literature has addressed this question. Secondary dispersal probably occurs to some extent, though Sekar et al. (in review b) shows it probably happens only rarely for chalta seeds. Also, elephant boluses from the same dung pile are sometimes spread out over a reasonably large area, making it possible that seeds from multiple boluses may survive and grow up as neighbors.

We cautiously suggest, therefore, that in the generous model two seeds from a single dung pile could survive and become successfully dispersed seeds through a combination of being spatially spread out during defecation and secondary dispersal.
Supplement References


moist evergreen forest in Thailand. *Journal of Tropical Ecology*, 22(02), 137–146. doi:10.1017/S0266467405002889


Sekar, N., Lee, C., & Sukumar, R. (in review). In the Elephant’s Seed Shadow: the prospects of domestic bovids as replacement dispersers of three tropical Asian trees.

Sekar, N., Sharma, N., Giam, X., & Sukumar, R. (in review b). Hazards of conspicuous fertilizer: how much seed predation occurs from Asian elephant dung?


Conclusion

Nitin Sekar

The effort to address a straightforward question—if Asian elephants go missing, can the remaining species compensate for them as seed dispersers?—has led us to a set of results that inform our understanding of the role of the largest animal species in ecological processes such as seed dispersal.

Firstly, there does appear to be such a thing as an Asian megafaunal fruit (Janzen and Martin 1982). In Buxa Tiger Reserve, 63% of Dillenia indica (chalta) fruit removed by terrestrial frugivores is consumed by elephants because the hardness of the chalta fruit inhibits broader frugivory. If domestic bovids, the most available replacement disperser, try to fill in for elephants, less than 1/16 as many seeds will survive gut passage and 2/3 as many of the defecated seeds germinate. Unless other species such as gaur somehow increase their consumption of chalta, our model indicates the number of chalta seeds successfully dispersed would likely decline by 54% without elephants.

Secondly, the loss of elephants is likely to be felt by a number of other species that are not strictly megafaunal fruits. Despite their low population densities, elephants are amongst the top frugivores of fruits that are accessible to animals as small as macaques and civets, removing 18% of frugivore-consumed Careya arborea (kumbhi) fruits and 10% of frugivore-consumed Artocarpus chaplasha (lator) fruits. While elephants do not dominate the consumption of these fruits, elephants’ other notable properties as dispersers mean that the dispersal of such plant species may still be affected by the absence of elephants. Since elephants’ gut passage rates of kumbhi seeds are higher than that of domestic bovids (the kumbhi’s most prominent frugivore), and since smaller species eat relatively few kumbhi fruits, the loss of elephants may lead to a 30% reduction in the successful dispersal of kumbhi seeds. For lator, which is heavily consumed by smaller species, median seed dispersal declines by an order of magnitude without elephants.
Despite this evidence, buried in the limitations and disclaimers scattered throughout this dissertation is the possibility that our tree study species and other plants may, at least in the short term, be resilient to the loss of one of their megafaunal dispersers (Guimaraes et al. 2008, Zaya and Howe 2009, Jansen et al. 2012). For the chalta, the ability to soften and become more accessible to smaller dispersers may prove to be adaptive in a world without the largest dispersers. For lator and kumbhi, domestic bovids and smaller frugivores may be able to attenuate the effects of elephant loss, and the timing of these species’ fruiting means their seeds could be carried away by monsoon water, perhaps aiding in the persistence of populations as they evolve a more sustainable dispersal regime. For all three species, the role of rodents in accidental seed dispersal may be more significant than is immediately apparent. Since our study of the dispersal of these three species was not comprehensive, it must be conceded that, even in disturbed landscapes such as Buxa, elephant-dispersed species may be able to weather moderate perturbations to their dispersal plan.

The natural question then is whether the sum of ecological and climatological stresses on such plant species today amount to a more-than-moderate perturbation (McConkey et al. 2012). Such inquiry is beyond the scope of this study. However, my work bolsters the argument that if one of society’s goals is to maintain the broader composition and character of the world’s remaining forests, the largest species, such as elephants, are likely to play a role commensurate with their size. Since their role as dispersers is non-redundant, we may say that elephants’ body size—which is linked to their digestive physiology and behavior—makes them a functional group unto themselves in seed dispersal in Buxa and, most likely, other modern tropical Asian ecosystems. More broadly, our research supports the notion that losing the largest and most physiologically unique—and thus, charismatic—species is likely to have measurable effects on ecological processes, furthering the juggernaut of global change our society has set in motion.

References:


Note on authorship

I was very fortunate to have Dr. R. Sukumar, Chia-Lo Lee, Netra Sharma, and Xingli Giam as co-authors for the chapters in this dissertation. Dr. Sukumar provided natural history knowledge that allowed me to embark on this project (for instance, suggesting *Dillenia indica* as a study species and Buxa Tiger Reserve as my study site), and he mentored me throughout my time in the field. He also carefully revised all my chapters with me, helping me hone my ideas. Finally, the elephant movement data which feature critically in chapters 3 and 5 were painstakingly collected by Dr. Sukumar and his team.

Chia-Lo Lee used Matlab to create the simulation models used for chapters 3 and 5. Often, I would describe to him what I wanted the model to do, and Chia-Lo would come up with a program do do it. Netra Prasad Sharma was a vitally important field assistant for all the work conducted for this dissertation, but I was not with him in the field for the data collection conducted for chapter 4; this means that he designed and manufactured the exclosure boxes for the dung, executed the experiment, and collected all the data. He provided valuable on-the-ground insights that helped shape experimental design. Xingli Giam helped me develop the statistical model used in chapter 4. He also contributed to the interpretation of the model. Finally, Dr. Jack Weiss of the Univeristy of North Carolina Chapel Hill, though not a co-author, essentially provided the statistical model fit to the seed transect data in chapter 2.

I conceived of the idea for this project, developed and honed the methodology, trained the staff, and collected the data with my staff. I made the original natural history observations featured in this document. I conceived of almost all the analyses in this paper, and I executed most of them by myself. I came up with the empirical probability model featured in chapters 3 and 5 (though I did not write the code for it). I created all the visuals except for those related to the chapter 2 seed transects. Finally, I wrote all the chapters in this dissertation, though I of course took revisions from my co-authors and committee members. While I was aided by my co-authors, this dissertation is predominantly my own work.
Acknowledgments

The PhD has been strange. On the one hand, it has been an isolating experience simply because I have been so much more invested in the success of this project than anyone I’ve worked with. Perhaps most PhDs share this characteristic, as they are essentially individualistic journeys. Since Princeton University’s Department of Ecology and Evolutionary Biology believes strongly in providing its doctoral students great autonomy—a blessing to anyone with initiative, including myself—the threat of professional loneliness is perhaps exacerbated. Yet it is this same attribute of the PhD that has revealed to me the bounty of human generosity that surrounds me. Since others have stood to gain little from my completion of this degree, I have been able to recognize just how selfless and charitable many have had to be for me to reach the end of this journey with a sound mind and body.

Andy Dobson, Henry Horn, David Wilcove, and Dan Rubenstein were a helpful committee. Andy made my time at Princeton possible; he instilled in me the principles that have guided my priorities as a PhD candidate, and he gave me the independence to realize my potential as a scientist (while dealing with much bureaucracy on my behalf). Henry and David were my mentors. Henry was especially helpful as I dealt with early insecurities and personal challenges in my first several years, and David has provided me crucial insights into the world of ecology and conservation policy. Dan helped me deal with the politics of being a graduate student, and boosted my confidence in my research project. All four provided useful feedback on my research. Simon Levin, Andrea Graham, and Rob Pringle have also been supportive.

Lolly O’Brien and Diane Carlino gave me lots of useful advice and help, and they also deserve to be designated as my committee members. Whatever it was my committee was able to do for me, it was only possible because of the organizational wizardry of Bernadette Penick, Geraldine Rhodes, Terry Guthrie, Siobhan Condran, and the late (and very much missed) Amy Bordvik. Across Washington Road in the GIS library, Tsering Wangyall Shawa also provided me a lot of patient support. Jesse Saunders, Axel Haenssen, and Rajeshri “Raj” Chokshi have
made the precariously tech-heavy work of modern science possible in our department. Over in McCosh, Dr. Margot Putukian helped me deal with a very poorly timed (second) ACL tear before my last field season.

There is not enough room here for a comprehensive list of the EEB students and post-docs that have supported me in the last six years. I will say that Corinne Kendall, Jenny Ouyang, Annette Trierweiler, and Jack Burdette are fantastic friends; they have all pitched in during times of personal travail. Ryan Chisholm, David Pattemore, Caroline Farrior, Sarah Batterman, Brian Higgins, Christina Faust, and Cara Brook floated into my world, helped me in some remarkable way, and asked nothing from me in return. Xingli Giam always welcomed statistical queries with open arms. Paul Williams, Anieke van Leeuwan, Erik Osnas, Nathan Gregory, and Maria Echeverry made my day-to-day life happier by being awesome officemates; Eno 111 is a shell of its former self when I am there without them. Daniel Stanton, Allison Shaw, Alex Washburne, Simon Leblanc, and Imene Goumiri were wonderful flatmates. Daniel in particular doubled as a mentor. Blair Roberts and Eili Klein made my cohort a friendly batch. 

While at Princeton, I have spent the most time with a handful of people outside EEB. These friends have broadened my horizons in ways that cannot be described succinctly on paper. They also looked after me with a quality that can only be described as Ubuntu. A special thanks to Phil Hannam, Dinsha Mistree, Derek Shiller, and Megan Nelson. Babasanmi (Victor) Oyeyemi was great companionship during the last lap of the race.

I spent about two years of my PhD in India, and so I naturally racked up karmic debt abroad as well. My sojourn in academia began because I stumbled upon a website featuring Dr. R. Sukumar, the world’s leading Asian elephant ecologist. I wanted to be him. He invited me to work with him in India before my PhD, shepherded me into the program at Princeton University, and provided me the guidance, wisdom, and political backing I needed to conduct this research.

Ahimsa Campos-Arceiz, Soumya Prasad, Andre Pittet, Kim McConkey, and Asmita Sengupta all shared scientific and/or methodological insights with me. The graduate students at the Centre for Ecological Sciences at the Indian Institute of Science, Bangalore, provided a
welcoming surrogate community during my brief and sporadic visits there. Karpagam Chelliah helped me set up shop in Buxa Tiger Reserve and kept me from being destroyed by my own ignorance. Milind Watve of the Indian Institute for Science, Education, and Research, as well as Amol Khedgikar, were helpful during my unsuccessful bid to launch a project in Maharashtra.

I stayed in the village of Rajabhatkhawa, where the Sharma family provided me a window into a different world. Pushpa Didi, Gita Ji, Keshab (Kallu), Nirman, Niruta, Sudha, Gopal, Shayli, Saibatri Didi, Urmila, and all their neighbors and friends showed me just how full and fulfilling village life can be. During my 15 months with them, I never once felt as irrelevant as I did when sitting alone in 111 Eno Hall. I also received great help from a set of multilingual field assistants, drivers, and cooks whose skill and knowledge made me question the relative usefulness of my formal education: Lachu Tim Sina, Suresh Roy, Bijay Mangar, Bikash Thappa, Dhiraj Chhetri, Dipak Subba, Chhottu Bastore, and Sanjay Lama meticulously collected much of the data that is the foundation of this work. Various officials and employees of the West Bengal Forest Department also aided our efforts, as did several captive elephants.

There is more. My family in India made this dissertation possible by exposing me to and instructing me in the realities of the subcontinent. Malathi Rajagopalan (Periamma), R. Rajagopalan (Periappa), M. Balakrishnan (Chitappa), Malini Balakrishnan (Chiti), and Swati Balakrishnan (cousin) participated directly in my efforts during my PhD, but my grandparents and other aunts, uncles, and cousins deserve my appreciation as well.

Then, there are the friendships that have proven unique in their quality, longevity and/or their intensity. Tuoyang Mu, James Norton, Bindhu Pamarthi, Shefa Sikder, and Mary Small were tremendously supportive during this solitary journey, assuring me that this dissertation, despite being focused on something so conceptual, would help me serve the world. I hope I prove them right. Karthik Balasubramanian, Danika Barry, Lois Mei En Kwa, Hudson Vaughan, Vidya Venkataramanan, and Krish Vigneswaran also called in to help me keep track of the big picture.
And finally, there are the people who have done the most to support both me and this dissertation. Thanks to my parents, Chandra and Padmini Sekar. They may regret the effect that those innumerable trips to the Birmingham Zoo had on my career trajectory, but they have always provided love and safe refuge when the world sent me home battered and torn. T.R. Krishna Kumar will be the first to tell you that he does not particularly care to understand what I am doing, but he will always try to know where I am and if I am ok—he enabled my adventures, and I hope every nephew and niece has an uncle who cares for them so profoundly. I have memorized the Indian cell phone number of Dr. Naman Shah—part brother, part peer, part travel companion, part prematurely confident (and yet so helpful) medical professional, and part guiding light for how to use one’s curiosity and intellectual acumen to make the world a better place. My actual sister, Samy, is my best friend in a way only a sibling can be but not all siblings are. Any third party that beholds the sacrifices she makes for me is perplexed by her selflessness; I perhaps have grown too accustomed to it. I am both proud of and annoyed by how inspiring I find her, and I thank her in particular for continuing to pretend that I give useful advice. Netra Prasad Sharma, the preternaturally talented farmer who served as my field assistant, is proof that the universe is not just. If I deserve a doctorate, so does he. Netra taught me Hindi; gave me food and shelter; kept me safe from wild elephants and snakes; enriched my worldview with his own natural history insights and testable hypotheses (latter not featured in this dissertation); designed and made many of the tools and apparatuses used in our work; helped me source and manage my research team; informed me when I was being taken advantage of or being unreasonable; collected mounds of data without me; and literally held me up when I could not stand myself. When I finally work in conservation, I hope I can honor Netra by treating unknown villagers with the respect I wish Buxa’s policy makers would show him.

Finally, I must dedicate this dissertation to Kennei. He did not live to see me finish this program. But if it weren’t for the lessons he taught me about how to live, or the meaning he gave to my day-to-day life growing up and while at Princeton, I would be an inferior and less happy person. Even if the articles in this dissertation are published or even cited a million times, this dissertation will still be the second most substantial thing I did in my youth after raising that dog.