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How much *Dillenia indica* seed predation occurs from Asian elephant dung?

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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 compared the number of seeds in boluses that are a) opened immediately upon detection (control boluses), b) made available only to small seed predators (<3 mm wide) for 1–4 months, and c) made available to all seed predators and secondary dispersers for 1–4 months. Using a model built on this experiment, we estimated that seed predation by small seed predators (most likely ants and termites) destroys between 82.9% and 96.4% of seeds in elephant dung between the time of defecation and the median germination date for *D. indica*. Exposure to larger seed predators and secondary dispersers did not lead to a significant additional reduction in the number of seeds per dung bolus. Our findings suggest that post-dispersal seed predation by small insects (<3 mm) substantially reduces but does not eliminate the success of elephants as dispersers of *D. indica* in a tropical moist forest habitat.

1. Introduction

Seed dispersal is 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 increasingly rare large-bodied animals (Cardillo et al., 2005; Terborgh et al., 2008; Hansen and Galetti, 2009) which are thought to be particularly effective at dispersing lots of seeds over substantial distances (Tchamba and Seme, 1993; Fragoso et al., 2003; Blake et al., 2009), even when the seeds are quite large (Chapman et al., 1992; Campos-Arceiz and Blake, 2011). 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—removal and predation of seeds has been documented from the faeces of numerous large-bodied frugivores ranging from gibbons to horses (McConkey, 2005a; 2005b; Andresen, 1999, Andresen, 2002; Balcomb and Chapman, 2003; 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 vary substantially amongst faeces 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 may serve as advertisements for a seedy meal. While research in

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the Neotropics suggest that being embedded in dung protects seeds (Janzen, 1982; Rios and Pacheco, 2006), there have been few efforts to measure levels of seed predation from elephant dung. Researchers have shown that species as varied as bush pigs (*Potamochoerus porcus*), red river hogs (*P. porcus*), sitatungas (*Tragelaphus spekii*), and savanna tree squirrels (*Paraxerus cepapi*) remove and predate upon seeds dispersed by African elephants (*Loxodonta africana*) (Cochrane, 2003; Magliocca et al., 2003; Midgley et al., 2012). Collectively, research indicates that post-dispersal seed predation from elephant dung is pervasive but does not sufficiently document seed predation or provide estimates of the probability of seed survival post-defecation.

We attempt here to advance the understanding of the fate of seeds in 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 and red jungle fowl, *Gallus gallus*) or infested with ants or termites, even during the dry season (November–March). It has been shown that i) elephants in Buxa disperse *Dillenia indica* seeds, ii) rodents consume *D. indica* seeds from un-dispersed fruit (Sekar and Sukumar 2013), and iii) *D. indica* seeds typically germinate in May just prior to the monsoon (Sekar et al., 2015). Thus, *D. indica* seeds in elephant dung could be vulnerable to predation by ubiquitous seed predators such as insects and rodents over a prolonged period of time.

Our research question, then, was as follows: does being embedded in elephant dung protect *D. indica* seeds from seed predation? We examined the following competing hypotheses:

H0. Exposure of elephant dung to seed predation leads to no reduction in the number of *D. indica* seeds in elephant dung.

H1. Exposure of elephant dung to seed predation will lead to a significant reduction in the number of seeds primarily due to *in situ* destruction of seeds by small seed predators (<3 mm wide; most likely insects).

H2. Exposure of elephant dung to seed predation will lead to a significant reduction in the number of seeds primarily due to removal of seeds by larger seed predators (>3 mm wide) such as rodents as well as secondary seed dispersers.

H3. Exposure of elephant dung to seed predation will lead to a significant reduction in the number of seeds due to both *in situ* destruction of seeds by small seed predators and removal of seeds by larger seed predators and/or secondary dispersers.

To arbitrate amongst these hypotheses, we executed a field experiment in which boluses from the same elephant dung pile were assigned to one of three treatments relating to exposure to seed predation. Although our research is exploratory, comparisons amongst these treatments allowed us to infer the relative importance of seed predation by small insects and seed removal by larger seed predators and secondary dispersers for *D. indica* seeds dispersed by elephants. We also estimated what proportion of seeds were likely to survive seed predation after dispersal by an elephant. This work thus takes us a step closer to understanding the role of elephants and seed predators in the seed dispersal ecology of a tropical moist forest.

2. Methods

2.1. Study area and study species

Our experimental approach is possible because of the strong relationship between Asian elephants (*Elephas maximus*) and the chalta tree (*D. indica*, family Dilleniaceae) in Buxa Tiger Reserve. Buxa Tiger Reserve (henceforth Buxa) is located in the northern region of the Indian state of West Bengal (26°30′–26°55′ N and 89°20′–89°55′ E, covering 761 km^2). Buxa has an average annual rainfall of c.4500 mm, and is predominantly a tropical moist forest habitat (Sukumar et al., 2003; Sekar et al., 2015). Chalta trees are found throughout the reserve (Sekar and Sukumar 2013).

Chalta trees are native to south and southeast Asia (Abdille et al., 2005; Campos-Arceiz et al., 2012) and arguably produce what are described as megafaunal fruits—fruits adapted to primarily attract large-bodied animals for the dispersal of their seeds (Janzen and Martin, 1982). Although the chalta's 6 mm seeds (averaging 103 per fruit) are smaller than those of the stereotypical megafaunal fruit, the indehiscent half-kilogram fruits (known as “wood apples”) 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, and 78% of elephant dung piles opened during the chalta's fruiting season had chalta seeds in them (Sekar and Sukumar 2013). Small rodents (apparently rat species) were sometimes found to access the seeds of fallen chalta fruit; emptied seed coats were found afterwards, suggesting the rats predated upon the seeds (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 (Sekar et al., 2015).

2.2. 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 (and potential secondary dispersal) from elephant dung before germination. From December through March, we located fresh elephant dung piles (estimated to be 0–2 days old) 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: “control”, “small insects only”, or “all seed removers” (hereafter “ASR”). Boluses in the “control” treatment were immediately opened up and the number of chalta seeds inside was counted (seeds and fecal matter were then discarded). These “control” boluses allowed us to estimate the original number of seeds per unit mass in the experimental boluses soon after defecation and prior to exposure to seed predation, allowing us to later estimate the proportion of seeds lost to seed predators. While the numbers of seeds in different boluses from the same dung pile are likely to be correlated, such a correlation is not necessary since we randomized treatment assignment across the boluses from each dung pile.

Boluses in the experimental “small 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 2-mm-wide mesh (with a diagonal of 2.8 mm) ensured that seed predators wider than 3 mm could not access the dung boluses; since chalta seeds are around 4 mm by 6 mm, this small mesh size was necessary to ensure that no whole chalta seeds could be removed from these boxes, as that would make it difficult to distinguish *in situ* destruction from secondary dispersal (as in Estrada and Coates-Estrada (1991)). Any seed disappearance from the dung in the boxes thus had to be due to *in situ* seed predation by small insects or other small organisms, and not due to secondary dispersal or predation by rodents.

Boluses in the “all seed removers” or “ASR” treatment were placed near those in the “small insects only” treatment in the same form as they were found. Thus, seeds in these boluses were susceptible to seed predation by insects <3 mm wide as well as larger