Sridhara, Sachin (2017) ***Examining spatio-temporal patterns of seed dispersal by a terrestrial non-obligate frugivore*****. PhD thesis, James Cook University.**

Examining spatio-temporal patterns of seed dispersal by a terrestrial non-obligate frugivore

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March 2017

A THESIS SUBMITTED

TO THE COLLEGE OF SCIENCE AND ENGINEERING

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education.

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Acknowledgements

I express my deepest gratitude to Will Edwards, David Westcott and Soumya Prasad, my supervisors. I thank Will for taking on a complete stranger from a faraway land, helping me deal with the university, and for his ever positive attitude. I thank Dave, foremost for having enough faith in me to convince Will on this adventure and for providing generous financial support to travel and obtain equipment; his moral, philosophical and diplomatic support has always eased me in to my tasks. Soumya has played a pivotal role in my PhD from before the application process, and worked in the background to support me throughout. I thank her for all the on ground assistance, financial support, and for her feverish excitement on seed dispersal. Together, the three of you have pulled me up when tardy but allowed me to prevail when I was finding my own ground, and have had my back through difficult times. This research would not have been possible without your intellectual and emotional input.

I'm indebted to AusAID for their generous scholarship which has allowed me to experience Australia; my horizons have undeniably expanded in this beautiful country. I appreciate the tremendous support extended by Alex Salvadore. The administrative staff at JCU, particularly Leanne Shillitoe, and members of the finance, estate, library, IT departments and GRS have been very helpful. My peers at JCU, my friends in Australia and the Hitchcocks welcomed me at all times. Adam McKeown from CSIRO has been a great sounding board and my interface to CSIRO.

Most importantly, I'm grateful to the Uttrakhand Forest Department for issuing permits in record time to carry out my work. Shri DVS Khati, Shri Dananjai Mohan, and Smt Neena Grewal were very supportive of my work and pressed their staff to provide timely assistance. Funding from AusAIS, the International Foundation of Science, IdeaWILD, MoEF, DST, AISRF, CSIRO and JCU was crucial to the completion of my research. Indian Institute of Science, National Center for Biological Sciences and Nature Science Initiative provided useful institutional and logistic support.

In the field, company and help from Basheer Baniya, Taukeer Lodha, Mumtaz Chechi, Netra Prasad, Shamshaad Baniya, Sadhique, Zareef Khan, Naushaad, and Meer Hamza, was the most crucial and enjoyable element of my research. They endured all my quirks with a smile and selflessly enabled my work. The warmth and hospitality of the Gujjars is unsurpassable;

they embody many of the values I can only cherish and have left a lasting impression on me. I have learnt much more from them than they ever will in my company. I thank them from the bottom of my heart for their friendship throughout my PhD years. Mumtaz and his family have lost more for science than anyone else I know. His sacrifice energizes my pursuits and I thank him on behalf of the entire scientific community for his courage and selflessness. NCF was a tremendous source of support to Mumtaz and their contribution is greatly appreciated. Mohan Joshi, Sayli Sawant, Nitin Sekar, Narendra Patil, Harish Prakash, and Priti Bangal provided their valuable time volunteering for my field data collection. I'm also thankful to the Kumars for their hospitality in Uttarakhand.

I cannot thank Ajith Kumar enough for being a moral and intellectual compass since I've known him. His unique mentorship has been a driving force in my scientific endeavour and his personality has inspired me to change in many ways. I thank scientists Larissa Bailey and Steve Railsback for their inputs with analyses and modelling. Bivash Pandav and Parag Nigam invested a lot of time and effort to help immobilize Chital for the study. It was very rewarding to work with them. I have no words to thank the open source R and NetLOGO community which provided a level of support that no organization/institution can match.

I would be remiss if I did not thank Center for Wildlife Studies, for providing me the break to switch from an engineering career. The boot camps in Bandipur, Nagarhole, Bhadra and Anshi-Dandeli are etched in my memories for life.

My family has been a witness to my weird journeys, supporting me all along the way. My parents have put my needs before theirs and have indulged me in more ways than I can imagine. My brother Sunil has supported us all through the toughest of times while silently enduring all our eccentricities; together with his wife Preethi, they are the spine of the family.

Finally, I thank my accomplice, fellow traveller, fierce critic and indefatigable friend, Meghna. Her unwavering faith in my abilities, beyond my own and her infinite warmth has lifted me from my lows, while her thoughtful criticism and dogged persistence has grounded me at all times. My personal and academic journey has been thoroughly meaningful in her company and I hope that my efforts are worth all the sacrifices she has made for me.

Statement of contribution of others

Nature of Assistance	Contribution	Contributors
Intellectual support	Supervision & conceptual guidance	Will Edwards (JCU, Australia) David Westcott (CSIRO, Australia) Soumya Prasad (JNU, India)
	Statistics & modelling	Larissa Bailey (CSU, USA) clarified concepts for Chapter 3. Steve Railsback (HSU, USA) provided some code for Chapter 5.
	Editorial	David Westcott, Will Edwards and Soumya Prasad provided comments on drafts written by me. Meghna Krishnadas assisted with presentation and revision.
Financial support	Scholarship	Sachin Sridhara received an AusAID Leadership Award to undertake the PhD. CSIRO (David Westcott) provided stipend for one month.
	Field research	Soumya Prasad was awarded a National Environmental Fellowship from Ministry of Environment and Forest, India, which partially funded field work.
		David Westcott and Soumya Prasad were awarded Australia India Strategic Research Fund grant that provided some more support for field work.
		Savings from scholarship helped fund a large portion of the field work.
	Field Equipment	International Foundation of Science, Sweden awarded a grant to Sachin Sridhara to procure GPS collars.
		IdeaWILD, USA awarded a grant to Sachin Sridhara towards field equipment (Binoculars, LASER rangefinder, compass).

		CSIRO (David Westcott) provided funds to procure chemicals required for immobilization.
	Travel	AusAID and CSIRO (David Westcott) provided funds to travel to India.
	Workshop	CSIRO (David Westcott) funded Sachin Sridhara to attend a workshop on Individual Based Modelling in the USA.
Administrative support		Indian Institute of Science (Soumya Prasad) included Sachin Sridhara on their permission to undertake field research for the first year.
		Ajith Kumar (NCBS, India) liaised with Forest Department to obtain permits for 2 years of field research.
		CSIRO (David Westcott) provided a laptop computer for 2 years of the PhD. Adam McKeown provided administrative support at CSIRO.
		Nature Science Initiative and Indian Institute of Science provided logistic support (field vehicle, field station).
Data collection	Permission	Forest Department, Government of Uttarakhand provided permits to undertake the research.
	Chital collaring	Parag Nigam and Bivash Pandav coordinated and immobilized Chital to deploy GPS collars.
	Field assistance	Basheer Baniya, Mumtaz Chechi, Taukeer Alam, Netra Prasad, Shamshaad Baniya, Mustafa, and Zareef Khan helped with data collection.
	Volunteers	Sayli Sawant, Mohan Joshi, Harish Prakash, Priti Bangal, Meghna Krishnadas, Nitin Sekar, and Narendra Patil volunteered to collect data.

Abstract

Seed dispersal is a key ecological process for plant regeneration. Being sessile organisms, plants rely on vectors (e.g. wind, animals) to disperse their seeds. In the tropics and sub-tropics, fruit-eating animals are vital dispersers for many plants, and the same plant species is often dispersed by several animal species. However, based on differences in body size, diet, and behaviour, frugivores differ in the quantities of fruit they consume and the spatial locations to which they carry seeds within a landscape. Because seed dispersal lays the template for germination and seedling survival, variation in spatial patterns of dispersal arising from different dispersers can have profound consequences for plant regeneration. Thus, assessing the contribution of dissimilar dispersers to spatial patterns of seed dispersal would provide a clearer understanding of the ecological mechanisms underlying plant community dynamics.

Our knowledge on several seed dispersers remain rudimentary. For example, large herbivores (> 2 kg) are found on nearly all continents and their diets include fruits in various amounts. Despite them being some of the largest consumers of fruit, studies on frugivory and seed dispersal by large herbivores are relatively sparse and the natural history and ecological understanding of their role in seed dispersal remains understudied. It has been suggested that large herbivores crucially assisted plant migration during past climatic changes. However, without detailed knowledge of their role as dispersers it is difficult to predict their contribution to shaping future plant communities, especially in the context of global land-use and climate change.

In my thesis, I assessed seed dispersal services provided by large herbivores. Specifically, I examined how the behaviour of a forest ruminant in response to food resources and predation risk influences the spatial patterns of seed rain they generate. I used Chital (*Axis axis*) a deer native to the Indian sub-continent, and tree species including *Terminalia bellerica* and *Ziziphus mauritiana* as a model system. I carried out the fieldwork in Rajaji National Park, a sub-tropical dry deciduous forest in Uttarakhand, India.

First, we reviewed information on large herbivores of Asia comprising of around 80 species. We compiled nearly 300 records of frugivory and seed dispersal from 27 large herbivore species for which diet information was available, but the data was rarely quantitative. The relationship between traits of fruits consumed by the herbivores and the traits of herbivores was examined. Larger-bodied herbivores consumed larger fruits on average (as measured by the maximum width of fruits), suggesting that body size affects patterns of frugivory by herbivores. Further, with the exception of ruminants (Bovids and Cervids) most herbivore families differed from one another in the type of fruits (e.g. size, colour) they consumed. Thus, large herbivores vary in their contribution to seed dispersal and may be more important to seed dispersal than previously though.

Next, I assessed how movement patterns of a medium-sized ruminant, Chital (*Axis axis*, 50 kg), influenced spatial patterns of seed rain for four tropical dry deciduous trees. Specifically, I examined how heterogeneity in topography and habitat influenced Chital movement patterns and consequently seed dispersal. I deployed GPS collars on seven Chital individuals. Chital movement was characterized as being short-range (small movements with rapid changes in direction) or long-range (moving large distances with little change in direction). Short-range movement was greater in areas that had an even mix of habitat types (providing food and cover) but less in rugged terrain. In comparison, long-range movements occurred in habitats with less cover. Notably, Chital space use and movement was not influenced by fruit availability but by factors that likely reflect predator avoidance. Further, seeds were more likely to be dispersed to areas with more Chital activity. Therefore, prey-predator interactions, more than spatial location of fruit trees, might affect spatial patterns of seed rain generated by medium-sized ruminants.

I then developed a novel analytical framework to characterize seed rain patterns of *Terminalia bellerica* generated by Chital. Specifically, using occupancy models I accounted for imperfect detection of seeds when sampling the forest floor. *Terminalia bellerica* seeds were not always detected even when present and detection varied among time periods. Seeds were less likely to be detected among taller ground vegetation. Seed rain patterns were best explained by a combination of Chital dung piles (indicating frequency of use) and the distance to the edge of closed canopy forest (proxy for flight distance). Temporal changes in seed rain patterns were predicted by a combination of grass and structural cover available in the plots. Our method is compatible with currently used field protocols for measuring seed rain, especially for terrestrial dispersers and allows more robust statistical inferences by explicitly modelling both the observation and ecological processes underlying spatial patterns of seed arrival.

Using the occupancy framework, I next examined seed rain patterns generated by Chital and contrasted them with other dispersers in the system namely pigs and birds. For this, I collected seed rain data for two species of trees (*T. bellerica* and *Ziziphus mauritiana*). Chital and pigs dispersed similar quantities of *Z. mauritiana* seeds but to very different number of locations. Chital dispersed seeds to nearly thrice the number of locations compared to pigs or birds. Although pigs transported far more seeds than birds, both dispersed seeds to similar number of locations. Further, seed rain by Chital varied less through time than pigs and birds. While the spatial distribution of grass and structural cover best explained seed rain patterns of Chital, fruiting trees predicted patterns generated by pigs and birds. Chital generate seed rain patterns that are very different from and likely more effective than pigs and birds.

Finally, I used individual-based simulation models to test whether seed rain patterns generated by Chital are driven by predator-prey interactions. Using my own data and that from other studies, I simulated four different scenarios where Chital behaved as grazers or frugivores, both in the presence or absence of perceived predation risk. I compared seed rain data from simulations against observed data. From simulations, I found that grazing behaviour in the presence of predation risk explained most variation in the observed data. Spatial concordance was also highest between observed data and simulations from grazing behaviour in the presence of predation risk. For a non-obligate frugivore such a Chital, predation risk is likely to strongly influence seed rain patterns.

Overall, my results show that the movement patterns of Chital and the seed rain they generate are influenced by habitat features that mediate predator avoidance behaviour and non-fruit resources such as grass and cover. Unlike highly frugivorous birds, non-obligate frugivores like ruminants likely ‘decouple’ seed rain from fruit tree distribution and perceived predation risk may be a key mechanism driving this process. The ecological insights combined with the methodological advances of my study will assist in bridging the research gap in understanding ecological differences among seed dispersers, particularly non-obligate terrestrial frugivores such as ruminant. The strong possibility for prey-predator interactions to influence the outcomes of seed dispersal by Chital is a novel and timely insight. My results have implications for ongoing global declines in large herbivores and top predators which could potentially alter seed dispersal mechanisms.

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General Introduction

Seed dispersal is a key ecological process governing the regeneration success of individuals, populations, species and the entire community of plants (Wang and Smith 2002, Levine and Murrell 2003). Being sessile organisms, plants rely on vectors (e.g. wind, animals) to disperse their seeds. In the tropics and sub-tropics, fruit-eating animals are vital dispersers for many plants, and the same plant species is often dispersed by many animal species (Jordano 2000). However, based on differences in body size, diet, and behaviour, frugivores differ in the quantities of fruit they consume and the spatial locations to which they carry seeds within a landscape (Jordano et al. 2007). In particular, the spatial locations to which dispersers transport seeds strongly influences subsequent processes such as seed predation, germination and seedling recruitment, which can have lasting impacts well into the adult life stages (Nathan and Muller-Landau 2000, Comita et al. 2010, Caughlin et al. 2014). Thus, assessing the contribution of dissimilar dispersers to spatial patterns of seed dispersal would provide a clearer understanding of the ecological mechanisms underlying plant community dynamics and provide insights on the underlying mechanisms driving such patterns (Russo and Augspurger 2004, Muller-Landau et al. 2008, Schupp et al. 2010).

In the tropics and sub-tropics, where a majority of plants are dispersed by animals, identifying the underlying drivers of spatial dispersal patterns requires an understanding of the disperser’s ecology (Westcott et al. 2005, Russo et al. 2006). Because several dispersers may interact collectively with the same plant species and in complex networks (Bascompte et al. 2003, Donatti et al. 2011), it is common to study a subset of the dispersers that represent the functionally distinct services provided (Dennis and Westcott 2006) and build up a more complete understanding of seed dispersal at the community level of plants and their dispersers. The literature on seed dispersal ecology has a disproportionate focus on certain types of dispersers, specifically highly frugivorous birds and primates, resulting in a paucity of information for other dispersers both in terms of taxa and their functional differences (Horn et al. 2011, Vidal et al. 2013, Sridhara et al. 2016).

Seed dispersal by large herbivores

Large herbivores (deer, antelope, tapirs, cattle) are found on nearly all continents and their diets include various amounts of fruits. Despite them being some of the largest consumers of fruit, studies on frugivory and seed dispersal by large herbivores are relatively sparse and the natural history and ecological understanding of their role in seed dispersal remains understudied (Sridhara et al. 2016). It has been suggested that large herbivores crucially assisted plant migration during past climatic changes. However, without detailed knowledge of their role as dispersers it is difficult to predict their contribution to shaping future plant communities, especially in the context of global land-use and climate change (Corlett and Westcott 2013).

Figure 0.1: Google Earth image indicating the position of Rajaji National Park (yellow dot) in Uttarakhand, India.

In this thesis, I assessed seed dispersal services provided by large herbivores. Specifically, I examined how the behaviour of a forest ruminant influences the spatial and temporal patterns of seed rain they generate. I used Chital (*Axis axis*) a deer native to the Indian sub-continent, and tree species including *Terminalia bellerica* and *Ziziphus mauritiana* as a model system. I carried out the fieldwork in Rajaji National Park, a tropical dry-deciduous forest in Uttarakhand, India (Fig 0.1). A mixture of *Shorea robusta* dominated stands, mixed forests, savannahs and open dry river-beds forms the key habitat types of Rajaji (Fig 0.2).

Figure 0.2: Typical landscape found in Rajaji National Park, India. Dry river-beds can be seen at the bottom of the image, immediately below savannah. Closed canopy forest extends all the way from savannah to the hill tops.

Overview of chapters

Chapter 1

This chapter is a review of information on large herbivores of Asia comprising of around 80 species. We compiled nearly 300 records of frugivory and seed dispersal from 27 large herbivore species for which diet information was available, but the data was rarely quantitative. We examined the relationship between traits of fruits consumed by the herbivores and the traits of those herbivores specifically to find whether body size and digestive physiology of large herbivores can explain the species level differences in types of fruits consumed. Larger-bodied herbivores consumed larger fruits on average (as measured by the maximum width of fruits), suggesting that body size affects patterns of frugivory by herbivores. Further, with the exception of ruminants (Bovids and Cervids) most herbivore families differed from one another in the type of fruits (e.g. size, colour) they consumed. Thus, large herbivores vary both in the extent and the type of fruits they consume, and in their contribution to seed dispersal processes. Compared to previous records from the neotropics (Bodmer 1991) which suggested a very limited role for large herbivores in seed dispersal, especially for deer, we found that deer in particular and large herbivores in general played a bigger role in seed dispersal than previously thought in tropical and sub-tropical Asia. Our review also highlighted the many gaps in our knowledge ranging from the diet to habitat use and movement patterns of large herbivores.

Figure 0.3: Fruits of four tree species consumed by Chital, with their corresponding seeds directly below them. Left to right: *Ziziphus mauritiana, Phyllanthus embelica, Ziziphus xylopyrus, Terminalia bellerica*. Scale calibrated in centimetres.

Chapter 2

Movement patterns of seed dispersers play an important role in determining the locations and distances to which seed are dispersed (Nathan and Muller-Landau 2000, Wang and Smith 2002, Côrtes and Uriarte 2013). I therefore assessed how movement patterns of a medium-sized ruminant, Chital (*Axis axis*, 50 kg), influenced spatial patterns of seed rain for four tropical dry deciduous trees (Fig 0.3). Because Chital are primarily grazers and their habitat use patterns are known to be strongly influenced by predator avoidance behaviour I predicted that movement patterns are unlikely to be influenced by fruiting trees (Schaller 1967, Raman 1997, Bagchi et al. 2003a, Vijayan et al. 2012). Specifically, I examined how heterogeneity in topography and habitat (which mediated predator avoidance) and availability of grass influenced Chital movement patterns and consequently seed dispersal. I deployed GPS collars on seven Chital individuals (Fig 0.4). Chital movement was characterized as being short-range (short movements with rapid changes in direction) or long-range (moving large distances with little change in direction). Short-range movement was greater in areas that had an even mix of habitat types (providing grass and structural cover) but less in rugged terrain. In comparison, long-range movements occurred in habitats with less structural cover. Notably, Chital space use and movement was not influenced by fruit availability but by factors that likely reflect predator avoidance (Laundre et al. 2010, Basille et al. 2015). Further, seeds were more likely to be dispersed to areas with few or no adult trees of the fruits they consumed, but patches that were better suited for bedding and foraging (Chital disperse most seed while bedding and ruminating - Prasad et al. 2006, Fig 0.5). Therefore, prey-predator interactions, more than spatial location of fruit trees, might affect spatial patterns of seed rain generated by medium-sized ruminants and this could decouple seed rain patterns from adult trees.

Figure 0.4: Two chital with GPS collars feeding at Rajaji National Park.

Figure 0.5: Seeds of *Ziziphus mauritiana* regurgitated by chital on the forest floor. Scale calibrated in centimetres (bottom half of the tape) and inches (top half of the tape).

Chapter 3

Chital like most terrestrial dispersers deposit seeds on the forest floor (Fig 0.5). Many of the current techniques used to locate and track seeds such as seed traps (Muller-Landau et al. 2008), fishing lines (Schupp 1988), and electronic tags (Suselbeek et al. 2013) are inappropriate for studying the fate of Chital dispersed seeds. Plots on the ground are routinely used to describe seed rain patterns (Herrera and García 2010, Morales et al. 2013) and are most appropriate for Chital. However, past applications of these methods have failed to take account the fact that seeds even when present in a plot may not be detected. As, a prelude to a study of seed deposition, I developed a novel analytical framework to characterize seed rain patterns of *Terminalia bellerica* generated by Chital, using occupancy models (MacKenzie et al. 2006). My goal was to explicitly account for imperfect detection of seeds when sampling the forest floor. To do this, I sampled 400 plots systematically laid in a 25 Ha area four times during the fruiting season. During each visit two individuals independently censused the plot. *Terminalia bellerica* seeds were not always detected even when present and detection varied among time periods. Seeds were less likely to be detected in taller ground vegetation. Seed rain patterns were best explained by a combination of Chital dung piles (indicating frequency of use) and the distance to the edge of closed canopy forest (likely a proxy for flight distance). Temporal changes in seed rain patterns were predicted by a combination of grass and structural cover available in the plots. Significantly, accounting for the detectability of seeds had a strong influence on our estimates and in turn the inferences made. Our method is compatible with currently used field protocols for measuring seed rain and allows more robust statistical inferences by explicitly modelling both the observation and ecological processes underlying spatial patterns of seed arrival.

Chapter 4

When multiple dispersers interact with plants it is important to assess the relative contribution of each species because dispersers contribute differentially to the dispersal process (Jordano et al. 2007, Schupp et al. 2010). I wanted to contrast the seed rain patterns generated by Chital with other dispersers in the system to better understand the relative role of Chital in particular but ruminants and large herbivores in general. Using the occupancy framework previously developed, I examined seed rain patterns generated by Chital and contrasted them with seed rain patterns generated simultaneously by other dispersers in the system, namely pigs and birds. For this, I collected seed rain data for two species of trees (*T. bellerica* – dispersed only by Chital and *Ziziphus mauritiana* – dispersed by Chital, pigs and birds). Chital and pigs dispersed similar quantities of *Z. mauritiana* but to very different locations. Chital dispersed seeds to nearly three times as many locations as did pigs or birds. Although pigs transported far more seeds than birds, both dispersed seeds to a similar number of locations. Chital dispersed varying quantities of seeds of both tree species as the season progressed but to similar number of sites, while pigs and birds dispersed varying quantities of seeds as the season progressed and to varying number of sites. While the spatial distribution of grass, structural cover and terrain ruggedness best explained seed rain patterns of Chital for both the tree species, fruiting trees predicted patterns generated by pigs and birds. By highlighting the differences in spatio-temporal patterns of seed rain generated by Chital, pigs and birds, and by identifying the potential drivers of these patterns this study underscores the importance of examining seed dispersal by medium-sized ruminants in particular and less-studied non-obligate frugivores in general.

Chapter 5

Understanding the mechanisms that drive observed seed rain patterns can be very useful to explain community wide seed dispersal and plant regeneration patterns (Muller-Landau et al. 2008). Insights on these mechanisms are vital to build predictive models of plant responses to various scenarios (Corlett and Westcott 2013, Mokany et al. 2014). However, empirically identifying the underlying mechanistic links in seed dispersal can be very challenging. Simulations based models provide an opportunity to test predictions theoretically and validate with empirically data (Morales et al. 2013, Rodríguez-Pérez et al. 2016). Findings from previous chapters indicate a consistent signal that predator-prey interactions may drive the seed dispersal patterns by Chital. I used individual-based simulation models to test whether predator-prey interactions indeed drive seed rain. Using my own data and that from other studies, I parameterized and simulated four different scenarios where Chital behaved as grazers or frugivores both in the presence and absence of perceived predation risk. I compared seed rain data from simulations against observed data. From simulations, I found that grazing behaviour in the presence of predation risk explained most variation in the observed data. Spatial concordance was also highest between observed data and simulations from grazing behaviour in the presence of predation risk. For a medium-sized ruminant such as Chital, predation risk is likely to strongly influence seed rain patterns, decoupling it from adult plants. While more empirical studies are required to confirm our results, the findings nevertheless have implications for ongoing declines in predators and large herbivores worldwide (Ceballos 2005, Dirzo et al. 2014)

Summary

Overall, results show that the movement patterns of deer and the seed rain they generate are influenced by habitat features and non-fruit resources such as grass and cover. Unlike highly frugivorous birds or primates, non-obligate frugivores such as medium-sized ruminants likely ‘decouple’ seed rain from fruit tree distributions. The ecological insights combined with the methodological advances of my study will assist in bridging the research gap in understanding ecological differences among seed dispersers, particularly non-obligate terrestrial frugivores like large herbivores. The strong possibility for prey-predator interactions to influence the outcomes of seed dispersal by Chital is a novel and timely insight. Combined results have implications for ongoing global declines in large herbivores and top predators and underscores the need to examine the role of ruminants in seed dispersal.

Chapter 1 Frugivory and seed dispersal by large herbivores of Asia

This chapter is based on a published book section by Sridhara et al. (2016) with minimal format edits:

Sridhara, S., K. McConkey, S. Prasad, and R. T. Corlett. 2016. Frugivory and Seed Dispersal by Large Herbivores of Asia. Pages 121–150 in F. S. Ahrestani and M. Sankaran, editors. The Ecology of Large Herbivores in South and Southeast Asia. Springer Netherlands.

Statement of contribution of others:

Sridhara, McConkey and Prasad collated the data. Sridhara and McConkey wrote the first draft with inputs from Prasad and Corlett. Subsequent drafts were revised by all authors.

1. Introduction

Seed dispersal is a key ecological process influencing the spatial patterns and population dynamics of plants (Wang and Smith 2002). Low rates of seedling recruitment under the canopies of parent trees makes seed dispersal essential for many plant species (Nathan and Muller-Landau 2000, Matthesius et al. 2011). Disruptions to the seed dispersal process can have profound consequences for ecosystem function and resilience (Terborgh 2013). In tropical ecosystems, 50 – 80% of plants are dispersed by vertebrate fauna (Jordano 2000). However, vertebrate frugivores are highly variable in their effectiveness of seed dispersal. Within the community of seed dispersers certain frugivore species tend to have disproportionately important functional roles (Jordano et al. 2007, Donatti et al. 2011). Large and highly mobile frugivores often have non-redundant seed dispersal roles in the habitats they occupy (Lundberg and Moberg 2003). Due to constraints on the size of seeds that can be processed by smaller frugivores, large-bodied frugivores can consume fruits that are accessible only to a limited number of frugivores, such as large or well protected fruits (Janzen and Martin 1982). Large frugivores also disperse very large quantities of seeds and over much longer distances compared to smaller frugivores within communities (Janzen and Martin 1982, Lundberg and Moberg 2003, Spiegel and Nathan 2007).

Large herbivores constitute some of the most wide-ranging fruit-eating animals in the world, with the incidence of frugivory being greatest among tropical species (Bodmer 1990). Tropical Asia supports nearly 80 species of large herbivores (> 2 kg) belonging to eight families (Groves and Grubb 2011) and occupying a wide range of habitats, from arid zones to rainforests (Wilson and Mittermeier 2011). Asia is a hot spot for deer radiation (Geist 1998), has the highest diversity of extant pig species (Meijaard et al. 2011) and the only forest-dependent rhinoceros species (van Strien et al. 2008). This high diversity and abundance of large herbivores may have been a key causative factor for the differences in the flora and fauna between tropical Asia and other tropical regions (Corlett 2007). Fruits are consumed by species from all herbivore families to varying degrees (Bodmer 1990, Corlett 1998), yet relationships between large herbivores and the seeds they disperse are poorly understood.

The relative role of large herbivores in seed dispersal can be understood when compared with the rest of the disperser community. However, comprehensive assessments of seed dispersal at community scales, especially for diverse tropical regions, are very limited. In an undisturbed tropical dry forest with an intact faunal assemblage in India, large herbivores had the greatest contribution to seed dispersal of the plant community; dispersing 31% of the 67 plants available (Prasad 2011). In a disturbed tropical wet forest in Malaysia, large herbivores interacted with 26% of 49 plant species (Yasuda et al. 2005), while in an relatively undisturbed tropical wet forest site in Thailand, large herbivores dispersed only 6% of the plant species, although they interacted with 18% of the plant community (Kitamura et al. 2002). One report from an African wet forest indicates that large herbivore interact with over 50% of the plant community (Gautier-Hion et al. 1980, 1985). However, except for Prasad (2011), few studies have used approaches that allowed robust sampling of frugivory by large herbivores which are mostly terrestrial frugivores feeding on fallen fruit. Consequently, these studies may have under-sampled the contribution of large herbivores. Additionally, most sites in tropical Asia have already suffered a decline of large fauna due to hunting and habitat degradation, and thus, large herbivores are likely to be under represented in these communities. While the existing community-wide datasets from tropical Asia, though incomplete, suggest variability in the relative role of large herbivores as dispersers, they nevertheless highlight a community-wide influence. Given the enormous potential of large herbivores in SSEA to play a functionally unique role in seed dispersal, a better understanding of their interactions with associated plant communities is essential.

Insights into the relationships between large herbivores and fruits in Asia are also vital due to the widespread population declines of many species caused by hunting, habitat destruction and competition from domestic livestock (Corlett 2007). Hunting in many parts of Asia has depressed large herbivore populations to critically low levels or extirpated them locally (Robinson and Bennett 2000, Corlett 2007). Additionally, the habitats of Asian large herbivores are among the most fragmented in the world (Riitters et al. 2000, Karanth et al. 2010). The consequences of such large-scale disturbances for seed dispersal can be dramatic, from preventing plant migration in the face of climate change to a total collapse of dispersal function

(McConkey et al. 2012, Corlett and Westcott 2013). Mitigating such effects requires a deeper understanding of the role of large herbivores as seed dispersers. In this chapter, we examine the nature of these interactions by reviewing known information on fruits consumed and seeds dispersed by large herbivores. First, we summarize studies examining the role of sensory cues in large herbivores to locate fruit in the forest. Next, we review fruit selection, the nature and outcome of fruit processing by large herbivores and examine the relationship between fruit size and herbivore body size. Finally, we conclude by discussing the effects historical and recent declines in large herbivores have had at the community level, in light of the interactions we describe above.

2. Data compilation

We compiled a database of fruits known to be consumed by large herbivores across tropical Asia and noted whether the seeds within them were either dispersed or destroyed. Data were collated from published articles, books, reports, theses, unpublished results and personal observations of researchers. Information on fruit traits such as length, width and weight of fruits and seeds, and fruit type were obtained from both primary and secondary sources. Secondary sources included digital floras, information from herbariums and databases maintained by individual researchers or institutions. Fruit and seed measurements were restricted to two dimensions – maximum length and width. When multiple measures existed or were provided as a range, the mean or mid-point was recorded, respectively. The diameter of globular fruits and seeds was taken as both length and width. Plants that were not identified to a species level, but had associated fruit trait data, were retained for the analysis. Herbivore action on seeds was recorded as dispersed or destroyed when available. If dispersal or predation records were ambiguous, fruits were recorded as being ‘consumed’ only.

Herbivore traits were obtained from a combination of primary and secondary sources. A single mean value was computed when ranges or multiple values were available. Traits recorded included body weight (kg), home range (ha), daily movement range (m), digestive physiology, and IUCN status. All binomial names follow the IUCN listing.

3. How do large herbivores locate and select fruit?

It is unlikely that large herbivores rely solely (or even largely) on sensory cues when locating fruits. Fruit crops last days or weeks, so returning to previously rewarding locations is a strategy that is probably used by all frugivores (Corlett 2011). A combination of spatial and temporal memory would allow long-lived animals to return annually to preferred fruiting plants (Campos-Arceiz and Blake 2011). However, sensory information is needed for precise location of individual fruits and for the detection of newly ripened fruit crops. As far as is known, all large herbivore species have the 'typical' forms of all the major mammalian senses: vision, touch, hearing, smell and taste.

Vision enables the herbivore to locate and identify food resources, including fruits. All large herbivore species that have been tested appear to be typical dichromats, with two spectrally distinct cone types. They are most sensitive in the blue to yellow-green part of the human visual spectrum and lack discrimination ability at the orange-red end (Ahnelt and Kolb 2000, Peichl 2005, Schiviz et al. 2008, Corlett 2011, Jacobs 2012). Fruits that are red or orange and eaten by large herbivores are likely to be eaten most by trichromatic primates or tetrachromatic birds (Corlett 2011). In low light the cones are inactive and rods take over, making vision monochromatic, with peak sensitivity in the blue-green. As in most mammals, rods dominate the retinas of all herbivores that have been studied. As well as colour, herbivores can potentially use brightness (lightness) to distinguish fruits from their background, under both high and low light conditions, but the relative importance of this is unknown.

Visual acuity may be more important than colour or brightness discrimination in locating fruit, but lack of standardization in the methods by which this is measured makes comparisons among taxa difficult. In general, it appears that acuity is low in large herbivores (Corlett 2011). Visual acuity is relatively higher in open-country species, such as horses, where it is presumably essential for predator avoidance, and lower in forest species, such as pigs and mouse deer (Schiviz et al. 2008, Sugnaseelan et al. 2013). Even at close range, domestic pigs failed to discriminate visual cues < 20 mm across (Zonderland et al. 2008). In contrast, Asian elephants can apparently discriminate cues 5 mm across at 2 m distance (i.e. at the tip of the trunk) (Shyan-Norwalt et al. 2009).

If an animal cannot see a fruit, it may be able to detect the fruit by either touch, the sound the fruit makes when falling, or by the smell of the fruit. The vibrissae (tactile hairs or whiskers) around the mouths of all herbivores are tactile sense organs (Ahl 1986) that may help detect fruits on the ground, although this has not been studied. A pig's entire snout seems to have the same function, and fallen fruits hidden in litter are presumably detected snout-first. Hearing is potentially useful for not only detecting the sound of falling fruits, but also the noise from feeding arboreal frugivores that many terrestrial frugivores follow (Prasad and Sukumar 2010). The ability to accurately localize sounds seems to vary considerably across large herbivores, being high in pigs and elephants, but low in domestic cattle (Heffner and Heffner 1992).

Olfaction is often assumed to have a dominant role in the mammalian sensory system, with the exception of primates (Corlett 2011), but comparisons between senses are difficult to make. Asian elephants are better at odour discrimination than humans, mice and macaques (Rizvanovic et al. 2013) and indirect evidence suggests that this may also be true for pigs and deer (Graves 1984, Rizvanovic et al. 2013). The sense of taste offers the last opportunity for rejecting a fruit before swallowing (Corlett 2011). Large herbivores appear to have the same five basic tastes as humans (sweet, salty, sour, umami and bitter) (Shine et al. 1998, Jiang et al. 2012). However, the details of what is detected as sweet or, in particular, bitter, are known to vary considerably across mammalian taxa and it is possible that this influences fruit choice in herbivores.

Finally, a diet based on sensory cues alone would inevitably be nutritionally unbalanced, since these cues are imperfect proxies for nutritional value (Corlett 2011, Cazetta et al. 2012). Preferences for colours, odours and tastes need to be fine-tuned by the post-ingestive physiological feedbacks that enable an animal to eat more of what it needs and less of what it does not need. This 'diet learning' ability has been widely demonstrated in domestic herbivores and can be assumed to be present in their wild relatives too (Provenza 1995, Yearsley et al. 2006).

4. Fruit (or seed) selection, processing and deposition

In addition to variation in sensory ecology outlined above, differences in body size, digestive physiology, nutritional requirements, and habitat specificity may influence fruit choice by large herbivores. The nature of seed processing, seed retention times and consequently the seed shadows generated by large herbivores for endozoochorously dispersed seeds are primarily influenced by the digestive anatomy and physiology of herbivores, which shows tremendous variation among herbivore families. The outcome of this plant-herbivore interaction determines whether the herbivore is a disperser or a seed predator, the distances to which seeds are transported and the deposition of seeds to particular habitats (Brodie et al. 2009a, Velho et al. 2012a, Jadeja et al. 2013). In this section we summarize relationships between fruit traits and the outcome of seed processing by large herbivores in relation to the digestive anatomy and physiology of large herbivores.

Based on their digestive anatomy and physiology, Asian large herbivores can be broadly classified into three groups which reflect similarities in seed processing: (1) foregut fermenters or ruminants (mouse-deer, muntjac, deer, antelope, and wild cattle), (2) simple-stomach frugivores (pigs, babyrousa) and (3) simple-stomach folivores (tapirs, wild ass, rhinoceros and elephant). Although processing varies within these groups, the overlap in characteristics merits a synthesis among the distinct groups.

4.1 Foregut fermenters (Tragulidae, Cervidae and Bovidae)

In SSEA, extant ruminants belonging to three families - Tragulidae (8 species), Cervidae (24 species), and Bovidae (10 species) - constitute the largest group of large herbivores. Ruminants range in size from 2 to 1000 kg; chevrotains (Tragulidae) and muntjacs (Cervidae) occupy the lower end of this spectrum (2—20 kg), while wild cattle (Bovidae; 240-850 kg) are comparable in size to rhinoceroses (Table 1.1). It has been suggested that the digestive physiology of ruminants may have evolved for a frugivorous diet, later diversifying for folivory (Bodmer 1989a, Gagnon and Chew 2000, Clauss et al. 2003).

Theories based on energetics, digestive physiology and allometry predict that smaller ruminants should consume more fruits than larger species (Jarman 1974, Hofmann 1989, Wenninger and Shipley 2000, Clauss et al. 2003). Specifically, energy requirements per unit mass increase with declining body size, necessitating small ruminants to ingest food items of high quality, such as fruits. Additionally, their smaller digestive tracts have faster passage rates associated with lower digestion efficiency (Hofmann and Stewart 1972, Demment and Soest 1985, Clauss et al. 2003). Conversely, fruits may not be dominant in the diet of larger ruminants, which are more efficient at processing more abundant lower quality food items such as grass and leaves (Clauss et al. 2013). Nevertheless, frugivory is reported from several species of ruminants (Table 1.2) and medium-sized ruminants can be seasonally very frugivorous (John Singh 1981). There are fewer reports of frugivory by larger ruminants such as wild cattle (genera *Bos* and *Bubalis*), nilgai (*Boselaphus tragocamelus*) or sambar (*Rusa unicolor)* compared to small and medium-sized ruminants such as muntjac *(Muntiacus muntjac)* and Chital *(Axis axis).* From available records, it appears that the extent of frugivory may be higher in small to medium-sized ruminants (e.g., Tragulids, muntjacs and *Axis* deer).

All ruminants house symbiotic bacteria in their fore-stomachs. While cervids and bovids have a four-chambered stomach, the third stomach chamber in tragulids is poorly developed or completely absent (Agungpriyono *et al.* 1992). Ruminants have strong molars and seeds can be destroyed during repeated chewing (Bodmer 1989b). While some ruminants have been documented to swallow fruits whole (Chen et al. 2001, Prasad et al. 2006, Jadeja et al. 2013), others may chew fruits too large to swallow (Feer 1995). The orifice between the first and second stomach chambers constrains the size of food particles that can pass through the fore-stomach, resulting in two distinct seed dispersal mechanisms. First, seeds that are small enough to pass through the fore-stomach (typically < 1 mm) are defecated intact (Demment and Soest 1985, Mouissie et al. 2005, Jadeja et al. 2013). Second, larger seeds, typically drupes (fleshy fruit which have seeds encased in a stony wall, providing strong protection) that can survive repeated mastication during rumination are spat out after being stored in the rumen (first stomach chamber) for several hours (Chen et al. 2001, Prasad et al. 2006). These two distinct mechanisms of dispersal are perhaps associated with significantly different seed retention times, survival probabilities, and germination success, all of which eventually determine the efficacy of ruminants as dispersers. Based on the limited number of both plant and ruminant species that have been examined for damage or germination, ruminants appear to play a key role in the dispersal of certain tropical plants, typically with drupes (Chen et al. 2001, Prasad et al. 2006, Brodie et al. 2009a). However, the fate of most seeds consumed by ruminants (i.e. whether they are dispersed or destroyed) remains unknown. There is a need to examine the exact nature of the interaction between ruminants and fruits, particularly for newly described ruminant species from tropical Asia (Dung et al. 1993, Rabinowitz et al. 1999, Groves and Grubb 2011).

4.1.1 Tragulidae

The small body size, crepuscular habits, elusive behaviour, and tendency to prefer dense undergrowth (Sridhara et al. 2013) has precluded reliable observations of frugivory by Tragulids until the more recent use of camera-traps (Prasad et al. 2009). From the literature we were able to tabulate fruits from 32 tree species in the diets of tragulids. Accounts of frugivory were restricted to three tragulid species, although eight occur in Asia. Records of fruits consumed by Tragulids were restricted to trees, mostly drupaceous and coloured green. Dispersal was confirmed for 6 species (all drupes), and seed predation recorded for one dry-fruited species (Yasuda et al. 2005). The largest fruits consumed and seeds dispersed by Tragulids were smaller than for other ruminant groups (Table 1.2).

4.1.2 Cervidae

We found frugivory records for only two species of muntjac, although 13 species are recognized in SSEA. For these, we were able to record instances of fruit consumption of 88 plant species. Fruits consumed were largely from trees, predominantly drupaceous, and were mostly yellow. A total of 15 species were recorded as being dispersed (11 drupes, 3 berries), and the largest fruits consumed and dispersed were similar in size

(Table 1.2). Seeds which were consistently destroyed (7 species – 4 drupes, 2 berries and 1 capsule) ranged from 10 x 8 mm to 25 x 15 mm.

We documented a total of 67 plant species whose fruit were consumed by larger cervids belonging to three genera: *Rucervus*, *Rusa* and *Axis*. Accounts of frugivory were restricted to 4 species, although 8 large cervid species occur in tropical Asia. Fruits consumed were mostly from trees, largely drupaceous, and predominantly yellow or green (Table 1.2). Dispersal records were confined to 24 plant species (15 drupes, 4 berries, 2 figs and 1 capsule). Seeds consistently destroyed (2 drupes, 2 berries and 1 capsule) varied from 15 x 9 mm to 25 x 15 mm.

4.1.3 Bovidae

Fruits from 38 plant species were documented to be consumed by bovids. Records of frugivory were restricted to 1 species each from the genera *Gazella*, *Naemorhedus, Tetracerus*, *Antilope*, *Capricornis*, *Boselaphus* and *Bos*, although 5 other species of bovids are found in tropical Asia. Fruits consumed were mostly from trees, drupaceous and equally likely to be black, green, yellow, or red. Twelve species were recorded as being dispersed (including 5 pods, 2 berries, 1 each of drupe and capsule), while no information was available on destruction of seeds.

4.1.4 Seed deposition

In general, there is surprisingly little information on the seed deposition patterns by ruminants. Brodie *et al.* (2009) found that muntjacs (*Muntiacus muntjac)* alone deposit seeds of *Choerospondias axillaris* in open microhabitats where their germination success is the highest, although sambar *(Cervus unicolor)* and gibbons (*Hylobates lar*) also disperse *C. axillaris*. Gut passage rates or seed retention times, which affect deposition patterns, are unknown for all but one species of ruminant, Chital *(Axis axis*). Chital retain the seeds of *Phyllanthus embelica* for 7-27 h before regurgitating them (Prasad et al. 2006). Studies on wild and domesticated ruminants from Europe and America indicate that gut passage rates range from 20 h to 5 d for medium to large ruminant species (Janzen et al. 1985, Schmidt et al. 2004). The uneven retention time of seeds combined with the large home ranges of medium-large ruminants (< 114 km^2 – Table 1.1) is expected to result in scattered seed deposition patterns and long seed dispersal distances (Vellend et al. 2003, Myers et al. 2004).

4.2 Simple-stomach frugivores (Suidae)

In Asia, the family *Suidae* comprises 12 species in three genera. Pigs and their relatives are primarily frugivorous, but are unique in comparison with other ungulates in supplementing their diet with a wide range of other food types including animal-matter.

Both pigs and babirusa are of medium-size, with weights ranging from 45-135 kg (pigs) and 70-100 kg (babirusa) (Table 1.1).The strong jaws and teeth, and irregular molar surfaces of pigs and babirusa make them well suited for crushing seeds (Meijaard et al. 2005). Domestic pigs have a well-developed caecum and spiral colon that are major sites for microbial digestion, with efficient cellulose digestion (Leus and Macdonald 1997). However, wild suid digestive physiology has rarely been investigated. Reports indicate that they are more folivorous than domesticated pigs (Leus and Macdonald 1997). The diet of *Sus scrofa* varies greatly among the habitats and regions in which it occurs (Ickes et al. 2001); both this species and *S. barbatus* appear to prefer fruit and consume it in abundance when available. Similarly, the digestive physiology of babirusa suggests that it is primarily frugivorous, or a frugivore-folivore (Leus 1994). Indeed, babirusa do show a preference for fruit (Leus 1994, Clayton 1997) and are more specialised in digesting fruit components and less efficient in digesting grass fibre than pigs (Leus 1994). Babirusa have enlarged stomachs compared to pigs as more fermentation occurs here than in the large intestine.

Published accounts also indicate significant variability in whether *Sus* are considered dispersers (Hamann and Curio 1999, Donatti et al. 2011) or predators of seeds (Campos and Ojeda 1997, Lynes and Campbell 2000, Curran and Leighton 2000, Meijaard et al. 2005), even for congeneric plant species (Campos and Ojeda 1997, Lynes and Campbell 2000). While the seeds of some fruit types (e.g., dry) are consistently destroyed (Curran and Leighton 2000), seed treatment is probably type- and species-specific and there may be significant differences in seed handling. Seeds from berries (10 of 12 species dispersed), pods (4 of 5 species) and complex fruit (6 of 6 species) were more likely to be dispersed than destroyed, while seeds from dry fruits (15 species) were always destroyed. Plant species with drupe fruit were equally likely to have their seeds dispersed (11 species) as destroyed (12 species). Seed predation by *Sus* can have profound effects on seed recruitment (Curran and Leighton 2000), while its potential role as a seed disperser in most Asian habitats may be less significant, albeit understudied (Hamann and Curio 1999). In temperate regions fruit forms 32 – 42% of the diet of *S. scrofa* (Diong 1982, Thomson and Challies 1988), while in *S. barbatus* stomachs investigated in Asia, crushed seeds were often, dominant (Caldecott 1991, Meijaard et al. 2005, Wulffraat 2006). Outside of their native range, there have been an increasing number of studies indicating an important dispersal role for introduced pigs, particularly where alternative native dispersers are scarce (Diong 1982, Fedriani and Delibes 2009, Matías et al. 2010, Donatti et al. 2011, O'Connor and Kelly 2012).

4.2.1 Babirusa

Information about frugivory by babirusa is largely anecdotal and the only evidence of seed dispersal comes from stomach contents (Clayton 1997). We found 21 records of frugivory for *B. babyrussa* and *B. togeanensis*, while no information exists for *B. celebensis*. Most records of frugivory were of drupaceous fruits from trees, equally likely to be coloured yellow, green, black or brown. Even if babirusa destroys the seeds of some species, they are one of the largest fruit-eating animals in their range, exceeded in size only by the anoa (*Bubalus depressicornis*) (Whitten et al. 1987).

4.2.2 Pigs

Available information on frugivory in *Sus* comes largely from the widespread *Sus scrofa* and *S. barbatus,* with limited records for *S. celebensis, S. cebifrons,* and *S. verrucosus.* In total, fruits of 97 species were recorded as being consumed, of which 30 species were reported to be destroyed and 32 dispersed. Fruits were mostly from trees and were predominantly drupaceous and red in colour. Generally, the seeds dispersed by *Sus* are small-medium sized (n = 12 species, with fruit length < 10 mm), but seeds up to 48 x 28 mm have been recorded to be dispersed.

4.2.3 Seed deposition

With gut passage rates of 2-4 days (O'Connor and Kelly 2012) and home range sizes of 6-34 km^2 (Saunders and Kay 1991, Caley 1997, Mitchell et al. 2009), *Sus scrofa* (and perhaps other pig species) may be effective long distance seed dispersers for some plant species (O'Connor and Kelly 2012). Further, defecation of seeds can be spaced over multiple days, producing scattered seed deposition patterns (O'Connor and Kelly 2012), which can be beneficial for seedling recruitment. *Sus barbatus* has unique ranging behaviour, whereby periodic mass migrations of individuals occur every few years, probably to coincide with predictable fruiting in *Dryobalanops* forests in the Malayan peninsula (Kawanishi and E. Sunquist 2008) or seasonally-fruiting *Dinochloa* bamboo in Borneo (Davies and Payne 1982). At other times the populations are mostly small and exhibit local movements only, although movements may increase as populations expand to exploit food sources(Kawanishi and E. Sunquist 2008). During annual migrations, *S. barbatus* may cover distances of 8-22 km per month, and 250-650 km in all (Caldecott 1991) and thus have the potential to disperse seeds over long distances.

4.3 Simple stomach folivores (Elephantidae, Rhinocerotidae, Equidae and Tapiridae)

Unlike ruminants (4.1) and pigs (4.2), simple stomach folivores belong to four different families with different phylogenetic histories: Elephantidae (1 Asian species), Rhinocerotidae (3 Asian species), Equidae (1 species in tropical Asia) and Tapiridae (1 Asian species). However, these species display similarities in their digestive systems and consequently show some similarities in their seed dispersal behaviour. Although collectively called "hindgut fermenters", fermentation in these animals actually occurs in the mid-gut, which results in distinctly different seed processing compared to foregut fermenters or simple-stomach frugivores. These large herbivores have simple stomachs, with symbiotic bacteria housed in the caecum and colon (Clemens and Maloiy 1982). The breakdown of cellulose is less efficient compared to foregut fermenters and faecal particle size is significantly larger, with faeces containing poorly-digested forage (Fritz et al. 2009). Thus, fruits and seeds are poorly digested and often pass undamaged through their guts. Since fermentation occurs in the caecum and colon, these animals can process low-nutrient food rapidly. This rapid food-processing gives them an advantage at large body sizes, as they are able to take in significantly larger quantities of food (Clauss et al. 2003). Perissodactyls (rhinoceroses, equids, and tapirs) have a compartmentalised colon (Stevens and Hume 1995), which makes their digestive systems more complex than elephants. Although fruit is typically not a predominant food item in the diet of elephants, rhinoceroses, wild asses and tapirs, the regular appearance of seeds in their dung indicate that they do consume a wide-range of fruit, sometimes in significant quantities (Table 1.2).

4.3.1 Elephants

Asian elephants (4000 kg) are the largest fruit-eating animals in Asia (Table 1.1). The extent of frugivory exhibited by elephants is highly variable (Campos-Arceiz and Blake 2011). Their mild masticatory action results in little or no seed damage in the mouth, although digestive seed predation in the gut has been reported (Campos-Arceiz et al. 2012). However, they are probably primarily seed dispersers.

Elephants consume fruits from a diverse range of life forms, but mostly from trees and herbs (Table 1.2), reflecting their diverse habitat use. Elephants were recorded to consume fruits from 84 species in our review. Types of fruit eaten were diverse, but most were pods, berries or drupes, and the seeds were usually dispersed. Fruits were mostly yellow, green or brown (Table 1.2). Elephants consume the largest fruits among large herbivores in Asia and can disperse seeds as large as 39 x 28mm.

4.3.2 Perissodactyls (Rhinoceroses, Tapirs and Equids)

4.3.2.1 Rhinoceroses

Rhinoceroses (750 – 2350 kg), second in size only to elephants, are predominantly folivorous. However, seeds and fruits are regularly found in their dung and latrines (Flynn 1978, Dinerstein 1991). The rarity of most rhinoceros species has prevented detailed investigation of the proportion of fruit in their diet. Frugivory has nevertheless been reported, and fruit of 37 plant species are recorded to be consumed by Asian rhinoceroses. These fruits are mostly from trees, usually dull coloured (green, brown or yellow), and are either berries or drupes. The relatively less diverse range of fruits consumed by rhinoceroses perhaps reflects their current rarity and habitat specialization.

4.3.2.2 Tapirs

Tapirs (350 kg) have been documented to disperse and destroy seeds. The dentition of tapirs is well suited for seed crushing (Campos-Arceiz et al. 2012) and seed fragments have been reported from dung of Neotropical tapir species (Janzen 1981). Like pigs, their function as dispersers or seed predators is variable. Captive tapirs have been documented to spit or swallow seeds whole and also defecate both viable and destroyed seeds (Campos-Arceiz et al. 2012). However, the extent of frugivory in tapirs in the wild is unclear, making any comparison with other simple-stomached herbivores difficult.

In our review, we found records of tapirs feeding on fruits from 21 species of plants. These fruits were all from trees, yellow, green or brown, and were complex fruits, berries or drupes. Tapirs are extremely variable in their seed treatment and often both disperse and destroy seeds from the same species (Campos-Arceiz et al. 2012). Of the 21 species we recorded as consumed by tapirs, five usually had the seeds destroyed, four had seeds destroyed as well as dispersed, two were dispersed and the remaining 10 were observations of frugivory only. Further, tapirs have difficulty handling large fruits and frequently spit seeds from large fruits (Campos-Arceiz et al. 2012). *Durio zibethinus* seeds (39 x 26 mm) are the largest reported to be dispersed by Asian tapirs (Holden et al. 2003, Campos-Arceiz et al. 2012).

4.3.2.3 Equids

The Asiatic wild ass (250 kg) is the smallest simple-stomached herbivore. Equids have small stomachs relative to their body-size and tend to process fruit slowly, limiting the quantity of food that can be consumed (Giffin and Gore 1989). The Asiatic wild ass has been studied in Israel, Iran and India, and seeds are frequently reported in dung and seedlings have been found near dung piles (Peled n.d., Shah 1993, Ghasemi et al. 2012), but detailed reports on extent of frugivory are unavailable. Similarly, there is no information on seed predation, although digestive seed predation has been reported for domestic horses (Janzen et al. 1985). In general, asses in the tropics are found only in desert regions, limiting their fruit consumption to berries, capsules and pods of herbs, shrubs, and sometimes trees.

4.3.3 Megafaunal fruit

It has been proposed that the largest fruit within tropical plant communities evolved in response to frugivory by “megafauna” - the largest terrestrial vertebrate frugivores (> 1000 kg; Guimarães et al. 2008). Analyses of elephant fruit and plant communities in South America suggest that megafaunal fruit fall into two categories: fruits 4–10 cm in diameter with up to five large seeds, and fruits > 10 cm diameter with numerous small seeds (Guimarães et al. 2008). In tropical Asia, elephants and rhinoceroses are able to swallow and disperse the largest seeds in the habitats they occupy (Cochrane 2003, Corlett 2011). In our review fruit that fit the “megafaunal fruit” syndrome featured prominently in the diets of elephants (19 of 50 plant species for which fruit width was available), rhinoceroses (10 of 24 plant species) and tapirs (9 of 13 plant species). The role of tapirs, however, in the dispersal of large seeds is variable; from studies on captive individuals, seeds of large fruits were less likely to be swallowed and more likely to be damaged, and only small-seeded species were regularly defecated in a viable condition (Campos-Arceiz et al. 2012). Fruits that fit the “megafaunal fruit” syndrome are known to be dispersed by smaller frugivores as well as other dispersal mechanisms such as wind or water (Cochrane 2003), and in a staggered successive manner with back-up dispersal mechanisms being invoked when megafauna fail to disperse the fruit (Sekar and Sukumar 2013). It remains to be tested if these fruit evolved in response to features of the sensory and digestive systems of large simple-stomached herbivores. No data on dispersal of megafaunal fruits exist for Asian equids, but in the Neotropics introduced horses appear to have replaced some of the seed dispersal services that were lost with the extinction of the megafauna around ten thousand years ago (Janzen and Martin 1982).

4.3.6 Seed deposition

Large simple-stomached herbivores process vast quantities of forage within a day, consequently exhibiting the longest known daily displacements rates and home ranges for terrestrial mammals. They also have long gut passage times (rhinoceroses 61-122 h, elephants 40-122 h, tapirs 63-235 h, ass 34-39 h), although this may not scale with body size, since the retention times of smaller foregut herbivores overlap (2-96 h, S. Prasad unpublished data). These large herbivores also undertake long, directed seasonal movements to access water, grasses in different stages of growth, or salt licks (Campos-Arceiz et al. 2008). Estimated seed dispersal distances for tapirs (Campos-Arceiz and Blake 2011) and elephants (Campos-Arceiz et al. 2008), indicate that these animals are effective long-distance seed dispersers. Asses and rhinoceroses are likely to be similarly capable of long-distance seed dispersal, although no data exist; Asiatic wild ass have daily movements of 4-11 km, and home ranges of 8-19 km^2, while rhinoceroses have home ranges of 5-50 km^2 and may travel up to 10 km within a day (van Strien et al. 2008).

Both elephants and rhinoceroses deposit seeds within large dung piles, which can provide suitable conditions for seedling recruitment, although this advantage may be partially offset by high seedling density and associated competition (Campos-Arceiz and Blake 2011). Rhinoceroses and tapirs frequently deposit seeds in latrines (Dinerstein 1991, O'Farrill et al. 2013), which can have both positive and negative consequences for seed recruitment (Gonzalez-Zamora et al. 2012, O'Farrill et al. 2013). While these are untested in rhinoceroses, latrines of *R. unicornis* were associated with distinct floras (Dinerstein 1991).

4.4 Relationship between body size of herbivores and size of fruit consumed

Seed size and weight are key determinants of recruitment success and seedling survival, consequently influencing the reproductive success of plants (Moles and Westoby 2006). Because frugivores can exert selective pressures on fruit and seed size (Forget et al. 2007), the constraint of frugivore body size on fruit traits needs closer examination. For instance, fruits with very large seeds are accessed only by a few frugivores that are often non-redundant in dispersal function, whereas fruits with smaller seeds usually have a wider suite of consumers and dispersers (Gautier-Hion et al. 1985, Kitamura et al. 2002). Indeed, recent evidence suggests that the functional extinction of large frugivores can cause rapid evolution in trees towards smaller seed sizes (Galetti et al. 2013) or shifts in plant communities in ecological time (Velho et al. 2012b).

Here, we examine the nature of the relationship between body size of large herbivores and the largest fruit they can consume. Fruit size is highly correlated to seed size and is therefore a good measure of the limits imposed by gape width of large herbivores on the size of seeds potentially dispersed (Forget et al. 2007). We analysed fruit and seed width (seed width = second-largest axis of the fruit or seed), which often determines if a fruit or seed is swallowed (Corlett 1998). Each species of plant and herbivore was considered to be an independent data point. We used generalized linear models and quantile regressions to examine whether the average and maximum width of fruit and seed consumed were constrained by the body size of large herbivores. To linearize the allometric relationship we log-transformed the predictor (i.e., body weight of herbivores) and used the log link function for Gaussian error distributions. We checked for over-dispersion and examined residuals graphically to check for normality and heteroscedasticity. All analyses were performed in R 3.0.1 (R-Core-Team 2013).

Although maximum fruit length, seed length, and width of seed consumed increased with body weight of large herbivores, the only significant relationship was with fruit width, suggesting that body size (correlated with gape width) of large herbivores can limit the sizes of fruits consumed (Fig 1.1). Results from the quantile regressions however, suggests that maximum fruit length alone shows a positive relationship with body weight for lower body weight (Fig 1.2a). Seed length may have such a relationship due to the long structure of pods and pod like fruits in the diet of large herbivores. Fruit width, seed length and seed width however, do not show any pattern with body size (Fig 1.2b, c, d) for the upper quantile (0.95). Because these three traits show a positive relationship for the other quantiles used (0.25, 0.5, 0.75) we could perhaps infer that fruit sizes consumed by smaller herbivores are on an average smaller than their larger counterparts. Taken together, these linear and quantile regression results do not suggest a strong link between disperser body mass and, fruit or seed size likely to consumed or dispersed. We conclude that more data may be necessary to elucidate these links and advice caution against reducing importance of larger species until such data has been assembled.

4.5 Overlap in fruit choice among Asian herbivores

We also assessed the similarity in the traits of fruits consumed by the different families of large herbivores found in Asia. We compiled data on the digestive system, maximum and minimum fruit length and width, maximum and minimum seed length and width, maximum and minimum fruit and seed weight, fruit type and fruit colour associated with each of the large herbivore species. This data was collated for seven of the eight families of large herbivores; Equidae was excluded due to the lack of information on fruit traits. We used the package 'FD' in software R to compute the dissimilarity in traits. Gower's dissimilarity index was used since it allows for categorical traits (fruit type and colour, in this case). Numbers close to 0 indicate greater similarity in fruit choice while numbers close to 1 indicate dissimilarity.

In general, our results suggest a degree of dissimilarity in the fruit choice by the different families of large herbivores, providing the first family-wise comparisons at a continental scale. Results indicate that fruit choice is most similar between cervids and elephants, followed by cervid and bovids (Table 1.3). The similarity between cervids and bovids may reflect the overlap in their digestive physiology and body size. The similarity between elephants and cervids, however, is surprising given the differences in their digestive physiology and sensory capabilities. Fruit choice may overlap based on the limited fruit characteristics we found and used in the analysis, perhaps due to sympatry of cervids and elephants throughout SSEA until recent times. Incorporating currently unknown information such as nutritional characteristics of fruits and the relative abundances of these fruits in the diet may alter the dissimilarity metrics when reassessed in the future. This similarity may also be cause due to the incomplete nature of the dataset. Nevertheless, our results, although preliminary, call into question the assumed non-redundancy of large herbivores as seed dispersers, specifically small-medium species in the families Cervidae and Bovidae. Tapirs are consistently dissimilar to most families, but it is unclear whether this reflects scarcity of information on frugivory or the uniqueness in their fruit choice. As other animals including bears, civets, macaques, and orangutans, also compete with large herbivores for fruits on the ground, fruit characteristics are as likely to have been shaped by these frugivores too. Finally, these results must be interpreted cautiously due to the incomplete nature of the dataset. Studies from more landscapes covering the entire suite of frugivores can help verify these patterns across regional, continental and global scales.

5 Other modes of seed dispersal by large herbivores

Apart from locating fruit actively, the consumption of fruits may be a passive activity when other plant parts (e.g. foliage, twigs) are being eaten. Janzen (1984) proposed that small fruits interspersed in the foliage maybe consumed inadvertently, even though the animals are not actively seeking them. Because small fruits may not provide sufficient rewards to the consumers, foliage serves the function of the fruit by 'packaging' seeds, which potentially leads to endozoochorous dispersal (Janzen 1984). Known as the 'foliage-as-fruit' hypothesis, this mechanism of dispersal is relevant to large herbivores, whose diet often consists predominantly of foliage. Several grasses, herbs and a few trees seemingly fit the requirements for this mechanism of seed dispersal in Asia (R. Corlett pers. obs.), although the hypothesis remains largely untested. Preliminary evidence supporting this hypothesis was found for elephants in Sri Lanka (Samansiri and Weerakoon 2008), three ruminants, and wild pigs in India (Middleton and Mason 1992), but was rejected for rhinoceroses in Nepal (Dinerstein 1991). More studies that test the hypothesis are necessary to assess its extent and significance for plant species.

Seeds of herbs and grasses can also be transported by adhering to the pelage or fur of animals. This mode of dispersal, referred to as epizoochory, has been reported for large herbivores because the body hair on these mammals enables the transport of certain kinds of seeds. European populations of *Sus scrofa* and certain temperate deer species effectively disperse seeds that attach to hair (Schmidt et al. 2004, Couvreur et al. 2004). However, there are no reports of epizoochory for any of the large herbivores from tropical Asia, although fruits and seeds with adaptations for external attachment are widespread in open habitats, where they often attach to human clothing (R. Corlett pers. obs). Reports suggest that pigs transport seeds of *Rafflesia* in their hooves (MacKinnon et al. 1997).

6 Large herbivore distributions and consequences for seed dispersal: past, present and future

The Asian tropics still harbour a number of large herbivores, but the abundance and range of most extant species have contracted over historical and recent times (Groves and Grubb 2011), and several additional species have become extinct since the Late Pleistocene. In this section, we summarize past and present distributions of herbivores, and assess the range of dispersal services that might have been lost in the Asian tropics.

All tropical terrestrial ecosystems, including several islands, have lost at least one megafaunal species (>44 kg) since the Pleistocene (Corlett 2011). Tropical Asia has experienced significant megafaunal losses at rates that are higher than some other continents (Corlett 2011). The drivers of this region-wide extinction of megafauna remain unclear, with both climate change and the arrival of *Homo* species being plausible explanations (Louys 2012). Herbivorous mammals, including elephants, stegodons, rhinoceroses, horses, bovids, and tapirs, constitute the largest group of extinct megafauna. Since the Late Pleistocene, at least two species each of elephants, stegodons, rhinoceroses and bovids, one species of giraffe, and at least one species of horse have gone extinct from south Asia (Chauhan 2008). The number of Late Pleistocene rhinoceros species is uncertain (Antoine 2012), but the distribution of the family has certainly declined (Corlett 2011). Similarly, at least one species each of elephant, stegodon, rhinoceros, horse and bovid, in addition to a giant tapir, have been lost from Southeast Asia (Mishra et al. 2010, Corlett 2011). All of these extinct species are likely to have consumed at least some fruit, like their extant relatives (Corlett 2010). Since their diversity, distributions and abundances were greater than today (Corlett 2010), they may have played a significant role in the evolution of modern fruits.

At present, ruminants are widely distributed, from the arid zones of western India to the rainforests of Indonesia and Philippines, but are predominantly found in woody habitats, ranging from savannah to rainforest (Eisenberg and Seidensticker 1976), and attain their highest densities in tropical dry forests and woody savannas (Karanth and Sunquist 1992). Most ruminants occur in woody environments and avoid disturbed environments, possibly restricting their functional roles to these habitats. A few ruminants, however, may occur at high densities in human dominated landscapes (e.g. Nilgai *Boselaphus tragocamelus*). *Sus* (pigs) is the most diverse and widely distributed genus among suids. *Sus* species are scattered across tropical Southeast Asia, primarily in forested habitats, with some species being able to persist in grasslands and cultivated areas. Most pig species partly forage in disturbed regions, and can occupy both forest and non-forest habitats (Table 1.1). The disturbance tolerance of suids varies considerably and only *S. scrofa* is a true habitat generalist and potentially a disperser of seeds across modified habitats. The three *Babyrousa* (babirusa) species are confined to Sulawesi or nearby islands (Indonesia), where they persist in forests and occasionally cultivated regions. *Porcula* comprises a single species found in tall grasslands in India and no frugivory information exists for this species. Elephants are found in a range of habitats, from alluvial grasslands to rainforest and are distributed widely from India to Indonesia. With the exception of Indian Rhino, *Rhinoceros unicornis*, all the Asian rhinoceroses have highly restricted ranges within the rain forests of South-east Asia (IUCN 2014). The Indian rhinoceros is found in grasslands and riverine forests in northern India and Nepal, a tiny fraction of its historical and Pleistocene ranges. The Asiatic wild ass is restricted to deserts and very dry regions of western India, while tapirs are found only in the rainforests of Southeast Asia (IUCN 2014). In summary, with few exceptions, most large herbivores are currently restricted to specific habitats within the continent, perhaps limiting the spatial extent of their seed dispersal function. However, elephants, often within a population, continue to utilize a range of habitats and probably remain responsible for long-range seed dispersal in a large mosaic of heterogeneous habitats for a wide range of plant species.

Apart from native large herbivores, free-ranging or feral buffalo, cows, horses and goats occur in many parts of tropical Asia (Dinerstein and Wemmer 1988, Middleton and Mason 1992). Although these feral and introduced animals have been documented to have detrimental impacts on plant populations (Scowcroft and Hobdy 1987, Moriarty 2004), they also function as seed dispersers (Middleton and Mason 1992, Giordani 2008), including dispersal of large fruits (Dinerstein and Wemmer 1988). Several Asian herbivores, including spotted deer (*Axis axis*), sambar (*Rusa unicolor*), blackbuck (*Antilope cervicapra*), and wild boar (*Sus scrofa)* have been introduced to other continents and become invasive in their introduced ranges (Moriarty 2004). These populations of introduced large herbivores may assist in the spread of both invasive and native plants (Moriarty 2004).

Most Asian large herbivores species are threatened by some combination of hunting, habitat loss, fragmentation, logging, competition from livestock, and hybridization with domestic species (IUCN 2013). Populations of many species are declining and their distributions are contracting, with larger species consistently more threatened than smaller ones (Table 1.1). Some smaller herbivore species, especially those that are habitat-specialists with very restricted ranges, are also at risk (Groves and Grubb 2011). It is not surprising therefore, that studies predicting future distributions of large herbivores in Asia present a grim prospect of further declines in their ranges and densities (Karanth et al. 2010, Corlett 2011). However, the impacts of these declines on seed dispersal processes are poorly understood. It has been suggested the loss of large mammals, including herbivores, can lead to declines in dispersal of large-seeded species, leading to a slow shift in forest community composition towards small-seeded, bird- and wind-dispersed species (Wright et al. 2007). Indeed, excessive harvest of muntjac (*Muntiacus muntjac*) in Thailand resulted in the decline of both seedling densities and seed dispersal of *Cheorospondias axillaris* (Brodie et al. 2009b).

Large, wide-ranging, habitat generalists such as elephants and pigs are especially important. They are likely to be regular dispersers of seeds across heterogeneous habitats and there is probably very low redundancy in their dispersal role in some habitats (Campos-Arceiz and Blake 2011). In the short term, plants may decline simultaneously with their key seed dispersers as has been noted in an elephant (Cochrane 2003) and deer (Brodie et al. 2009b) dispersed species. Long term consequences of herbivore declines on plants with no redundant seed dispersers may include range contraction and local extinctions (Corlett and Westcott 2013). However, plants that are seemingly dependant on megafaunal dispersers may have evolved mechanisms to be dispersed by other frugivores. For instance, rodents and introduced livestock disperse seeds of plants thought to be entirely dependent on megafauna extinct 10000 years ago (Janzen and Martin 1982, Guimarães et al. 2008). Recent evidence from India also demonstrates that small and medium-sized herbivores, specifically native ruminants such as deer can provide ‘back-up’ dispersal services to megafauna-dispersed trees, albeit to a much lesser extent (Sekar and Sukumar 2013). Additionally, these small-medium sized herbivores, although not capable of accessing the wide range of fruits available to much larger megafauna, have been documented to be disperse more plant species than their larger counter parts in both wet and dry tropical forests of Asia (Prasad 2011). We therefore suggest a rethinking of the importance placed on small and medium sized herbivores as seed dispersers. While conservation efforts have often focussed on charismatic megafauna and should continue to do so, the unique and diverse dispersal services provided by small- and medium-sized herbivores should also be integrated into conserving planning.

7 Conclusion

We set out to produce a quantitative summary of frugivory and seed dispersal by large herbivores in tropical Asia. However, we found very little quantitative information on plant-herbivore interactions in the region. Our understanding of the extent of frugivory by herbivores, especially for smaller species, is incomplete. We also understand very little about fruit choice, seed processing and gut retention times of seeds dispersed by herbivores. These gaps in our understanding severely restrict our ability to assess dispersal services lost due to extinctions of large herbivores, and the potential future impacts if herbivore species currently under threat continue to decline. Most importantly, with the current limitations on our understanding of seed dispersal by large herbivores in tropical Asia, we are unable to predict shifts in herbivore-plant interactions for the future under changing climates and land-use. A robust understanding of plant-herbivore interactions in heterogeneous landscapes is critical to plan management strategies that address the anticipated impacts of climate change and associated drivers on biodiversity (McConkey et al. 2012, Corlett and Westcott 2013). Large herbivores can effectively disperse seeds very long distances away from parent trees (Vellend et al. 2003, Myers et al. 2004), potentially facilitating migration of plants at rates suitable to track climatic changes as predicted for the future (Corlett and Westcott 2013).

It has been suggested that lost ecological services may be reinstated by reintroducing species into their former ranges, or by introducing ecologically equivalent species (taxon substitutes) into areas that have experienced extinctions of fauna involved in key ecological processes (Ehrlich and Mooney 1983). Faunal reintroductions to address lost seed dispersal services have been undertaken at a few sites, e.g. Aldabra tortoises in Mauritius - (Hansen et al. 2008). However, before attempting this in tropical Asia we need a better understanding of the seed dispersal services provided by large herbivores and of the community-level consequences of species reintroductions, especially novel introductions. Additionally, given the high human pressures and the continued use of forests in tropical Asia, it is imperative that we mitigate these threats (e.g. fragmentation or hunting) that have led to the decline of large herbivores, before attempting reintroductions.

We hope this review will initiate further enquiry into seed dispersal services provided by large herbivores in tropical Asia, and extend the emphasis of research beyond documenting their distributions and abundances to studying their ecological function.

Acknowledgements

We thank the following people for providing data on fruits consumed by herbivores and other information: Asmita Sengupta, Chanpen Saralamba, Freddy Pattiselanno, Firmann Aldy, Matt Heydon, Meghna Krishnadas, Robert Steinmetz, Stephan Wulffraat, and Naveed Khan. Farshid Ahrestani, Mahesh Sankaran, David J. Chivers, and David A. Westcott made useful comments on the manuscript.

Species	Family	IS	SC	WT	HR	DMR	HAB	DA	Ref.
Tragulus javanicus	Tragulidae	DD	22	2	4.85	546	Forest	R-3C	1, 2
Moschiola indica	Tragulidae	LC	6	3	-	-	Forest	R-3C	3
Tragulus napu	Tragulidae	LC	10	7	2.5	-	Forest	R-3C	251
Muntiacus atherodes	Cervidae	LC	18	16	6.2	-	Forest	R-4C	1
Muntiacus muntjak	Cervidae	LC	78	20	6	-	Forest	R-4C	1, 3, 4
Tetracerus quadricornis	Bovidae	VU	2	20	-	-	Open forest	R-4C	5
Gazella bennettii	Bovidae	LC	10	23	-	-	Grassland	R-4C	6
Antilope cervicapra	Bovidae	NT	1	30	766	-	Grassland	R-4C	7
Axis porcinus	Cervidae	EN	11	37	51.25	252	Grassland	R-4C	8
Sus cebifrons	Suidae	CE	2	45	-	-	Forest	S-FR	9
Sus celebensis	Suidae	NT	1	55	-	-	Generalist	S-FR	9
Sus barbatus	Suidae	VU	31	70	-	500	Forest	S-FR	9
Babyrousa babyrussa	Suidae	VU	8	70	-	-	Forest	S-FR	10
Axis	Cervidae	LC	40	72	169	-	Open forest	R-4C	3, 11
Sus verrucosus	Suidae	EN	2	90	-	-	Open forest	S-FR	9
Rucervus eldii	Cervidae	EN	8	100	814.5	-	Open forest	R-4C	12, 13
Babyrousa togeanensis	Suidae	EN	6	100	-	-	Forest	S-FR	9
Sus Scrofa	Suidae	LC	62	135	1800	8400	Generalist	S-FR	9, 14
Rusa unicolor	Cervidae	VU	73	200	900	-	Forest	R-4C	3, 11, 15
Boselaphus tragocamelus	Bovidae	LC	15	240	8800	2150	Open forest	R-4C	16
Equus hemionus	Equidae	EN	15	250	2800	7500	Desert	S-FO	17
Tapirus indicus	Tapiridae	EN	16	350	1275	2160	Forest	S-FO	18, 19
Dicerorhinus sumatrensis	Rhinocerotidae	CE	18	750	2500	7500	Forest	S-FO	20
Bos gaurus	Bovidae	VU	23	850	11200	4000	Forest	R-4C	11, 21
Rhinoceros sondaicus	Rhinocerotidae	CE	5	1350	14500	-	Forest	S-FO	22
Rhinoceros unicornis	Rhinocerotidae	VU	14	2350	5000	-	Grassland	S-FO	23, 24
Elephas maximus	Elephantidae	EN	84	4000	41700	4000	Generalist	S-FO	25, 26, 27

Table 1.1 Traits of large herbivores recorded to consume fruits, listed by increasing weight; IS - IUCN status: DD - data deficient, LC - least concern, NT - near threatened, VU - vulnerable, EN - endangered, CE - critically endangered; SC - number of species whose fruits were consumed; WT - body weight in kg; HR: home range in hectares; DMR – daily movement rate in m; HAB - habitat type; DA - digestive anatomy: R-3C - ruminant with 3 chambered stomach, R-4C - ruminant with 4 chambered stomach, S-FR - simple-stomach frugivore, S-FO - simple-stomach folivore.

References: 1- (Heydon 1994), 2 - (Yasuda et al. 2005), 3 - (Prasad 2011), 4 - (Kitamura et al. 2002), 5 - (Baskaran et al. 2011), 6 - (Dookia and Jakher 2007), 7 - (Jadeja et al. 2013), 8 - (Dhungel and O'Gara 1991), 9 -(Meijaard et al. 2011), 10 - IUCN species account, 11 - (Schaller 1967), 12 - (Aung et al. 2001), 13 - (McShea et al. 2001), 14 - (Mitchell et al. 2009), 15 - (Sankar 1994), 16 - (Khan 1994a), 17 - (Ghasemi et al. 2012), 18 - (Campos-Arceiz et al. 2012), 19 - (O'Farrill et al. 2013), 20 - (Flynn 1978), 21 - (Krishnan 972), 22 - (Corbet and Hill 1992), 23 -(Dinerstein and Wemmer 1988), 24 - (Dinerstein 1991), 25 - (Samansiri and Weerakoon 2008), 26 - (Forget et al. 2007), 27 - (Campos-Arceiz and Blake 2011).

Group	Life form of plants	Fruit type	Fruit colour	Largest fruit consumed	Largest seed dispersed
Tragulidae	Tree 32	Drupe 15; Berry 5; Capsule 3; Pod 2	Green 10; Yellow 3; Brown 3	80x80mm	23x17mm
Muntjacs	Tree 78; Liana 6; Shrub 3; Palm 1	Drupe 30; Berry 17; Capsule 10; Fig 6; Pod 1	Yellow 30; Red 12; Black 12; Purple 7; Orange 6	87x84mm	80x80mm
Large cervids	Tree 53: Shrub 6; Vine 4; Liana 3	Drupe 30; Berry 17; Pod 8; Fig 2	Yellow 11; Green 8; Red 6; Black 5	548x19mm	35x17mm
Bovidae	Tree 27; Shrub 5; Vine 3; Herb 2	Drupe 12; Pod 8; Berry 7	~3 each of Black, Green, Yellow, Red	548x19mm	9x7mm
Babirusa	Tree 11; Vine 1	Drupe 6; Complex fruit 3; Berry 2; Pod 2	Yellow, Green, Black, Brown ~2 each	350x125mm	48x28mm
Pigs	Tree 47; Shrub 8; 4 of Palm & Grass; 3 of Vine & Herb	Drupe: 23; Dry fruit 15; Berry 12; Complex fruit 6; Pod 5	Red 18; Yellow 11; Brown 8; Green 5; Black 4; Orange 4; Purple 4; White 3; Blue 2; Pink 1	350x125mm	48x28mm
Elephants	Tree 45; Herb 19; Vine 10; Grass 8; Shrub 6; Palm 2	Pod 22; Berry 20; Drupe 16; Complex fruit 9; Grass 7; Capsule 4; Dry fruit 1	Yellow 13; Brown 10; Red 9; Green 5; Black 3; Purple 3; Orange 1	375x175mm	39x26mm
Rhinoceros	Tree 19; Herb 6; Vine 4; Shrub 3	Berry 9; Drupe 6; Capsule 5; Complex fruit 4; Pod 4	Brown 7; Red 4; Yellow 4; Green 3; Purple 2; Orange 1; White 1	300x200mm	30x23mm
Tapirs	Tree 15	Complex fruit 6; Capsule 4; Drupe 4; Berry 2	Green 4; Yellow 3; Brown 2; 1 each of Red, Purple, Black and Orange	132x100mm	39x26mm
Wild ass	Herb; Shrub; Tree	NA	NA	NA	NA

Table 1.2: Traits of fruit and seed consumed or dispersed by large herbivores of Asia.

	Tragulidae	Cervidae	Bovidae	Suidae	Tapiridae	Rhinocerotidae	Elephantidae
Tragulidae	0	0.63	0.63	0.6	0.49	0.67	0.69
Cervidae	0.63	0	0.28	0.44	0.72	0.58	0.23
Bovidae	0.63	0.28	0	0.47	0.75	0.48	0.42
Suidae	0.6	0.44	0.47	0	0.58	0.64	0.53
Tapiridae	0.49	0.72	0.75	0.58	0	0.75	0.61
Rhinocerotidae	0.67	0.58	0.48	0.64	0.75	0	0.55
Elephantidae	0.69	0.23	0.42	0.53	0.61	0.55	0

Table 1.3: Dissimilarity in the traits of fruits consumed by the different families of large herbivores of Asia. Values towards 0 indicate similarity in traits, while values towards 1 indicate dissimilarity.

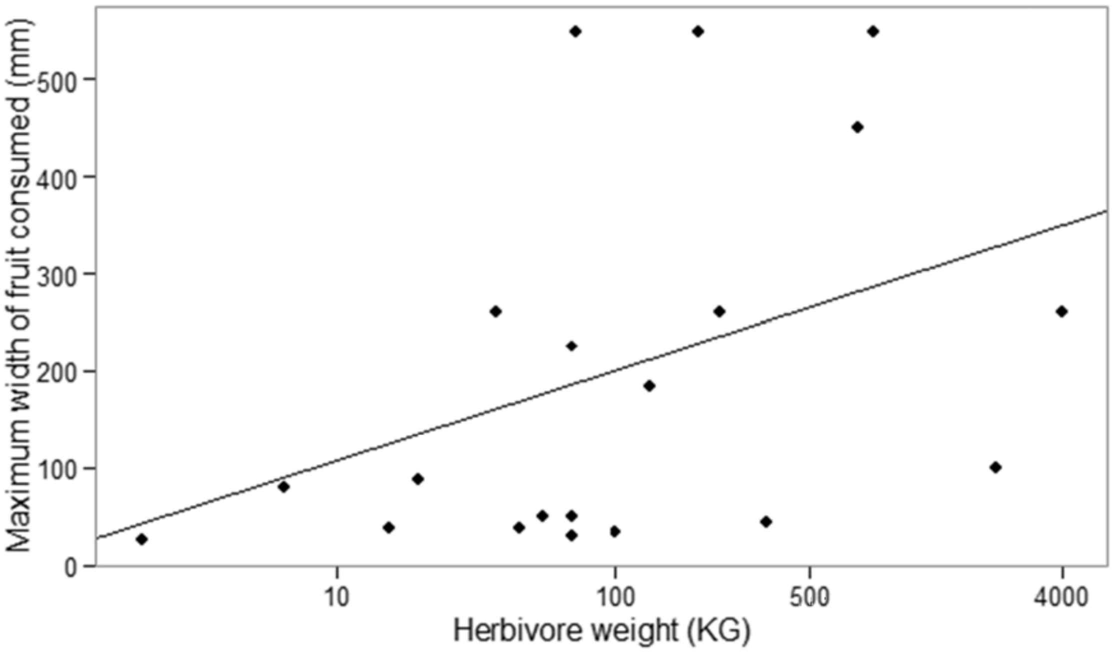

Figure 1.1 Relationship between body weight of large herbivores in tropical Asia, and the maximum width of fruits consumed

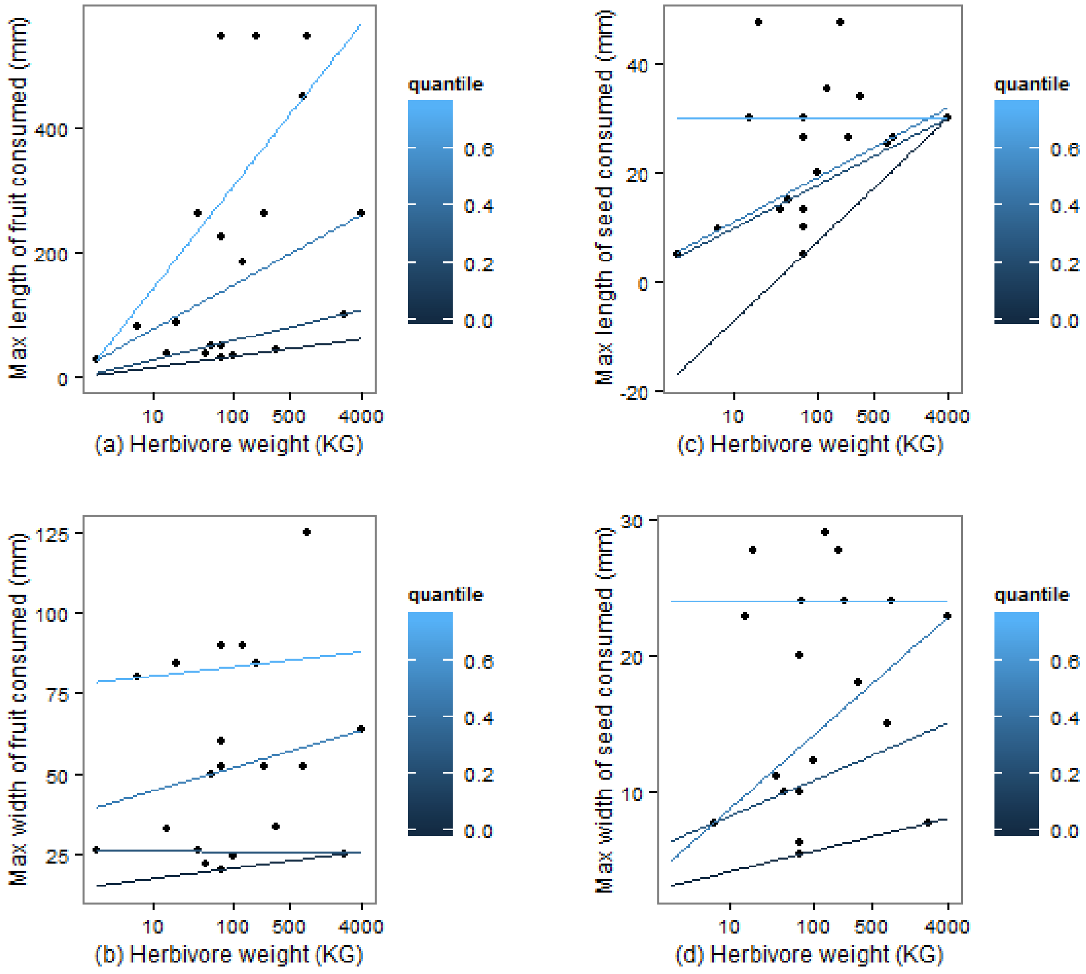

Figure 1.2: Quantile regressions of fruit traits (a) maximum length of fruit consumed, (b) maximum width of fruit consumed, (c) maximum length of seed consumed and (d) maximum width of seed consumed as a function of herbivore body weight.

Chapter 2: Movement patterns of a non-obligate frugivorous ruminant decouples seed rain patterns from adult trees

This chapter is based on a manuscript in preparation:

Sridhara, S., Prasad S., Edwards, W. and D. A. Westcott. Movement patterns of a non-obligate frugivorous ruminant decouples seed rain patterns from adult trees.

Statement of contribution of others:

Sridhara designed the study with inputs from Westcott, Prasad and Edwards. Sridhara collected data, and performed the analysis. Parag Nigam immobilized Chital to deploy GPS collars. Bivash Pandav coordinated the immobilization procedure. Sridhara wrote the first draft, and revised the subsequent drafts with Westcott, Will and Prasad.

Movement patterns of a non-obligate frugivorous ruminant likely decouples seed rain patterns from adult trees

Abstract

Disperser behaviour is a vital determinant of the seed dispersal patterns of plants that rely on animal vectors. When dispersers are largely frugivorous they preferentially deposit seed close to or under conspecific and synchronously fruiting heterospecific plants. However, when dispersers are only occasionally frugivorous the patterns of seed rain are probably influenced by the spatial positioning of non-fruit resources mediated by ecological processes other than foraging. This is especially likely when seeds are retained for up to several hours before deposition. I tested this prediction on Chital (*Axis*, 50 kg), a medium-sized ruminant, which is primarily a grazer but also a seed disperser that retains seeds for up to 27 hrs. As the case for many other medium-sized ruminants, availability of grass and cover from predators, and perhaps not the availability of fruits, is likely to play a key role in influencing movement patterns of Chital and consequently on seed dispersal. Specifically, I examined how heterogeneity in topography, habitat and key resources (grass and fruits) influenced Chital movement patterns and consequently seed dispersal. I deployed GPS collars on seven Chital individuals. Chital movement was characterized as being short-range (movement likely associated with foraging and seed deposition) or long-range (movement likely associated with search and predator avoidance behaviour). Short-range movement was greater in areas that had an even mix of habitat types (providing food and structural cover) but less in rugged terrain. In comparison, long-range movements occurred in habitats with less cover. Notably, Chital space use and movement was not influenced by fruit availability but by factors that likely reflect trade-offs between predator avoidance and resource tracking. Finally, seeds were more likely to be dispersed to areas with more Chital activity (those with less cover and higher grass availability), and not associated with adult fruit trees. We demonstrate that Chital, a non-obligate frugivore decouples seed rain from adult plants. Habitat use mediated by predator avoidance, and

not the spatial location of adult fruit trees, likely drives seed rain patterns generated by Chital.

Introduction

Animal mediated seed dispersal is a crucial ecological process for plants. Especially in the tropics and sub-tropics, between 70 to 90 % of the plants are dispersed by animals (Jordano 2000, Herrera 2002). Through their handling and transport of fruit and seeds, animal dispersers influence all stages of seed dispersal from the number of fruits they consume to the locations and distances to which seed are dispersed (Wang and Smith 2002, Schupp et al. 2010). Patterns of animal mediated seed dispersal exert a crucial influence on seed fate, potentially determining a seed's exposure to natural enemies (Velho et al. 2009), its probability of germination and recruitment (Klinger and Rejmánek 2010), and can have lasting impacts even in to the adult stages of plants (Russo and Augspurger 2004, Valenta et al. 2015). Therefore, examining how disperser behaviour influences seed dispersal patterns is crucial to understanding plant regeneration and population dynamics (Wang and Smith 2002, Schupp et al. 2010).

Animal behaviour is often invoked to explain and predict the outcome of plant-frugivore interactions. (Westcott et al. 2005, Russo et al. 2006, Morales et al. 2013). Nevertheless, it is thought that seed dispersal is fundamentally an indirect interaction among plants mediated through animal behaviour (Albrecht et al. 2015). This premise arises partly from the lack of plant-frugivore specialization which is reflective of the high diet plasticity of frugivores (Carnicer et al. 2009, Schleuning et al. 2011). Further, many observed patterns of seed dispersal are well explained by the spatial distribution of adult conspecific and simultaneously fruiting heterospecific plants, without having to invoke the behaviour of specific dispersers. For example, the influence of fruiting plants on seed rain patterns documented at small spatial scales (Morales et al. 2012, Rodríguez-Pérez et al. 2014, Martínez and García 2014), may persist even at medium to large scales when conspecific or co-fruiting heterospecific plants function as foci for movement by providing feeding or perching roosts (Carlo et al. 2013, Abedi-Lartey et al. 2016, Razafindratsima and Dunham 2016a). While these seed dispersal patterns emerge in highly frugivorous disperser communities (e.g. obligate avian or primate frugivores), it is unclear whether the spatial distribution of fruiting trees has a universally strong influence on disperser behaviour, and therefore on patterns of seed rain.

In diverse disperser communities in which dispersers vary widely in traits such as body size and digestive physiology, many species interact only opportunistically with fruits (Kissling et al. 2009, Donatti et al. 2011). Several mammalian herbivores (e.g. deer, tapirs and elephants), mammalian omnivores (e.g. jackals, pigs, and bears), tropical and temperate fishes, and even omnivorous birds are opportunistic or non-obligate frugivores and functionally distinct from highly frugivorous dispersers such as small birds, bats or primates (Dubost 1984, Zhou et al. 2011, Horn et al. 2011, Morales et al. 2013, Viana et al. 2013, Sridhara et al. 2016, Carlo and Morales 2016). Because these seed dispersers often track non-fruit resources, retain seeds for medium to long periods of time (10-60 hrs) and move relatively large distances, it is possible that conspecific or heterospecific plants may exert minimal influence on their activity post fruit consumption and, ultimately, on the spatial patterns of seed dispersal (Long et al. 2015, Sridhara et al. 2016). Increasing evidence suggests that interactions between opportunistic or non-obligate frugivores and plants can have a strong influence on plant population dynamics and could be more common than previously assumed (e.g. Zhou et al. 2011, Sridhara et al. 2016, Carlo and Morales 2016). Many non-obligate or opportunistic frugivores are crucial dispersers and can play disproportionately key roles for plant community dynamics (Campos-Arceiz and Blake 2011, Carlo and Morales 2016). Thus, examining the interaction between opportunistic or non-obligate frugivores, and conspecifics and co-fruiting heterospecifics trees will enable a better understanding of spatial seed dispersal patterns.

When fruiting trees and their distribution minimally influence disperser behaviour—as is likely for some non-obligate frugivores—such dispersers may ‘decouple’ seed rain from adult trees. Specifically, dispersers might deposit many seeds away from adult conspecifics thereby generating seed rain patterns that are independent of adult fruit tree distribution. This is especially likely when dispersers are less dependent on fruiting resources and have long seed retention times (Guttal et al. 2011). Any decoupling of seed rain patterns from the spatial distribution of adults could have a number of implications for processes beyond seed dispersal. Particularly, post-dispersal seed fate and seedling survival is influenced by proximity to conspecific and heterospecific adults, mediated through seed predation or pathogen pressure (Velho et al. 2009, Bagchi et al. 2014, Comita et al. 2014). Decoupling seed rain from adult plants may release seeds from the negative effects of conspecific proximity and could lead to enhanced germination (Hirsch et al. 2012a).

We tested the prediction that a non-obligate frugivore with relatively long seed retention time decouples seed rain from adult conspecifics on Chital (*Axis axis*), a widely distributed deer native to India. Although predominantly a grazer, Chital consume and disperse seed of several tree species making them an especially suitable species with which to test our prediction (Sridhara et al. 2016). Like many medium-sized ruminant Chital have long seed retention times and their habitat-use patterns are primarily influenced by forage availability (grass) and the extent to which a habitat influences their ability to detect and avoid predators (Bhat and Rawat 1995, Ramesh et al. 2012). We therefore predicted that movement patterns will reflect these resource requirements and will in turn influence seed deposition. Specifically, we expected that grass availability, predator avoidance behaviour mediated by habitat structure and topographical features would be primary determinants of their movement patterns. Because Chital are likely to trade-off conflicting resource and habitat requirements, we anticipated that areas that provide a combination of the different habitats types are more likely to influence movement rather than habitats that provide any single resource. In turn, we expected that the distribution of non-fruit resources would provide a better explanation of the spatial patterns of seed rain generated by Chital than would fruiting trees. In order to test these predictions, we first characterized movement patterns of Chital. Then, we examined the correlation between these movement patterns and the different resources needed by Chital—fruiting trees, grass, and cover that allow detection of, and escape from, predators (Owen-Smith et al. 2010, Laundré 2010). Finally, we examined the relative influence of these different resources on seed deposition patterns produced by Chital to test if seed rain was spatially independent (decoupled) from adult tree distribution.

Methods

Study system

We undertook the study in Rajaji National Park, part of the Shivalik foothills of the lesser Himalayas. Situated in the state of Uttarakhand, India, Rajaji's forest types have been categorized as northern Indian moist deciduous forest and northern tropical dry deciduous forest (Champion and Seth 1968). Chilla, the administrative unit within Rajaji where the study was conducted, is characterised by rugged hills ranging from 400 to 1000 m in altitude. The area is drained by seasonal rivers and streams with the valleys supporting extensive grasslands. The major associations are mixed forests comprising of tree species such as *Terminalia alata, Anogeissus latifolia, Lagerstroemia parviflora, Holoptelia integrifolia, Ehretia laevis, Aegle marmelos,* and Sal *(Shorea robusta)* dominated stands. Savannahs occur mostly along rivers beds but can be found scattered throughout the park and in all terrains. Our sampling was conducted in two areas within Chilla – Sukkasoth and Meethawali. Nearly 100 people belonging to 20 families of the pastoral community of Gujjars live in settlements on the fringes of Sukkasoth, along with approximately 500 head of livestock (chiefly buffalo *Bubalis bubalis* and cattle *Bos taurus*). Meethawali has had no human settlements since 2001, when they were relocated to outside the park.

Chital disperse seeds of several tree species that bear fruit between October and March (Sridhara et al. 2016). Being a terrestrial frugivore, Chital depend on other frugivores (primarily primates, *Macaca radiate* and *Semnopithecus hector*) or on natural fruit fall to access fruit. Chital swallow fruits after some mastication and regurgitate relatively larger seeds while defecating smaller ones (Sridhara et al. 2016). In this study we examined relationships between Chital movement and seeds from four species of trees, *Terminalia bellerica, Phyllanthus embellica, Ziziphus xylopyrus* and *Ziziphus mauritiana*. Both *T. bellerica* and *P. embellica* are medium to large trees producing almost globular or ovoid fruits of mean radius 15 and 10 mm respectively. Both *Z. xylopyrus* and *Z. mauritiana* are small- to medium-sized, armed trees producing globular fruits of mean radius 12 and 7 mm respectively (Sridhara et al. 2016). Seed size of the four species varies from 5 to 20 mm diameter with globular or ovoid shapes and are all regurgitated by Chital.

Data collection

We deployed GPS enabled radio collars on Chital to describe their movement patterns. To fit collars on the neck of the deer, an experienced veterinarian immobilized them using a dart gun loaded with ketamine and medetomidine. Upon fitting the collar, a reversal drug was injected and the animal was monitored from a distance until it came to and resumed normal activities. All standard animal handling procedures were vetted by an animal handling ethics committee (James Cook University Animal Ethics Permit #A1934) and strictly observed to ensure that the animal experienced minimal stress. We deployed GPS enabled collars on 7 individuals, programmed to acquire a location every 10 minutes (henceforth ‘fix’). The radio collars, manufactured by eObs GmbH, Germany weighed 0.75 kg, less than 5% of the body weight of the individuals (50-75 kg). The location data was stored on board the collar and was wirelessly downloaded on to a portable base-station. Data was downloaded from as far away as 500 meters and often times when the animal was visually located to be just a few meters away. Care was taken not to disturb the animal during the process of data download which lasted between 10 - 30 minutes. Of the seven individuals, four were collared nearly six to twelve months prior to the start of this study. We collected all data from November 2014 to March 2015. One of the individuals collared in Meethawali was predated after a month of our sampling commencement. Within a fortnight we deployed the collar on another individual in Sukkasoth area. In all, five individuals were collared in Sukkasoth, and two in Meethawalli.

Our main sampling approach was to isolate the locations of Chital acquired in a period of one month, and sample the corresponding area used by each of the animals by systematically dividing the space in to grids. The choice to use one month as a block of data was based on a combination of the duration of fruiting of our focus tree species (3-5 months), the large scale of sampling required (up to 1300 hectares), and the undulating nature of the area which presented logistical challenges. Grids were of size 200 x 200m and were placed adjacent to each other. This sampling was undertaken three times - late November to mid-December 2014, mid to late January 2015, and late February to early March 2015 corresponding to movement from mid-October to mid-November 2014, December 2014, and mid-January to mid-February 2015 respectively. Approximately, 20 to 60 grids were sampled for each animal in each of three visits.

All variables were measured at or around the centroid of each of the grids. We established a plot of size 5mx5m laid at the centroid. Within these plots we (i) estimated the availability of grass as an indicator of grazing resources, (ii) counted the number of fresh dung piles of Chital and other wild and domestic ungulates as an indicator of the intensity of Chital use, and (iii) counted the number of seeds dispersed by Chital belonging to the four tree species of interest. Next, we estimated the amount of structural cover (lateral cover provided by vegetation) present within a circle of radius 25m centred at the grid's centroid. Finally, within this circle we also counted the number of adult trees with GBH > 30 cms, recorded the number of trees bearing fruit and estimated the quantity of fruit on each tree (in categories of 0, 1-10, 11-100, 101-1000 and so on). We included trees species whose fruits are consumed by Chital at any time during the year. These tree species were *Aegle marmelos, Cassia fistula and Diospyros melanoxylon*.

While sampling the grids, we mapped the three structurally different habitat types present in the area using a GPS. They were i) open habitat – areas devoid of woody vegetation (mostly river or stream beds and meadows with very little grass), ii) savannahs – areas with continuous grass cover but discontinuous tree cover, and, iii) closed canopy forest – forest patches with continuous canopy cover. These mapped areas were overlaid on Google Earth images and visually inspected to confirm the boundaries of each habitat. We calculated the extent of each of the three habitat types within the grid and computed an index of habitat evenness using Shannon's Diversity Index. An index value closer to 1 means that a grid is composed of equal parts of all three habitats and values closer to 0 means that grid was composed entirely of just one of the three habitat types. Using freely available digital elevation models (SRTM), we computed mean terrain ruggedness for each of the grids.

Analyses and modelling approach

Characterising movement patterns: Analysing movement patterns in the context of seed dispersal must be done at a temporal resolution matching the gut passage time of the seeds. Chital are known to retain seeds for up to 27 hrs with a mean time of 14 hrs (Prasad et al. 2006). It was therefore sufficient for us to use location data form every hour. This also ensured that measurement error of fixes (3-5m) would only minimally impact distances between two consecutive fixes. The distribution of step lengths – the distance between two consecutive locations, and turning angles – the angle between two consecutive steps, are attributes of movement patterns often used to discern the different movement patterns and their associated drivers (Patterson et al. 2008). Studies of other ruminants demonstrate that movement can be broadly categorized into two modes, short-range (also called encamped) and long-range (also called exploratory) (Morales et al. 2004). Short range movement mode is associated with short step lengths and very variable turning angles (less directional), and is more likely during periods of foraging and resting. Long-range movement mode is associated with more directional displacement and large step lengths, and is more likely when animals are moving between habitats, escaping predators or are in low resource areas. We used these two modes because they are known to be associated with high and low profitable areas, underpinning resource distribution in other grazing species and are therefore suitable for our study (Fryxell et al. 2008). For ruminants short-range movement is likely to be strongly associated with resting and rumination, the activities during which seed regurgitation is most likely to occur (Prasad et al. 2006), but also to include some foraging. Consequently, this difference in the behavioural context associated with the different movement modes necessitates a separate examination of the two movement modes. Specifically, factors influencing one mode of movement need not necessarily influence the other. We used Bayesian methods outlined in Morales et al (2004) and Beyer et al (2013), to categorize each fix as either being part of short-range or long-range mode of movement, through program JAGS and R.

Factors influencing movement patterns: Using software QGIS we identified the total fixes within each of the sampled grid and also differentiated fixes based on whether they were part of short-range or long-range movement modes, because these modes correspond to distinct behavioural contexts. We then modelled separately the number of short-range and long-range fixes in a grid as a function of measured variables, in a generalized linear mixed models (GLMM) framework. In our exploratory analyses, we started by using the individuals as random effects and the different sampling occasions as fixed effects and random effects. We found that variation among the different individuals was so low that the group level intercept and slope explained very little variation and therefore these were not included in our final candidate set. We also did not include sampling occasion and individuals as fixed effects based on the lack of statistical support (confidence interval of parameter estimates included zero and the corresponding AIC was also much higher). Because our grids are systematically laid, our data is unlikely to be spatially independent. To account for this we divided the entire sampling area into several zones, each 1 km^2 in area, and estimated a random intercept for each of the zones. One kilometre corresponds to the maximum daily displacement of the deer during the period. Within each zone 16 of our sampling grids could be accommodated. To further account for spatial dependence, we included in all our models a predictor which was the mean number of fixes obtained in the neighbouring grids. This was included both as a fixed effect, and a random slope was calculated for each spatial zone. The fixes within each grid were modelled using negative binomial error structures since they represented count data.

Factors influencing seed rain patterns: We used a GLMM framework with a logistic structure to model whether any seeds of the four species were found in each grid against predictors described above. A group level intercept was modelled for each spatial zone. A set of candidate models were constructed to test our expectations.

Model selection was based on AICc using techniques described in Burnham and Anderson (2002). All modelling was done in program R using package glmmADMB. Software JAGS interfaced through R, was used to identify whether fixes belonged to short-range or long-range movement mode. QGIS was used for certain GIS related tasks. Bayesian models were run for 10000 iterations, discarding the first 1000 samples and retaining estimates from every 10th iteration .

Results

Characterizing movement patterns

Results from the Bayesian analyses were reliable since R-hat values converged to 1 (Gelman and Rubin 1992). Each fix could be characterized as being drawn from one of two underlying movement modes – short-range or long-range. As expected, histograms of step length indicate that short-range movement was associated with a distribution of step lengths clearly skewed towards short distance while long-range movement had a wider distribution of step lengths (Fig 2.1a). Approximately 60% of these steps were in the zero category indicating that the animals were resting. Histograms of turning angles also showed that short-range movement was associated with a much wider distrbution of values while that of long-range movement was denser around 180 degrees (Fig 2.1b)

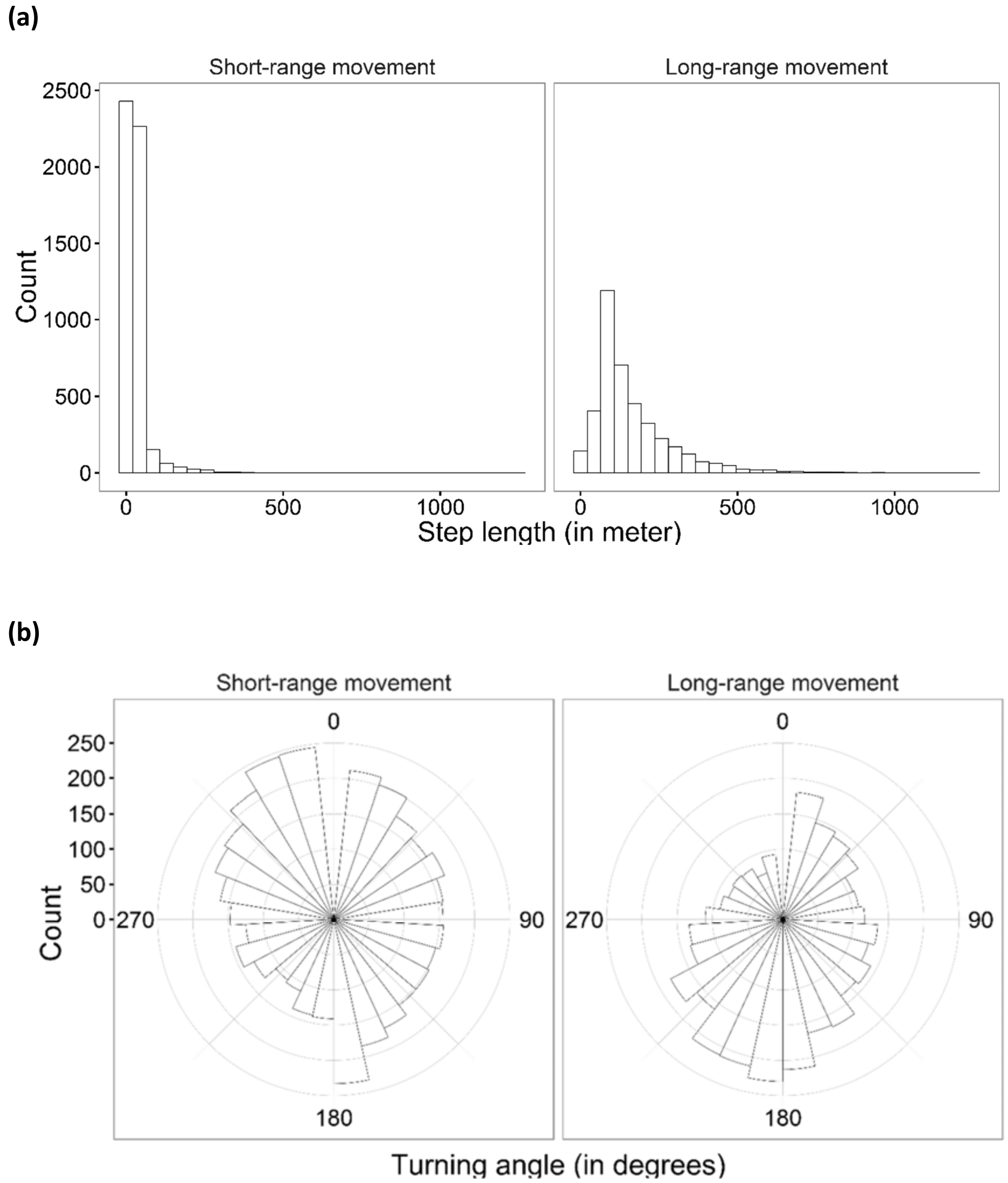

Figure 2.1: Histograms of (a) step lengths and (b) the turning angles associated with short-range and long-range movement modes of Chital

Factors influencing movement patterns

We constructed a total of 11 candidate models to assess factors likely to influence both short-range and long-range movement of Chital. Table 2.1a and 2.1b summarize the model selection results for short-range and long-range modes respectively. An additive effect of terrain ruggedness and habitat evenness best predicted short-range mode of movement by Chital, whereas an additive effect of terrain ruggedness and structural cover best predicted observed patterns of long-range movement. Terrain ruggedness was a strong predictor of observed movement pattern of Chital, negatively influencing both short-range (-0.29 ±0.06, p<0.001 – Fig 2.2a) and long-range modes (-0.24 ±0.04, p<0.001 – Fig 2.2c); its effect attenuated by about 20% for long-range mode. Habitat evenness had a positive influence on short-range movement (0.14 ±0.06, p=0.03 – Fig 2.2b) and long-range movement (0.18 ±0.05, p<0.001 - Fig 2.2d). However, for long-range movement, models with habitat evenness as a predictor ranked significantly lower than models without (Table 2.1). Structural cover had a marginally significant negative influence on short-range movement (-0.10 ±0.06, p=0.08) despite being closely ranked to the top model. On the other hand, structural cover had a strong negative influence on long-range movement mode (-0.21 ±0.05, p<0.001), with the slope being more than twice as that of short-range movement mode. For both the modes of movement, models with number of adult trees (> 30 cm DBH) or number of dung piles of wild ungulates performed poorly. Availability of grass did not influence short-range or long-range movement. We found no support for models that incorporated fruit resources either as the number of adult trees in fruit or as an estimate of total fruit available. Finally, visual inspection of model residuals in space suggested that spatial dependence was minimal in our top ranking model.

	Model		AIC$_C$	ΔAIC$_C$	np	w
	Fixed effects	**Random effects**				
(a)	Ruggedness + Habitat evenness	Spatial zone	3269.2	0	7	0.58
	Ruggedness + Structural cover		3270.9	1.7	7	0.25
	Ruggedness		3271.7	2.4	6	0.17
	Habitat evenness + Structural cover		3283.4	14.1	7	<0.1
	Structural cover		3286.7	17.5	6	<0.1
	Habitat evenness		3286.9	17.7	10	<0.1
	Trees >30 cm DBH		3288.6	19.3	6	<0.1
	Dung piles of wild ungulates		3290.7	21.5	6	<0.1
	Grass		3291.0	21.7	6	<0.1
	Number of fruiting trees		3291.1	21.8	6	<0.1
	Total fruit available		3291.5	22.3	6	<0.1
(b)	Ruggedness + Structural cover		3055.4	0	7	0.97
	Ruggedness + Habitat evenness		3063.1	7.7	7	0.02
	Structural cover + Habitat evenness		3068.2	12.9	7	<0.1
	Ruggedness		3075.5	20.1	6	<0.1
	Structural cover		3077.2	21.8	6	<0.1
	Habitat evenness		3085.3	30.0	6	<0.1
	Trees >30 cm DBH		3102.5	47.1	6	<0.1
	Total fruit available		3103.1	47.7	6	<0.1
	Grass		3103.8	48.4	6	<0.1
	Number of fruiting trees		3105.2	49.8	6	<0.1
	Dung piles of wild ungulates		3105.2	49.8	6	<0.1

Table 2.1: Summary of models used to assess factors influencing (a) short-range and (b) long-range movement of Chital. Parameters were modelled either as ‘Fixed effects’ or as ‘Random effects’. In all models “mean number of a fixes in neighbouring grid” was included as a fixed effect in addition to being used to estimate a random slope and intercept for each of the spatial zones (random effect). AIC$_C$ – small sample size corrected Akiake Information Criteria; ΔAIC$_C$ – difference in AIC$_C$ between each model and the model with lowest AIC$_C$; np – number of parameters estimated in the model; w – model weight or the relative support for the model.

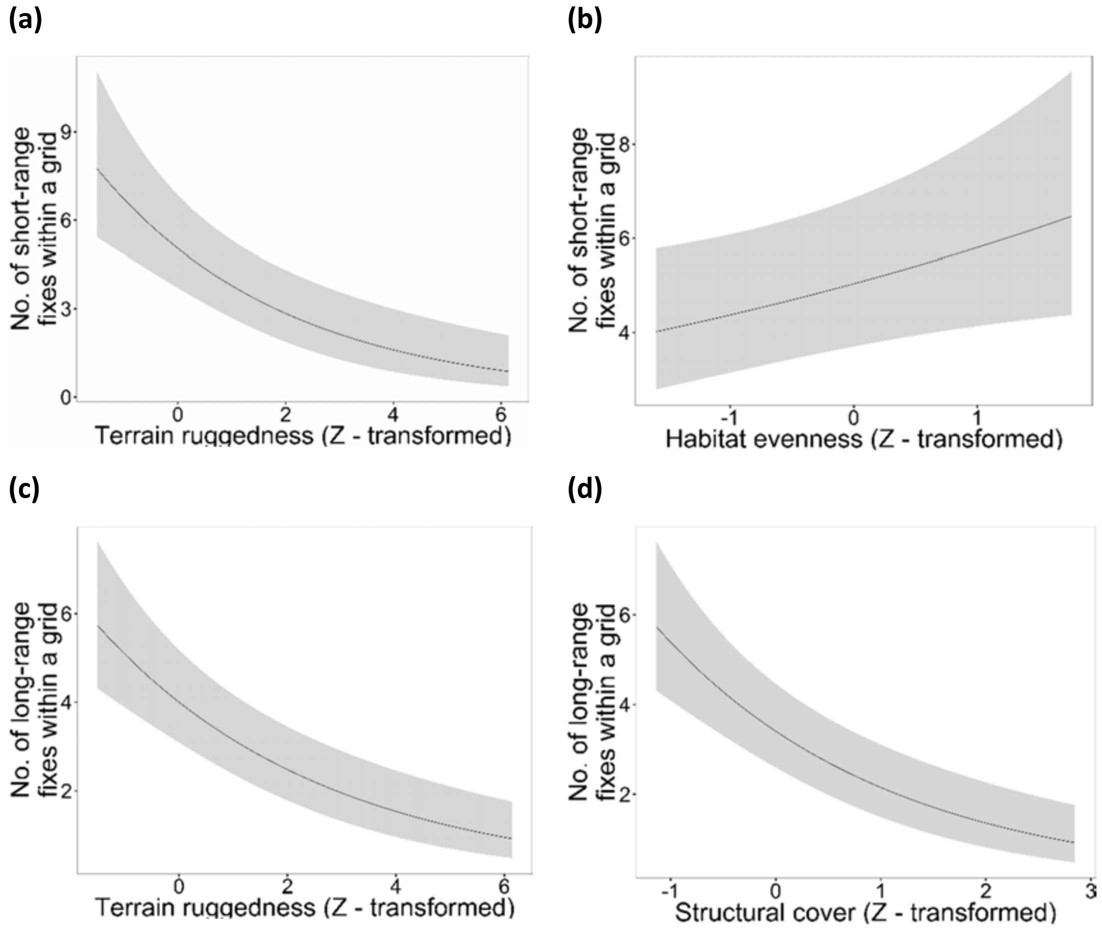

Figure 2.2: Predictions from top model indicate that short-range movement patterns of Chital were (a) negatively influenced by terrain ruggedness and (b) positively influenced by habitat evenness. Long-range movement patterns of Chital were negatively influenced by both (c) terrain ruggedness and (d) structural cover. All predictor variables were z-transformed to allow easy comparison across different variables. Ribbons represent 95% lower and upper confidence intervals of predicted values.

Factors influencing seed dispersal patterns

Ten candidate models were used to assess the influence of various measured variables on seed dispersal patterns of deer. Except for Chital dung piles, no other parameter was found to influence observed patterns of seed dispersal (Table 2.2). Chital dung piles had a positive influence on the probability of seeds being dispersed to the sampling plot (0.57 ±0.12, $p < 0.001$ – Fig 2.3). All models in Table 2.2, included a random intercept estimate for the different spatial zones.

Models	AIC$_C$	ΔAIC$_C$	np	w	
Fixed effects	Random effects				
Chital dung piles	Spatial zone	344.4	0	3	1
Fixes of Chital		364.5	20.1	3	<0.1
Structural cover		365.2	20.8	3	<0.1
Trees (>30 cm GBH)		365.8	21.4	3	<0.1
Ruggedness		366	21.6	3	<0.1
No. of fruiting trees		366.3	21.9	3	<0.1
Wild ungulate dung piles		366.3	22.0	3	<0.1
Total fruit		366.4	22.0	3	<0.1
Grass		366.4	22.0	3	<0.1
Habitat evenness		366.4	22.0	3	<0.1

Table 2.2: Summary of models used to assess factors influencing the probability of seeds being dispersal by Chital. Parameters were modelled either as ‘Fixed effects’ or as ‘Random effects’. In all models a random intercept was estimated for each of the spatial zones (random effect). AIC$_C$ – small sample size corrected Akiake Information Criteria; ΔAIC$_C$ – difference in AIC$_C$ between each model and the model with lowest AIC$_C$; np – number of parameters estimated in the model; w – model weight or relative support for the model.

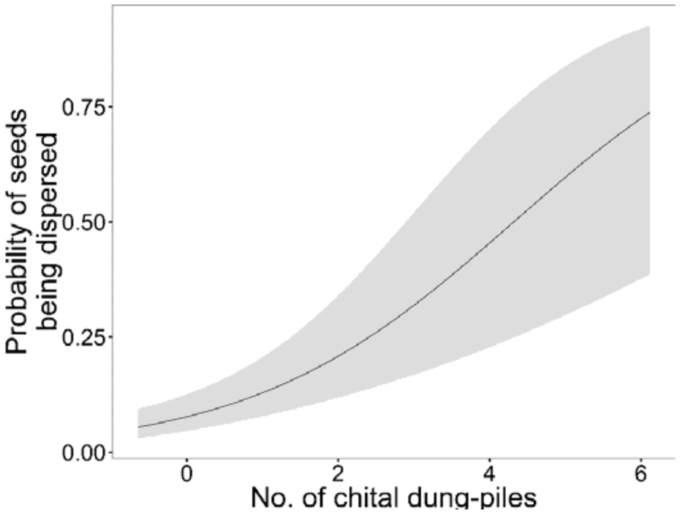

Figure 2.3: Predictions from top model show the positive nature of relationship between the probability of a seeds being dispersed and the number of Chital dung piles in a grid. Predictor variables were z-transformed; ribbons indicate 95% lower and upper confidence intervals of predicted values.

Discussion

Our goal was to understand whether the non-fruit resource requirements of a non-obligate frugivorous ruminant influences its movement patterns and consequently decouples seed deposition patterns of seeds from the spatial distribution of adult fruit trees. We first characterized Chital movement patterns as short-range or long-range. Then, we tested whether fruiting resource distribution, grazing resources, cover from predators or topography better predicted observed movement patterns. We then assessed the potential influence of several measured variables on movement patterns, and on observed seed rain patterns. Our combined results show that fruiting trees did not influence movement patterns and habitat use by Chital. Instead, we found that topographical and habitat features best predicted observed patterns, especially short-range movement which was most likely to influence seed deposition. Finally, we found that the probability of seed being deposited was higher in grids more intensively used (measured as dung-piles). The presence of fruiting trees or higher quantities of fruit in a grid did not predict observed seed rain.

Characterizing Chital movement patterns

We characterized the movement patterns of Chital using two attributes of movement – step-length and turning angle. We identified two distinct movement modes in all Chital individuals reliably using Bayesian techniques (Fig 2.1), as seen in other medium-sized ruminants from temperate regions (Morales et al. 2004, Haydon et al. 2008, Beyer et al. 2013). Short-range and long-range modes are thought to primarily represent foraging and searching behaviour respectively and therefore were treated as distinct behavioural responses when modelling the influence of various measured abiotic and biotic variables (Fryxell et al. 2008, Nathan et al. 2008). Specifically, in the case of a ruminant, short-range movement are associated with rumination, the behaviour state during which most seeds are likely to be regurgitated (Prasad et al. 2006, Brodie and Brockelman 2009).

Correlates of Chital movement patterns

In general, topography and attributes of the habitat better predicted observed movement patterns than did any single resource such as grass or structural cover. As expected, we found that Chital preferred less rugged terrain in general and these results are consistent with natural history observations and previous studies where Chital were found to prefer flatter terrain (Bhat and Rawat 1995, Bagchi et al. 2003a, Ahrestani et al. 2012). Differences in space use based on topography and habitat features could contribute to niche segregation among large herbivores (Hopcraft et al. 2010). Because Chital are often sympatric with many other large herbivores, it remains to be seen whether such niche segregation in turn has implications for spatial patterns of seed dispersal for fruit species consumed by multiple large herbivores in our system (Moe and Wegge 1994, Bhat and Rawat 1995, Bagchi et al. 2003b). Notably, fruiting resources—both the number of fruiting trees and the total available fruit—performed poorly in explaining observed patterns of short-range or long-range modes of movement.

Further, most short-range (short-range) movements, likely associated with feeding or resting, occurred within areas that had an even mix of different habitats (river bed, savannah, and forest). Grids containing an equal proportion of open, savannah, and closed canopy forest not only provide foraging resources but also suitable habitats to avoid predators (Moe and Wegge 1994, Bagchi et al. 2003a, Creel et al. 2014, Pokharel and Storch 2016). On this basis we had hypothesized that grids with a more even composition of different habitats would be favoured by Chital for foraging and resting, activities encompassed under short-range movements. More homogeneous grids in contrast provide largely one or another kind of resource and might therefore be less attractive overall. Accordingly, neither grass nor structural cover alone seemed to explain short-range movement of Chital (Table 2.1). Hence, we suggest that the observed patterns reflected a trade-off between foraging and predator avoidance behaviour as has been seen in various temperate large herbivores such as elk, moose, roe-deer (e.g. Hebblewhite and Merrill 2009, Mabille et al. 2012, Mysterud 2013, van Beest et al. 2016).

In comparison, long-range (long-range) movement occurred most prominently when there was less cover from predators. We had thought that grids with higher structural cover would be less attractive to a grazer like Chital because of low grass availability and they would therefore rapidly move through such areas (longer step lengths). Contrary to our expectation however, greater vegetation cover was associated with lower levels of long-range movement. Because vegetation cover could also provide hiding areas for predators, Chital might perceive such areas as high risk due to lowered predator detection and thereby avoid areas with high structural cover altogether (Creel et al. 2014, Basille et al. 2015). Perhaps Chital moved in the long-range mode in areas with low vegetation cover while searching for or transiting to more optimal habitats. This would not preclude their use of resources present in these areas but this would occur at lower levels. However, similar to short-range movement, long-range movement also decreased in more rugged terrain suggesting that rugged topography was a general deterrent of Chital habitat use (Bagchi et al. 2003b). Differences in space use based on topography and habitat features could contribute to niche segregation even among large herbivores (Hopcraft et al. 2010). Because Chital are sympatric with ruminants (and other large herbivores) that disperse seeds of the same plant species (Sridhara et al. 2016), niche segregation among the ruminant species (Moe and Wegge 1994, Bhat and Rawat 1995, Bagchi et al. 2003b) could generate functionally non- redundant seed dispersal patterns as has been seen with other large herbivores (Polak et al. 2014).

Chital resource use and resulting seed deposition

We found that whether a seed was dispersed by Chital to a location was independent of the number of trees or the total fruit available fruit within the neighbourhood of 25m, in line with our expectation. Because Chital's intensity of use (measured as dung piles) was often in areas with few or no fruiting trees (measured as no. of fruiting trees and total fruit available) these results suggest that Chital were likely dispersing seeds away from adult trees. This is in contrast with other frugivorous dispersers such as small birds, bats and even some primates which deposit seeds "contagiously" or disproportionately close to conspecifics (Carlo et al. 2013, e.g. Côrtes and Uriarte 2013, Fedriani and Wiegand 2014, Razafindratsima and Dunham 2016a) but similar to other large herbivores such as tapirs (Bueno et al. 2013) and blackbuck (Jadeja et al. 2013) but even rodents (Hirsch et al. 2012a).

Since we did not monitor seed germination or seedling establishment success, we cannot conclusively state whether seed rain patterns generated by Chital translate to enhanced survival of seeds and seedlings and whether these benefits carry on to the adult stages. Nevertheless, theory and empirical evidence suggest that dispersal of seeds away from parent trees results in lowered levels of mortality by fungal pathogens, insects, and mammalian seed predators and could lead to higher germination and recruitment success (Wenny and Levey 1998, Kwit et al. 2004, Bell et al. 2006, Hirsch et al. 2012a, Salazar et al. 2013, Fricke et al. 2014). Thus, Chital might add to the services of other dispersers such as birds and bats that deposit seeds under co-fruiting heterospecific trees, by facilitating escape from density-dependent mortality due to natural enemies (Kwit et al. 2004, Hirsch et al. 2012a).

Chital are more likely to disperse seeds when undertaking short-range (short-range) movements because these movements incorporate the resting and rumination periods when Chital regurgitate a majority of the seeds (Prasad et al. 2006, Li 2013). Thus, correlation of seed rain with high activity areas viewed together with correlation of Chital short-range movement with evenly mixed habitats and less rugged terrain, suggest that seeds are more likely to be dispersed to locations with an even mix of habitats. These locations are most likely to be used by Chital for resting and bedding, because resting and bedding sites of ruminants are generally chosen to allow easy detection of predators but also provided adequate protection, i.e. areas that have a mixture of relatively open habitats in proximity to high structural cover to flee from predators (Brodie and Brockelman 2009). Therefore, an interaction between Chital and their predators could be a crucial component of seed dispersal patterns by this disperser. Although Howe (1979), in a theoretical study based on small birds, examined the influence of predation risk on frugivory, it was done only in the context of time spent on foraging and not explicitly tied to dispersal patterns. Since predation risk is widely accepted to play a key role in the large-scale habitat use and behavioural responses of ruminants (Brown and Kotler 2004, Kuijper et al. 2013, Hopcraft et al. 2014), we suggest that prey-predator interaction could be a potential mechanism by which Chital decouple seed rain from adult trees.

Conclusion

We found that Chital, a non-obligate frugivorous ruminant, by using areas which had an even composition of different habitat types dispersed seeds away from fruiting trees – or decoupled them from adult conspecifics. The habitat use by Chital and its seed deposition patterns, is very reflective of Chital simultaneously responding to predation threats and tracking crucial resources. We posit that behaviours governing predator avoidance might indirectly but strongly influence where seeds are dispersed by Chital and other similar medium-sized ruminants. Yet, downstream consequences of ruminant behavioural responses to perceived risk or 'landscape of fear' (Laundre et al. 2010) has received little attention in relation to seed dispersal. Although our insights are based on ruminants, it is likely that many dispersers in general but non-obligate frugivores in particular, routinely make decisions similar to our study species (Morales et al. 2013, Carlo and Morales 2016, Rodríguez-Pérez et al. 2016). By extending our research focus to a diverse range of dispersers that include a wide range of traits, we will better understand the underlying mechanisms driving seed dispersal patterns.

Acknowledgements

We thank the Uttarakhand Forest Department for providing research permits. Parag Nigam and Bivash Pandav helped collar Chital. Support from Mumtaz, Taukeer, Basheer, Sadhique, and Netra Prasad was vital in collecting field data. Meghna's inputs and comments helped improve the writing and presentation substantially.

Chapter 3: Accounting for imperfect seed detection while modelling seed rain patterns generated by a terrestrial disperser: a novel application of site occupancy models

This chapter is based on a manuscript in preparation:

Sridhara, S., Prasad S., Edwards, W. and D. A. Westcott. Accounting for imperfect seed detection while modelling seed rain patterns generated by a terrestrial disperser: a novel application of site occupancy models

Statement of contribution of others:

Sridhara designed the study and collected data. Sridhara performed the analysis with inputs from David, Soumya and Will. Larissa Bailley clarified the modelling approach. Sridhara wrote the first draft, and revised the subsequent drafts with Westcott, Will and Prasad.

Accounting for imperfect seed detection while modelling seed rain patterns generated by a terrestrial disperser: a novel application of site occupancy models

Abstract

Spatial patterns of seed dispersal influence crucial ecological processes that govern plant community dynamics. Locating, tracking and monitoring seeds are fundamental steps in understanding the processes that generate seed rain patterns. However, seeds dispersed by animals can be hard to locate and are therefore not likely to be detected in a sampling unit even when present. Yet, seed rain patterns are routinely modelled without accounting for the specific observation error of imperfect detection of seeds, potentially resulting in incorrect inferences about spatio-temporal patterns of seed rain. Using occupancy models, we developed a novel framework to characterize spatial and temporal patterns of seed rain generated by a terrestrial disperser. This approach allows us to identify the potential factors influencing seed rain patterns while modelling and accounting for errors in detection. Correcting for imperfect detection allows more robust inferences of the correlates of seed arrival. We illustrate our approach using seed rain data of *Terminalia bellerica* generated by a deer (Chital – *Axis axis*) in a tropical forest of India. We systematically sampled 25 Ha of forest at 400 locations, each visited four times during the fruiting season by two observers to record seed arrival and measure covariates. Detection probability of seeds was < 1 (0.19 to 0.86). Seeds were less likely to be detected in taller vegetation. The probability of a seed being dispersed to a plot increased (estimated through parameter 'ψ' - a measure of spatial variation in seed rain) increased with the number of Chital dung piles (a proxy for activity) and decreased with distance to closed canopy forest. The temporal variation in seed rain - estimated through parameter 'ε', decreased with increasing grass availability and structural cover. We demonstrate the utility of our approach in simultaneously modelling observation and ecological process, while highlighting the novel ecological insights our study provides on seed dispersal ecology of deer in particular. Finally, we

make recommendations on how to extend our approach to several scenarios in seed dispersal studies.

Introduction

Seed dispersal is a key ecological process influencing plant recruitment at individual, population, and community levels (Wang and Smith 2002). Spatial patterns of seed rain determines potential germination success and sets the template for downstream processes such as seed predation (Russo 2005), seedling recruitment (Svenning 2001), gene flow (Wang and Smith 2002) and density-dependent seedling survival (Harms et al. 2000). Ultimately, by determining the locations to which different species are transported, seed dispersal contributes to mechanisms governing species distributions and plant co-existence (Levine and Murrell 2003). A better understanding of the spatial ecology of seed dispersal can help predict the responses of plant communities to environmental change (Muller-Landau et al. 2008) , especially with land-use conversion and climate change in an increasingly human-dominated world (Corlett and Westcott 2013).

Spatial seed rain patterns have been described both directly - by tracking seeds (Russo 2005, Suselbeek et al. 2013, Yi et al. 2014) and indirectly - using modelling techniques that do not require the physical path of seeds to be traced (e.g. Westcott et al. 2005, Kuparinen 2006). However, to track seeds beyond seed deposition, through subsequent processes such as secondary dispersal, seed predation, germination or seedling establishment, it is essential to monitor seeds in their natural habitats (Wang and Smith 2002). For instance, the widely used seed dispersal effectiveness framework, which assesses the relative contribution of multiple dispersers to seed dispersal, requires the fate of seeds to be followed until germination or recruitment (Schupp et al. 2010). Research examining the consequences of dispersal on seedling recruitment and eventually on mechanisms of co-existence also monitor seeds and their transition to seedlings (e.g. Bleher and Böhning-

Gaese 2001, Brodie et al. 2009a, Herrera and García 2010, Carlo and Morales 2016). Locating seeds in space and over time, i.e. seed rain, is the first step in monitoring seed fate, and is thus fundamental to describing and understanding spatial patterns of seed dispersal.

Locating seeds however, can be notoriously difficult. Failing to locate seeds when they are present can potentially bias results and change inferences regarding the importance of different correlates of seed rain. Seeds are rarely so conspicuous that they are detected perfectly on the forest floor, especially when the forest floor has a complex structure in which seeds of a certain size, shape, or colour blend-in. For tropical and sub-tropical trees, a majority of which are dispersed by animals (Jordano 2000), search efforts are likely compounded by how seeds are distributed in space. Animals frequently disperse seeds patchily, in clumps, and at non-random locations, complicating the type of search required and often making detection more difficult (Hardesty and Parker 2003, Fragoso et al. 2003, Russo and Augspurger 2004). Marking fruits and seeds with radio tags (Suselbeek et al. 2013), placing nets above the ground (also called seed traps) to capture seeds before they reach the forest floor (e.g Muller-Landau *et al.* 2008), or clearing the forest floor of all vegetation and litter (e.g. Morales *et al.* 2013) are some commonly used techniques to improve detection of seeds. However, these techniques could themselves influence how seeds are dispersed. Moreover, current methods implicitly assume that the observed spatial patterns of seeds are in fact the true and final patterns (however see Hirsch et al. 2012b). The few indirect attempts at modelling imperfect observations only rectify the error in the number of seeds observed, but not the issue of seeds being undetected altogether (e.g. Hille Ris Lambers et al. 2002, Bagchi et al. 2014).

Imperfect observations are pervasive in ecology and in some situations could lead to incorrect inferences if not suitably modelled (Kellner and Swihart 2014). Modelling philosophies now espouse dealing with imperfect observations explicitly and have led to the development of various modelling techniques (Yoccoz et al. 2001, Williams et al. 2002, Martin et al. 2005, Royle and Dorazio 2009). Techniques developed for animal population analysis and management deal with imperfect detection using the capture-recapture framework to estimate densities (Williams et al. 2002), and have been extended to estimate another state variable - occupancy (MacKenzie et al. 2002). Estimating occupancy - the proportion of area occupied by a species - is the central goal of site occupancy models while explicitly accounting for the fact that a species may not be detected even when present in the sampling unit, i.e. probability of detection is <1. These models, initially conceived for vertebrate taxa, have been applied to other taxa (plants, invertebrates, pathogens) and even to human medicine, paleontology, and political science (Bailey et al. 2014). In this family of models, multiple surveys are conducted in sampling units called ‘sites’ within which an entity of interest (animal, plant) is either detected or undetected. An entity occurs in a ‘site’ with certainty if recorded. However if the entity is not recorded in a site and a value of zero is assigned to the site, it could imply either that the entity was not present or that it was present but was not detected. Modelling exercises demonstrate marked differences in the inferences drawn when not explicitly accounting for these two distinct zero-generating processes in data (Martin et al. 2005, MacKenzie 2006).

Recording seeds from several locations during multiple surveys (either from seed traps or from plots on the ground) is analogous to detecting animals (or plants) in site occupancy studies. The most important advantage of this framework is the ability to model the ecological process (generation of seed rain patterns) separately from the observation process (detecting seeds at a plot) (MacKenzie et al. 2006). Modelling approaches that do not account for detection probability will confound true absence of seeds from a plot with non-detection of seeds in a plot. Consequently the inferences drawn about spatial patterns of seed dispersal are not purely reflective of the actual variation in where seeds were deposited, but also subsumes differences in our ability to detect the seeds. For instance, if seeds were consistently under-detected in habitats with thick understory (due to poor visibility), we are likely to conclude that sites with thick understory are unfavourable for dispersal, even though seeds may have been dispersed to such sites but simply not detected.

Our motivation in incorporating the occupancy framework in seed dispersal studies arises from a need to describe the spatial patterns of seed rain generated by a terrestrial disperser, and identify the potential drivers of such patterns. Chital (*Axis axis*) is a widely distributed deer (Cervidae) native to the Indian sub-continent, dispersing seeds of several trees (Sridhara et al. 2016). Because they regurgitate or defecate seeds onto the forest floor, standard methods of capturing dispersed seeds such as raised seed traps are inappropriate. Further, clearing plots on the ground is intrusive (e.g. in our sampling scheme an area of nearly 0.5 Ha would have had to be cleared), likely to bias results through disperser avoidance, and would be logistically demanding. Even then, clearing the ground of all vegetation is unlikely to result in perfect detection of seeds. For these reasons, we chose to sample plots on the ground, minimally modifying the substrate or vegetation already present. In doing so, we realized that not all seeds on the forest floor were likely detected. In this regard our study faced a problem common to all studies of terrestrial dispersers, like the majority of mammal and reptilian species, but also ground dwelling birds, and even insects. Detection is inevitably imperfect and though we would like to account for observation errors, the main goal of our study, like that of others, is to elucidate the drivers of spatial seed dispersal patterns.

In a novel application of site occupancy models, we assessed the potential drivers of spatial seed dispersal patterns of a tropical deciduous forest tree (*Terminalia bellerica*) generated by Chital, while explicitly modelling the observation errors of detecting seeds. We modelled detection probability of seeds as a function of vegetation height and substrate type of the plot (open, vegetation, debris etc). Next, and more importantly, we assessed whether availability of grass, structural cover, distance to closed canopy forest, quantity of fruits in a 50m radius, and distance to nearest fruiting tree influenced spatial seed rain patterns, and the temporal changes in these patterns. Finally, we provide guidelines to generalize our novel approach for other sampling scenarios and make recommendations on both spatial and temporal replicates.

Methods

Study site and data collection

We undertook the study in the foothills of Himalayas within the Chilla Range of Rajaji Tiger Reserve, Uttarakhand, India. Forest type of Rajaji have been categorized as northern Indian moist deciduous forest and northern tropical dry deciduous forest (Champion and Seth 1968). Chilla range, where the study was conducted, mostly comprises of rugged hills varying in altitude from 400 to 1000 m. Valleys, which support extensive grasslands, are almost always drained by seasonal or perennial rivers. The major tree associations are mixed forests comprising of tree species such as *Terminalia alata, Anogeissus latifolia, Lagerstroemia parviflora, Holoptelia integrifolia, Ehretia laevis, Aegle marmelos,* and Sal *(Shorea robusta)* dominated stands. Savannahs occur mostly along rivers beds but can be found scattered throughout the park and in all terrains. *Terminalia bellerica* are medium to large trees producing globular or ovoid fruits of mean radius 15 mm with ovoid seeds having a length of up to 20 mm (Sridhara et al. 2016). Chital regurgitate the seeds of *T. bellerica*.

We identified a 25 Ha (500m x 500m) area of dry-deciduous forest free of anthropogenic disturbance, and systematically subdivided it into grids (hereafter ‘site’ or ‘sites’) of size 25mx25m, creating 400 sites in total. The 25 Ha study area encompassed the three major habitat types found in the region, namely – open dry river beds, savannah comprising of continuous grass cover but discontinuous tree cover, and closed canopy forest (CCF). Within the 25 Ha study area, we located all adult trees of *T. bellerica* and mapped their location using a GPS. The trees with fruit were monitored during each sampling occasion and the number of fruit was recorded in categories of 0, 1-10, 11-100, 101-1000 and 1001-10000. We similarly mapped and monitored adult trees of *Aegle marmellos, Phyllanthus embelica, Ziziphus mauritiana,* and *Ziziphus xylopyrus*, the fruits of which are known to be consumed by Chital. When trees were close to one another with overlapping canopy, we treated them as a single individual. At the centre of each of the 400 sites we established a single circular seed plot of 2 m radius. Two observers independently visited each of the 400 plots once every 25-35 days, for a total of four times within the fruiting season of *T. bellerica* – October 2015 to March 2016.

During each visit, observers recorded three sets of data. First, the two observers independently noted whether at least a single seed was detected in each plot (1) or not (0), and following which seeds, if any, were removed from the plot. Next, observers recorded a suite of variables that either influenced the detection probability of seeds or the probability of seed dispersal and extinction. Variables measured at the plot were percentage grass available in four 1x1 m quadrats and percentage structural cover available in a 25m radius. Within the plot we counted the number of dung piles of Chital, measured the height of ground vegetation and identified the substrate type. For each plot we also computed or estimated distance to closed canopy forest (CCF), an index of fruit availability which summed fruits available in a 50m buffer for conspecific trees only, and for all species included. Distance to the nearest conspecific fruiting tree, and distance to nearest fruiting tree (including hetero-specific species whose fruits Chital are known to consume) were also computed for each site.

Occupancy modelling

Site occupancy models are used to estimate the proportion of area occupied by a species, using a mark-recapture framework (MacKenzie et al. 2006). Originally conceived for animal population monitoring, occupancy models estimate parameter '**ψ**', interpreted as the *proportion of sites occupied* for the entire study area, or the *probability that a site is occupied by the study species* for any particular site (MacKenzie et al. 2002). In our study we interpret '**ψ**' as the *proportion of sites to which seeds are dispersed* for the entire study area, or as *the probability that a seed is dispersed to* a particular site within the study area. Further, the models also estimate '**p**', the probability of detecting at least one individual of the study species at a site, given that it is present. In our study, 'p' is the *probability of detecting at least one seed at a site, given that it is present*'.

Detection probability is estimated by assuming that the entity of interest (animal, plant, or seed in our case) either occupies a site throughout the study period, or does not, and this state never changes during the study period. This assumption, called closure, is vital for estimation of '**p**'. To estimate the probability of detection of seeds '**p**', multiple observations are made by visiting the sampling sites repeatedly and noting whether seeds were found or not. Likelihoods are constructed as a set of probabilistic arguments based on whether seeds were detected ('1') or not detected ('0') during each visit. For example, in a study with four surveys, detection history of a sampling site where at least one seed was detected in the 1st and 4th visit but not in the 2nd and 3rd is '1001' and its corresponding likelihood is

$$\psi\,[\,p_1\,(1-\,p_2)(1-\,p_3)p_4]$$

where p_1, p_2, p_3, and p_4 are probability of detecting seeds in visit 1, 2, 3, and 4 respectively; and '**ψ**' is the probability of a seed being dispersed to the site (MacKenzie et al. 2002). Non detection of seeds either means that the seeds were not present in the site or were present and not detected. The likelihood of sites where no seeds are detected in any of the visits is

$$\psi\,(1-\,p)^T+(1-\,\psi)$$

where T is the number of visits made to each site - 4 in this study (MacKenzie et al. 2002). Assuming independence of the sites, the product of all terms (one for each site) constructed in this manner creates the model likelihood for the observed set of data, which can be optimized to obtain maximum likelihood estimates of the parameters. When dispersal probability and detection probabilities are constant across sites, the combined model likelihood can be written as

$$\mathrm{L}\,(\psi, \mathbf{p}) = \left[\psi^{\mathrm{n}} \prod_{\mathrm{t}=1}^{\mathrm{T}} \mathrm{p}_{\mathrm{t}}^{\mathrm{n}_{\mathrm{t}}}\ (1-\mathrm{p}_{\mathrm{t}})^{\mathrm{n}-\mathrm{n}_{\mathrm{t}}}\right] \mathrm{x} \left[\psi \prod_{\mathrm{t}=1}^{\mathrm{T}} (1-\mathrm{p}_{\mathrm{t}}) + (1-\psi)\right]^{\mathrm{N}-\mathrm{n}}$$

where T is the number of visits, n is the number of sites in which seeds were detected on at least one visit, n_t is the number of occasions in which at least one seed was detected, and N is the total number of sites (MacKenzie et al. 2002). Both '$\boldsymbol{\psi}$' and '**p**' can be modelled as a function of measured covariates (MacKenzie et al. 2006) allowing us to test hypothesis and make inferences about the study system.

Dynamic occupancy models

The major assumption of closure - sites remaining closed to emigration or immigration during the entire season of sampling - is central to estimate detection probability for the single season model described by MacKenzie *et al.* (2002). For our study, assumption of closure would mean that seeds are neither added nor removed from sites during the season. Because Chital consume *T. bellerica* fruits and disperse seeds throughout the season (Sridhara pers obs) sites are likely to experience 'colonization' of seeds between two consecutive visits. Additionally, Chital may not disperse seeds to sites it had done so previously, due to change in resources (e.g. reduction of grass); so sites may also experience 'extinction' of seeds between two consecutive surveys. Seed predation is unlikely to contribute to the process of 'extinction' because we found through camera trapping that seeds of *T. bellerica* are not cached but predated *in situ* (Sridhara, unpublished data). Therefore, the assumption of closure was very likely to be violated. Dynamic occupancy models (also called multi-season models) specifically relax this assumption of closure by modelling data across multiple seasons (MacKenzie et al. 2003). The basic survey design is similar to a single-season model but replicated across several seasons. The different seasons are called ‘primary sampling periods’ across which ‘colonization’ or ‘extinction’ events can occur, while the surveys within a season comprise the ‘secondary sampling period’ during which closure is assumed. Apart from ‘**ψ**’ and ‘**p**’, MacKenzie *et al.* (2003) introduced two additional parameters in the dynamic occupancy model, ‘**γ**’ or colonization probability and ‘**ε**’ or extinction probability. For our study we interpret ‘**γ**’ as *the probability that at least one seed is dispersed to a site in primary sampling period ‘t’ given that no seeds were dispersed during primary sampling period ‘t-1’*, and ‘**ε**’ as *the probability that no seeds are dispersed to a site in primary sampling period ‘t’ given that at least one seed was dispersed during primary sampling period ‘t-1’*. The detailed model construction, parameters estimation and their likelihoods are presented in MacKenzie *et al.* (2003). In our study we used a multi-season model similar to that of Otto et al (2013). Although our sampling was in a single fruiting season, each of the four visits to the plot is analogous to a primary sampling period, and the two independent observations made by the two observers, represent two secondary sampling periods. In all, we had *four primary sampling periods consisting of two secondary sampling periods each*. An example detection history of ‘10 00 11 00’ means that observer 1 detected at least one seed in primary sampling period 1 while observer 2 did not; no seeds were detected by either observers in primary sampling period 2 and 4, while both observers detected at least one seed in primary sampling period 3. For simplicity, we refer to the primary sampling period as the ‘sampling occasion’.

Hypothesis, model construction and analysis

Although our main goal was to identify potential drivers of the spatial patterns of seed dispersal (i.e. parameter ‘**ψ**’), our approach allowed us to model two additional parameters namely ‘**p**’ – the detection probability, and either ‘**ε**’ – the extinction probability or ‘**γ**’ – the colonization probability. Based on a preliminary analysis we found

'γ' to be very low (0.02 to 0.05) and therefore we chose to model '**p**', 'ψ' and 'ε' with each parameter having its own set of corresponding predictors. We constructed models based on previous studies and a priori expectations from our own system.

To estimate probability of seed dispersal ('ψ') we first constructed models that examined the influence of the spatial distribution of fruits. Support for these models would agree with previous results mostly from avian seed dispersers (e.g. Morales *et al.* 2012). To this end, four models were constructed using (a) distance to the closest conspecific adult fruiting tree, (b) distance to the closest adult fruiting tree (including hetero-specific individuals), (c) sum of conspecific fruits available in a radius of 50m, and (d) sum of all fruits available in a radius of 50m, as predictors. Because Chital are a non-obligate frugivore, classified as a grazer, we expected non-fruiting resources to play a significant role in determining its space use and in turn influencing seed deposition patterns (Schaller 1967). Our next set of models to estimate 'ψ' included availability of grass, availability of structural cover, number of Chital dung piles, and distance to closed canopy forest as single predictors. Finally, since Chital are known to be highly risk averse we expected Chital to use areas that not only allowed easier detection of predators but also provided quick refuge when pursued (Bagchi et al. 2003b, Vijayan et al. 2012). To test these expectations on parameter 'ψ' we constructed more models specifically using the variables number of Chital dung piles, availability of cover, and distance to CCF. These models included two predictors and the interaction between them.

To estimate 'ε' we constructed simple models using availability of structural cover, grass and fruits as predictors. Detection probability of seeds '**p**' was modelled as a function of substrate height and substrate type. We approached the modelling process in two steps, as is done with occupancy studies. First we constructed models to identify the best structure for '**p**'. The best model was selected based on Akiake Information Criterion corrected for small sample sizes (AIC_C). Once the top model was identified, we retained its model structure for ‘**p**’ while constructing several models that included covariates for ‘ψ’ and ‘ε’. All modelling was done in software R using package RMark. The ‘RDOccupPE’ model was used to fit data, which estimates parameters ‘ψ’, ‘ε’ and ‘**p**’, and computes the values of ‘γ’ based on the estimates of ‘ε’.

ψ	ε	***p***	np	AIC$_C$	ΔAIC$_C$	w
1	1	Height * Substrate + SO	15	900.78	0.00	1.00
1	1	Height + Substrate + SO	11	922.83	22.06	0.00
1	1	Height + SO	7	925.30	24.52	0.00
1	1	Height * Substrate	12	929.40	28.62	0.00
1	1	Height	4	934.30	33.52	0.00
1	1	Substrate + SO	10	936.29	35.51	0.00
1	1	Height + Substrate	8	936.70	35.93	0.00
1	1	SO	6	939.35	38.57	0.00
1	1	1	3	952.94	52.17	0.00
1	1	Substrate	7	954.93	54.15	0.00

Table 3.1: Top ranked models used to assess probability of detection of *T. bellerica* seeds. ψ - covariates used to model probability of dispersal, ε – covariates used to measure probability of extinction, ***p*** – covariates used to measure probability of detection; ‘1’ means an intercept only model, np – number of parameters estimated in the model, AIC$_C$ – small sample size corrected Akiake Information Criterion, ΔAIC$_C$ – difference in AIC$_C$ between each model and the model with lowest AIC$_C$, w – model weight. ‘*’ indicates additive and multiplicative effects, ‘+’ indicates additive effect only, and. Height – height of vegetation at sampling plots, Substrate – type of substrate at sampling plot, SO – sampling occasion or primary sampling period.

Results

Detection probability

During the four sampling occasions we detected at least one seed on 102 instances and located, in total, 598 seeds of *T. bellerica* dispersed by Chital. Number of seeds dispersed per site, for only those sites which received seeds and for all sites (400) varied from 2.71 to 6.47, and from 0.05 to 0.68 respectively, across the four sampling occasions. Table 3.1 summarizes the results of the first step of the analytical process where we modelled detection probability -'***p***' - of *T. bellerica* seeds dispersed by Chital, as a function of the measured covariates. The top model from Table 3.1 suggests that an interaction between vegetation height and substrate type best explained the patterns of detection histories observed. The top model also supported our expectation that detection probability varies across sampling occasions, with the lowest being 0.19 (±0.14) in the last SO and the highest being 0.86 (±0.07) in the 3rd SO (Fig 3.1). Vegetation height negatively influenced detection probability (Fig 3.2) while substrate types had a vast differential influence in the last SO compared to the first three (Fig 3.3). Seeds, if present, were more likely to be detected in plots whose vegetation height was lower rather than higher.

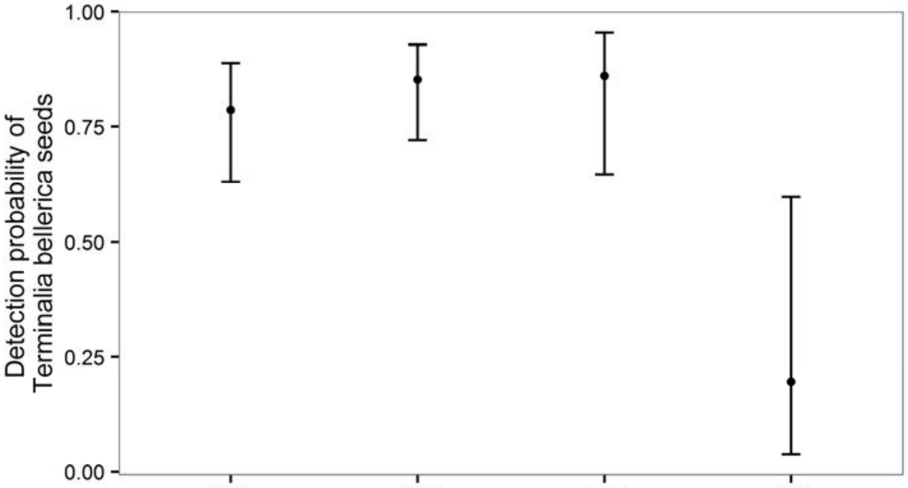

Figure 3.1: Detection probability of T. bellerica seeds. SO1 – SO4 are the four sampling occasions or primary sampling periods. Error bars indicate the upper and lower confidence intervals (95%) of the estimates.

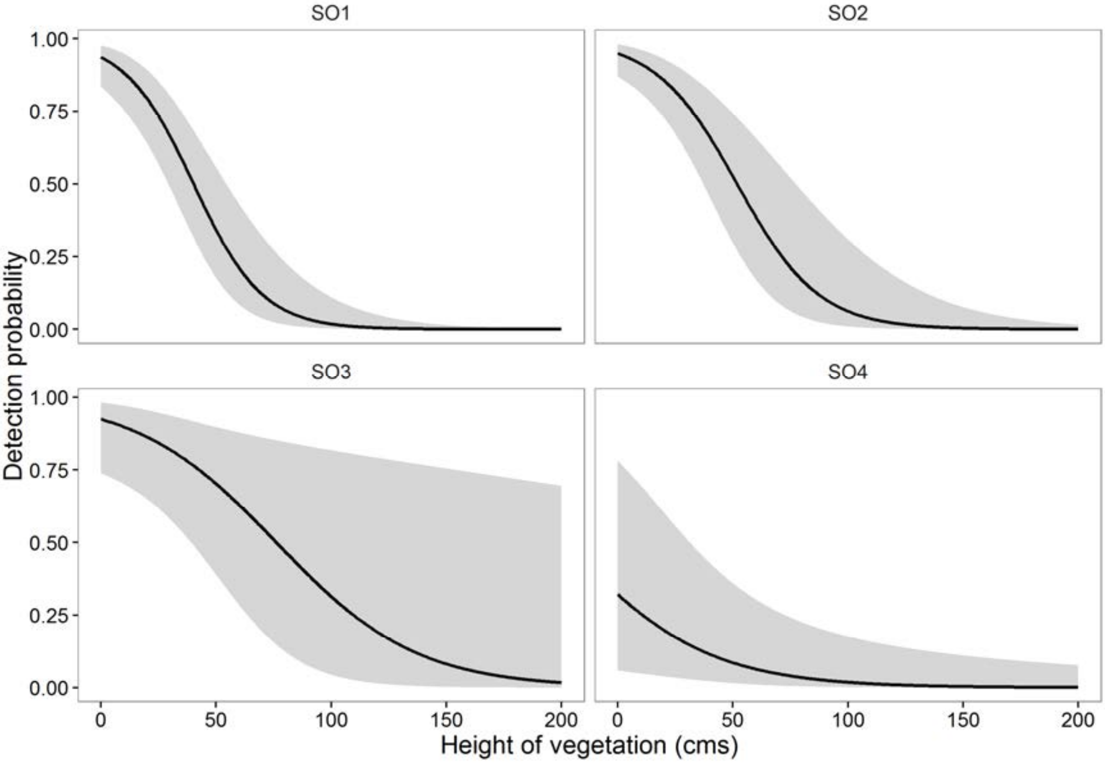

Figure 3.2: Detection probability of *T. bellerica* seeds was negatively influenced by vegetation height. SO1 – SO4 are the four sampling occasions or primary sampling periods. Grey ribbon indicates the upper and lower confidence intervals (95%) of the estimates.

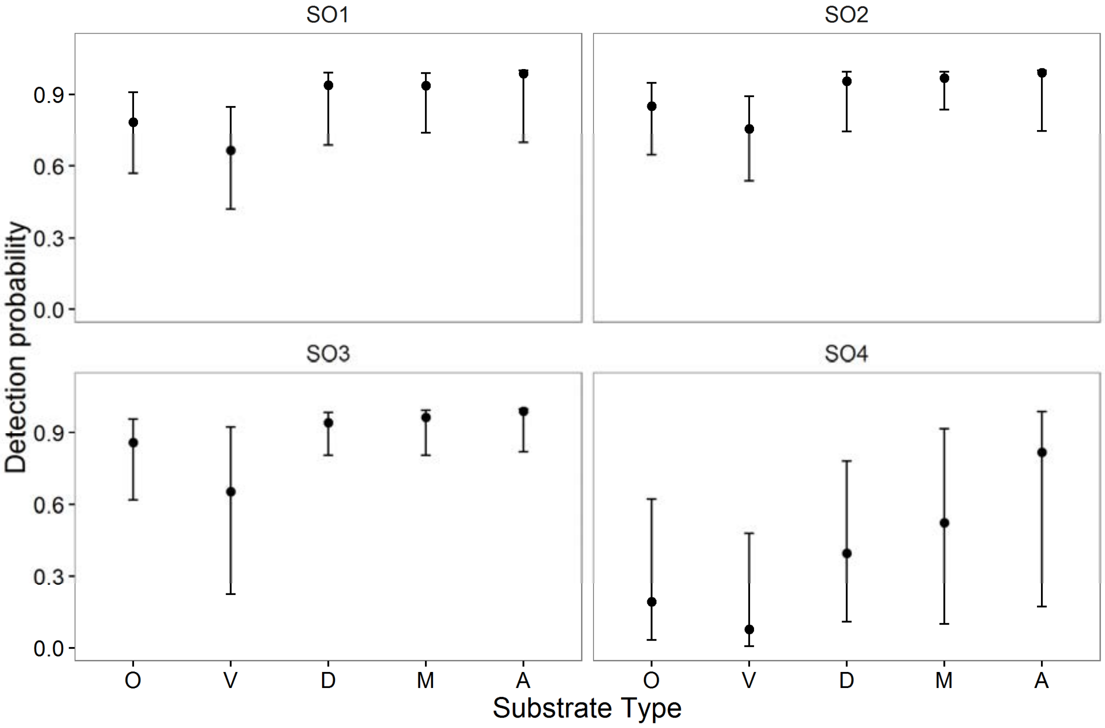

Figure 3.3: Detection probability of *T. bellerica* seeds was differentially influenced by substrate type. O: open / bare ground, V: Vegetation, D: debris consisting of grass, leaves, twigs and branches, M: combination of two or more substrates previously listed, A: combination of V and D only. SO1 – SO4 are the four sampling occasions or primary sampling periods. Error bars indicates the upper and lower confidence intervals (95%) of the estimates.

Spatial patterns of seed dispersal

We modelled both the seed dispersal probability 'ψ' and extinction probability of dispersed seeds across two sampling occasions 'ε' using a candidate model set based on a priori expectations. Top models suggest that similar to parameter '**p**', parameter 'ψ' varies across the different sampling occasions ranging from 0.04 (±0.019) to 0.11 (±0.016), with estimated values seeing an improvement of 7% to 20% for the first three SO and a 280% jump for the last SO (Fig 3.4) compared to the actual observed values. In the top ranking models, 'ψ' was best explained as an interaction between Chital dung piles and distance to closed canopy forest (CCF - Fig 3.5), both influencing the parameter positively. We found that for sites closer to the edge of closed canopy forest (CCF) the probability of Chital dispersing *T. bellerica* seeds increased as number of Chital dung piles increased (Fig 3.5). In contrast, at sites farther away from the edge of CCF, the seed dispersal probability was relatively lesser, and decreased as number of Chital dung piles increased (Fig 3.5).

Temporal patterns of seed dispersal

Models that estimated 'ψ' for each sampling occasion performed much better at explaining observed temporal changes in seed dispersal patterns than models that assumed a constant 'ψ' across sampling occasions (Table 3.2). Parameter 'ψ' was highest in the second sampling occasion and least in the fourth. Local extinction probability, 'ε' was best explained by structural cover alone in the top model, and as an additive effect of grass availability and structural cover in the closely ranked second model. Extinction probability 'ε' was negatively influenced by grass as expected (Fig 3.6), but contrary to our expectation, structural cover influenced local extinction negatively (Fig 3.7). Between two sampling occasions, Chital were less likely to continue depositing seeds to sites that contained less grass. Similarly, between two sampling occasions, Chital were less likely to deposit seeds to sites that contained less structural cover.

ψ	**ε**	**p**	np	ΔAIC_C	*w*
Chital dung piles * Distance to CCF + SO	Cover + SO	Height * Substrate type + SO	24	0.00	0.40
Chital dung piles * Distance to CCF + SO	Grass + Cover + SO	Height * Substrate type + SO	25	0.89	0.26
Chital dung piles + SO	Cover + SO	Height * Substrate type + SO	22	2.09	0.14
Chital dung piles + Grass + SO	Cover + SO	Height * Substrate type + SO	23	2.72	0.10
Chital dung piles + Distance to CCF + SO	Cover + SO	Height * Substrate type + SO	23	2.83	0.10
Fruit availability (TB species) + SO	Cover + SO	Height * Substrate type + SO	22	16.77	0.00
Distance to CCF + SO	Cover + SO	Height * Substrate type + SO	22	18.28	0.00
Grass + SO	Cover + SO	Height * Substrate type + SO	22	18.43	0.00
Intercept only	Intercept only	Height * Substrate type + SO	15	19.70	0.00
Nearest TB fruiting tree + SO	Cover + SO	Height * Substrate type + SO	22	20.21	0.00
Cover + SO	Cover + SO	Height * Substrate type + SO	22	20.88	0.00
Fruit availability (all species) + SO	Cover + SO	Height * Substrate type + SO	22	20.91	0.00
Nearest fruiting tree + SO	Cover + SO	Height * Substrate type + SO	22	20.94	0.00

Table 3.2: Top ranked models used to assess probability of dispersal and extinction of *T. bellerica* seeds. 'ψ' - covariates used to model probability of dispersal, 'ε' – covariates used to measure probability of extinction, 'p' – covariates used to measure probability of detection, np – number of parameters estimated in the model, ΔAIC_C – difference in AIC_C between each model and the model with lowest AIC_C, w – model weight. '*' indicates additive and multiplicative effects whereas '+' indicates additive effect only. TB – *T. bellerica*, CCF – closed canopy forest, SO – sampling occasion or primary sampling period.

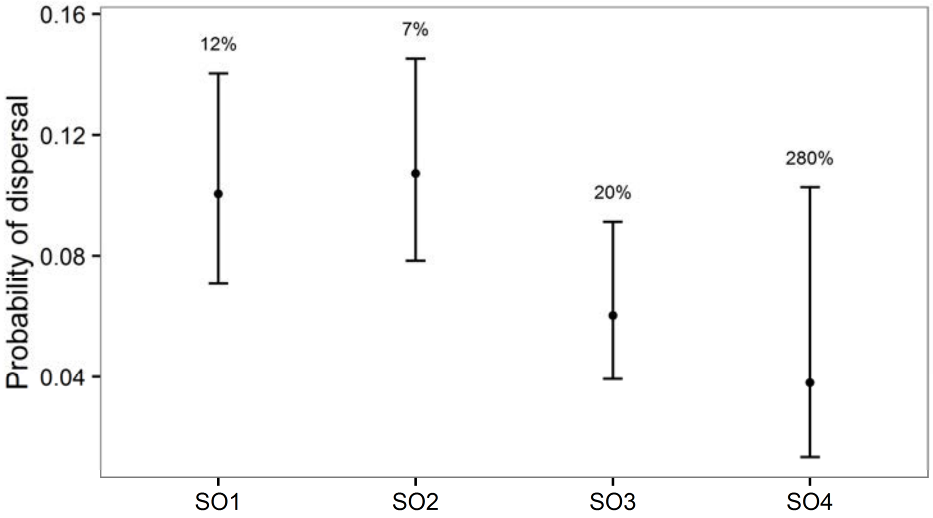

Figure 3.4: Probability of dispersal of *T. bellerica* seeds – 'ψ'. SO1 – SO4 are the four sampling occasions or primary sampling periods. Error bars indicate the upper and lower confidence intervals (95%) of the estimates. The numbers show the percentage increase in number of predicted sites to which seed were dispersed compared to observed data.

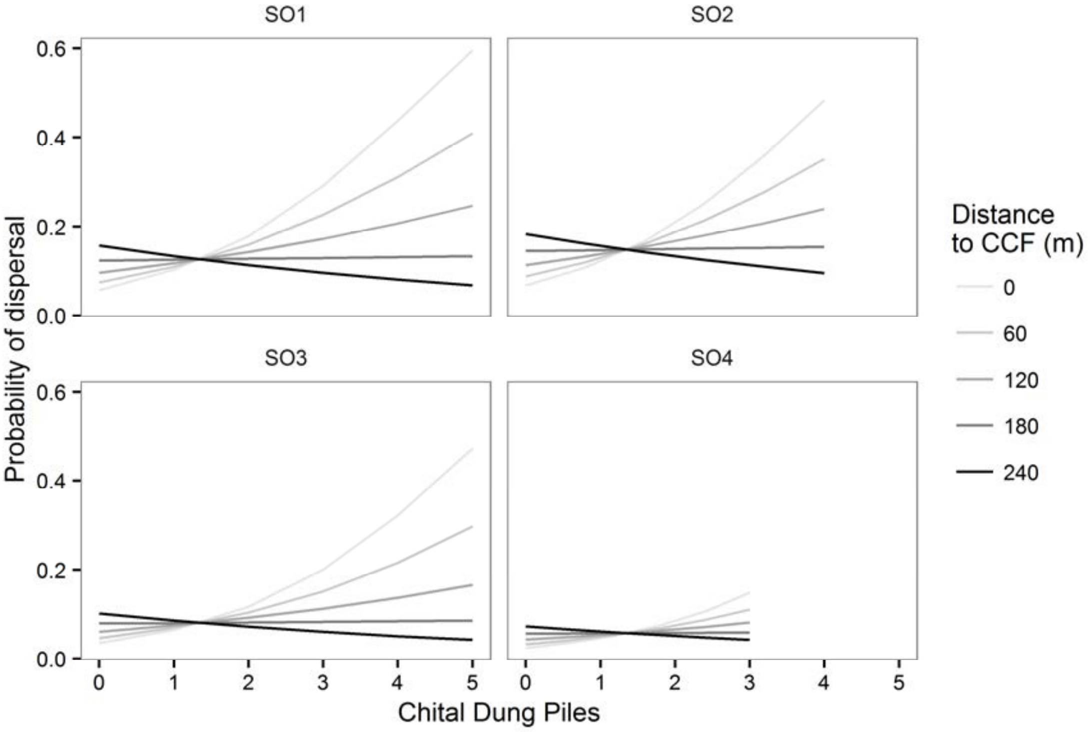

Figure 3.5: Probability of dispersal of *T. bellerica* seeds – 'ψ' from top model is visualized as an interactive effect between Chital dung piles and distance to closed canopy forest (CCF). SO1 – SO4 are the four sampling occasions or primary sampling periods.

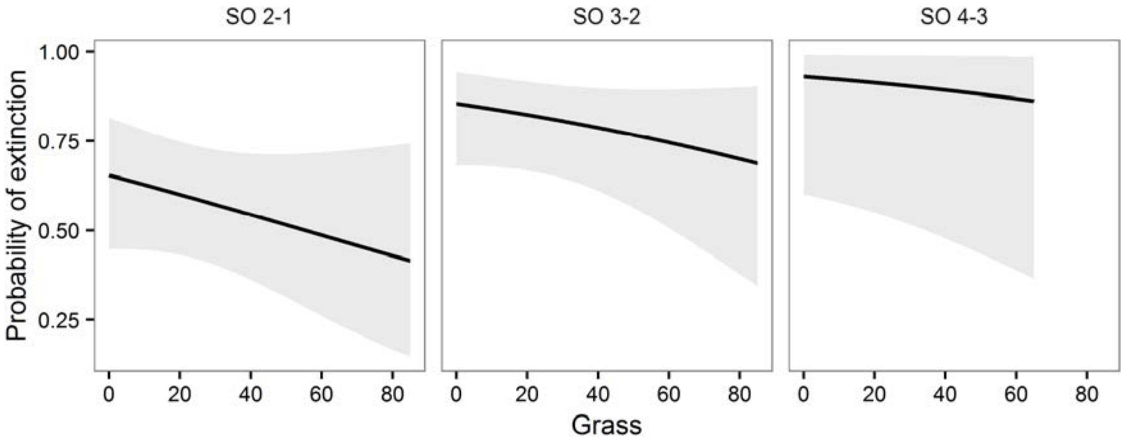

Figure 3.6: Probability of extinction of *T. bellerica* seeds – ‘ε’ from top model is negatively influenced by grass availability. SO 2-1, SO 3-2 and SO 4-3 represent the transition between two consecutive sampling occasions or primary sampling periods.

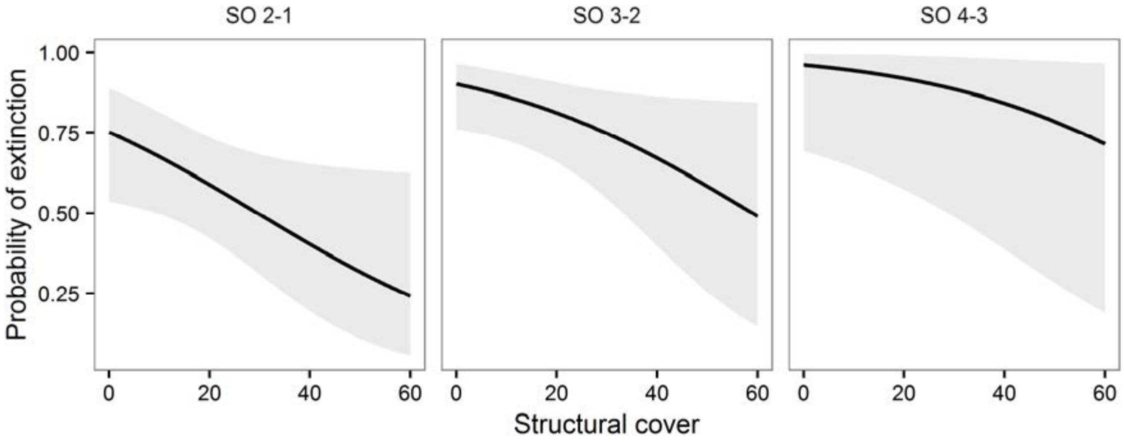

Figure 3.7: Probability of extinction of *T. bellerica* seeds – ‘ε’ from top model is negatively influenced by structural cover. SO 2-1, SO 3-2 and SO 4-3 represent the transition between two consecutive sampling occasions or primary sampling periods.

Discussion

We set out to identify the factors likely to influence spatial patterns of seed dispersal by Chital, while explicitly accounting for observation errors arising through imperfect detection of seeds on the forest floor. We found that seeds of *T. bellerica* dispersed by Chital were not detected even when present. The probability of detecting seeds changed during the four visits to the plots and decreased when height of vegetation in the plot increased. The spatial patterns of dispersal were best predicted by an interaction between number of Chital dung piles in the site and distance of the site to closed canopy forest. Temporal changes in these spatial patterns were best predicted by grass availability and structural cover in a site. Unlike avian seed dispersers, spatial and temporal changes in seed rain patterns were not explained by the distribution of fruiting resource either in space or time.

Detection probability of seeds

Our finding that detection probability of seeds - '**p**' - was < 1 (0.19 to 0.86, Fig 3.1), suggests that seeds even when present, were not detected despite our best efforts. Unsurprisingly, seeds were less likely to be detected, even when present, with taller vegetation in sampling plots (Fig 3.2). Seed detection was likely to vary with different substrates (e.g open, vegetation - Fig 3.3). Substrate type has been documented to influence detection probability of animal signs (e.g. Jeffress et al. 2011, Harihar and Pandav 2012), but ours is the first quantification of the influence of substrate on detecting seeds. Notably, we found that there was a consistently high chance of seeds going undetected on bare ground (indicated by 'O' in Fig 3.3) suggesting that clearing vegetation in all the seed plots would not have mitigated observation errors for *T. bellerica* seeds dispersed by Chital. Detectability of seed on bare ground may have been imperfect perhaps because the colour of *T. bellerica* seeds provide little contrast on sandy and dry soil substrates (the seeds and substrate have similar colours), and are hidden among vegetation or debris in other substrates (despite sufficient contrast). In summary, despite the large size of *T. bellerica* seeds, detection was imperfect and our approach allowed us to quantify the errors in our detection.

Spatio-temporal patterns of seed dispersal by Chital

Our results also provide novel insights into the spatial patterns of seed dispersal by Chital. Seed dispersal probability - 'ψ' - was higher at more intensely used (greater number of Chital dung piles) sites when close to the edge of closed canopy forest (CCF), and higher at less intensely used sites when far from the edge of CCF. Chital disperse most of the seeds during bedding (Prasad et al. 2006, Brodie and Brockelman 2009) when they are vulnerable to predation. Therefore, during bedding Chital prefer habitats in which they can detect their predators easily, such as the more open savannahs (Schaller 1967, Vijayan et al. 2012), but remain close to patches with high structural cover such as CCF to flee from attacks by stalking predators such as tigers and leopards (Schaller 1967, Karanth 2001). However farther away from CCF, Chital are less likely to bed and therefore may deposit seeds in less intensely used sites (lower number of dung piles). Our results suggest that the risk averse behaviour of Chital, driven by predator avoidance has a stronger influence on where they choose to bed and therefore disperse seeds. Unlike studies of avian frugivores (e.g. Morales and Carlo 2006, Carlo and Morales 2008, Herrera et al. 2011), we found no support for the expectation that distribution of fruiting trees influenced spatial seed rain patterns generated by Chital (Table 3.2).

We found that patterns of seed dispersal by Chital vary within the fruiting season of *T. bellerica* (Fig 3.4). Our approach provides the flexibility to model this variation either using parameter 'γ' or 'ε'. We expected that Chital, being grazers, were less likely to use sites where grass diminished as the season progressed. Consequently, Chital were less likely to disperse seeds to such sites. Often studies evaluate the patterns of seed dispersal as a cumulative effect at the end of the season (Morales et al. 2013). Recent evidence suggests that the timing of seed dispersal even within a season can influence germination and other subsequent stages of plant recruitment (Naoe et al. 2011, Yamazaki et al. 2016). The application of dynamic occupancy models as done in this study can help better understand the correlates of seed arrival through time and potentially aid in understanding the long term evolutionary consequences of timing of seed dispersal at the community level of plants (Razafindratsima and Dunham 2016b).

Interpreting seed rain patterns in the occupancy framework

Our principle goal, as with many seed dispersal studies, was to identify factors that influenced spatial and temporal seed rain patterns (Nathan and Muller-Landau 2000, Wang and Smith 2002). The seed dispersal parameter, 'ψ', estimated using likelihood methods in a logistic regression framework, can be interpreted in two ways. First, for the entire study area, 'ψ' is *the proportion of sites to which seeds are dispersed by Chital*. In our study Chital were estimated to disperse seeds to between 4% (16) and 11% (44) of the 400 sites during the four sampling occasions. Because 'ψ' is estimated for every site based on the site specific co-variates that were measured, our approach allows a second interpretation of 'ψ', that is *the probability of a seed being dispersed by Chital to* any particular site. We envision the first interpretation of 'ψ' to be a useful addition to any study that classifies a disperser community functionally (Dennis and Westcott 2006). Estimates of 'ψ' can complement metrics such as quantity of fruit consumed or movement patterns, to gain insights in to the spatial spread of dispersed seeds (Dennis and Westcott 2006). For instance, 'ψ' could be different for two dispersers consuming the same quantity of fruits of a plant species underscoring functional differences in spatial patterns of seed dispersal by different dispersers.

Considerations for sampling design

We encourage researchers to carefully identify and measure variables likely to influence seed detection. For example, height of vegetation, substrate type, seed colour and size, and habitat type are likely to influence detection. Because observers themselves could influence detection we strongly suggest developing a standard protocol to be used across observers, and to randomly shuffle observers between teams to reduce observer bias (e.g. MacKenzie et al. 2002).

The number of sampling occasions would depend on the duration of fruiting of the targeted plant species and logistical constraints. The number of sampling occasions required would also depend on the temporal scale at which seed rain patterns are being analysed. More sampling occasion would allow a finer examination through time, which may be relevant for dynamically changing systems (e.g. Rodríguez-Pérez et al. 2016). For a plant species with long fruiting seasons or when trying to examine large scale patterns of seed dispersal, many temporal replicates may be logistically challenging. In such a scenario, it may be necessary to decrease the number of sites being sampled and increase the number of observers during each temporal replicate (MacKenzie and Royle 2005). In contrast, when fruiting duration is very short or when repeated surveys are difficult, temporal replicates could be substituted with spatial replicates to build detection histories based on a single survey (MacKenzie et al. 2006). Single survey design however, would preclude estimation of parameters 'ε' or 'γ', and the opportunity for making any inferences about the temporal nature of the seed rain patterns. We refer the reader to a study by MacKenzie & Royle (2005) that uses simulations to identify optimal sampling efforts for different combinations of primary and secondary sampling occasions. Wrong choice of sample sizes or sampling design can result in biased parameter estimates for site occupancy models (Welsh et al. 2013). The consequence of these trade-offs to sampling have been discussed in the context of animal occupancy studies but are equally relevant to seed dispersal (MacKenzie and Royle 2005, Kendall and White 2009, Rota et al. 2009, Guillera-Arroita 2011, Lele et al. 2012, Bailey et al. 2014).

Model implementation

Occupancy modelling can be undertaken using a variety of tools ranging from interactive software (Program Presence, MARK) to packages for software R (unmarked and RMark) which implement the most commonly used models formulations and their extensions. We demonstrated a fairly complex implementation of occupancy, but even greater sophistication is possible. Software such as WinBUGS, JAGS or STAN allow modelling complex relationships through hierarchical approaches that estimate group level (random effects) slopes or intercepts (Kéry and Royle 2008, Bolker et al. 2013). Incorporating occupancy modelling based analysis in seed dispersal can therefore be easy accomplished through simple software or can be flexibly tailored for specific scenarios that requires complex models.

Conclusion

We demonstrated that the occupancy framework can account for imperfect detection of seeds while characterizing seed rain patterns, an important ecological consideration.

Accounting for detection enhances the confidence about errors of estimates, and can even modify the inferences made from the study (Martin et al. 2005, Royle and Dorazio 2009, Kellner and Swihart 2014). With minimal changes and careful considerations of study design (e.g. number of temporal replicates and observers), our approach can be easily adapted for most seed dispersal studies that routinely use spatially and temporally replicated surveys to measure seed rain (Muller-Landau et al. 2008, Morales et al. 2013).

Acknowledgements

We are thankful to Uttarakhand Forest Department for issuing research permits. Funding was provided by AusAID, DST & MoEF from India, IdeaWild from USA, JCU and CSIRO. We thank NSI, NCBS, and IISc for institutional support. The analysis benefitted from discussions with Larissa Bailley. Sachin is especially grateful to Mumtaz Chechi, Basheer Baniya, Shamshaad Baniya, Mustafa and Zareef Khan for their able assistance in the field, and Ajith Kumar for administrative support. Meghna Krishnadas supported all stages of this work, and her inputs on presentation helped improve the manuscript substantially.

Chapter 4: Functionally different dispersers produce contrasting and similar spatio-temporal patterns of seed rain

This chapter is based on a manuscript in preparation:

Sridhara, S., Prasad S., Edwards, W. and D. A. Westcott. Functionally different dispersers produce contrasting and similar spatio-temporal patterns of seed rain

Statement of contribution of others:

Sridhara designed the study with inputs from Westcott, Prasad and Edwards. Sridhara collected data, and performed the analysis. Sridhara wrote the first draft, and revised the subsequent drafts with Westcott, Prasad and Will.

Functionally different dispersers produce contrasting and similar spatio-temporal patterns of seed rain

Abstract

When multiple animal species disperse seeds of plants they often contribute differentially to the several stages of seed dispersal. Understanding the relative role of dispersers is essential to identify the key dispersers of the plant. Using the previously developed occupancy framework, we examined seed rain patterns generated by Chital and contrasted them with other dispersers in the system, namely pigs and birds, to identify the similarities in spatio-temporal seed rain patterns and the potential factors driving these patterns. Due to differences in the diets and habitat use of the three dispersers, we predicted their spatio-temporal seed rain patterns to be very different. Specifically, Chital would generate seed rain patterns explained by resources that reflect its grazing diet and predator avoidance behaviour but not fruiting trees. In comparison pigs and birds would generate seed rain patterns that were explained by fruiting resource distribution. To test these predictions we collected seed rain data of *Ziziphus mauritiana* (dispersed by Chital, pigs and birds) and contrasted them with seed rain data of *Terminalia bellerica* (dispersed by Chital only). Spanning an area of 25 Ha, we systematically sampled 100 sites (50mx50m) with four seed plots each, surveyed four times during the fruiting season. Chital and pigs dispersed similar quantities of *Z. mauritiana* seeds but to very different number of locations. Chital dispersed seeds to nearly thrice the number of locations compared to pigs or birds. Although pigs transported far more seeds than birds, both dispersed seeds to similar number of locations. Chital dispersed varying quantities of seeds as the season progressed but to similar number of sites, while pigs and birds dispersed varying quantities of seeds to varying number of sites as the season progressed. While the spatial distribution of grass, structural cover and terrain ruggedness best explained seed rain patterns of Chital, fruiting trees predicted patterns generated by pigs and birds. By highlighting the differences in spatio-temporal patterns of seed rain generated by Chital, pigs and birds, and by identifying the potential drivers of these patterns our study underscores the importance of examining seed dispersal by ruminants in particular and less-studied non-obligate frugivores in general.

Introduction

Plants that rely on animals to transport their seeds are typically dispersed by multiple animal species (Gautier-Hion et al. 1985, Kitamura et al. 2002, Bascompte et al. 2003, Donatti et al. 2011). But dispersers vary in the quantity of fruits they consume, the manner in which they handle and process seeds, and the locations or distances to which they transport seeds (Bascompte et al. 2003, Jordano et al. 2007, Schupp et al. 2010). These differences in the contribution of dispersers to seed dispersal can have profound consequences for plant regeneration (e.g. Spiegel and Nathan 2007, Brodie et al. 2009a, Bueno et al. 2013) and the loss of functionally distinct and non-redundant dispersers can be debilitating for plant demography (Pérez-Méndez et al. 2016, Sekar et al. 2017). Understanding the functional role of different dispersers and whether they provide redundant seed dispersal services to plants has therefore become increasingly relevant in the face of global declines of many seed dispersers (Corlett 2011, McConkey et al. 2012).

Animals provide seed dispersal services in a multitude of ways. For instance, dispersers may differ in the type and quantity of fruits they consume (Gautier-Hion et al. 1985, Donatti et al. 2011, Dehling et al. 2016) or how they process seeds in their guts and duration for which they retain them (Traveset and Verdu 2002, Traveset et al. 2007). A particularly crucial functional difference among dispersers is their movement patterns that influences the kind of locations and distances to which seeds are dispersed (Nathan and Muller-Landau 2000, Wang and Smith 2002). Differences in the spatial locations to which seeds are dispersed by different dispersers can have consequences on seed predation and seedling recruitment, influencing later stages of plant regeneration (Kwit et al. 2004, Spiegel and Nathan 2007, Brodie et al. 2009a). Characterising the differences in spatial patterns of seed rain generated by different dispersers and the identifying the potential drivers of these patterns is essential to assess the relative importance of dispersers to plant demography (Nathan and Muller-Landau 2000, Jordano et al. 2007, Schupp et al. 2010).

Spatial variation in seed rain patterns alone may be unable to explain observed differences in germination and seedling recruitment (Norden et al. 2007). Temporal variation in seed arrival, mediated largely by animal dispersers in tropical forests, is also known to strongly influence early stages of plant regeneration of not just individual plant species but that of the entire plant community (Norden et al. 2007, Paine and Harms 2009). In particular, timing of seed dispersal can determine quantity of seeds transported, germination success and seedling recruitment rates (Verdú and Traveset 2005, Carnicer et al. 2009). The combined effects of the timing of fruiting, consumption by dispersers and seed dispersal may even have evolutionary consequences for fruiting synchrony among plant species (Razafindratsima and Dunham 2016b). Despite the potentially vital role of timing in seed dispersal few studies examine the temporal variation in seed rain generated by different dispersers, let alone understand the probable drivers of these differences among functionally different dispersers.

Many community-wide studies of functionally different dispersers often examine very similar species such as birds, primates, and lizards (Spiegel and Nathan 2007, McConkey et al. 2014, Rother et al. 2016, Pérez-Méndez et al. 2016). Few studies span a diverse set of dispersers (McConkey and Brockelman 2011, Mokany et al. 2014). Consequently the functional role of certain types of dispersers such as large mammalian herbivores, mammalian carnivores, avian carnivores, fresh water fishes remain poorly understood, despite being key dispersers (Zhou et al. 2011, Horn et al. 2011, Vidal et al. 2013, Sridhara et al. 2016). Expanding community-wide studies to include these poorly studied groups is not only important to gain a more complete understanding of seed dispersal, but is also timely. Many disperser groups, especially large herbivores are experiencing global declines in populations (Ceballos 2005, Dirzo et al. 2014). Predicting the consequences on the loss of large herbivores is currently challenging because insights gleaned from functionally very dissimilar dispersers such as avian frugivores, or primates are not applicable to them (Sridhara et al. 2016).

In this study our aim was to contrast the functional role of under-studied medium-size ruminant, specifically deer Chital – *Axis axis* and pigs – *Sus scrofa*, in generating spatio-temporal seed rain patterns of *Ziziphus mauritiana* and contrast them with services provided by a better documented disperser group, birds. Further, we wanted to identify the potential factors likely to drive these patterns. We predicted differences in both spatial and temporal patterns of seed rain generated by the three different disperser groups (Chital, pigs and birds). Due to their highly frugivorous diets, we expected spatio-temporal seed rain patterns generated by birds to be influenced largely by the distribution of fruiting resources, including co-fruiting heterospecifics (e.g. Morales and Carlo 2006). Because pigs exploit ephemeral resources such as fruits we expected the spatio-temporal seed rain patterns they generate to also be dependent on fruit distribution, but less so than birds due to the omnivorous diet of pigs (Sridhara et al. 2016). In contrast, we expected that seed rain patterns generated by Chital, which are predominantly grazers, to not correlate with the distribution of fruits. Instead, because Chital are grazers (Schaller 1967), we predicted grass availability to influence habitat use and consequently their seed rain patterns. Further, Chital disperse seeds (through regurgitation) mostly when bedding (Prasad et al. 2006) and bedding sites are chosen to enable easy detection of predators (Brodie and Brockelman 2009). Hence, we predicted seed deposition to be higher in areas with low structural cover (better predator detection). Since grass and structural cover are temporally less variable than fruit availability of *Z. mauritiana*, we predicted that Chital would generate the least temporally variant seed rain patterns. To confirm whether seed rain patterns by Chital are indeed independent of fruiting resources, we also examined seed rain of *Terminalia bellerica*, which is primarily dispersed by Chital. We accounted for imperfect detections of seeds, arising from the need to sample seeds from the forest floor, using the occupancy modelling framework developed in Chapter 3.

Methods

Study system

We undertook the study in Rajaji National Park, part of the Shivalik foothills in lesser Himalayas, within the state of Uttarakhand, India. Rajaji's forests have been categorized as northern Indian moist deciduous forest and northern tropical dry deciduous forest (Champion and Seth 1968). Chilla range, where the study was conducted, has rugged hills ranging from 400 to 1000 m in altitude. The area is drained by seasonal rivers and streams with the valleys supporting extensive grasslands. Savannahs occur mostly along rivers beds but can be found scattered throughout the park and in all topographical contexts. Our sampling was conducted in a location near which nearly 30 people (5 families of the Gujjars) live along with approximately 75 heads of livestock (buffalo *Bubalis bubalis* and cattle *Bos taurus*).

Ziziphus mauritiana, a small- to medium-sized deciduous, armed tree produces globular fruits and globular or ovoid seeds of mean radius four and three mm respectively (Sridhara et al. 2016). Fruits are dispersed by a number of animal species including two species of bears, Chital, pig, two species of civets, porcupine, and several species of birds (at least 6 species). However, statistical analysis was undertaken for only Chital (60-90 Kg), pig (35-50 Kg) and several species of birds (0.01 - 0.150 Kgs) as seed rain data from other species was inadequate. Due to differences in scat morphology, seeds embedded in fecal matter can be easily identified as being dispersed by bears, pigs, civets or porcupines, although it is impossible to visually differentiate among the species of bears or civets. Regurgitated seeds can also be identified as being dispersed by Chital or birds due to the differences in extent to which the pulp is removed from the seeds, although the identity of the bird species is impossible to establish visually. Both Chital and pigs depend on primates (*Macaca radiata* and *Semnopithecus hector*), birds or natural fruit fall to access fruit when it is beyond their reach. The other tree species, *Terminalia bellerica*, is a medium to large deciduous tree producing ovoid fruits and seeds with a mean radius 12 and 8 mm respectively (Sridhara et al. 2016). Chital are the primary dispersers of this tree in the landscape, eating fruits discarded by primates or those that have fallen down. Birds and pigs have never been recorded to consume their fruits. Both the tree species bear fruit between October and March.

Sampling design

We identified a 25 Ha (500m x 500m) study area, of dry-deciduous forest encompassing the three major habitat types found in the region, namely – open dry river beds, savannah comprising of continuous grass cover but discontinuous tree cover, and closed canopy forest. Within the study area, we located all adult trees of *Terminalia bellerica* and *Ziziphus mauritiana*, mapping their location using a GPS. The trees with fruit were monitored during each survey and the number of fruit was recorded in categories of 0, 1-10, 11-100, 101-1000 and 1001-10000. When trees were close to one another with overlapping canopy, we treated them as a single individual. The study area was systematically divided into grids (henceforth ‘site’ or ‘sites’) of size 50mx50m, creating 100 sites in total. Within each site we realized four circular seed plots (henceforth ‘plot’) of radius 2m placed equidistant in a 2x2 matrix resulting in a total of 400. Two observers visited each of the 400 plots once every 25-

35 days, four times within the fruiting season of *Terminalia bellerica* and *Ziziphus mauritiana* – October 2015 to March 2016.

During each visit, observers recorded three sets of data. First, the two observers independently noted whether a seed was detected in at least one of 4 plots within a site (1) or not (0), following which any seeds found were removed from the plot. Next, observers recorded a suite of variables that influenced (i) the probability of detecting seeds (ii) the spatial pattern of seed rain and (iii) the temporal patterns of seed rain. Variables measured at the plot were percentage of grass available in four 1x1 m quadrats and percentage of structural cover available in a 25m radius. Within the plot we counted the number of dung piles of both Chital and domestic livestock, measured the height of ground vegetation and identified the substrate type. For each plot we computed or estimated an index of fruit availability which summed fruits available in a 50m buffer for each of the two trees in our study and for all species known to be consumed by birds. Additionally for each site, we computed distance to the nearest conspecific fruiting tree, and distance to nearest fruiting tree (including hetero-specific species whose fruits Chital and birds are known to consume), and the average number of fruits available in the neighbouring sites.

Analytical methods

We used a capture-recapture based site occupancy models, to model spatial patterns of seed rain and the temporal changes to these patterns as a function of measured co-variates, while simultaneously accounting for imperfect detection of seeds (MacKenzie et al. 2006). A detailed explanation of model formulation and its application to our study is explained in Chapter 3. Using dynamic occupancy models we estimated parameter 'ψ' - *proportion of sites to which seeds are dispersed*, for each of the disperser groups (Chital, pig, birds). This allowed us to assess factors influencing the spatial patterns of seed rain. Next, we estimated 'γ' - *the probability that at least one seed is dispersed to a site given that no seeds were dispersed during the previous visit* or 'ε' - *the probability that no seeds are dispersed to a site given that at least one seed was dispersed during the previous visit.* Parameters 'γ' and 'ε' were used to assess the factors likely to influence temporal changes in the observed seed rain patterns across the four sampling occasions. Finally, we also estimated parameter 'p' - the *probability of detecting at least one seed in a site, given that it is present.* While all the above parameters are modelled as a function of measured co-variates using a generalized logistic regression, '*p*' is estimated by constructing a set of probabilistic arguments based on whether seeds were detected ('1') or not detected ('0') during each visit to the site, also called detection history. An example detection history for a site in our study is '10 00 11 00'. The string of 1's and 0's means that observer 1 detected at least one seed in 1st visit while observer 2 did not; no seeds were detected by either observers in the 2nd and 4th visit, while both observers detected at least one seed in the 3rd visit. Our model assumes that no new seeds are dispersed between the two observations made by two observers during a visit, a reasonable assumption considering that these observations were always made 5-15 minutes apart. This assumption is essential to the estimation of the detection probability *'p'*. Another important assumption is that the two observations are independent. We maintained independence by ensuring that observers separately surveyed the plot and only revealed whether they detected a seed or not after both the observers completed the survey. Any seeds found were removed from the plots.

We constructed candidate models sets to assess the influence of measured co-variates for each tree species and disperser combination (e.g. *T. bellerica* – Chital, *Z. mauritiana* – bird) based on our hypotheses. We chose to model 'ψ' because we were interested in spatial seed rain patterns, and estimated either 'γ' or 'ε' to model temporal seed rain patterns. Package RMark in program R, allows any combination of two parameters to be estimated but not all three ('ψ', 'γ', 'ε'). First, we assessed the influence of measured co-variates on detection probability '*p*' (parameter 'ψ' and 'γ' or 'ε' were modelled as intercept only) and identified the best model based on AICc (small sample size corrected Akiake Information Criteria). We retained the model structure from the previous step and next modelled both 'ψ' and 'γ' or 'ε' based on the set of candidate models. Our choice to model 'γ' or 'ε' for each tree species – disperser combination was based on whether standard error and parameter estimates were unaffected by boundary conditions (estimates close to 0 or 1), and did not have very large standard errors (MacKenzie et al. 2006, Welsh et al. 2013). For Chital, our candidate model set included fruiting resources (sum of fruits within a site, distance to closest fruiting tree), grass, structural cover and count of livestock dung as independent variables. To model patterns of seed rain generated by pig, we fixed 'p' to 1 because our data and preliminary analysis suggested that detection probability was likely to be close to one (the two independent observers had identical detection histories throughout). In the candidate models for pigs, we included substrate type, grass and fruiting resources (sum of fruits within a site, distance to closest fruiting tree) as independent variables. Finally, to model bird seed rain, our candidate models not only included fruit distribution of *Z. mauritiana* (sum of fruits within a site, distance to closest fruiting tree), but also that of other tree species fruiting during the study and known to be consumed by birds (e.g. *Ficus rumphii, Ficus religiosa and Limonia sp.*), and the sum of fruits in the neighboring grids. We included fruit in the neighboring grids because empirical data from several studies suggest that visitation and removal rates of fruits and seed rain patterns are influenced by the distribution of fruits in proximity (Carlo and Morales 2008, Morales et al. 2012, Albrecht et al. 2015). All co-variates were checked for collinearity prior to the analyses. All analyses were done using software R and package RMark.

Results

In all, 100 sites with four seed plots each were surveyed four times between October 2015 and March 2016. A visualization of data illustrates the varying spatial and temporal seed rain patterns for different tree species – disperser combinations sampled across four months (Fig 4.1). The total number of seeds dispersed every month varied among the different tree species – disperser combinations. Chital dispersed fairly consistent number of seeds of *T. bellerica* every month showing a declining trend (Fig 4.2). The number of *Z. mauritiana* seeds dispersed not only varied among disperser groups but also across the different months for each disperser group, all showing an initially increasing followed by a decreasing trend (Fig 4.2).

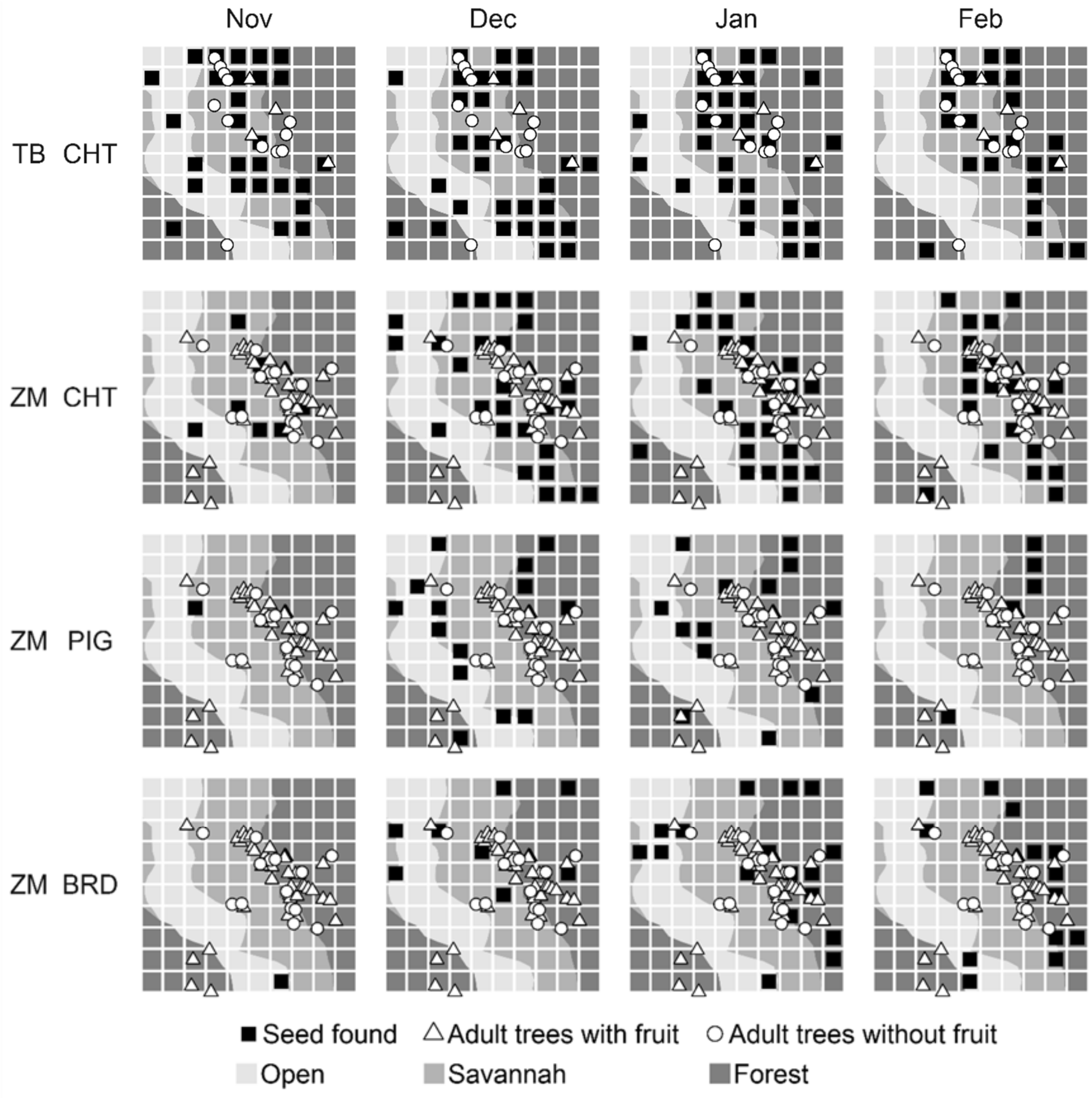

Figure 4.1: Patterns of seed rain of *Terminalia bellerica* (TB) and *Ziziphus mauritiana* (ZM) generated by Chital (CHT), pig (PIG) and birds (BRD). White grids represent the 100 sampled sites spanning 25 Ha and located in three different habitat types (Open, Savannah, and Forest). Grids were sampled during November 2015 (Nov), December 2015 (Dec), January 2016 (Jan) and February 2016 (Feb). Trees in the first row of panels represent *T. bellerica* species, and *Z. mauritiana* in the rest. The circles and triangles indicate whether trees bore any fruit at all during the season or not, and not the dynamic changes in fruit availability as the season progressed.

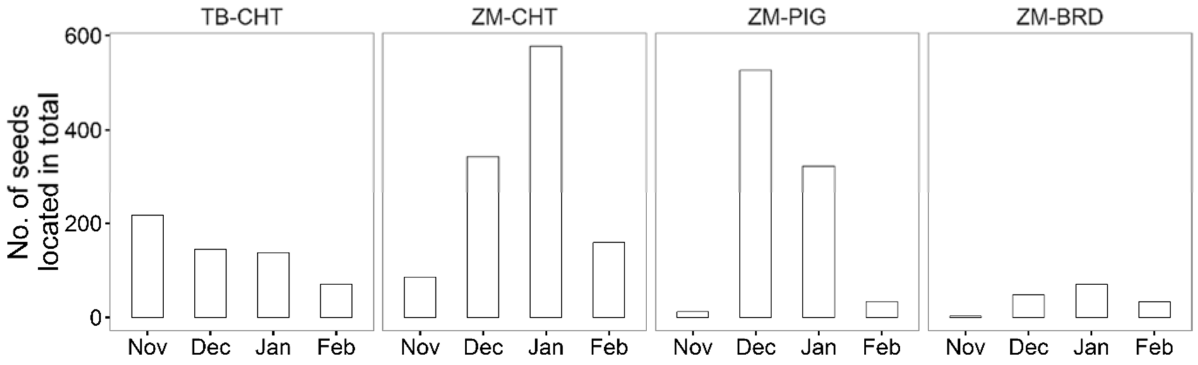

Figure 4.2: Total number of seeds of *Terminalia bellerica* (TB) and *Ziziphus mauritiana* (ZM) identified as being dispersed by Chital (CHT), pig (PIG) and birds (BRD) during November 2015 (Nov), December 2015 (Dec), January 2016 (Jan) and February 2016 (Feb).

As a first step in modelling spatio-temporal seed rain patterns, we modelled detection probability of the different tree species – disperser combinations as a function of measured covariates. We summarize the estimated parameter estimates from the top ranking model based on AICc (Table 4.1). Detection probability of *T. bellerica* seeds dispersed by Chital were best explained by an additive effect of substrate and habitat. Substrate did not influence detection probability of *Z. mauritiana* regardless of whether birds or Chital dispersed them. Instead, the presence of *T. bellerica* seeds influenced detection probability of *Z. mauritiana* seeds dispersed by both Chital and birds. In addition to substrate, habitat also influenced the detection of *Z. mauritiana* seeds dispersed by Chital (Table 4.1). Detection probabilities were fairly consistent across the months, and was highest *for Z. mauritiana* seeds dispersed by birds, followed by *T. bellerica* and *Z. mauritiana* seeds dispersed by Chital (Fig 4.3).

	Covariate	β (±SE)
TB - CHT	Intercept	2.09 (±0.98)
	Substrate	Covered: -0.30 (±0.92)
		Mixed: 1.52 (±0.75)
	Habitat	Open: -3.55 (±0.97)
		Savannah: 0.38 (±0.62)
ZM - CHT	Intercept	0.33 (±0.68)
	Other seed	Present: 1.58 (±0.49)
	Habitat	Open: -2.30 (±0.76)
		Savannah: 0.17 (±0.72)
ZM - BRD	Intercept	1.87 (±0.43)
	Other seed	Present: -0.94 (±0.78)

Table 4.1: Summary of model estimates for detection probability *'p'* of *T. bellerica* (TB) and *Z. mauritiana* (ZM) seeds dispersed by Chital (CHT), and birds (BRD). The intercept represents (i) 'Open' substrate and 'Closed canopy forest' habitat in the case of TB – CHT, (ii) other seed 'Absent' and 'Closed canopy forest' habitat in the case of ZM – CHT, and (iii) other seed 'Absent' in the case of ZM – BRD.

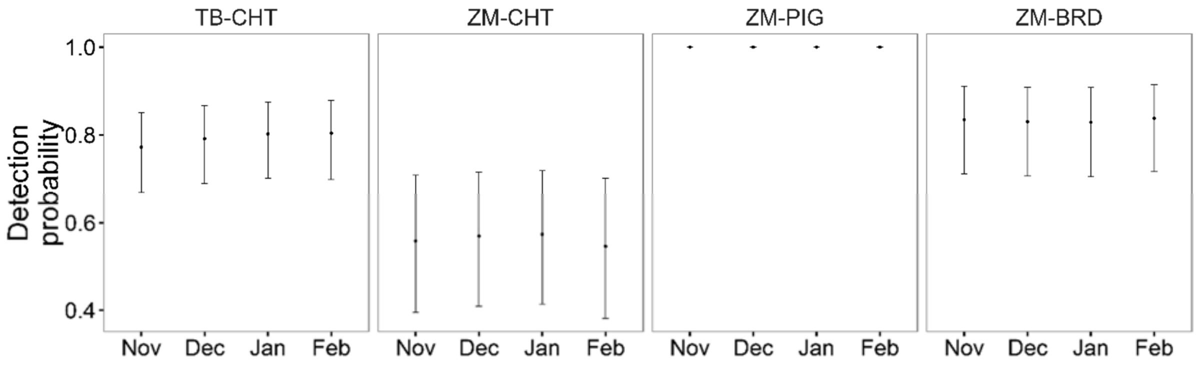

Figure 4.3: Detection probability of seed of *T. bellerica* (TB) and *Z. mauritiana* (ZM) dispersed by Chital (CHT), wild pig (PIG) and birds (BRD) during November 2015 (Nov), December 2015 (Dec), January 2016 (Jan) and February 2016 (Feb).

Next, we assessed the potential factors influencing spatial and temporal patterns of seed rain using a candidate set of models for each tree species – disperser combination. Table 4.2 summarizes results by listing the co-variates in our top raking models (according to AICc) influencing both spatial and temporal seed rain patterns of all the tree species – disperser combinations. There were vast differences in covariates influencing seed rain patterns across the three disperser groups. Models for seed rain generated by Chital found support for a combination of grass, structural cover and terrain ruggedness. Seed rain patterns generated by pigs and birds were a combination of factors reflecting fruit distribution: distance to nearest fruiting tree to the site, sum of fruits within the site or sum of fruit within all the neighbouring sites (Table 4.2). The proportion of sites to which seeds were dispersed varied among the different tree species- disperser combination (Fig 4.4). Colonization probability of seeds – 'γ' were, in general, much smaller than extinction probability of seeds – 'ε' (Fig 4.5). Seeds dispersed by Chital (both *T. bellerica* and *Z. mauritiana*) had a higher colonization probability compared to seeds dispersed by pigs or birds; this pattern was reversed for extinction probability – seeds dispersed by pigs and birds had much higher extinction probability compared to seed dispersed by Chital (Fig 4.5).

	Spatial variation (ψ)	β (±SE)		Temporal variation	β (±SE)
TB - CHT	Grass	0.56 (±0.13)	γ	Structural cover	-0.89 (±0.23)
	Structural cover	-0.54 (±0.21)		Ruggedness	-0.35 (±0.17)
ZM - CHT	Structural cover	-0.67 (±0.22)	γ	Grass	0.28 (±0.18)
				Structural cover	-0.64 (±0.26)
ZM - PIG	Distance to nearest *Z. mauritiana* in fruit	0.40 (±0.24)	ε	Distance to nearest *Z. mauritiana* in fruit	-1.73 (±0.69)
ZM - BRD	Sum of fruits from all tree species consumed by birds	0.49 (±0.16)	ε	Sum of fruits, from all tree species consumed by birds, in neighbouring sites	-0.42 (±0.35)

Table 4.2: Summary of model estimates for 'ψ', and 'γ' or 'ε' of *T. bellerica* (TB) and *Z. mauritiana* (ZM) dispersed by Chital (CHT), pigs (PIG) and birds (BRD). The columns 'Spatial variation' and "Temporal variation" describes the variables predicting (ψ) and (ε or γ) respectively, from the top model for that particular tree species – disperse combination. Temporal covariates modelled varied for each tree species - disperser combination and the actual parameter estimated (γ – colonization probability or ε – extinction probability) is indicated in the column immediately preceding 'Temporal Covariate'.

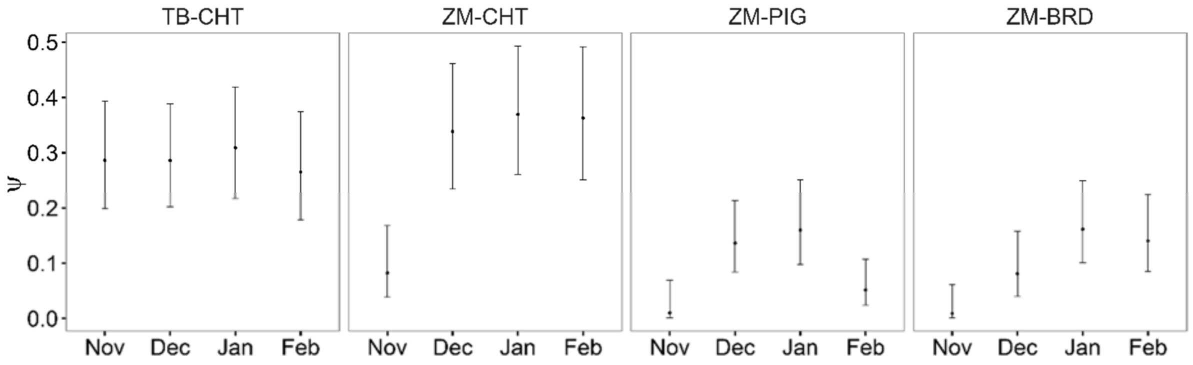

Figure 4.4: Estimates of 'ψ' – the proportion of sites to which seeds are dispersed - for seeds of T. bellerica (TB) and Z. mauritiana (ZM) dispersed by Chital (CHT), wild pig (PIG) and birds (BRD) during November 2015 (Nov), December 2015 (Dec), January 2016 (Jan) and February 2016 (Feb).

The spatial patterns of seed rain generated by birds were strongly influenced by fruit distribution (Table 4.2). The temporal changes in these patterns were also explained by fruit distribution, specifically, the sum of fruits in the neighbouring sites of all species consumed by frugivorous birds (Table 4.2). In sum, birds were likely to disperse seeds to sites that contained a larger quantity of fruits (not just from *Z. mauritiana*), and less likely to continue dispersing seeds to sites which had lower number of fruits in the neighbourhood. Both the spatial and temporal patterns of pig-generated seed rain were influenced by fruiting resources, similar to birds, however unlike birds pigs were more likely to disperse *Z. mauritiana* seeds to sites farther away from fruiting conspecifics than to those located close to fruiting adult conspecifics. Pigs were also less likely to continue dispersing *Z. mauritiana* seeds to sites close to fruiting *Z. mauritiana* across two replicate surveys. Spatio-temporal seed rain patterns generated by Chital were best explained by the distribution of grass, structural cover and terrain ruggedness of the sites, rather than the distribution of fruits. Based on the top raking models, Chital were likely to disperse *T. bellerica* seeds to sites that had more grass and less structural cover, and *Z. mauritiana* seeds to sites that had less structural cover (Table 4.2). Temporal changes in seed rain patterns generated by Chital were influenced by grass, cover and terrain ruggedness (Table 4.2). Chital were less likely to disperse *T. bellerica* to sites with greater structural cover and terrain ruggedness, if they had not dispersed to these sites in the preceding month. For *Ziziphus mauritiana,* sites with higher grass were more likely to receive seeds from Chital if no seeds were dispersed to them in the preceding month. In contrast, sites with lower structural cover were more likely to receive Chital dispersed seeds if no seeds were previously dispersed to this site (Table 4.2).

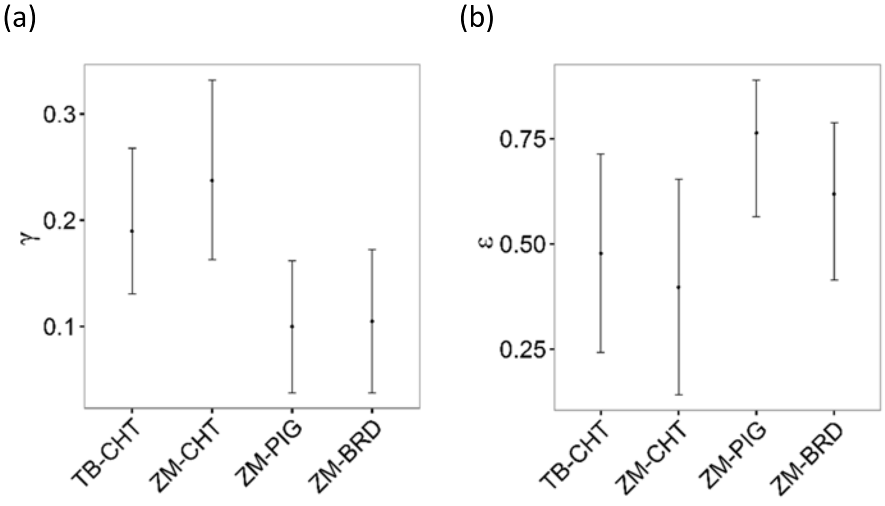

Figure 4.5: Estimates of ‘γ’ – colonization probability and ‘ε’- extinction probability for seeds of *T. bellerica* (TB) and *Z. mauritiana* (ZM) dispersed by Chital (CHT), wild pig (PIG) and birds (BRD).

Discussion

We set out to contrast spatio-temporal seed rain patterns generated by three functionally different dispersers—Chital, pigs, and birds—and to identify the associated drivers of these differences. Our results were broadly in agreement with our predictions regarding the potential factors likely to influence the spatio-temporal variation in observed seed rain (Table 4.2). Further, we found both similarities and dissimilarities in the spatio-temporal seed rain patterns generated by Chital, pigs and birds. While birds and pigs generated seed rain data best explained by the distribution of fruits, Chital generated seed rain explained by structural cover and grass availability (Table 4.2). Birds generated the most time varying seed rain pattern followed by pigs. Chital, on the other hand generated the least temporally variant seed rain pattern (Fig 4.4).

Spatial variation in seed rain patterns

Bird-generated seed rain of *Z. mauritiana* are in general agreement with patterns from other avian dispersers, especially obligate frugivores, whose seed deposition patterns are strongly correlated with the spatial distribution of fruiting trees (e.g. Morales and Carlo 2006, Morales et al. 2012). Accordingly, we found that birds dispersed *Z. mauritiana* seeds to sites that had a higher quantity of both conspecific and co-fruiting heterospecific fruits and rarely to sites that had no fruits. In comparison pigs dispersed *Z. mauritiana* seeds away from fruiting trees. Since there is little quantitative information on habitat use by pigs, no specific insights from previous studies predict that pigs are likely to deposit seeds farther away from fruiting trees (Ballari and Barrios-García 2014, Sridhara et al. 2016). However, the observed spatial patterns of *Z. mauritiana* seed rain generated by pigs is likely explained by this animal's omnivorous diet, known to include grass, tubers, leaves, eggs and even carrion. Since pigs would move to track these multiple resources, their movement may not be restricted to the vicinity of fruiting trees, suggesting why seed are deposited farther away from fruiting trees (Sridhara et al. 2016).

Seed rain patterns generated by Chital aligned well with our prediction that grass and structural cover would be key determinants of Chital habitat use and consequently seed rain. While areas with high grass are preferentially used, areas with high structural cover are avoided by Chital (Raman 1997, Ramesh et al. 2012, Vijayan et al. 2012). Comparing Chital-generated seed rain for two tree species with markedly different spatial distributions (*T. bellerica* and *Z. mauritiana*) helped establish that, as expected, other resources such as grass and structural cover, rather than fruit tree distributions, are better predictors of seed deposition by this herbivore. Notably, structural cover was the most prominent predictor of seed rain by Chital. We infer that the importance of low structural cover in our models known to aid detection of predators, is reflective of top-down effects that predators exert on habitat use by Chital (Schaller 1967, Bagchi et al. 2003a, Ahrestani et al. 2012), which in turn appears to influence seed dispersal patterns by Chital.

Temporal variation in seed rain patterns

In line with our expectations Chital produced the most temporally consistent seed rain patterns among the three dispersers. The two key resources for Chital, structural cover and grass were much less variable through time than fruiting densities (Sridhara, unpublished data) explaining the consistency in observed seed rain. Chital dispersed varying quantities of seeds as the season progressed (Fig 4.2) but to similar number of sites (Fig 4.4) corroborating that seed deposition was independent of variation in fruit availability even though fruit removal by Chital has been shown to be dependent of fruit availability (Prasad and Sukumar 2010). Pigs and birds, on the other hand, dispersed varying quantities of seeds as the season progressed (Fig 4.5) and to varying number of sites (Fig 4.2) likely reflective of their dependence on fruiting resource whose abundance varies as the season progresses.

The timing of seed arrival through dispersal is known to play a role in influencing seed predation, seedling survival and eventually the diversity of the seedlings community (Verdú and Traveset 2005, Norden et al. 2007, Myers and Harms 2009). However, the relatively long seed dormancy periods in many tropical dry forest tree species (Khurana and Singh 2001) could dilute any benefits accrued due to differences in timing of seed dispersal by different dispersers. We tried monitoring seeds for natural germination, but no germination occurred during the five months of the study period. Further examination on timing in seed dispersal especially in the context of seed dormancy, germination, and patterns of seedling establishment is required.

Functional similarities and differences among dispersers

Our results provide several insights on the similarities and differences in the seed rain patterns generated by the three disperser groups. Birds and pigs dispersed *Z. mauritiana* seeds to similar number of sites, but pigs dispersed significantly higher quantities of seeds. Seed of *Z. mauritiana* dispersed by birds may experience high levels of density- and distance-dependent pressures due to their proximity to adult trees (Kwit et al. 2004). The consequences of pigs dispersing large number of *Z. mauritiana* seeds to few locations in a clumped manner is likely to be a trade-off between density-dependent pressures and release from specialized predators (Beckman et al. 2012). On the other hand, Chital dispersed *Z. mauritiana* seeds to more number of sites than pigs, but both dispersed similar quantities of seeds. The uniform pattern of seed deposition by Chital (in savannah habitat, Fig 4.1) could release seeds from density-dependent predation effects but attract generalist predators (Beckman et al. 2012). Apart from varying degrees of spatial aggregation, differences in outcome of gut treatment (birds regurgitate seed with a layer of pulp, pigs defecate seeds in faecal matter often embedded in pulp, Chital regurgitate seed entirely devoid of pulp) will further influence seed predation pressure and germination success (Traveset and Verdu 2002, Traveset et al. 2007).

All three dispersers deposited *Z. mauritiana* seeds to different kind of sites. Birds and pigs transported seeds to sites in savannah and forest habitats, but to varying distances away from adult trees. In comparison, Chital dispersed seeds to sites almost entirely within savannah habitats and in a uniformly spaced manner (Fig 4.1). The combined results suggest that the Chital, pigs and birds generate complementary spatial seed rain patterns of *Z. mauritiana* with the Chital dispersing more seeds to more number of locations and farther away from fruiting trees. Temporal variation of seed rain for *Z. mauritiana* generated by pigs and birds were qualitatively similar and differed from those generated by Chital (Fig 4.5) suggesting that the birds and pigs were functionally similar to one another (more variant and influenced by fruiting trees) but different from Chital (less variant and independent of fruiting trees).

Modelling seed rain patterns in the occupancy framework

Based on the premise that we were likely to miss detecting seeds camouflaged by the forest floor, we explicitly modelled imperfect detection in our analyses. We found that detection probability of dispersed seeds differed for the two tree species and the disperser involved (Fig 4.3). Seed traits (size, colour and contrast with respect to the substrate) and the state of dispersed seed (e.g. embedded in scat, covered with pulp or not) mediated by differential treatment of seeds in the gut of different dispersers could influence seed detection. For example, *Ziziphus mauritiana* seeds dispersed by birds have a thin layer of pulp still attached to the seed rendering them bright yellow and more easily detectable compared to dull colour of seeds regurgitated by Chital. Importantly, our approach allowed us to model the observation process (i.e., the detection probability) in addition to the ecological process (i.e. the drivers of the spatio-temporal patterns of seed rain) (MacKenzie et al. 2006, Royle and Dorazio 2009). With minimal changes and certain careful considerations (e.g. how many temporal replicates and observers are needed), our approach can be easily adapted for most seed dispersal studies that routinely use multiple surveys in time to measure seed rain (Muller-Landau et al. 2008, Morales et al. 2013).

Conclusion

Spatio-temporal seed rain patterns by functionally different dispersers, especially medium-sized ruminants such as Chital and pigs have rarely been documented, let alone contrasted (however see Brodie et al. 2009a). Most studies typically examine fairly similar disperser species such as frugivorous birds (Morales et al. 2013, Rodríguez-Pérez et al. 2016), or primates (McConkey et al. 2014, Razafindratsima and Dunham 2015). We demonstrated that our analytical framework which incorporates occupancy models provides a suitable and robust approach to examine seed rain patterns across different dispersers while explicitly accounting for observation errors. By highlighting the differences in spatial and temporal patterns of seed rain generated by Chital, pigs and birds, our study underscores the importance of examining seed dispersal by medium-sized ruminant in particular and less-studied non-obligate frugivores in general (Sridhara et al. 2016). We show that dispersers could be functionally classified based on the differences in their spatio-temporal seeds rain patterns they generate. Further, by identifying the factors likely to influence observed seed rain patterns we are closer to unravelling mechanistic linkages of seed dispersal by forest ruminants. Our combined insights can be useful in predicting plant responses to environmental change (Mokany et al. 2014) and have implications for ongoing declines of large herbivores, which may eventually influence downstream processes including seed dispersal (Corlett 2011, McConkey et al. 2012, Ruxton and Schaefer 2012, Dirzo et al. 2014).

Acknowledgements

Uttarakhand Forest Department issued permits to undertake the study. Funding was provided by AusAID (scholarship), DST-India, MoEF - India and IdeaWild – USA, JCU and CSIRO. We thank NSI, NCBS, and IISc for institutional support. Mumtaz Chechi, Basheer Baniya, Shamshaad Baniya, Mustafa and Zareef Khan provided crucial assistance in the field; Ajith Kumar provided administrative support. Meghna Krishnadas supported all stages of this work, but her inputs on presentation helped improve the manuscript substantially.

Chapter 5: Can predation risk perceived by a seed disperser influence spatial seed rain patterns? A preliminary test using individual-based simulations of a tropical ruminant

This chapter is based on a manuscript in preparation:

Sridhara, S., Prasad S., Edwards, W. and D. A. Westcott. Can predator risk perceived by a seed disperser influence spatial seed rain patterns? A preliminary test using individual-based simulations of a tropical ruminant

Statement of contribution of others:

Sridhara designed the study with inputs from Westcott, Prasad and Edwards. Sridhara collected data, developed the model and performed the analysis. Steve Railsback provided some guidance with model development. Sridhara wrote the first draft, and revised the subsequent drafts with Westcott, Prasad and Will.

Can predator risk perceived by a seed disperser influence spatial seed rain patterns?

A preliminary test using individual-based simulations of a tropical ruminant

Abstract

Many plants rely on animals to transport their seeds to favourable locations. Animal behaviour is a key influence on the spatial patterns of seed rain generated by animals and is often mediated by distribution of fruits. However, when dispersers are not very frugivorous (e.g. non-obligate frugivores), behaviours contributing to seed deposition patterns (e.g. movement and habitat-use) are likely to be governed by non-fruiting resources and ecological processes not linked to fruit distribution. For example, many large mammalian herbivores such as ruminants (deer, antelope, chevrotains etc) disperse seeds. Yet the spatial distribution of fruits is not a key determinant of their habitat use and movement patterns perhaps because they are non-obligate frugivores. Because many ruminants are grazers and highly risk averse we predicted that the seed rain patterns they generate will reflect the underlying trade-offs between predator avoidance and forage (grass, leaves etc.) tracking behaviour. We tested this prediction on spatial seed rain patterns generated by a deer (Chital, *Axis axis*) for a deciduous tree, *Ziziphus mauritiana*, using a combination of empirical data and simulations. We expected that Chital (a grazer) would deposit more seeds in habitats (specifically savannahs) where perceived predation risk is lower but forage (grass) availability is higher. First, we collected seed rain data by intensively sampling 400 plots systematically laid in an area of 25 Ha. Next, we constructed stochastic, individual-based simulation models to incorporate different Chital behaviour (grazing and frugivory, with and without predation risk) and generate seed rain patterns. We then examined to what extent observed seed rain patterns were explained by our simulation models. We found that grazing behaviour in the presence of perceived predation risk had the highest spatial concordance with observed data, followed by grazing in the absence of perceived predation risk. Our study underscores the need to examine disperser behaviour in a context broader than their interaction with fruiting plants alone. Furthermore, our results, though preliminary, suggest current global declines in predator populations have broader implications for ecosystems.

Introduction

Spatial patterns of seed dispersal influence crucial early stages in plant regeneration such as germination and seedling recruitment (Wang and Smith 2002, Levine and Murrell 2003). Understanding the underlying mechanisms driving spatial patterns of seed dispersal is vital to predict the responses of individual plants, species and communities to environmental and ecological changes (Nathan and Muller-Landau 2000, Muller-Landau et al. 2008, Corlett and Westcott 2013). Elucidating these mechanisms however, can be challenging. This is especially true when animals act as vectors of seed dispersal because animal dispersers vary widely in their behaviour (Nathan and Muller-Landau 2000, Wang and Smith 2002). Understanding animal generated spatial seed rain patterns requires examining the behaviour of dispersers in relation to fruit tree distribution in the landscape, but also the complete repertoires of behavioural responses to a suite of ecological/environmental influences (Westcott et al. 2005, Morales et al. 2013).

The mechanisms driving seed rain patterns are fairly well understood for certain dispersers such as highly frugivorous avian birds or primates (Carlo and Morales 2008, Morales et al. 2012, McConkey et al. 2014, Razafindratsima and Dunham 2015, 2016a, Albrecht et al. 2015). Empirical and simulation based studies have shown that conspecific and co-fruiting heterospecific plants play a significant role in driving both the distances to which seeds are dispersed and their spatial aggregation (e.g. Rodríguez-Pérez et al. 2014, Razafindratsima and Dunham 2016a). However, strong associations between individual plant species and their dispersers is not widespread, especially when those dispersers are only opportunistically frugivorous (Bascompte et al. 2003, Kissling et al. 2009, Schleuning et al. 2011). Many seed dispersers are opportunistic frugivores. Nevertheless, these species provide crucial seed dispersal services for individual species and the entire plant community (Zhou et al. 2011, Donatti et al. 2011, Horn et al. 2011, Sridhara et al. 2016, Carlo and Morales 2016). In the absence of strong associations between non-obligate frugivores and fruit resources, the behavioural responses that contribute to seed rain patterns (e.g. movement patterns, habitat use) are likely to be governed primarily, if not entirely, by resources and processes that are not the same as those governing obligate frugivores.

Numerous large mammalian herbivores, especially ruminants (deer, antelope, wild cattle etc.) disperse seeds of several plants even though fruits often form a small proportion of their diet (Dubost 1984, Kitamura et al. 2002, Sridhara et al. 2016). For the vast majority of forest ruminant species, the primary factors influencing movement and habitat-use is a combination of resource availability and predation risk (e.g. Godvik et al. 2009, van Beest et al. 2010, Thaker et al. 2010, Creel et al. 2014, Hopcraft et al. 2014). The relative levels of predation risk in different parts of the landscape is well known to reflect the level of fear of predation a prey species perceives, i.e. the 'landscape of fear', and strongly governs space use by prey species such as ruminants (Laundre et al. 2010, Gallagher et al. 2017). With seed retention times varying from 7 to 90 hours, most ruminants can be expected to spend a considerable amount of time between the time of fruit consumption and its deposition, trading-off predation risk and access to required resources (Sridhara et al. 2016). Therefore, for dispersers such as ruminants, there is a need to not only consider fruit availability but also forage availability and prey-predator interactions, to fully understand the mechanisms driving spatial seed dispersal patterns.

In this study we provide a preliminary test of the expectation that predators may influence habitat use patterns of a ruminant which in turn influences the seed rain pattern they generate. We tested this prediction on Chital (*Axis axis*, 50 kg) a widely distributed deer native to the Indian subcontinent. Although classified as a grazer, Chital consume fruits and disperse seeds of several plant species and are thought to be very risk averse, making them especially suitable to test our expectations (Schaller 1967, Clauss et al. 2002, Ghuman et al. 2010, Sridhara et al. 2016). Conducting empirical studies to examine the influence of predation can be logistically very challenging. We therefore employed simulations to test our expectations, an approach that has been frequently used to examine the influence of disperser behaviour on spatial patterns of seed dispersal, and validated them against observed patterns of seed rain (Morales and Carlo 2006, Carlo and Morales 2008, Morales et al. 2013, Rodríguez-Pérez et al. 2016).

Chital are predated by tigers (*Panthera tigris*) and leopards (*Panthera pardus*) that stalk before pursuing the animals for short distances (Karanth 2001). Therefore, Chital are known to avoid habitats such as forests where predator detection is poor (due to high structural cover), but nevertheless use areas close to habitats with high structural cover to flee from predators upon detection (Schaller 1967, Vijayan et al. 2012). Their key foraging resource – grass – is less abundant in forest habitats and more abundant in savannah or grassland habitats (Karanth and Sunquist 1992, Bagchi et al. 2003a, 2003b). In contrast, fruiting resources are more abundant in forest habitats (Khan 1994b, Raman et al. 1996, Raman 1997). Chital disperse large seeds through regurgitation, and mostly when bedding (Prasad et al. 2006). During bedding they are especially vulnerable to predation and therefore, we expected Chital to disperse seeds predominantly to savannah and grassland habitats, where predator visibility is high. Additionally we hypothesized that seeds will not be dispersed very far away from forest patches, because Chital are unlikely to bed in these areas that do not have structural cover in the vicinity. We tested these predictions by collecting seed rain data of *Ziziphus mauritiana*, a tree dispersed by many species including Chital and comparing them against seed rain generated by an individual-based simulation model.

Methods

Study site and system

The study was conducted in Rajaji National Park, located in the state of Uttarakhand, India. Classified as northern Indian moist deciduous forest and northern tropical dry deciduous forest (Champion and Seth 1968), Rajaji has three broad habitats; open river-beds, savannah – with continuous grass cover but discontinuous tree cover and, closed canopy forest. Closed canopy forest are either mixed species forests or *Shorea robusta* dominated stands. Chital and other large herbivore such as muntjac (*Muntiacus muntjac*) sambar (*Cervus unicolor*), and nilgai (*Boselaphus tragocamelus*) occur at high densities (Harihar et al. 2011). The principle predators of Chital in the landscape are tigers (*Panthera tigris*) and leopards (*Panthera pardus*).

Field data collection

We selected a 25 Ha area of forest to intensively sample for seed rain of *Ziziphus mauritiana*, a species dispersed by Chital as well as several other mammal and bird species (Chapter 4). We divided the 25 Ha systematically into 400 grids and placed a seed plot (2m radius) at the centre of each grid, resulting in a matrix of 20x20 seed plots 25m apart from each other. We sampled seed rain throughout the season of fruiting, from October to February. During the sampling we also recorded the availability of grass from four 1m^2 plots around the seed plot and estimated the availability of structural cover in a circle of diameter 25m centred at the sampling plot. We also mapped all the adult *Z. mauritiana* trees both with and without fruit within the 25 Ha area, and quantified the fruit crop of each tree. Finally, to parameterize the model with real data we collected movement data from seven Chital fitted with GPS collars (Chapter 2),

Model description

Model development: To test our expectations we developed an agent based simulation model and created four different simulation scenarios representing different patterns of both frugivory by model Chital and perceived predation risk in the model landscape. The stochastic, individual-based and spatially-explicit simulation model generated seed rain patterns based on the activity of model Chital in response to resource and habitat distribution. In the first scenario, model Chital consumed fruits 80% of the time, grass for the remaining 20% and perceived no predation risk in the landscape (‘frugivory with no predation risk’). In the second scenario, the only difference was that model Chital perceived predation risk in the landscape (‘frugivory with predation risk’). Models for the above two scenarios were constructed to compare our results with well documented patterns from avian disperser systems (Morales et al. 2012, Rodríguez-Pérez et al. 2014). In the third simulation scenario, Chital consumed grass 80% of the time, fruits for the remaining 20% and perceived no predation risk (“grazing with no predation risk”). In the fourth and final scenario, model Chital were again grazers but perceived predation risk in the landscape (“grazing with predation risk”). This final scenario is most reflective of our current knowledge of Chital’s diet and behaviour (Sridhara et al. 2016). Henceforth the use of the term scenario refers to one of four models outlined above. The model was developed in free software NetLOGO version 5.2.1.

Model initialization: All models regardless of the scenario being simulated, were initialized as below, to make simulation comparable across scenarios. We first generated a virtual landscape with the same distribution of the three habitat types (open, savannah, and closed canopy forest) as was observed on our 25 Ha study area. The values of grass and structural cover assigned to each habitat cell were drawn from a distribution fitted to observations made from the corresponding habitat types (Fig 5.1 A to D). The model was spatially scaled to match the study area; each unit in the virtual landscape corresponded to 2.5m on the ground. Next, we placed model *Z. mauritiana* trees in the virtual landscape at the same relative locations at which they were found in the study area. The fruit crop on the trees was assigned from an exponential distribution fitted to observed values (Fig 5.1 E). To compute the fruit fall at a tree, a number, used as the proportion of the fruit crop currently on the tree, was drawn from a normal distribution N ($\mu = 0.05$, $\sigma^2 = 0.01$). The computed fruit-fall was the total fruit available at the tree for consumption and subtracted from the fruit crop of the tree. We next placed Chital randomly in the landscape at densities and group sizes observed at Rajaji and other similar forests (Karanth and Sunquist 1992, Bagchi et al. 2004, Harihar et al. 2011). To place the Chital in groups, we identified a random centre for the entire group around which individuals were positioned. The distance between group members was a random number between 1m and the maximum observed distance between individuals of a Chital herd (Ghuman et al. 2010).

Model simulation: Once initialized, simulation proceeded in the following steps regardless of scenario. The model was executed in discrete time steps corresponding to 10 real world minutes. The time step was chosen to match movement patterns recorded from Chital fitted with GPS from our study site, which were programmed to acquire a location every 10 minutes. At each time step, model Chital would either forage or rest. If Chital were in rest 'mode' they would not move during the time step. But, if they were in forage 'mode' they would consume fruit or grass (depending on the scenarios) and move to a new location. The duration of both the rest and forage modes of behaviour were drawn from normal distributions fitted to observed movement data (Fig 5.1 G and 5.1 H). At the end of the time step, if Chital had remained in a behaviour mode for longer than the randomly assigned duration, it would switch from that behaviour mode (foraging or resting) to the other (resting or foraging).

Since each time step of the simulation was treated as an equivalent of 10 minutes, one simulated day consisted of 144 time steps (24 hours * 6 time step of 10 minute each). A total of 30 model days were simulated before seed rain data were analysed. Fruit-fall of each tree was updated at the beginning of each model day. All individuals were set to forage ‘mode’ at the start of the simulation. Details of how they foraged, moved and dispersed seeds are described below

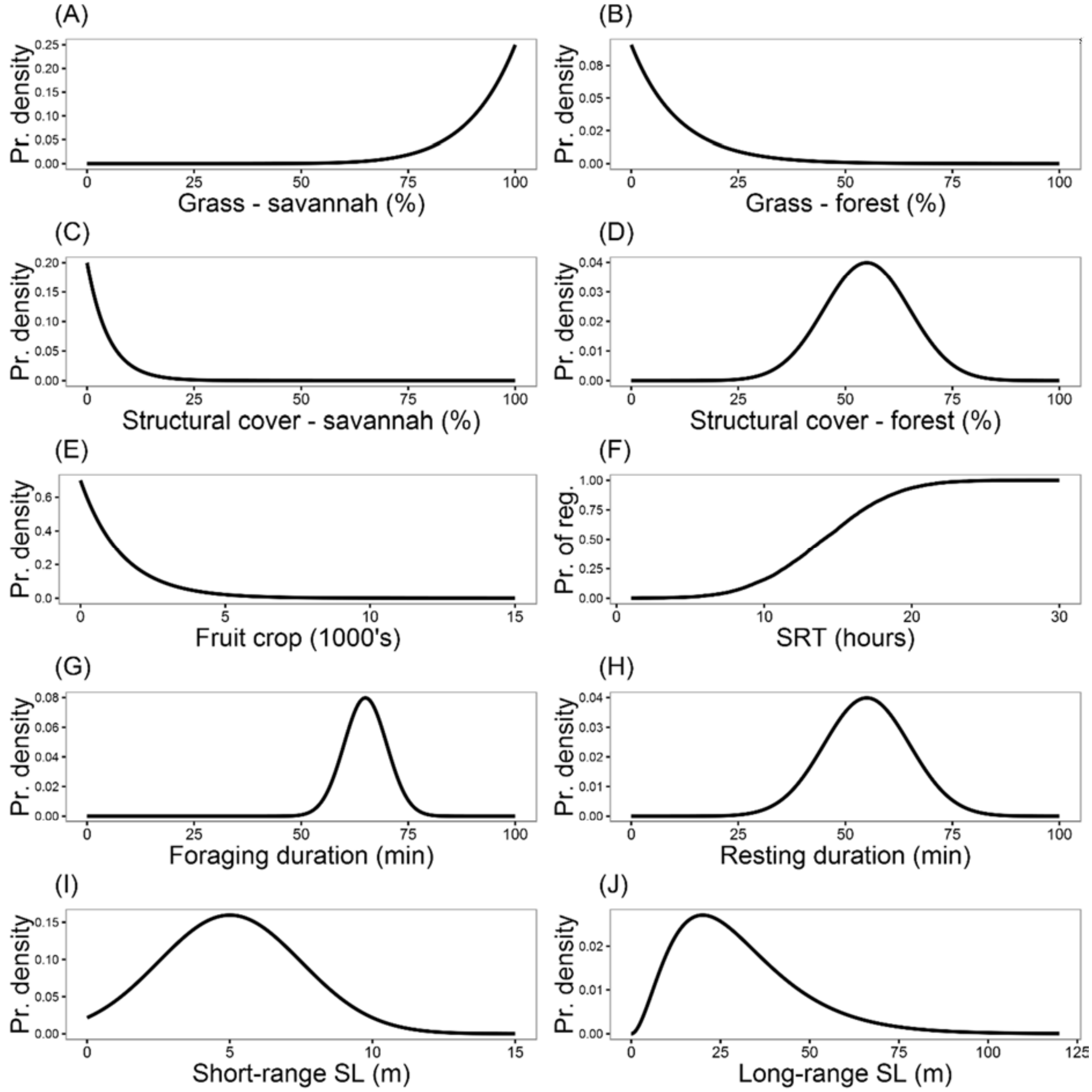

Figure 5.1: Distributions of various parameters used in the simulations. Pr. density is the probability density of the parameter. Percentage grass in habitat cells within savannah (A) and forest (B). Percentage structural cover in habitat cells within savannah (C) and forests (D). Fruit crop of tree (E). F – Probability of a seed being regurgitated - Pr. of reg., was calculated from seed retention time; i.e. SRT. Foraging duration (G) and resting duration (H) were drawn from slightly different normal distributions. Step lengths were categorized into two types: (I) short-range step lengths (Short-range SL) and (J) long-range step-lengths (Long-range SL) from Chital locations acquired every 10 minutes through GPS collars.

Foraging module: In grazing model scenarios, the grass intake quantity was subtracted from grass availability of the corresponding cell the Chital was on. Intake values were based on previous studies on Chital (Narendra Prasad and Sharatchandra 1984) and a similarly sized grazer - *Antelope cervicapra* (Baskaran et al. 2016). In frugivory model scenarios, the number of fruits consumed were removed from the fruit-fall of the nearest tree. Removal rates were based on previous information from camera traps (Prasad et al. 2009) and from count of seeds found in regurgitated piles, recorded when collecting seed rain data. When fruits were consumed, the time of consumption was recorded for every model Chital.

Movement module: Upon consumption of fruits or grass, each group of Chital would move to a new location. In the 'frugivory with no perceived risk' scenario, Chital would remain at the same fruit tree if fruits were available for consumption or move to the closest fruiting tree when no fruits were available at the current tree, regardless of what type of habitat the tree was in. On the other hand, in 'frugivory with predation risk' scenario, Chital moved to trees farther away if the current habitat cell had high structural cover, but to closer trees when the current habitat cells had low structural cover. Chital stayed for longer at a tree when habitat cell had low cover and for shorter duration when they had high cover regardless of the fruit-fall at the tree. A current habitat cell was considered to have low or high structural cover if its value was lesser than or greater than the mean structural cover over the entire virtual landscape respectively.

In 'grazing with no predation risk' scenario, the first step in moving involved computing the distance by which it should move. This distance was computed as a linear and negative relationship of the grass available in the current habitat cell the Chital was located on; i.e. it would move larger distances for low values of grass availability and smaller distances for high values. Once the movement distance was determined, in the second and final step of movement module, Chital would move to the cell which had the highest grass-availability among all cells at that computed distance, regardless of habitat-type of the cell. Maximum distance movable was determined from a distribution of short-range step lengths (Fig 5.1 I).

In 'grazing with predation risk' scenario, displacement distance of Chital was determined linearly as before if, structural cover was low in the current habitat cell. But if structural cover at the current location was high, displacement distance was drawn from a distribution of step-lengths fitted to observed data of long-range movement patterns of Chital (Fig 5.1 J).

This final distance was larger if the Chital was farther away from the edge of savannah (i.e. greater than Chital flight distance – estimated in other studies) and forest habitat and shorter if the current habitat cell was closer to open or savannah habitat (less than Chital flight distance). After determining the displacement distance, in addition to finding the habitat cell with the highest grass-availability, habitat cell with the least structural cover was selected in this scenario.

Regardless of the scenario, the final location to which animals would move, was actually the group centre around which all the individuals of a group would be located. The distance between group members was again chosen randomly between zero and the maximum observed distance between individuals of a Chital herd.

Regurgitation module: At the end of each time step, any fruits consumed by Chital would be regurgitated at its current location based on the probability distribution fitted to observed seed retention times – Fig 5.1 F (Prasad et al. 2006). Because Chital and many other medium-sized ruminants are known to regurgitate up to 75% of the seeds while ruminating in rest posture (Prasad et al. 2006, Sridhara et al. 2016), we incorporated this bias in the model Chital.

Model validation

We validated the model outputs against observed seed rain using the approach outlined in (Rodríguez-Pérez et al. 2016), by undertaking a virtual survey in the model landscape. Specifically, the number of seeds dispersed at relatively the same locations at which actual seed rain data was collected from the 25 Ha study area, was recorded. First, we calculated the amount of variation in the observed seed rain data explained by simulations, as the generalized coefficient of determination (adjusted R^2) assuming Gaussian errors. Next, we estimated the spatial concordance in the distribution of observed and simulated seed rain using partial Mantel-r test available in 'vegan' library of program R. A Mantel-r test was performed at two levels; first to compare whether seeds were found or not in a plot (seed presence), and second, to compare the number of seeds found in each plot (seed number).

Results

Field data

Seed rain data collected from 400 plots showed a strong bias toward savannah patches (Fig 5.2). Visualization of seed rain data shows the spatial spread of dispersed *Z. mauritiana* seeds among the different habitats within the study area (Fig 5.3). Results from the previous logistic regression analysis (Chapter 4) show that structural cover negatively influenced the probability of whether a seed was found (β = -0.67 ±0.26).

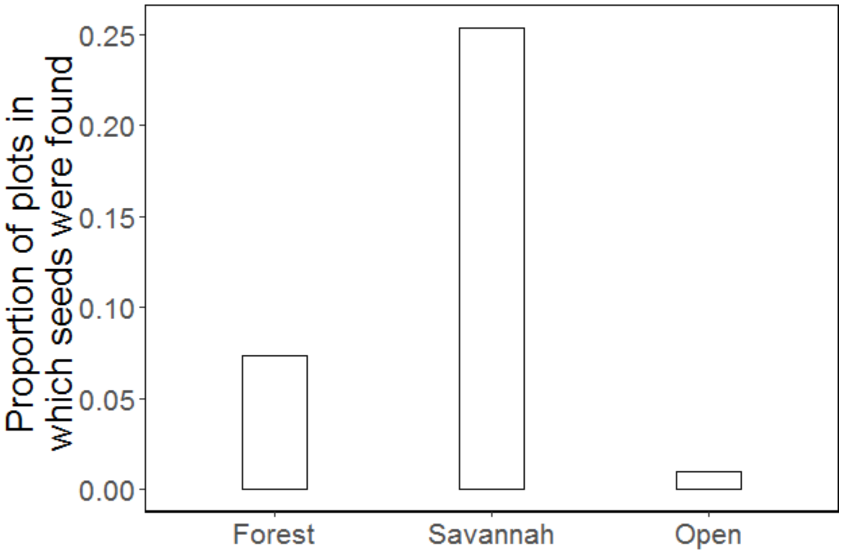

Figure 5.2: Observed seed rain indicates that many more plots located within savannah habitat received *Z. mauritiana* seeds dispersed by Chital (nearly four and 20 times more compared to seed plots in forest and open habitat respectively).

Figure 5.3: Observed seed rain patterns in the three habitat types found within the 25 Ha study area. White boxes indicate the 400 grids at the centre of which plots were sampled for seeds.

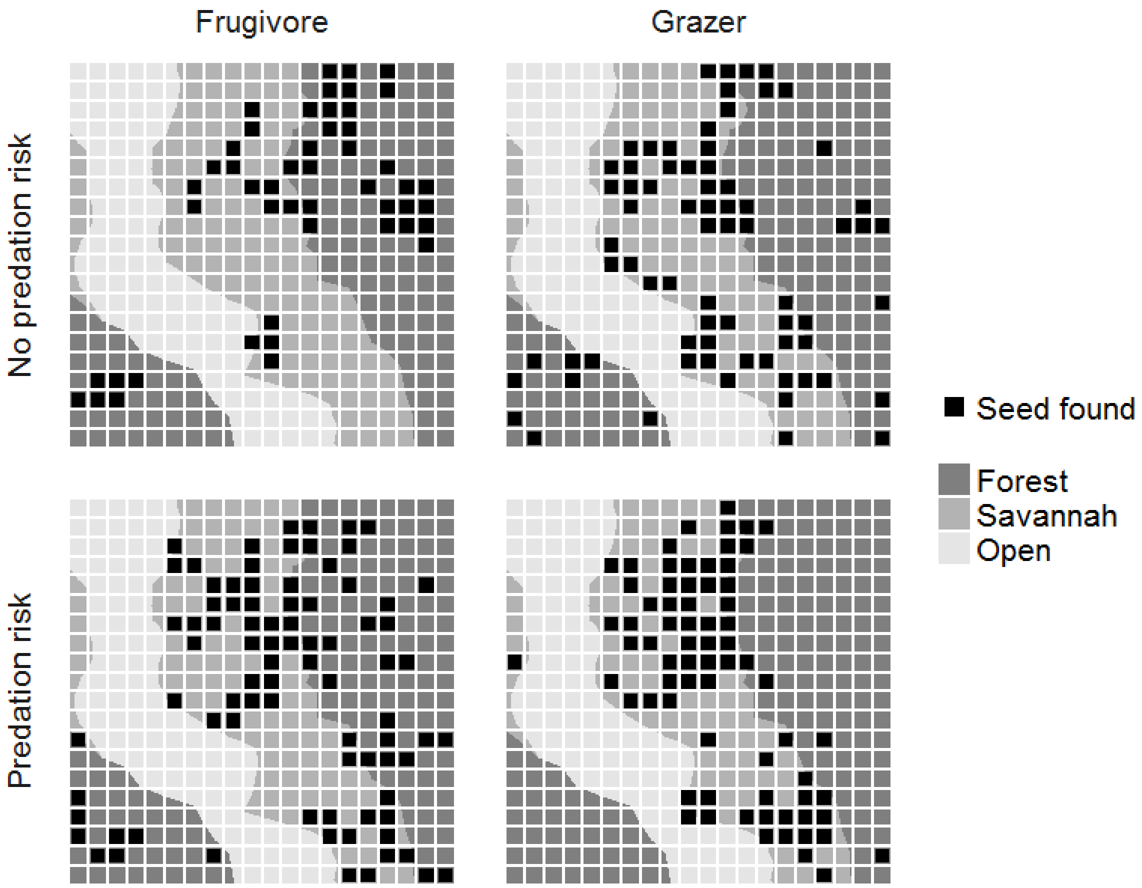

Figure 5.4: Seed rain patterns from simulations, spread across the three habitat types within the study area (forest, savannah and open). White boxes indicate the 400 grids at the centre of which plots were sampled for seeds. The four panels represent the two diet and predation risk scenarios.

Simulation Scenario	R^2	Seed presence	Seed number
Frugivory with no predation risk	- 0.07	<0.01 (0.66)	-0.02 (0.43)
Frugivory with predation risk	0.19	0.19 (0.02)	0.21 (0.16)
Grazing with no predation risk	0.30	0.33 (0.08)	0.28 (0.03)
Grazing with predation risk	0.38	0.41 (<0.01)	0.37 (<0.01)

Table 5.1: Results showing the spatial concordance of simulated seed rain against observed seed rain for different simulated scenarios of diet and behaviour. R^2 corresponds to the generalized coefficient of determination between observed and simulated seed rain data. The columns ‘Seed presence’ and ‘Seed number’ indicate the Mantel-r test value of observed vs simulated seed rain data. Values closer to 1 suggest greater spatial concordance. ‘Seed presence’ quantifies spatial concordance based on whether or not a seed was found in a plot (both observed and simulated values). ‘Seed number’ test quantifies spatial concordance based on the number of seeds found in a plot (both observed and simulated values). The probability of the test results are indicated within brackets.

Simulations

Seed rain patterns from simulations varied for the different diet and behaviour scenarios (Fig 5.4). Grazing with predation risk scenario explained the most variation (38 %) in observed seed rain data as seen by the adjusted R^2 values (Table 5.1). Grazing without predation risk scenario was the next best scenario, explaining 30% of the variation in observed seed rain. Both the frugivory scenarios (with or without perceived predation risk) were either unable to explain any variation or explained substantially less of the observed data. Spatial concordance between simulated and observed seed rain data as indicated by Mantel-r test was again highest for grazing with predation risk scenario. In comparison, spatial concordance for frugivory in the presence of predation risk, though statistically significant, was nearly 50% lower (Table 5.1). Grazing without predation risk was marginally significant and was the second most spatially concordant with observed seed rain (Table 5.1). Finally, Mantel-r test for seed number indicated that only simulations with grazing behaviour were statistically significant, both with and without predation risk. The scenario with the greatest spatial concordance with observed seed number within the plots of seeds was grazing with predation risk.

Discussion

Our objective was to identify the likely mechanisms driving observed seed rain patterns generated by a non-obligate frugivore Chital. Specifically, we hypothesized that Chital would use habitats in relation to resource availability and perceived predation risk, and this habitat use pattern would eventually influence their seed dispersal patterns. We used simulation models to generate seed rain data and tested it against observed seed rain patterns. Our results showed that even with simple simulation models, observed seed rain patterns of Chital are best explained by grazing behaviour in the presence of predation risk and not by frugivory that is spatially dependent on adult *Z. mauritiana* trees.

Observed seed rain pattern of *Z. mauritiana* by Chital showed a strong bias towards savannah habitats (Fig 5.2, 5.3) and is very reflective of previous findings that grass availability is generally higher in grasslands and savannahs and consequently associated with large groups of Chital spending more time in these habitats (Raman 1997, Ramesh et al. 2012). Through model validation, we found that amongst the four simulated scenarios (frugivory or grazing – with or without predation risk), grazing under predation risk explained the most variation (38%) in, and showed the greatest spatial concordance with observed seed rain patterns of Chital (0.41, Table 5.1, Fig 5.4).

Values of spatial concordance from our results are not as high as those seen from similar simulation models based on avian dispersers (Rodríguez-Pérez et al. 2016). This is, perhaps, due to the fact that a range of alternative environmental effects determining overall behavioural patterns were not included. For example, our simulations did not incorporate complex habitat use patterns driven by processes such as; thermoregulation (use of cover when temperature is high), group size dynamics (large groups may use high risk areas if resource availability is high), and topographical features (Chital avoid rugged terrain) (Bhat and Rawat 1995, Raman 1997, Bagchi et al. 2003b, Gallagher et al. 2017). It is therefore unlikely the models captured full range of behaviours. Nevertheless, even with our simple simulations of grazing and predator avoidance behaviour, up to 38% of the variation in observed data was explained. This suggests that the effect of predation pressure on the spatial distribution of Chital activity, and, in turn, on the patterns of seed rain they generate must be strong enough to be identifiable using simple simulation models. Incorporating additional behavioural data is likely to result in even more realistic model prediction and lend further support for the role for prey-predator interactions in seed dispersal by Chital.

Our results show how Chital generated seed rain differs from that of obligate avian frugivores and primates. Avian frugivores and primates such as lemurs are known to bias seed rain towards adult conspecific plants and co-fruiting heterospecific plants due to their strong dependence on fruiting resources (Carlo et al. 2013, Razafindratsima and Dunham 2016a). In contrast, we found that habitat and their associated non-fruiting resources (specifically, grass and structural cover) influence seed rain patterns. However, these seed patterns, are mediated by biotic interactions (prey-predator) rather than habitat per-se. Habitats, or specifically the variation in cover is known to influence seed deposition by even opportunistic avian frugivores (Morales et al. 2013, Carlo and Morales 2016). Visitation and fruit removal rates by Chital are influenced by neighbourhood densities of adult conspecific plants independent of the habitat type (Prasad and Sukumar 2010). Yet our results show that fruiting trees have little influence on observed rain patterns, further corroborating that behavioural responses of Chital to predation risk was likely the primary driver of seed rain patterns biased towards open areas.

The pattern of seed rain generated by Chital is qualitatively similar to patterns generated by other large herbivores – tapirs (*Tapirus terrestris*) and specifically ruminants black buck (*Antelope cervicapra*) – in that seeds are dispersed to open habitats with few or no adult conspecifics (Jadeja et al. 2013, Bueno et al. 2013). Blackbuck males deposited *Prosopis juliflora* seeds away from adults plants to open grasslands, but this was largely a result of the males being attracted to lek sites during the mating season, rather than being a response to predation risk, as was the case in our study (Jadeja et al. 2013). Muntjacs were also found to disperse seed to micro-habitats that had lesser tree canopy above, however, no estimates of conspecific density was made in the vicinity of the deposition sites (Brodie et al. 2009a). Although ruminants in particular and large herbivores in general may frequently deposit seed away from adults, the underlying behavioural mechanism may differ between species and in time, e.g. in and outside breeding season. Furthermore, many avian dispersers, even when closely related, are known to bias seed rain towards open areas (Herrera et al. 2010, 2011, Morales et al. 2013). Whether these are driven by predation risk remains to be seen. Opportunistic frugivores (also called generalist frugivores) by biasing seed rain towards open areas have been shown to play a disproportionate role in the regeneration (Carlo and Morales 2016). Whether Chital, by biasing seed rain to open are, are also crucial seed dispersers needs to be examined.

Future directions and conclusion

The simulation model in our study was relatively simple. Nevertheless, it enabled a preliminary test of the effects of predation risk on seed deposition by Chital. The simulated results might have shown greater concordance with the field observations had the models incorporated other behaviours influencing habitat use by Chital, e.g. group dynamics through fusion and fission known to influence habitat use and predator avoidance behaviour (Fortin et al. 2009, Rubenstein 2014). Additionally, characteristics of movement such as directional bias and memory effect could be incorporated (Fryxell et al. 2008, Nathan et al. 2008). Finally, the distribution of trees and the spatial configuration of habitats could be varied in models to test the effect of interaction between these resources on seed dispersal.

We have provided evidence, through simulation models and empirical data, that spatial patterns of seed rain could indeed be generated from an interplay of resource distribution and perceived predation risk in different habitats. Although such patterns are more likely to be most easily detected in species such as Chital and other ruminants, our insights may be relevant to many other dispersers including obligate frugivores in certain contexts. We recommend that dispersal studies consider disperser behaviour in a wider context to better inform our knowledge of the mechanistic underpinning of seed dispersalecology. Finally, the principle predator of the Chital, tiger has experienced dramatic range contractions (Johnsingh et al. 2010). Because such population declines of top predators are being documented at a global scale (Ceballos 2005, Dirzo et al. 2014), our results not only have implication for plants dispersed by Chital and other ruminants, but broadly for the functioning of ecosystems.

Acknowledgements

We thank the Uttarakhand Forest Department for providing permits to undertake this study in Rajaji National Park. Funding to attend a modelling workshop was generously provided by Dave Westcott. Steve Railsback provided advice on building the individual-based model and provided comments during early stages. Support from Mumtaz, Basheer, Zareef, Mustafa and Netra Prasad was vital in collecting field data. Meghna provided support at all stages of this work

Synthesis

Background

Seed dispersal is a complex ecological process and a crucial influence for plant regeneration, eventually contributing to ecosystem functioning (Wang and Smith 2002, Levine and Murrell 2003, Jordano et al. 2011, Ruxton and Schaefer 2012). With environmental change underway globally, it is predicted that the process of seed dispersal is particularly vulnerable and could disrupt many ecological interactions (McConkey et al. 2012, Corlett and Westcott 2013). This is especially true in the tropics and sub-tropics, where many of the animal dispersers that provide crucial dispersal services to a majority of the plants (Jordano 2000) are severely threatened (Galetti and Dirzo 2013, Dirzo et al. 2014). Understanding the mechanisms underlying seed dispersal is crucial to predict the consequences of global change and inform mitigation measures (Mokany et al. 2014, 2015)

Our knowledge on the seed dispersal services provided by many different disperser groups remains rudimentary. For example, large herbivores such as deer, tapirs and cattle disperse seed of many plant species, although fruits often forms small proportion of their diet. Yet quantitative information on the exact nature of seed dispersal is relatively much poorly known than for species such as avian frugivores, primates, or bats (Sridhara et al. 2016). Nevertheless, in certain ecosystems, ruminants such as deer and antelope consume the fruits of between 20% to 50% of the tree species in the habitat (Dubost 1984, Prasad 2011). However, many large herbivores are experiencing population declines or have been completely extirpated in parts of their range (Karanth et al. 2010, Dirzo et al. 2014, Sridhara et al. 2016). Decline in disperser populations can have ecological (McConkey and Drake 2006) and evolutionary (Galetti et al. 2013) consequences for plant regeneration and have been documented for plant species dispersed by deer (e.g. Brodie et al. 2009b).

This is the context in which I set out to gain a better understanding of the functional role of ruminants in seed dispersal. I based my study on the seed dispersal by Chital (*Axis axis*), a deer native to the Indian sub-continent. Broadly my goal was to understand the seed dispersal services provided by Chital. Specifically, I started with a literature review on large herbivores of Asia and examined several closely related aspects of the spatio-temporal patterns of seed dispersal by Chital. In this final chapter I summarize the central findings from each of the chapters and suggest future research avenues.

Frugivory and seed dispersal by large herbivores of Asia: gaps and opportunities

Our review in Chapter 1 revealed that many species of large herbivores from Asia disperse seeds of multiple species of plants. These dispersal services are provided in varied ecosystems: rainforests, seasonally dry forests, savannahs and even arid landscapes such as deserts. While the role of large species such as elephants and rhinoceros has been well documented (Dinerstein 1991, van Strien et al. 2008, Campos-Arceiz and Blake 2011), our review highlighted the role of small and medium-sized species, that have largely been neglected or considered seed predators in the past (Bodmer 1991, Bodmer and Ward 2006). Significantly, the review clearly shows major gaps in our knowledge of frugivory and seed dispersal by large herbivores. While for some species even basic natural history like the distribution, plant species consumed or dispersed is missing, for many other species quantitative information on fruit consumption rates, movement patterns or their relative role in dispersal community is unknown. Because many of the species face local extinction, and population declines, insights on their seed dispersal services are of timely importance (Corlett 2002, Dirzo et al. 2014). At the same time, since some species are widely distributed, and new methods allow quantification of their dispersal services (Prasad et al. 2009, also see Chapter 3), there is a great opportunity to include insights from large herbivores in theoretically and empirically advancing our knowledge on frugivory and seed dispersal (Sridhara et al. 2016).

Chital movement patterns decouple seed rain patterns from adult tree distribution

In Chapter 2, I found that movement patterns of Chital are strongly correlated with terrain ruggedness, habitat evenness and structural cover but not fruit availability or the presence of adult conspecifics and synchronously fruiting hetero-specifics. The two modes of movement of Chital, short-range and long-range (Morales et al. 2004, Beyer et al. 2013), were correlated with habitat evenness and structural cover respectively, in agreement with results from Chital (Bhat and Rawat 1995, Raman 1997, Bagchi et al. 2003a, Vijayan et al. 2012) and other ruminants (Mendoza and Palmqvist 2008, Godvik et al. 2009, Mabille et al. 2012). Next, we found that seeds were deposited to places where activity was high (e,g, resting and foraging sites). Since 80% of the seed deposition of the examined tree species occurs during rumination (Prasad et al. 2006), a behaviour encapsulated in short-range movement mode, we conclude that seeds are predominantly dispersed to sites that have an even mix of the three habitat types found in the landscape, and unlikely to have too many adult conspecifics in the vicinity. In sum, Chital likely decouple seed rain patterns from adult plants, which can enhance plant regeneration due to escape from predators and increased colonizing potential (Bell et al. 2006, Hirsch et al. 2012a, Salazar et al. 2013).

Since short-range movement patterns of Chital were not predicted by any single resource used by Chital (structural cover or grass) but by an even mix of habitats, I postulate that the foraging behaviour in synergy with predator avoidance behaviour is a strong influence of seed rain patterns (Laundre et al. 2010, Laundré 2010, Kuijper et al. 2013). Further research should examine the eventual consequences of decoupling seeds for germination and recruitment. Because Chital are sympatric with other ruminants which also disperse many of the same species of plants, but differ in their habitat use patterns (Bagchi et al. 2003a, 2003b), studying other species of ruminants can help understand the combined contribution of ruminants to seed dispersal.

A framework to analyse spatio-temporal seed rain patterns generated by a terrestrial disperser: novel application of occupancy models

In Chapter 3, I demonstrate that occupancy models can be used to identify the factors potentially influencing spatio-temporal seed rain patterns generated by a terrestrial disperser. This methodological conceptualization was necessary since Chital disperse all seeds on the forest floor and locating them can be an imperfect process. Our modelling framework explicitly accounts for the fact that seeds even when present in sampling unit may not be detected, an aspect that is ignored in most seed dispersal studies. As a result, our modelling approach allows for more robust inferences by separating factors that influence our ability to detect seeds from factors that drive the spatial patterns of dispersal

(MacKenzie et al. 2006). Specifically, in our study we found that the detection of seeds dispersed by Chital reduced when vegetation in the sampling unit was taller. While the probability of a seed being dispersed to a sampling unit was correlated with Chital dung piles and the distance from closed canopy forest, temporal change in these patterns were explained by. The new framework can be employed to analyse data collected routinely in many seed dispersal studies (Morales et al. 2013, Rother et al. 2016) with minimal changes to sampling design. Further, there is tremendous scope to extend our approach to multi-year and multi-scale studies, community wide seed rain data and even when seeds are falsely identified to wrong species.

Chital generated seed rain patterns and their potential drivers differ from patterns generated by pigs and birds, both in time and space

Seed dispersal by different disperser groups are often variable and their impact on plant regeneration can be similar to one another or non-redundant (Jordano et al. 2007, McConkey and Brockelman 2011, Bueno et al. 2013, Polak et al. 2014). Whether the disperser groups are redundant or not has serious implications for plant regeneration, especially in the context of frugivore loss (Galetti et al. 2013, Pérez-Méndez et al. 2016). In Chapter 4, using the framework developed in Chapter 3, I examined the relative role of Chital in generating seed rain patterns of *Ziziphus mauritiana* in comparison with two other dominant dispersers of the tree, namely birds and pigs. Further, I also identified the potential factors influencing these observed differences in seed rain. I found that both the spatial and temporal patterns of seed rain generated by Chital was very different from either birds or pigs and correlated with vastly different abiotic and biotic factors. Specifically, dispersal by Chital was largely influenced by grass availability and low structural cover (Schaller 1967, Raman 1997, Bagchi et al. 2003a, Ramesh et al. 2012) and was reflective of its grazing and predator avoidance behaviour (Sundararaj et al. 2012, Vijayan et al. 2012). Most significantly, Chital disperse the most number of seeds to the most number of sites and the patterns was relatively the least variable in time. By highlighting the differences in spatio-temporal patterns of seed rain generated by Chital, pigs and birds, our study underscores the importance of examining seed dispersal by ruminants in particular and less-studied non-obligate frugivores in general. The parameter 'ψ' – the proportion of sites to which seeds are dispersed – estimated in our framework and indicating the spatial spread of generated seed rain, could be used as an additional attribute while functionally classifying dispersers groups in a community (Dennis and Westcott 2006).

Chital likely generate observed seed rain patterns as a response to perceived predation risk and grass availability

In the previous 3 chapters, I found repeatedly that seed rain and movement patterns of Chital were reflective of their response to predation risk and forage availability. Perceived predation risk mediated by habitat heterogeneity (i.e. landscape of fear) is well known to influence movement patterns of large herbivores, particularly ruminants (Laundre et al. 2010, Creel et al. 2014). Whether behavioural responses to predation risk has downstream consequences for the functional role of ruminants has been rarely explored, especially for seed dispersal. In the 5th chapter I found that among four different scenarios simulated using individual based models, response to perceived predation risk and grass availability best explained observed seed rain patterns from the field. That fear of predators could potentially influence seed dispersal patterns is a novel insight despite being theoretically explored in a very different context (Howe 1979). There is tremendous scope to incorporate increasing levels of complex Chital behaviour such as group dynamics, energetics, and collective behaviour (Rubenstein 2014, Gallagher et al. 2017) in the simulation models and to understand the mechanisms driving seed rain using the pattern oriented modelling approach (Grimm et al. 2005).

Concluding remarks

The findings of my thesis further our understanding of seed dispersal by ruminants. In particular, they provide a quantitative assessment of the patterns themselves and identify the potential mechanisms underlying seed rain patterns generated by Chital. Additionally, novel analytical frameworks enable easier examination of seed dispersal by terrestrial vectors. This combined information is going to be useful in carrying out further research on functional role of ruminants in seed dispersal by ruminants in particular and seed dispersers in general. Results corroborate known information about Chital space use, while providing new insights on patterns of seed dispersal by Chital. Further investigation in to seed dispersal can produce very relevant ecological information and have the potential to inform conservation in many scenarios (e.g. over harvest of Chital dispersed fruits, decline in Chital and predator populations, etc).

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