Seed dispersal effectiveness of samango monkey
(*Cercopithecus albogularis schwarzi*)

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Abstract

The effectiveness of a seed disperser is dependent on the impact it has on plant fitness. For fruiting species, plant fitness is dependent on the behaviour of its mutualists in (a) reducing seed mortality and (b) increasing the likelihood of future reproduction. The main aim of this thesis was to assess how intergroup variability in the feeding and movement behaviour of a highly social frugivore, influences seed dispersal effectiveness (SDE) and plant fitness. I achieved this by deconstructing the different components of seed dispersal, the quality of dispersal and the quantity of dispersal and investigated how the behaviour of samango monkeys influenced each component. Germination experiments demonstrated that although removal of germination inhibiting fruit pulp through seed-spitting increased germination potential compared to the mechanical and scarification of seeds via seed-swallowing, plants may trade quality for quantity, as the SDE of samango monkeys was greater for swallowed seeds. Time budget analysis showed that intergroup variability in feeding behaviour led to differences in the quantity of seeds dispersed by each group Movement behaviour analysis showed that differences in habitat quality influenced the quality of dispersal. Gut passage time analysis provided a reliable estimate of a gut passage time window between 16.63 – 25.12 hrs. The findings of this study highlight intergroup variability in SDE of neighbouring groups of social foraging frugivores, which possibly arose through ecological constraints associated with group size

(Janson & van Schaik 1988; Chapman & Chapman 2000b). Intergroup variability in SDE could have important consequences on the maintenance of forest systems and the recruitment in, and colonization of, secondary forest or open habitats. Variation in SDE within animal populations can have important implications for spatial demographics in plant communities, and this thesis highlights the importance of including intergroup variability seed dispersal models.

Declaration

No portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification at this or any other university or other institute of learning.

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Most of all, thanks to the samango monkeys and all of the wildlife I encountered in South Africa, you changed my life, especially the leopard for allowing me to share her silent world, just for a moment.

Dedication

I dedicate this thesis to Nellie Stringer, whose love empowered me,

and Paul Stringer, in whose memory I strive to accomplish all that I can.

Chapter 1

General Introduction

> *"If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent thinking"*
>
> Aldo Leopold (1953, p. 190)

Frugivory and seed dispersal form a critical mutualistic relationship between plants and animals (Farwig & Berens 2012; Eriksson 2016). This relationship represents the only mobile life stage of plants (Nathan & Muller-Landau 2000) and is therefore crucial for maintaining forest dynamics (Terborgh et al. 2002). Plants rely on frugivores to disperse seeds away from the parent (Janzen 1970; Connell 1971) and enhance germination and seedling establishment (Terborgh et al. 2002; Traveset et al. 2007). The effectiveness of dispersal is defined as the contribution it has on plant fitness or the future reproduction of a plant (Schupp 1993), which can be quantified as a product of the quantity of seeds they disperse and the quality of the dispersal services they provide (Schupp 1993; Schupp et al. 2010). These components are determined by the behaviour of the disperser and the habitat into which seeds are dispersed (Schupp 1993; Schupp et al. 2010). In social foraging animals such as primates, behaviour can be constrained by, and vary as a consequence of, the social and physical environments they inhabit (Chapman & Chapman 2000b; Grove 2012).

In this thesis, I assess aspects of the seed dispersal effectiveness (SDE) (Schupp 1993; Schupp et al. 2010) of samango monkeys (*Cercopithecus albogularis schwarzi*), an arboreal and frugivorous non-human primate (hereafter primate), through investigation of the effect of seed handling mechanisms on seed germination (*Chapter 3*), the passage time of seeds through the gastrointestinal tract (*Chapter 4*), and the influence of foraging behaviour (time spent feeding and movement behaviour) on the seed dispersal effectiveness (*Chapter 5*) of two groups of samango monkeys.

1.1 | The Importance of Seed Dispersal

1.1.1 | Defining Dispersal

The multifaceted components of ecosystem biota maintain healthy ecosystem functioning (Gaston 2000; Thompson 2011), however biodiversity loss through anthropogenic mediated habitat fragmentation and degradation threatens ecosystem functioning (Fahrig 2003; Hooper et al. 2012). The continued conversion of land for agriculture and urban settlement, most notably through deforestation (Flinn & Velland 2005; Kissinger et al. 2012), are primary drivers of habitat fragmentation and degradation globally (Zhang et al.

2007; Haddad et al. 2015). A significant consequence of deforestation is the pressure placed on the maintenance of forest dynamics through the loss of seed dispersers (Farwig & Berens 2012).

In ecology, the term 'dispersal' describes the "*unidirectional movement of an organism away from its place of birth*" (Levin et al. 2003 p. 576). However, as discussed by Schupp et al. (2010), there is no universally accepted definition of seed dispersal. Plants are sessile organisms for which dispersal occurs during a single mobile life stage (Fig. 1.1) in which propagules (mature ovules containing an embryo (Nathan & Muller-Landau 2000; Vander Wall et al. 2005a)) are released and potentially transported by abiotic vectors such as wind or water, or biotic agents such as animals (Levin et al. 2003; Cousens et al. 2008). In the majority of vascular plants, mature ovules are seeds, formed as a result of sexual reproduction through pollination services (Vander Wall et al. 2005b).

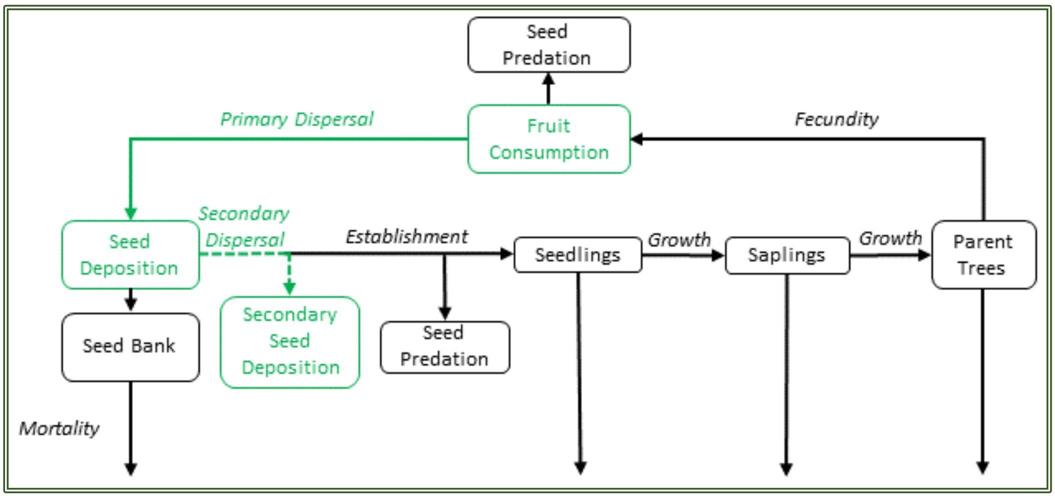


Fig 1.1 Frugivore-mediated seed dispersal facilitates the single life stage in which fruiting plants are mobile (dispersal – in green) through fruit consumption and subsequent deposition of seeds, and in some cases by secondary dispersal (dashed green lines) of partially consumed fruit and seeds by granivores and seed hoarders (adapted from Nathan & Muller-Landau 2000; Vander Wall et al. 2005a; Beckman & Rogers 2013).

Animal mediated seed dispersal mechanisms include ingestion and deposition of seeds internally (endozoochory), carrying seeds adhered externally (epizoochory), scatter hoarding (dyszoochory), seed-caching (synzoochory) and in two separate primary and secondary dispersal phases by two different dispersers (diplochory) (van der Pijl 1969; Clark et al. 2002; Vander Wall & Longland 2004; Couvreur et al. 2005; Gómez et al. 2019). Seeds dispersed by endozoochory tend to be contained within a dry pod or nutritious fleshy fruit and which are mutualistic evolutionary adaptations of the propagule to (a) attract primary and/or secondary dispersers, and (b) remain with the disperser to facilitate transportation away from a source point (Howe & Smallwood 1982; Wenny 2001; Tewksbury 2002; Couvreur et al. 2005); although seeds do not necessarily need to be transported away from the crown of the parent tree in order to be defined as dispersed (Schupp et al. 2010). It is thought that the fleshy tissue of fruits, containing one or many seeds, are functionally adapted to attract seed dispersers (Eriksson 2016). For example, avian-dispersed fruits are commonly small, appear in large quantities, are coloured within the red-blue colour spectrum and often lack olfactory cues (Gautier-Hion et al. 1985; Tamboia et al. 1996). Mammal-dispersed fruits on the other hand tend to be larger, coloured within the green-red spectrum and have olfactory cues indicating their ripeness (Gautier-Hion et al. 1985; Tamboia et al. 1996). Furthermore, increasing sizes of seeds can progressively restrict endozoochory to larger species (Balcomb & Chapman 2003). While seeds facilitate the dispersion of plants (Vander Wall et al. 2005a), seed dispersal has several functions which influence plant fitness (Wenny 2001).

1.1.2 | Functions of Seed Dispersal

Seed dispersal by frugivores is a mutualistic relationship between frugivores that rely on fruits as food resources, and fruiting trees that rely on frugivores to increase survival of progeny (Chapman & Onderdonk 1998; Farwig & Berens 2012). From an evolutionary perspective, seed dispersal has several functions which have a major influence on plant fitness (Wenny 2001), and which are vital in the maintenance of intact and remnant forests, as well as forest regeneration, especially in fragmented and degraded forests (Clark et al. 1999; Terborgh et al. 2002). Firstly, seed dispersal functions as the main mechanism of gene flow within and between populations (Matthysen 2012), facilitating the spatial and genetic structure of plant populations at the local and landscape level (Levin et al. 2003; Gelmi-Candusso et al. 2017). Secondly, seed dispersal can function as an escape mechanism (Howe & Smallwood, 1982) by reducing density- and distance-dependent and responsive mortality (Schupp 1992; Wenny 2001; Terborgh 2012). For example, under the Janzen-Connell hypothesis (Janzen 1970, 1971; Connell 1971) high densities of seeds, seedlings and saplings around the parent plant drives both competition for resources and density- and distance-responsive 'enemies', namely pathogens and herbivores that predate on conspecifics within high-density and close-distance vicinities (Janzen 1970, 1971; Connell 1971). Thus lastly, seed dispersal can function to transport seeds to microsites where conditions are favourable for germination and survival (Nathan & Muller-Landau 2000), termed 'dispersal quality' (McKey 1975). It is suggested that differences in dispersal quality by seed dispersal vectors led to fruit-frugivore coevolution (Wenny 2001). It is therefore important to understand the relative role of seed dispersers so that conservation management plans incorporating the requirements of seed dispersers, such as corridors between habitats, can be formed (Andresen et al. 2018; Chapman & Dunham 2018).

1.2 | The Role of Frugivores in Seed Dispersal

There is a rich body of evidence of the importance of vertebrates in seed dispersal (Chapman & Onderdonk 1998; Bleher & Bohning-Gaese 2001; Wenny 2001; Traveset et al. 2007; Chapman et al. 2016). In tropical ecosystems, vertebrates are estimated to account for 95% of seed dispersal (Terborgh et al. 2002) and in temperate ecosystems, vertebrates account for approximately 60% of seed dispersal (Howe & Smallwood 1982). Frugivores predominantly disperse seeds through endozoochory and their behaviour impacts on plant fitness directly during ingestion, gut passage and defaecation (Schupp 1993; Traveset et al. 2007) and indirectly during daily travel (Calviño-Cancela 2004).

1.2.1 | Direct Impact of Frugivores on Seeds

Feeding behaviour can have a direct impact on seed germination and plant fitness through the different handling mechanisms that frugivores use to process fruits and seeds (Table 1.1). Firstly, dropping partially consumed fruit can release the fruit from the tree and facilitate secondary dispersal by terrestrial frugivores (Seufert et al. 2010). Secondly, partial (Prins & Maghembe 1994) or complete removal of fruit pulp releases seeds from chemicals that inhibit germination (*the disinhibition effect*) and decrease the risk of fungal-mediated mortality (Traveset & Verdú 2002). Spat or regurgitated seeds can then be removed by secondary dispersers such as granivores, remain within the seed bank, germinate or perish (Lambert 2001; Seufert et al. 2010).

Table 1.1 The influence of frugivore seed handling mechanisms on germination (adapted from Traveset & Verdú 2002; Traveset et al. 2007; Samuels & Levey 2005; Robertson et al. 2006).

Handling	Mechanism	Effect on Seeds	Description
Dropping	Disinhibition Effect	Chemical Inhibition	Partial removal of fruit pulp may release seed from germination inhibiting molecules and chemicals.[a]
	Secondary Dispersal		Granivores and terrestrial frugivores move seeds to suitable microsite.
	Seed Predation following dispersal		Destruction of seeds by granivores or pathogens.
Spitting & Regurgitation	Disinhibition Effect *plus*	Chemical Inhibition	Removal of fruit pulp releases seed from germination inhibiting molecules and chemicals.
	Scarification Effect	Mechanical Alteration of Seed Coat	Physical alteration of the seed coat through oral processing, can facilitate imbibition.
	Seed Predation		Seed destroyed through oral processing.
	Secondary Dispersal		As Above.
	Seed Predation following dispersal		As Above.
Swallowing	Disinhibition Effect *plus*	Chemical Inhibition	As Above.
	Scarification Effect *plus*	Mechanical Alteration of Seed Coat	As Above.
	Gut-Passage Effect *plus*	Mechanical & Chemical Alteration of Seed Coat	Physical actions and digestive fluid alter the seed coat during gut-passage, which can facilitate imbibition.
	Fertiliser Effect	Fertilisation from Faecal Matrix	Enhanced germination nutrients from provided by the faecal matrix.
	Seed Predation		As above or in gut passage.
	Secondary Dispersal		As above dung beetles.
	Seed Predation following dispersal		As Above.

[a] e.g. Prins & Maghembe 1994

Thirdly, passage through the gut or fine oral processing can enhance germination by breaking seed dormancy through mechanical and chemical scarification of the seed coat (*the scarification effect*) which, in addition to releasing the seed from inhibiting chemicals through pulp, may facilitate imbibition of water and gases (Traveset & Verdú 2002; Baskin & Baskin 2014). Passage time through the gut is highly variable between and within species and between food items (Varela & Bucher 2006; Figuerola et al. 2010; Elfström et al. 2013), which can influence the extent to which seeds are scarified (Petre et al. 2015a). Finally, the faecal matrix can enhance seed germination through a fertilising effect, or can have a lethal effect by facilitating the growth of fungus, increasing the risk of pathogen attack *(the fertiliser effect)* or by attracting dung consumers (Traveset & Verdú 2002; Traveset et al. 2007). The faecal matrix can also facilitate secondary dispersal by dung beetles (*Scarabaeidae*) (Nichols et al. 2008; Culot et al. 2018).

1.2.2 | Indirect Impacts of Frugivores on Seeds

As well as seed handling mechanisms, feeding behaviour can have indirect impacts on plant fitness by influencing the quantity of seeds dispersed (Zwolak 2018). For example, individuals within populations of *Didelphis albiventris* (white-eared opossum) (Cantor et al. 2013), *Alouatta palliata* (mantled howler monkey) (Dáttilo et al. 2014) and *Rousettus aegyptiacus* (Egyptian fruit bat) (Herrera et al. 2008) demonstrate different dietary preferences. In these populations, individuals differed in the species of fruit they consumed and therefore the number of seeds they dispersed (Zwolak 2018). The timing of foraging behaviour can influence how far seeds are dispersed and the quality of microsite deposition. For example, seeds ingested by toucans (*Ramphastos* spp.) in the morning were dispersed farther than at other times, whereas seeds ingested in the afternoon were more likely to be dispersed in clumps under roosting sites (Kays et al. 2011). In social foraging animals such as birds and primates, time budget decisions regarding when, where and for how long to forage are influenced by the decisions of others and can vary as a consequence of the social and physical environments (Krebs 1980; van Schaik 1983; Marshall et al. 2012). For example, mean food intake rate can increase or decrease as individuals adjust vigilance behaviour (Krebs 1980; Roberts 1996), conspecific aggression (Beauchamp 1998) and resource guarding (Janson & van Schaik 1988) in relation to their position within the group and the behaviour of neighbours (Marshall et al. 2012).

The structure of the physical environment, such as the distribution of resources, can also have indirect impacts on plant fitness by influencing the quality of seed deposition through the dispersers movement behaviour (Schupp et al. 2010). Increased movement between resource patches can alter likelihood of dispersal into either suitable microhabitats or novel environments (Zwolak 2018). This can be both positive through escape from negative density-dependent mortality (Janzen 1970, 1971; Connell 1971) and deposition into ephemeral suitable microsites (Zwolak 2018), or it can be negative as spatial autocorrelation of habitat quality can reduce the likelihood of deposition into suitable microsites the farther seeds are dispersed from the parent tree (Zwolak 2018).

Models of seed dispersal typically include measures of the effect of a disperser's behaviour on seed germination following treatment in the mouth or gut (reviewed in Robertson et al. 2006; Traveset et al. 2007; Fuzessy et al. 2016), the quantity of seeds dispersed (e.g. Lucas & Corlett 1998; Wehncke et al. 2004), dispersal distance and/or spatial distribution of depositions (Lambert & Chapman 2005; Gonzalez-Zamora et al. 2012; Petre et al. 2015b), or a combination of two or more of these measures (e.g. Rogers et al. 1998; Otani & Shibata 2000; Bravo 2009; Matías et al. 2010).

1.3 | Theoretical Framework: Seed Dispersal Effectiveness

1.3.1 | Mutualistic Interactions

Animal mediated seed dispersal is a mutualistic interaction that has an immediate outcome (e.g. the spitting or swallowing of a seed) and a delayed outcome (e.g. germination or mortality of the seed), the effects of which can impact the fitness of the interacting partners (Schupp et al. 2017). The act of transporting seeds away from a source location is a critical step in the survive-demise dichotomy for individual seeds, which sets the scene for changes in plant population dynamics, population ranges and community structure

(Nathan & Muller-Landau 2000; Dennis & Westcott 2007; Westcott 2007). Animal mediated seed dispersal is complex and all frugivores are not equal in the seed dispersal services they provide (Niederhauser & Matlack 2015), with intraspecific and interspecific variation observed at the local and landscape scales (Zwolak 2018; Snell et al. 2019). Such differences arise from the complex mechanisms, variable outcomes and the frequency of occurrence of the processes involved during seed dispersal (Schupp et al. 2010; Zwolak 2018).

The impact of mutualistic interactions on the fitness of interacting partners, can be assessed through an effectiveness concept (Schupp 1993). The effect of a mutualist on its partner is a function of the product of the frequency of the interaction (how often it occurs) and the outcome of the interaction when it does occur (Schupp 1993; Schupp et al. 2017). For seed dispersal, effectiveness is a product of the quantity of seeds dispersed and the outcome or quality (McKey 1975) of the dispersal (Schupp 1993), which form the two major components of the Seed Dispersal Effectiveness (SDE) framework (Fig 1.2) (Schupp 1993; Schupp et al. 2010).

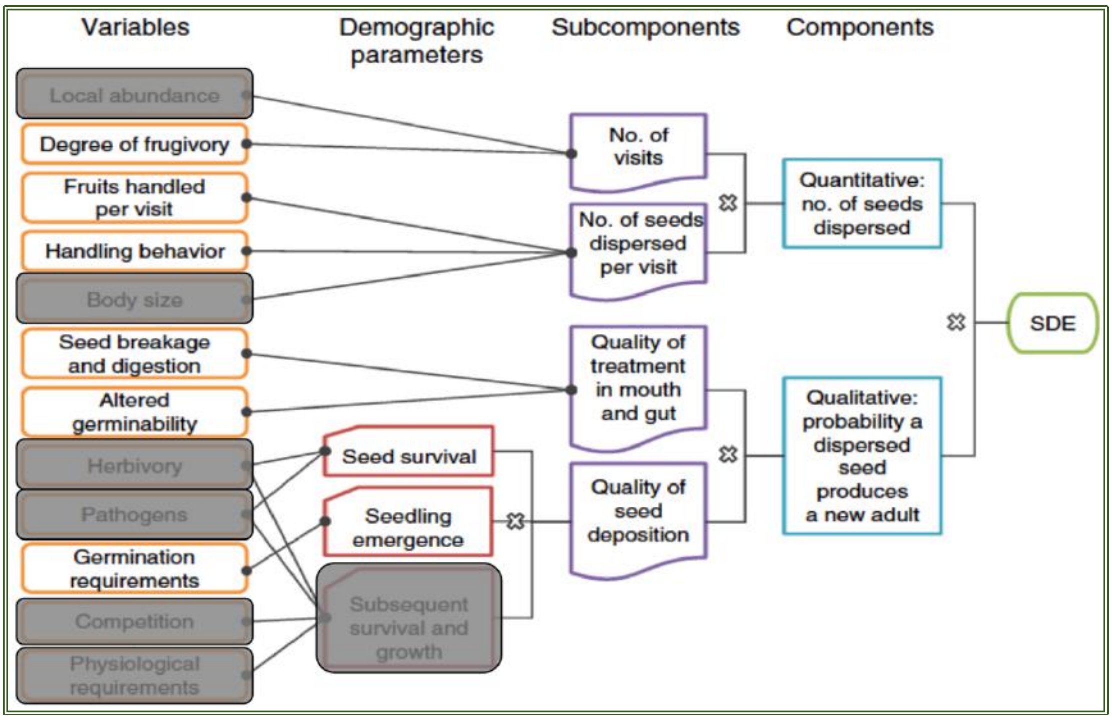


Fig 1.2 The variables encased within the subcomponents and components of the Seed Dispersal Effectiveness (SDE) Framework that influence plant fitness (Schupp et al. 2010). Shaded variables are not considered in this thesis due to logistical constraints of time and resources.

The SDE framework was originally conceived by Schupp (1993) as Seed Disperser Effectiveness, defined as "…*the contribution a disperser makes to the future reproduction of a plant*" (Schupp 1993: p. 16), and based on the measure of "…*the number of new adults produced by the dispersal activities of a disperser, relative to the number produced by others*" (Schupp 1993; p. 16). The framework of Schupp (1993) built on components of Seed Dispersal Quality (SDQ), described by Reid (1989) as the probability of a seed being dispersed to a site suitable for establishment and germinating ('disperser efficiency') and the proportion of seedlings that a disperser is responsible for dispersing ('disperser effectiveness'). In the SDQ framework, disperser efficiency was measured as the seed shadow or patterns of seed dispersal produced by a disperser (Reid 1989). Disperser effectiveness was measured as a function of the density of the disperser population, the number of seeds an individual dispersed, the efficiency that a seed was deposited in a site suitable for establishment, and the probability that a seed will germinate and establish following dispersal (Wheelwright & Orians 1982; Reid 1989). Thus, the original SDE framework focussed on quantifying how a disperser affected plant recruitment (Schupp et al. 2010). On the other hand, seeds can be dispersed by multiple vectors of the same species, by an assemblage of different species and even through two distinct phases of dispersal involving two distinct dispersal agents (Vander Wall & Longland 2004; Schupp et al. 2010).

The SDE framework was renamed seed dispersal effectiveness to account for the multiple agents that are involved in the seed dispersal process (Schupp et al. 2010). The two major components can be measured as products of subcomponents (Fig. 1.2) in which variables act to influence plant fitness (Schupp 1993). As such, the impact a disperser has on plant fitness is the product of the number of seeds dispersed per unit of time and the probability that a seed produces a new adult, or SDE = Quantity x Quality (Schupp 1993; Schupp et al. 2010).

1.3.2 | Dispersal Quantity

The quantity component of SDE combines observational data on the feeding behaviour and activities of a disperser. Dispersal quantity is typically measured as the product of number of seed dispersed per visit and the number of visits (per unit of time) (Schupp 1993; Schupp et al. 2010), although variables used to calculate the quantity of dispersal vary between studies. Observational data are typically assessed using surveys of dispersers at specific feeding trees or through activity budget analyses that include durations of feeding sessions and seed processing (e.g. Beaune et al. 2013a), Some studies have combined the number of visits with the number of seeds recovered from faecal samples (e.g. Figueroa-Esquivel et al. 2009), and some have used a proxy measurement such as body mass to estimate the potential number of seeds being dispersed (Mokotjomela et al. 2016).

1.3.3 | Dispersal Quality

The quality of dispersal is typically measured as the product of the effect of seed handling on germination and the quality of seed deposition into microsites which favour survival and growth (Quality of treatment x Quality of deposition; Fig 1.2) (Schupp 1993; Schupp et al. 2010). The quality of treatment measures how seed handling mechanisms influence the germination of seeds following processing in the mouth or gut of a frugivore (Schupp 1993). As discussed by Schupp et al. (2010), seeds do not necessarily have to be transported away from the immediate vicinity of the parent tree to have been dispersed. The quality of deposition therefore focusses on the environment into which a seed is deposited, which may include variables such as competition, herbivory and pathogens that may act to reduce the probability of a seed surviving into adulthood (Fig. 1.2) (Schupp et al. 2010). Dispersal quality is typically assessed through seed germination experiments (quality of treatment), distance from conspecifics and habitat or environmental variability in terms of where seeds are deposited (quality of deposition) (Schupp et al. 2010).

While it could be argued that dispersal quantity is relatively straight forward to assess, there is bias in the methodological approaches in assessment of dispersal quality, which may affect the conclusions of such studies. This bias is most notable in germination experiments designed to assess the effect of seed processing mechanisms on seed germination. For example, few studies (e.g. Corlett and Lucas 1990; Dominy and Duncan 2005; Gross-Camp and Kaplin 2011) focus on seed-spitting or investigate the role of the faecal matrix (e.g. Tutin et al. 1991; Valenta and Fedigan 2009; Anzures-Dadda et al. 2016). A 2005 review of 99 studies found that 77% of studies used the comparison between germination of gut-passed and manually extracted seeds in their study design (Samuels & Levey 2005). These studies did not include entire fruit, where seeds are untreated, as control groups and therefore, do not wholly address the effect of gut-passed seeds (Samuels & Levey 2005). As previously discussed (section 1.2), removal of fruit pulp acts as a disinhibitory effect which may increase germination potential of seeds (Prins & Maghembe 1994; Traveset & Verdú 2002). Because of the earlier review, I wanted to assess what has been adopted since 2005 in terms of experimental design in germination experiments assessing the effect of seed processing mechanisms on germination.

I conducted a Web of Science topic search (which includes title, abstract and keywords) for the period January 2005 to May 2019 using GERMINATION, SEED, EXPERIMENT OR DISPERS*, "GUT PASSAGE" OR "SEED HANDLING" OR SPIT* as search terms, indicated that there is still a prominent bias in the comparative treatments included in seed dispersal studies. The search, which was filtered for mammals only, generated 212 papers in total, 69 of which investigated the likelihood of seed germination following spitting by, or passage through the gut of, mammal seed dispersers (Appendix Table A.1). The main approach omitted from studies was the inclusion of entire fruits as a control group (Samuels & Levey 2005; Fuzessy et al. 2016) and 76% of studies still used manually extracted seeds as controls, demonstrating a lack of progression. Furthermore, 76% of studies excluded the fertiliser effect and just 9% included mechanical scarification of de-pulped seeds along-side gut-passed seeds. Without isolating each fundamentally different mechanism, the absolute role of primates on seed germination is confounded (Samuels & Levey 2005).

An additional issue is that many experiments are conducted *ex-situ* in laboratories (e.g. Kankam and Oduro 2012; Lessa et al. 2013), growth chambers and incubators (e.g. De Carvalho-Ricardo et al., 2014; Maldonado et al., 2018), while few studies (e.g. Chen et al., 2016; Sánchez de la Vega and Godínez-Alvarez, 2010) conduct germination experiments in the field where natural environmental conditions fluctuate. Experiments conducted in controlled conditions often report that the effect of gut passage on seed germination is consistently higher than controls, whilst in field experiments, studies most often report no significant difference (Fuzessy et al. 2016), highlighting the importance of well-designed and controlled *in situ* studies.

1.3.4 | Seed Dispersal Effectiveness Landscape

The SDE can be visualised in a SDE landscape (Fig. 1.3), which plots the dispersal quantity (*x*-axis) and dispersal quality (*y*-axis), and where isoclines represent possible combinations of SDE (Schupp et al. 2010). The SDE landscape demonstrates that where dispersal quality is low, even a four-fold increase in dispersal quantity does not substantially increase overall SDE (Schupp et al. 2010). Similarly, if dispersal quantity is low, large increases in quality would not substantially increase overall SDE.

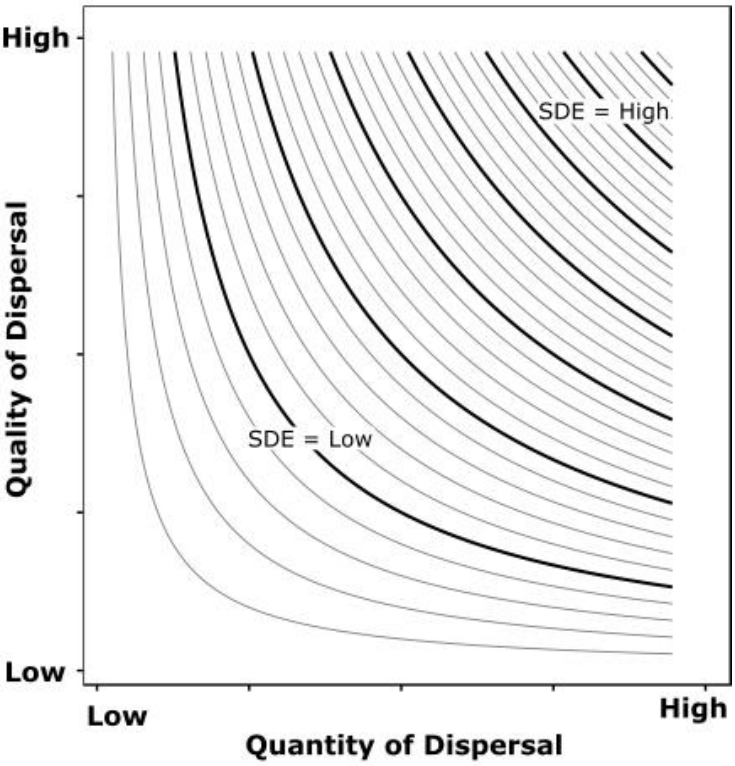


Fig. 1.3 The SDE landscape (adapted from Schupp et al. 2010; p. 337) combining the quantity and quality components of SDE and where isoclines represent all possible combinations of quantity x quality.

1.3.5 | Flexibility of the Seed Dispersal Effectiveness Framework

The SDE framework is highly flexible and can be used at a variety of scales. Previous studies have utilised the SDE framework to evaluate the effectiveness of a species at the local (e.g. Rodríguez-Pérez & Traveset 2010; Albert 2012; Beaune et al. 2013) and landscape scale (e.g. Chaves et al. 2011; Montaño-Centellas 2013), as well as the interspecific effectiveness of sympatric bird dispersers (e.g. Figueroa-Esquivel et al. 2009; Montaño-Centellas 2013; Sun et al. 2014; Mokotjomela et al. 2016; Fricke et al. 2019), sympatric mammal dispersers (e.g. Martins 2006; Brodie et al. 2009; McConkey et al. 2014, 2018), and inter-order sympatric dispersers (e.g. González-Castro et al. 2015; Nogales et al. 2017) at the community level, demonstrating the framework's flexibility. Studies evaluating variation between individuals at the species level have identified behavioural, physiological and morphological traits that affect patterns of seed dispersal (Zwolak 2018). These traits include sex-related differences in feeding (e.g. Herrel et al. 2004) and mating (e.g. Karubian et al. 2012) behaviour and age-related differences in feeding (e.g. Culliney et al. 2012) behaviour . However, to date there have been few studies (e.g. Phiphatsuwannachai et al. 2018) that evaluate intergroup SDE variability and, while interspecific variation in seed dispersal is well documented (e.g. Muller-Landau *et al.* 2008, Traveset *et al.* 2007), intergroup variability in SDE is still poorly understood.

1.4 | Seed Dispersal by Primates

1.4.1 | Why Primates?

Primates are a particularly useful taxa for intergroup comparisons of SDE. Group size among primate populations is a highly variable adaptation of sociality, often constrained by ecological properties of their environment (Chapman & Chapman 2000; Grove 2012). Under these constraints, it is proposed that larger groups experience increased within-group feeding competition (Janson & van Schaik 1988) and that rapid depletion of resources forces foraging across greater areas than smaller groups (Chapman & Chapman 2000). Increased foraging area can increase seed dispersal distance away from the parent (Chapman & Russo 2006), although it can also result in reduced feeding time and therefore lower quantities of dispersed seeds (Karubian & Durães 2009). Collectively, primates vary in body size, home range and feeding guilds (Garber 1987; Bufalo et al. 2016; Fuzessy et al. 2016), display a wide variety of feeding behaviours and fruit handling techniques (Garber & Lambert 1998; (Fuzessy et al. 2016) and can process fruit in different ways resulting in spitting, swallowing or predation of seeds (Corlett & Lucas 1990), such that the quality of dispersal may differ even for the same plant species (Zwolak 2018; Snell et al. 2019). Primates are often the largest arboreal frugivores within the areas they inhabit (Chapman & Onderdonk 1998; Gross-Camp & Kaplin 2005; Bueno et al. 2013; Sato 2018) and can consume larger fruits and seeds than most birds (Chapman & Onderdonk 1998; Balcomb & Chapman 2003). Primates inhabit many ecosystems and have a broad distribution across habitats under threat from anthropogenic disturbance (Estrada et al. 2017) and understanding the role primate populations have in the habitats in which they live can inform landscape conservation efforts (Arroyo-Rodríguez & Fahrig 2014; Chapman & Dunham 2018).

Many primate species rely on forests and there is an increasing amount of literature on the threats primates face because of anthropogenic disturbance including habitat destruction (e.g. Myers et al. 2000; Rovero et al. 2012; Wich et al. 2014; Linder and Palkovitz 2016; Estrada et al. 2017; Strona et al. 2018). Indeed, while 60% of primate species are threatened with extinction, 76% of species are threatened due to land conversion to agriculture (Estrada et al. 2017). The loss of primates from dispersal networks are likely to have cascading effects on plant communities and ecosystem functionality (Chapman & Onderdonk 1998; Farwig & Berens 2012; Bello et al. 2015; Peres et al. 2016; Chapman & Dunham 2018).

1.4.2 | Quantity and Quality: Primates as Effective Dispersers

Primates are regarded as important and effective seed dispersers (Chapman 1995; Andresen et al. 2018) and key dispersers in complex ecological networks (Chapman 1995; Gómez & Verdú 2012; Fuzessy et al. 2016; Chapman & Dunham 2018). Studies are often based upon either the quantity of dispersed seeds or the quality of treatment during gut passage that positively influences seed germination or a combination of both (Andresen et al. 2018; Chapman & Dunham 2018) (Table 1.2).

For example, germination success of spat, dropped and gut passed seeds demonstrated that white-faced capuchins (*Cebus capucinus*) were more effective dispersers through seed swallowing than dropping and spitting seeds (Valenta & Fedigan 2009); black-handed spider monkeys (*Ateles geoffroyi vellerosus*) are effective seed dispersers as they consumed large quantities of fruit, defaecated large quantities of intact seeds, and germination following gut passage was enhanced (Chaves et al. 2011); Similarly, white ruffed lemurs (*Varecia variegata*) demonstrated their effectiveness as dispersers as they also consumed large quantities of seeds and deposited seeds far enough away from parent plants to minimise density-dependent mortality (Moses & Semple 2011). The SDE framework demonstrated that lar gibbons (*Hylobates lar*), were consistently more effective dispersers than other mammal frugivores, as they swallowed large quantities of fruit crops (~38-81%) and dispersed 99% of handled seeds away from the parent plant, from which more seedlings survived to 1-year (McConkey et al. 2015).

Table 1.2 Demonstration of the diversity in measures of dispersal quantity and quality employed by studies investigating primate as effective seed dispersers

Measure of Dispersal Effectiveness		*Species*	Study
Quantity	Quality	Common Name	
Number of fruit species consumed, proportion in diet, number of faecal samples containing seeds, number of seeds processed.	Viability and germination success of spat and gut passed seeds, dispersal distance, deposition site, dispersal patterns.	*Macaca leonina* northern pigtailed macaques	Albert et al. 2013
Fruit and seed processing mechanisms, daily seed rain calculated as seeds per faeces x defecation rate x bonobo density.	Viability and germination success of gut passed seeds, gut passage time of seeds, dispersal distance.	*Pan paniscus* bonobo	Beaune et al. 2013
None	Deposition patterns, germination success of gut passed seeds.	*Alouatta caraya* black and gold howler monkeys	Bravo 2009
None	Deposition patterns and microsite influence on secondary dispersal, germination success of gut passed seeds.	*Cercopithecus nictitans* putty-nosed monkey	Chapman et al. 2010
Quantities of fruit consumption, number and composition of defaecated seeds.	Deposition patterns, germination success of gut passed seeds.	*Ateles geoffroyi vellerosus* black-handed spider monkeys	Chaves et al. 2011
Diet composition.	Germination success of gut passed seeds.	*Eulemur sanfordi* Sanford's brown lemur	Chen et al. 2016
Diet composition, number of seeds recovered from faecal samples	Germination success of gut passed seeds, habitat utilisation	*Chlorocebus pygerythrus* vervet monkey	Foord et al. 1994

Table 1.2 Continued

None	Spatial association between lemurs and food plants, germination of gut passed seeds.	*Microcebus griseorufus* Malagasy reddish-grey mouse lemurs	Génin & Rambeloarivony 2018
Proportion of fruit crop consumed.	Dispersal distance, germination success of gut passed seeds.	*Nomascus gabriellae* southern yellow-cheeked crested gibbon	Hai et al. 2018
Number of seeds recovered from faecal samples.	Viability and germination success of gut passed seeds.	*Gorilla gorilla gorilla* western lowland gorilla	Haurez et al. 2018
Number of seeds recovered from faecal samples.	Viability and germination success of gut passed seeds.	*Papio anubis* olive baboon	Kunz & Linsenmair 2008
Probability of a seed being handled	Probability a handled seed would survive to a 1-year seedling.	*Hylobates lar* lar gibbon	McConkey et al. 2015
Number of seeds recovered from faecal samples	Dispersal distance, viability and germination success of gut passed seeds.	*Varecia variegata* white ruffed lemurs	Moses & Semple 2011
Diversity of seeds recovered from faecal samples; number of seeds recovered from faecal samples per individual	Deposition patterns, germination success of gut passed seeds.	*Gorilla gorilla gorilla* western lowland gorilla	Petre et al. 2015
Number of seeds recovered from faecal samples	Viability and germination success of gut passed seeds, seedling growth.	*Varecia rubra* red-ruffed lemur	Razafindratsima & Martinez 2012
Number of seeds spat out and recovered from faecal samples	Dispersal distance, germination success of spat and gut passed seeds, monitoring of *in-situ* seedlings.	*Macaca mulatta* rhesus macaque	Sengupta et al. 2014
Differences in the diversity and number of seeds recovered from faecal samples between primate species.	Comparisons of dispersal distance and germination success of spat and gut passed seeds between primate species.	*Trachypithecus auratus* Javan lutung *Macaca fascicularis* long-tailed macaque	Tsuji et al. 2017

Table 1.2 Continued

None	Germination success of spat, dropped and gut passed seeds.	*Cebus capucinus* white-faced capuchins	Valenta & Fedigan 2009
Time feeding in individual trees	Dispersal distance, deposition patterns	*Cebus capucinus* white-faced capuchins	Wehncke et al. 2004
Number of seeds recovered from faecal samples.	Germination success of gut passed seeds	*Pan troglodytes* chimpanzee	Wrangham et al. 2008
None	Comparison of dispersal distance between primate species	*Alouatta seniculus* red howler monkey *Lagothrix lagotricha* Humboldt's woolly monkey	Yumoto et al. 1999
Comparison of feeding rate in a single tree *Ziziphus cinnamomum* between primate species, number of *Z. cinnamomum* seeds recovered from faecal samples.	Monitoring of *in-situ* germination success	*Cebus apella* brown capuchin monkey *Ateles paniscus* black spider monkey	Zhang & Wang 1995

The majority of studies assessing seed dispersal by primates focus the quality of dispersal on the effect of gut passage reporting an increase in the number of seeds germinating and decrease in latency to germinate (time from seed deposition to germination) (e.g. Stevenson et al. 2002; Valenta and Fedigan 2009; Sengupta et al. 2014; Petre et al. 2015; Muñoz-Gallego et al. 2019). For example, seeds swallowed by bonobos (*Pan paniscus*) had 25% increase in germination success following passage through the bonobo's gut compared to manually de-pulped seeds (Trolliet et al. 2016). Fig (*Ficus* spp.) seeds swallowed by brown howler monkeys (*Alouatta fusca*) had 37% increase in germination success following gut passage compared to manually depulped seeds (Figueiredo 1993). A meta-analysis on neotropical primates found that overall, gut passage increased seed viability by 33% and decreased germination latency (time to germination) by 20% (Fuzessy et al. 2016). It is postulated that passage through the gut alters seed physiology, releasing the seed from dormancy, allowing germination to occur at a greater rate than would otherwise ensue (section 1.2) (Traveset et al. 2007).

Physical properties of food items can also influence gut passage time. For example, seed mass, shape, size and specific gravity can influence the time seeds remain in the digestive tract (Garber 1986; Tsuji et al. 2010). Smaller seeds may also become trapped within the folds of the gut. Gut passage time of seeds may subsequently influence dispersal distances (Tsuji et al. 2010) and the conditions into which seeds are deposited (González-Di Pierro et al. 2011). Gut passage time has been widely studied in primates (Cabre-Vert & Feistner 1995; Lambert 1998; Norconk et al. 2002; Remis & Dierenfeld 2004; Tsuji et al. 2015; Bai et al. 2019) and can vary considerably (Lambert 1998). It is thought that both body size and digestive strategy can explain the large variation of gut passage times observed in primates (Lambert 1998; Clauss et al. 2008; Blaine & Lambert 2012).

There is a general trend that gut passage time increases between the smallest and the largest sized primates (Lambert 1998). There is also a general pattern for frugivorous primates, whose diets contain greater quantities of simple carbohydrate such as glucose and fructose, to display reduced gut passage times compared with folivorous and exudativorous primates, whose diets consist of greater quantities of complex structural carbohydrates such as cellulose (Lambert 2002; Clauss et al. 2008; Cabana et al. 2017). Cellulose is a major constituent of plant cell walls and many primates rely on non-fruit plant matter as a major source of energy. Unlike simple carbohydrates, digestion of cellulose depends on fermentation which, like in other herbivorous vertebrates, occurs through fermentation in the primate gastrointestinal tract and can increase gut passage time and therefore the time seeds are subject to digestive processes (Chivers & Hladik 1980).

Gut passage studies measure the time it takes a focal element to travel through the gastrointestinal tract between ingestion and defaecation. Several indices are used to calculate gut passage times including Transit Time (TT), defined as the time of the first appearance of the focal elements in faeces, Time of Last Appearance (TLA), defined as the time of the last appearance of the focal elements in faeces and Mean Retention Time (MRT) defined as the mean gut passage time of the focal elements from ingestion to excretion (Blaxter et al. 1956; Warner 1981). Several different insoluble particulate markers have been used for gut passage studies; artificial markers such as 2-3 mm plastic beads and plastic ribbon (e.g. Maisels 1994; Lambert 2002), glitter (Cabana et al. 2017) and polystyrene and cellulose acetate beads (Power & Oftedal 1996). *In-situ* studies in other primates, for example, bonobo *(Pan paniscus)* (Beaune et al. 2013), spider monkeys *(Ateles belzebuth)* (Link & Di Fiore 2006) and woolly monkeys *(Lagothrix lagothricha)* (Stevenson 2000) have used seeds from infrequently ingested fruit items to estimate gut passage times. However, relying on infrequently ingested fruit means ensuring continuous observation of the focal animal for the entire sampling period to avoid further feeding on focal tree species (Stevenson 2000). In capuchins (*Cebus* spp.) and tamarins (*Saginus* spp.), for which gut passage time is relatively short (Oliveira & Ferrari 2000; Valenta & Fedigan 2010), observational-based studies of gut passage time using seeds from infrequently ingested fruit can be reliable (Heymann et al. 2012). For primate species of which gut retention time is relatively longer, such as guenons (*Cercopithecinae*), this method can be unreliable and much more difficult to accomplish (Heymann et al. 2012). As such, there is a need for more robust *in-situ* methods of assessing gut passage time in species with relatively long retention times.

1.4.3 | Guenons

Guenons are Old World monkeys endemic to sub-Saharan Africa (Enstam & Isbell 2007), with a broad distribution from Ethiopia to South Africa (Lawes 1990; Grubb 2003). They are predominantly arboreal and occupy a wide variety of primary and secondary forest habitats including woodland, bamboo, swamp, lowland and montane (Butynski 2005; Enstam & Isbell 2007) making them ideal models for seed dispersal studies. Guenons belong to the sub-family *Cercopithecinae,* or the cheek-pouched monkeys (Grubb 2003), with morphological adaptations to a diet high in fruits and seeds (Enstam & Isbell 2007). These adaptations include a simple stomach (Bruorton & Perrin 1988), dentition such as bunodont, high-crowned molars (Kay 1978) and cheek pouches, which are used to store food and contain a high level of α-amylase, a saliva enzyme involved in pre-digestion breakdown of starch (Murray 1975). When full, these cheek pouches can hold the same volume as the stomach (Rowell & Mitchell 1991) allowing for the transport of twice as many seeds, making seed-spitting perhaps as important as seed-swallowing in terms of seed dispersal (Corlett & Lucas 1990).

The majority of primates species are seed swallowers (Lambert 1999; Clark et al. 2002; Dominy & Duncan 2005), however *Cercopithecinae* are unique in that they display multiple seed-processing mechanisms. Guenons are seed-swallowers of seeds smaller than 4 mm (on longest axis), seed-spitters of seeds larger than 4 mm (Lambert 1999; Gross-Camp & Kaplin 2011; Linden et al. 2015) and seed destroyers, as they can crush seeds during oral processing of fruits and often consume unripe fruits (Wrangham et al. 1998; Lambert 1999). Mechanical and chemical scarification of seeds during oral processing may have similar effects to the scarification effects during gut passage, though to a lesser degree (Anzures-Dadda et al. 2016), or may have only a disinhibitory effect through pulp removal.

Seed dispersal in *Cercopithecus* spp. has been well studied (Table 1.3). Overall, studies have shown that cercopithecines are important dispersers for many species as spat seeds (Lambert 2001; Gross-Camp & Kaplin 2011) and defaecated seeds (Foord et al. 1994; Poulsen et al. 2001; Chapman et al. 2010) exhibited greater germination than control seeds. Furthermore, the faecal matrix increased germination compared to entire fruits (Gross-Camp & Kaplin 2011). Removal of fruit pulp and seed-spitting by cercopithecines has also been shown to reduce mortality from fungal pathogens (Lambert 2001). However, the SDE of a guenon monkey has yet to be quantified and my study aims to fill this gap in knowledge.

Table 1.3 Studies of seed dispersal by *Cercopithecus* spp.; Methodologies: DA Diet Analysis; DP Deposition Patterns; SD Secondary Dispersal; GE Germination Experiments (treatments: E Entire fruit; D Disinhibition, manual pulp removal; G Gut-Passage, seeds recovered from faecal samples; F Fertiliser, seeds sown in the faecal matrix; Sp spat out seeds, (c) Control Treatment), GR Gut retention time Ex *ex-situ.*

Study	*Species* common name	Focus of Study	Methodologies Employed	Influence on Seed Dispersal
Chapman et al. 2010	*Cercopithecus nictitans* putty-nosed monkey	Ecological role of *C. nictitans* in forest conservation and regeneration	DP faecal sample/habitat analysis SD seed removal GE D(c), G, Sp	G enhanced and Sp reduced seed germination; faecal matter did not influence secondary dispersal.
Cordeiro et al. 2004	*Cercopithecus mitis doggetti* blue monkey	Seed dispersal of invasive exotic tree	Disperser assemblage Seeds dispersed per visit	*C. mitis* a functional disperser of invasive tree
Foord et al. 1994	*Cercopithecus aethiops* vervet monkey (*Chlorocebus*)	Rehabilitation of sand dune forest	DA behavioural observation, faecal sample analysis GE D(c), G	Germination of 1/5 species higher after G, 4/5 no different
Gross-Camp & Kaplin 2011	*Cercopithecus l'hoesti* l'Hoest's mountain monkey *Pan troglodytes* chimpanzee	Comparison of seed handling/processing and seed defaecation	DP behavioural observations of seed handling / microhabitat analysis GE F, Sp monitoring *in-situ* GE E(c), Sp, G, F, D (plots)	*In-situ*: Sp higher germination than F Plots: 82% removed or died, F higher germination, Sp not different to E
Gross-Camp et al. 2009	*Cercopithecus l'hoesti* l'Hoest's monkey *Pan troglodytes* chimpanzee	Comparison dispersal by frugivore assemblages	Focal tree observations Seeds dispersed per visit	*C. l'hoesti* dispersed greater number of seeds for 2/5 species

Table 1.3 Continued

Kaplin & Moermond 1998	*Cercopithecus mitis doggetti* blue monkey *Cercopithecus l'hoesti* l'Hoest's monkey	Comparison of seed handling/processing and seed defaecation	DA behavioural observation, faecal sample analysis DP behavioural observations of seed handling and habitat analysis	Both defaecated large quantities of intact seeds, *C. l'hoesti* dispersed more in open and disturbed habitats
Kaplin et al. 1998	*Cercopithecus mitis doggetti* blue monkey	Seasonal fruit influence on dietary plasticity and seed dispersal potential	DA behavioural observation, faecal sample and plant density analysis GE D (dropped by monkeys), G	GE only dropped seeds germinated Seed defaecated intact, fig seeds most common, diet changed seasonally
Kiepiel & Johnson 2019	*Cercopithecus mitis labiatus* samango monkey	Fruit removal and seed dispersal of toxic seeds	Camera traps to identify dispersers and fruit processing mechanisms GE E(c), D	Samango monkey - primary disperser through pulp removal and dropping or spitting
Lambert 1999	*Cercopithecus ascanius* red-tailed monkey *Pan troglodytes* chimpanzee	Comparison of seed handling/processing, dispersal method and dispersal distance	DP behavioural observations of seed handling, dispersal distance and microhabitat analysis	*C. ascanius* demonstrated fine oral processing and species-dependent spitting, *P. troglodytes* coarse oral processing and reduced spitting
Lambert 2001	*Cercopithecus ascanius* red-tailed monkey	Services provided to seeds other than dispersal	DP behavioural observations of seed handling and dispersal distance SD experimental patches of seeds GE E(c), Sp	Seed-spitting reduced seed mortality from fungal pathogens and increased germination compared to controls
Lambert 2011	Multiple *Cercopithecus* spp. and other primates	Primates as umbrella species for forest conservation	DP behavioural observations of seed handling	*Cercopithecus* spp. best fitted umbrella species criteria
Seufert et al. 2010	*Cercopithecus albogularis schwarzi* samango monkey	Secondary seed removal	Camera traps	Primates drop fruits and seeds making them available to terrestrial animals

Table 1.3 Continued

Linden et al. 2015	*Cercopithecus albogularis schwarzi* samango monkey	Seed dispersal by samango monkeys in Afromontane forest	DA behavioural observation, faecal sample analysis DP behavioural observations of seed handling	Predominantly frugivorous 72%, diverse fruit content in diet, seed-spitting and seed-swallowing
Poulsen et al. 2001	*Cercopithecus cephus cephus* moustached monkey *Cercopithecus nictitans nictitans* white-nosed guenon *Cercopithecus mona pogonias* crowned guenon	Seed dispersal within a primate community	Primate densities using faecal samples GE D (c), G DP dispersal distance from GPS location and gut retention time GR Ex	GR *C. c. cephus* ~23.8 hr GR *C. m. pogonias* ~ 21.4 hr All seed viable, one species G germination greater than D
Righini et al. 2004	*Cercopithecus aethiops* vervet monkey (*Chlorocebus*)	Effect of primates on *Ficus* seed germination	GE D(c), G from *ex-situ* feeding GR Ex	GR of 50% of seeds 19.8 hrs G germination higher than D

Within primates, guenons show increased gut passage time compared to similar sized primate species (Lambert 1998; Lambert 2002), with studies reporting gut passage times between 21.4 hrs in *C. mona mona* (crested Mona monkey) (Poulsen et al. 2001) and 40.6 hrs in *C. mitis* (blue monkey) (Clemens & Phillips 1980). Guenons exhibit considerable feeding flexibility with consistently large proportions of both fruit and non-fruit plant parts in their diets (Butynski 2005; Enstam & Isbell 2007; Blaine & Lambert 2012; Coleman & Hill 2014). It is suggested that *Cercopithecus* spp. digestive strategies include extended retention time of food for fermentation and extraction of nutrients from a diet high in fibrous material (Lambert 1998; Lambert 2002).

Prior research on *Cercopithecus* spp. gut passage times have all been conducted in captivity and predominantly in zoological collections (Chapter 4). In captivity, subjects' diets consist of commercial food pellets supplemented with domestic fruits and vegetables, and movement is generally more limited (e.g. Maisels 1994; Lambert 2002; Blaine & Lambert 2012). Wild animals are generally more active than captive animals, and energy expenditure can also influence gut passage times (Blaine & Lambert 2012). In addition, the 'captivity effect' (Martin et al. 1985), whereby the gastrointestinal tract can become reduced in captivity, can also reduce gut passage rates (Milton 1984; Martin et al. 1985; Blaine & Lambert 2012). As such, captive studies may paint a misleading picture of gut passage time in primates adapted to high-fibrous and considerably flexible diets, and therefore a more reliable method of estimating gut passage time in wild primates is needed.

1.5 | Thesis Structure

This thesis presents an investigation into the seed dispersal effectiveness of an arboreal forest guenon, the samango monkey (*Cercopithecus albogularis schwarzi*), using some of the variables from the SDE framework (Fig 1.4). In this introduction I have given an overview of the ecological importance of seed dispersal and the significance of primates in their role as primary seed dispersers. I have highlighted some bias in methods currently utilised to study different components of SDE distinct. Firstly, in experiments that aim to assess the effect of seed handling mechanisms on germination, there is still a bias to exclude entire fruits as a relevant control and the majority of studies exclude the fertiliser and effect. Secondly, all of the research on gut passage times of guenons has been conducted *ex-situ*. As such, there is bias towards measuring gut passage times of captive subjects, which may paint a misleading picture of gut passage time in primates adapted to high-fibrous and highly flexible diets. Thus, there is a need to develop a reliable method of estimating gut passage time in wild primates. Lastly, whilst the use of the SDE framework has grown in recent years, there is currently a lack of research focussing on SDE variability between neighbouring groups within populations.

My three data chapters address the aforementioned gaps in order to broaden our knowledge of the effectiveness of primates as seed dispersers. Each of the following data chapters (Chapters 3-5) is presented in journal article format. Chapter 2 details the study site and outlines the general methodology I employed to conduct this research. Chapter 3 addresses a subcomponent of the qualitative component of the SDE framework and assesses the quality of samango monkey seed processing mechanisms and the effect on seed germination of three locally abundant fruit species. Chapter 3 also highlights the need for ecologically relevant treatments in germination studies. In Chapter 4, I further assess the qualitative component of SDE by estimating the passage time of seeds through samango monkey guts. I adapt methods used in *ex-situ* studies of cercopithecine gut passage for use *in-situ* and critically assess its suitability for use in the field. In Chapter 5 I link results from the germination experiments in Chapter 3 with behavioural data analysis to estimate SDE in samango monkeys for three locally abundant fruit species and to estimate intergroup variability in SDE and explore one aspect of animal behaviour in shaping seed dispersal. Finally, in Chapter 6, I summarize the results from the previous data chapters and present a general discussion on the effectiveness of samango monkeys as seed dispersers and the impacts intergroup variability could have on plant fitness. I review how the results could shape future research and conservation directives for this endangered primate.

1.6 | Aims of Thesis (Statement of Objectives)

Quality of Dispersal (Fig. 1.4)

i. **Aim 1: Determine the quality of samango monkey seed dispersal**
    a. How do individual fruit processing behaviours exhibited by samango monkeys, influence the quality of treatment that seed processing mechanisms have on seed germination potential? *(Chapter 3)*
    b. What is the impact of intergroup variability in movement behaviour on the quality of seed deposition? *(Chapter 5)*

ii. **Aim 2: Develop a reliable method for estimating gut passage in wild primates**
    a. Can a gut retention experimental method be used in captivity be adapted for use in the field? *(Chapter 4)*
    b. What is the passage time of seeds through the gastrointestinal tract of samango monkeys following ingestion? *(Chapter 4)*

Quantity of Dispersal (Fig 1.4)

iii. **Aim 3: Determine the quantity of samango monkey seed dispersal**
    a. What is the daily activity budget of samango monkeys? *(Chapter 5)*
    b. How does foraging behaviour influence the quantity of seeds dispersed? *(Chapter 5)*

c. What is the impact of intergroup variability in time budgets on the quantity of seeds dispersed per day? *(Chapter 5)*

Seed Dispersal Effectiveness (Fig 1.4)

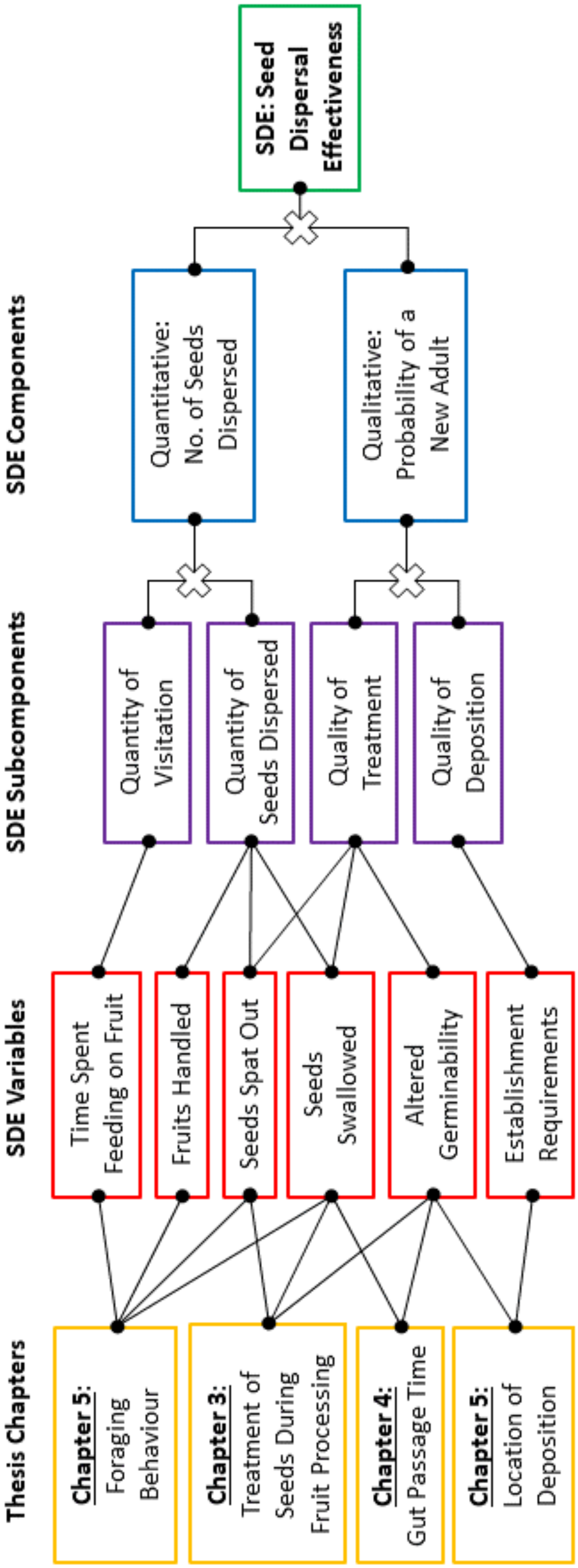
iv. **Aim 4: Determine the impact of frugivory by samango monkeys on plant fitness**

d. Are samango monkeys providing effective dispersal equally to the fruit species they consume? *(Chapter 5)*

v. **Aim 5: Investigate the impacts of animal sociality on plant fitness?**

e. How does sociality influence seed dispersal effectiveness in animal-plant mutualisms? *(Chapter 5)*

Fig 1.4 Chapters of this thesis in which each of SDE variables considered during this study are assessed.



Chapter 2

General Methodology

As individual methods sections accompany each data chapter (journal article format), this chapter provides background information on the study species, further details on the field site and the timescale of fieldwork and includes information on preliminary methods not described in other chapters.

2.1 | Ethical Statement

The majority of this study involved non-invasive behavioural sampling. Part of the study required provisioning two monkeys with small amounts of fruit impregnated with wooden beads. Ethical approval was obtained from Liverpool John Moores University's (LJMU) Life Sciences Ethical Review Process, under clearance through LJMU's Use of Live Animals in Unregulated Research Protocol, permit number NK_ SS/2016-1, and the Animal Welfare Ethical Review Board at Durham University. Fieldwork was carried out with permission from the Limpopo Province Department of Economic Development and Tourism, adhering to the legal requirements of South Africa and following guidelines from the Association for the Study of Animal Behaviour (ASAB 2012).

2.2 | Study Species

2.2.1 | Life History

Samango monkeys (*Cercopithecus albogularis*, Sykes 1931) are medium-sized, sexually dimorphic (males ~7.6 kg, females ~4.4 kg; Harvey & Clutton-Brock 1985) arboreal forest guenons, with a life-span between 20-33 years for females (Cords & Chowdhury 2010). Female guenons are philopatric (Cords 2002) and live in multi-female, single-male (hereafter 'resident male') groups of typically up to ~45 individuals (Skinner & Chimimba 2005). Males loosely associate with small 'bachelor' groups, or remain solitary, after leaving their group just before sexual maturity between 6-8 years (Henzi & Lawes 1987). Breeding is seasonal occurring over a two to three month period (Swart & Lawes 1996) between November - July, depending on sub-species and geographic location (Linden et al. 2016), when bachelor and/or solitary males temporarily coalesce around one or more groups, mating with females and contesting the resident male for his position within the group (Henzi & Lawes 1987, 1988).

2.2.2 | Distribution and Ecology

Guenons have a broad distribution from Ethiopia to South Africa (Fig. 2.1) (Lawes 1990; Grubb 2003; Kingdon et al. 2008). They live in a diverse range of habitats including woodlands, mangrove forests, swamp forests and sand forests along the edges of the Kalahari and Sahara Deserts (Butynski 2005; Kingdon et al. 2008). Guenons can adapt to human modified landscapes (Nowak et al. 2017b) and are tolerant of degraded habitats (Albert et al. 2014), however are restricted to areas with indigenous forest patches for reproduction and recruitment (Lawes 1990; Linden et al. 2016; Parker 2018). They are listed as least concern by the International Union for the Conservation of Nature (Kingdon et al. 2008). Whilst widespread and common in many areas, some subspecies inhabit increasingly isolated forests and are locally threatened (Kingdon et al. 2008; Linden et al. 2016). In South Africa, three subspecies of samango monkey exist; *C. a. erythrarchus, C. a. labiatus,* and *C. a. schwarzi,* (Fig. 2.2) (Dalton et al. 2015).

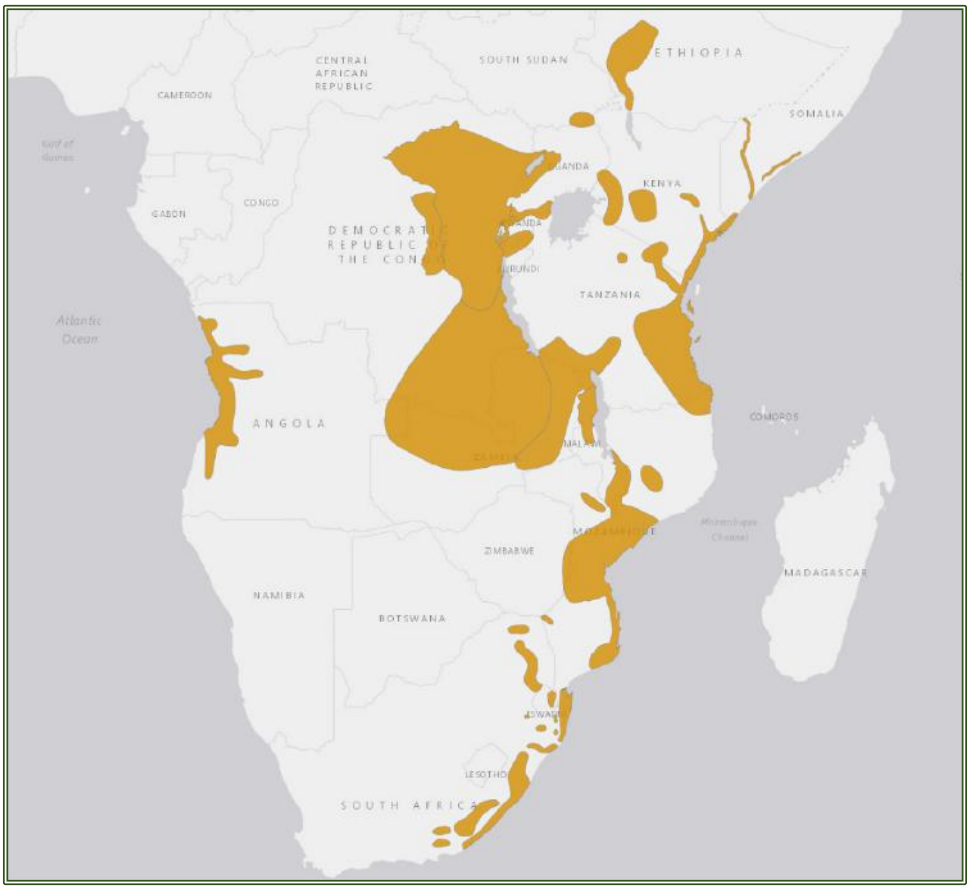


Fig. 2.1 Distribution of guenon monkeys (*Cercopithecus* spp.) across sub-Saharan Africa (Source: Kingdon et al. 2008)

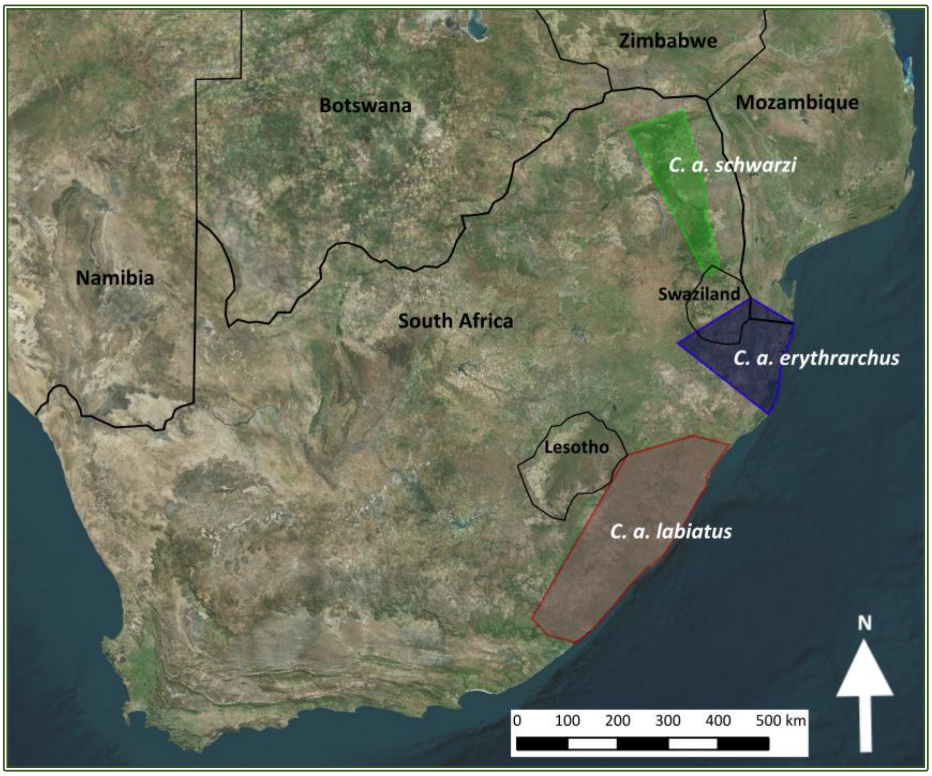


Fig. 2.2 Estimated distribution of three subspecies of samango monkey (*Cercopithecus albogularis*) in South Africa and Swaziland (adapted from Linden et al. 2016).

Cercopithecus albogularis schwarzi (Fig. 2.3) are South Africa's only true forest-dwelling primate, highly dependent on high-canopy evergreen forest (Linden et al. 2015; Parker 2018). The subspecies *C. a. schwarzi* is listed as locally endangered on the Red List of Mammals of South Africa, Lesotho and Swaziland (Linden et al. 2016). A major threat to the survival of *C. a. schwarzi* is deforestation and habitat fragmentation, resulting from agricultural expansion and urbanisation (Linden et al. 2016). Other threats include hunting pressure and more frequent contact with humans through urbanisation (Linden et al. 2016). The range of *C. a. schwarzi* encompasses the Soutpansberg Mountain range in Limpopo Province in the north, down to the Drakensberg Mountain range in

Mpumalanga Province and Swaziland (Fig 2.2) (Dalton et al., 2015). It is likely that mountain populations of samango monkeys are isolated from neighbouring populations due to lack of connecting habitat (Swart & Lawes 1996; Linden et al. 2016).

Fig. 2.3 Samango monkey (*Cercopithecus albogularis schwarzi*) consuming a broom cluster fig (*Ficus sur*) at Lajuma, Soutpansberg Mountain, South Africa

2.2.3 | Diet

Samango monkeys are frugivorous-omnivorous (Bruorton & Perrin 1988), with fruit typically comprising >50% of their diet (Lawes 1991; Chapman et al. 2002; Coleman & Hill 2014a; Linden et al. 2015). Figs, the fruit of *Ficus* spp. trees, are an important resource for samango monkeys (Shanahan et al. 2001; Linden et al. 2015) and they are the only large-bodied arboreal species that feed on medium to large sized fruits in the canopy layer of South Africa's evergreen forests (Coleman & Hill 2014, Linden *et al.* 2015, 2016). However, like most guenons, samango monkeys exhibit considerable dietary flexibility with consistently large proportions of both fruit and non-fruit plant parts in their diets (Blaine & Lambert 2012; Coleman & Hill 2014; Linden et al. 2015).

Across their range, leaves can comprise >40% of their diet (Coleman & Hill 2014), and it is suggested that *Cercopithecus* spp. digestive strategies include extended retention time of food for fermentation and extraction of nutrients from a diet high in fibrous material (Chivers & Hladik 1980; Lambert 1998, 2002). Samango monkeys have an extended caecum and colon, increasing the volume of gastrointestinal tract and fermentation capacity, suggesting adaptation to a flexible diet that can contain high levels of cellulose (Bruorton & Perrin 1988; Bruorton et al. 1991). Extended retention times may present an advantage to seed dispersal by exposing the seed to scarification processes for an extended period of time (Section 1.2.1), thereby increasing the germination potential of seeds. Extended retention times may also present an advantage by increasing the dispersal distance away from conspecifics (Section 1.2.1). However, this would greatly depend on the behaviour associated with travelling, such as speed, direction and tortuosity, as well as ecological factors such as distribution of resources (Section 1.2.2). Samango monkeys also utilise cheek pouches to store food (Lambert 2005a; Linden et al. 2015), which present a further mechanism for seed dispersal (Section 1.4.3).

2.2.4 | Threats and Conservation Priorities

In South Africa, samango monkeys are threatened by increasingly fragmented habitat as a consequence of both the natural isolation of the mountainous landscape and anthropogenic disturbance (Linden et al. 2016). Agriculture and plantation forestry are of particular threats to samango monkeys as these industries further fragment landscapes removing important corridors and connecting habitat (Swart & Lawes 1996; Linden et al. 2016). Habitat fragmentation can have important ecological consequences for the long-term survival of species (Estrada et al. 2017). These consequences include a reduced carrying capacity of the habitat, resulting in a decrease in population numbers and further isolation (Haddad et al. 2015; Estrada et al. 2017).

The fragmentation of samango monkey habitat through expanding anthropogenic land use has increased the contact between the monkeys and humans (Albert et al. 2014; Linden et al. 2016; Di Bitetti 2019). Where samango monkeys do exist alongside agricultural and plantation land, conflicts with farmers and landowners arise through crop-raiding and crop damage (von dem Bussche & van der Zee 1985; Lawes et al. 1990; Linden et al. 2016; Di Bitetti 2019). Human-wildlife conflicts present further threats to samango monkey populations including collisions on roads, bushmeat hunting, electrocution on game fencing, and accidental or intentional snaring (Linden et al. 2016), which can further reduce population numbers.

Habitat fragmentation and isolation of dispersal vectors can have several limitations for seed dispersal, and the SDE of dispersal vectors. Firstly, isolation can reduce colonisation into new habitats and range expansion (Howe & Smallwood 1982). Contraction of habitats may increase conspecific density and reduce the availability of microsites suitable for seedling establishment (Section 1.2.2). Secondly, reduced population densities of dispersal vectors can limit the number of seeds dispersed away from conspecifics, increasing density-dependent mortality (Muller-Landau 2007; Caughlin et al. 2015) and reducing the SDE of dispersers (McConkey & O'Farrill 2016). Lastly, extirpation of a dispersal vector may result in reduced or even irreplaceable dispersal services (Albert et al. 2014; Caughlin et al. 2015; McConkey & O'Farrill 2016). As South Africa's largest forest-dwelling primate (Linden et al. 2016), reduction of habitat for, or loss of samango monkeys, may impact seed dispersal of many important forest plant species, many of which are endemic to South Africa (Hahn 2006; Mostert 2006).

The isolation of samango monkeys in South Africa requires conservation efforts and management plans to be specific for the populations of each subspecies. Such planning requires detailed understanding of the genetics for each subspecies to preserve genetic diversity (e.g. Dalton et al. 2015), as well as the ecological traits of each subspecies (Linden et al. 2016; Galán-Acedo et al. 2019). Ecological traits include home range size, trophic guild and habitat type amongst others (Galán-Acedo et al. 2019), as well as how the monkeys interact with the habitats on which they rely. Data on ecological traits can guide management of indigenous forests and restoration of connecting habitat between isolated groups (Coleman & Hill 2014; Linden et al. 2016; Nowak et al. 2017; Parker 2018).

2.3 | Study Site

2.3.1 | Soutpansberg Mountain Range

Fieldwork was conducted at the Primate and Predator Project, hosted at the Lajuma Research Centre (23°02'23"S, 29°26'05"E) situated at the western edge of the Soutpansberg Mountain Range, in the Limpopo Province of South Africa (Fig. 2.5), between August 2017 and May 2018. The Soutpansberg has an altitudinal range between 1150 to 1750 m.

The Soutpansberg lies within South Africa's newest and largest UNESCO (United Nations Educational, Scientific and Cultural Organisation) Man and the Biosphere (MAB) reserve, the Vhembe Biosphere Reserve (VBR), designated in 2009 and covering 3,070,000 ha (Pool-Stanvliet 2013). The aim of the VBR is to address the conservation of biodiversity alongside the conservation and promotion of the social, ecological and cultural components of the Vhembe district and the indigenous people within it (Pool-Stanvliet 2013; Pool-Stanvliet et al. 2018). As well as its rich cultural heritage, the Soutpansberg is a recognised Centre of Plant Endemism and Biological Diversity (van

Wyk & Smith 2001). The Soutpansberg is home to one third of Southern Africa's tree species (Hahn 2006) and is therefore an area of high conservation value (Hahn 2006; Mostert 2006).

2.3.2 | Lajuma Research Centre

Lajuma Research Centre is a Natural Heritage Site situated within the Luvhondo Nature Reserve, which forms part of the VBR. On site elevation ranges from 1150 m to the peak of Mount Lajuma at 1748 m, the highest point of the Soutpansberg (Coleman 2013). The geology on site is characterised by pink quartzite and sandstone, with acidic sandy and shallow soils, except within the mistbelt at the base of the southern slopes, where deeper peaty soils act like reservoirs, holding orographic mist and slowly releasing water to mountain streams (Mostert et al. 2008). Local climate conditions are mesothermal with distinct cool dry winter (April to September) and warm wet summer (October to March) seasons (Munyati & Kabanda 2009). Annual rainfall averages at ~724 mm, although is highly variable (Willems 2007).

2.3.3 | Flora and Fauna

The principal biomes present across the Soutpansberg are forest, savannah and grassland (Mucina & Rutherford 2006). At higher altitudes, montane grasslands dominate the plateaus, while south-facing ridges of the mountain range receive orographic mist and increased localised rainfall (Mostert 2006) which support high-canopy evergreen (mistbelt) forests at their base (Linden et al. 2015). Away from the ridges, the evergreen forest transitions into semi-deciduous woodland, thicket, grassland and intersecting riverine forest (Maltitz et al. 2003; Mucina & Rutherford 2006). The matrix of habitats is further fragmented by agriculture, commercial plantations and residential areas.

Flora on the Soutpansberg are highly diverse, comprising >50% of species present in Southern Africa (Hahn 2006). Vegetation at the study site is characterised by a complex mosaic of vegetation types (Maltitz et al. 2003; Mostert et al. 2008). Northern Mistbelt Forest, incorporating the Limpopo Mistbelt Forest and Soutpansberg Forest vegetation types, are evergreen Afrotemperate forests (Geldenhuys & Mucina 2006) confined to the southern slopes where soils are damp (Mostert et al. 2008). Afrotemperate forests are situated within South Africa's Afromontane region and contain 5.35% of South African plant species (Lötter & Beck 2004). Soutpansberg Moist Mountain Thicket vegetation type is characterised by a low closed thicket structure, with no definition between the tree and shrub layers, heights of between 1.5-4 m and >80% canopy cover (Mostert et al. 2008). Soutpansberg Mountain Bushveld has an open canopy woodland structure and vegetation is adapted to water stress and unpredictable rainfall (Mostert et al. 2008).

All five of South Africa's non-human primate species are represented at the study site, and samango monkeys are sympatric with vervet monkeys (*Chlorocebus aethiops*), chacma baboons (*Papio ursinus*), thick-tailed greater galago (*Otolemur crassicaudatus*) and southern lesser galago, (*Galago moholi*). Samango monkeys regularly forage in close proximity to other primates and crested guinea fowl (*Guttera pucherani*), rock hyrax (*Procavia capensis*), southern tree hyrax (*Dendrohyrax arboreus*), red forest duiker (*Cephalophus natalensis*), bushbuck (*Tragelaphus scriptus*), common warthog (*Phacochoerus africanus*) and banded mongoose (*Mungos mungo*). Frugivore diversity in Afrotemperate forests is typically low, with a higher proportion of avian rather than mammalian seed dispersers (Chapman et al. 2016). Samango monkeys are the largest arboreal mammal within the canopies of the Afrotemperate evergreen forests (Linden et al. 2015). As such, samango monkeys may be important primary dispersers for these forests through spitting and swallowing seeds or carrying seeds away from parent plants in cheek pouches. They may also facilitate secondary dispersal by other mammals by dropping partially consumed fruits under the canopy of fruiting trees (Seufert et al. 2010). The main predators of samango monkeys on site are leopards (*Panthera pardus*), crowned eagle (*Stephanoaetus coronatus*) and African rock python (*Python sebae*) (Coleman & Hill 2014).

2.4 | Study Groups

In this study I followed two groups of well habituated samango monkeys, “Barn” group, comprising approximately 40 individuals and “House” group, comprising approximately 60-70 individuals (Emerson et al. 2011; Coleman & Hill 2014; Nowak et al. 2014; Parker 2018), between December 2017 and May 2018. Both groups comprised one resident male, multiple females, and their sub-adult and infant offspring. Between March and May, four to six bachelor males joined both groups intermittently for the mating season. The monkeys have been studied since 2004 (Ian Gaigher, pers. comm.) and I was able to follow them at a minimum distance of five metres, using binoculars when they were high in the canopy. Guenons are difficult to identify, particularly in large groups and in montane, high-canopy environments (Coleman 2013; Linden et al. 2015; Parker 2018). Some individuals in both groups had been ear-tagged for a previous study (Russell Hill, pers. comm.) and others were recognisable through injuries and other novel features, however as data required for the present study focussed on group identity, I decided not to focus on recognisable individuals that might bias data collection.

2.5 | Focal Plant Species

Chapters 3 and 5 focus on three locally abundant fruit species commonly found in the diet of each samango monkey group. This selection was based samango monkey feeding preferences studies conducted during 2015 – 2017. Mean annual percentage of time spent feeding on each fruit species in the diet was calculated using data previously collected by the Primate and Predator Project, as described by Coleman (2013). From the list of 36 species samango monkeys were recorded as consuming, I subsequently selected the ten most consumed fruit species (Table 2.1).

Table 2.1 The ten fruit species most consumed by samango monkeys at Lajuma, South Africa 2015-2017 inclusive, calculated as mean annual percentage of time spent feeding.

Plant Species	Common Name	Percentage of Time Spent Feeding 2015 - 2017
Ficus sur	broom-cluster fig	9.43%
Ficus burkei	common fig	9.32%
Ficus cratestoma	forest fig	8.68%
Searsia chirindensis	red currant	7.13%
Celtis africana	white stinkwood	6.48%
Searsia pentheri	crowberry	6.01%
Trichilia dregeana	forest mahogany	5.32%
Syzygium cordatum	common water-berry	4.27%
Ekebergia capensis	Cape ash	3.57%
Rhoicissus tomentosa	forest grape	2.90%

From this list, focal species for this study were selected if (1) there were sufficient numbers of seeds found in faecal samples for two of the treatments in the germination experiments (Chapter 3), and (2) there were trees with enough fruit low enough for me to collect without arborist equipment for three of the treatments in the germination experiments. During this study, the fruiting seasons for *Celtis africana, Ekebergia capensis, Searsia pentheri* and *Rhoicissus tomentosa* commenced later than expected and there were not enough monkey-dispersed seeds or fruit for their use in this study. This was largely due to severe droughts (El Niño events) and extremely high temperatures during the rainfall seasons across southern Africa between 2014 and 2016 (Maponya & Mpandeli 2016; Archer et al. 2017; Kolusu et al. 2019). Samango monkeys did not consume *Trichilia dregeana* seeds and therefore this species could not be included in this study. There were sufficient seeds and fruits available within the timescale of this study from five fruit species; three *Ficus* spp., *Searsia chirindensis* and *Syzygium cordatum*. As such, the germination experiments (Chapter 3) and SDE analyses (Chapter 5) are focussed on these five species. The fruiting seasons of *S. chirindensis* and *S. cordatum* occurred only during the wet season and we collected data on *Ficus* spp. for only six weeks during the dry season. For this reason, we did not include seasonal effects of behaviour in any analyses. Further details on each of the species are given in Chapter 3 and images of the seeds are given in Appendix Fig. A.1.

2.6 | Data Collection

2.6.1 | Hardware and Software

Behavioural data were recorded on a Yoga Tab 3 tablet (Lenovo Group Ltd., Beijing, China) powered by Android 5.1 OS (Google Inc., Mountain View, California, USA), using Prim8 mobile behavioural data collection software (McDonald & Johnson 2014). Location data were collected using an eTrex10 GPS (Garmin International Inc., Olathe, Kansas, USA). Temperature (ºC) and relative humidity (%) were recorded at 30-min intervals in each seed nursery using Easy-Log USB 2+ data loggers (Lascar Electronics, Salisbury, UK). Supplementary data were recorded in paper notepads. All GPS data were downloaded onto a computer using Garmin Basecamp (Version 4.4.7, Garmin Ltd., Olathe, Kansas, USA) and converted to GIS compatible files.

2.6.2 | Faecal Sample Collection

Samango monkey faecal samples were collected between August 2017 and May 2018 from both groups. Data from these samples were used for seed germination experiments in Chapter 3 and for calculation of the quality component of the SDE framework in Chapter 5. The protocol for the collection, processing and storage of the faecal samples is detailed below. Faecal samples were also collected during the gut retention trials in Chapter 4. These samples were collected and processed using the same protocol, although were not stored or used in any other analyses.

Fresh faecal samples were collected *ad libitum* during daily follows by SS and by Primate and Predator Project research assistants, from all age-sex classes (for definition of age-sex classes, see section 2.6.5). Each sample was collected in a separate plastic bag and given a unique code consisting of the date, time, and group identity. The unique code and age-sex class of the individual were noted on the bag. Prior to collection, a photograph of the faecal sample was taken from waist height (approximately 1.2 m) and the photograph number noted on the collection bag. The location of the faecal sample was taken using GPS, recorded using the same unique identification code. Data from each bag were transferred to a spreadsheet (Excel Version 16.28 Microsoft Corporation, Washington, USA). Faecal samples were stored overnight in dark sealed plastic boxes to keep them cool and processed at dawn the following day. Between December 2017 and March 2018, before processing, faecal samples were checked for *Ficus* spp. or *S. chirindensis* seeds, with some samples being used without further processing for the Fertiliser Effect treatment in germination experiments, details of which are given in section 2.6.3 and Chapter 2.

Faecal samples not used as the Fertiliser Effect treatment in germination experiments were first washed then dried, and the contents identified, counted and stored for use in germination experiments. To wash a sample, it was transferred to a fine mesh net (<1 mm mesh) and gently washed in fresh water, piped directly from the forest, to remove digesta (Fig. 2.5). Once clean, the sample was laid out inside a cardboard tray marked with its unique identification code and air-dried inside a secure tent for 48 hours (Fig. 2.5).

Fig. 2.5 Processing samango monkey faecal samples by (A) transferring each sample to a fine mesh net, (B) rinsing away digesta in fresh water and (C) air-drying in a secure tent for 48 hrs.

Once the sample was dry, we collected all entire seeds and examined seeds greater than 2 mm diameter for damage visually, using a lens with 10x magnification and discarding those with visual damage to the seed coat or endocarp (Kunz & Linsenmair 2008). Seeds were identified using an extensive seed library located at Lajuma Research Centre. Seeds that could not be identified using the library were given a number and identified once the plant species from which it came was located and identified using an identification book (Coates-Palgrave 2002).

In total 783 faecal samples were recovered from samango monkeys, 48 of which did not have photographs and/or GPS data and were discarded. A further two samples contained no seeds. Collectively, the remaining 733 faecal samples contained 435,369 entire seeds of 42 different plant species (Table 2.2). Of these 26 were identified to be from 15 families; 23 were identified to species and 3 were identified to genus. There were 16 unidentified species. On average (mean ±SD) faecal samples contained 2.4 ±1.2 different species and 592 ±866 seeds per sample. The number of seeds of each species varied between faecal samples (Table 2.2).

Table 2.2 Mean (±SD) entire seeds per sample, range (min - max, where applicable), total number of seeds retrieved and number (n) of faecal samples containing each seed species recovered from samango monkey faecal samples August 2017-May 2018 inclusive at Lajuma, South Africa

Family *Species* (common name)	*n* Samples	Seeds Recovered		
		Mean/Sample	Range min-max	Total
Anacardiaceae (sumac)				
Searsia chirindensis (red currant)	215	20 (±33)	1 - 243	4,484
Searsia pentheri (crowberry)	60	94 (±144)	1 - 705	5,633
Searsia spp. (species unidentified)	20	8 (±16)	1 - 65	164
Apocynaceae (dogbane)				
Carissa bispinosa (forest num-num)	2	3 (±2)	1 - 4	5
Carissa edulis (climbing num-num)	80	4 (±4)	1 - 24	282
Rauvolfia caffra (quinine tree)	34	2 (±1)	1 - 4	53
Cannabaceae (hemp)				
Celtis africana (white stinkwood)	31	3 (±6)	1 - 34	100
Capparaceae (caper)				
Capparis fascicularis var. *fascicularis* (caper-bush)	80	5 (±5)	1 - 27	370
Fabaceae (legume)				
Pterolobium stellatum (red wing)	2	7 (±7)	2 - 12	14
Vachellia sieberiana var. *woodii* (paper thorn)	1	1(-)	NA	1

Table 2.2 Continued

Malvaceae (mallow)				
Grewia spp. (-)	1	1(-)	NA	1
Meliaceae (mahogany)				
Ekebergia capensis (cape ash)	118	3 (±4)	1 - 15	395
Moraceae (mulberry)				
Ficus spp. (fig)	718	593 (±855)	1 - 6,906	425,510
Myrtaceae (myrtle)				
Eugenia natalitia (forest myrtle)	2	1(-)	NA	2
Psidium guajuava (common guava)[a]	33	8 (±14)	1 - 77	268
Syzygium legatii (mountain water wood)	1	(-)	NA	1
Oleaceae (olive)				
Olea capensis (black ironwood)	1	1(-)	NA	1
Olea europaea subsp. *Africana* (wild olive)	1	2(-)	NA	2
Passifloraceae (passionflower)				
Adenia gummifera var. *gummifera* (monkey rope)	2	1 (-)	NA	2
Rhamnaceae (buckthorn)				
Ziziphus mucronata subsp. *mucronata* (buffalo thorn)	3	1(-)	NA	3
Rubiaceae (coffee)				
Afrocanthium mundianum (rock alder)	1	1(-)	NA	1
Keetia gueinzii (climbing turkey-berry)	44	5 (±4)	1 - 19	198
Sapotaceae (sapodilla)				
Englerophytum magalismontanum (Transvaal milkplum)	32	3 (±2)	1 - 9	91
Vitaceae (grapevine)				
Cyphostemma anatomicum (-)	14	2 (±1)	1 - 5	23
Rhoicissus rhomboidea (bastard forest grape)	16	3 (±3)	1 - 12	41
Rhoicissus tomentosa (wild grape)	218	6 (±6)	1 - 42	1,241
Unidentified				
Unidentified 1	2	3 (±2)	1 - 4	5
Unidentified 2	1	1 (-)	NA	1
Unidentified 3	1	3 (-)	NA	3
Unidentified 4	1	6 (-)	NA	6
Unidentified 5	9	5 (±6)	1 - 5	43
Unidentified 6	1	4 (-)	NA	4
Unidentified 7	16	4 (±4)	1 - 17	71

Table 2.2 Continued

Unidentified 8	4	3 (±2)	4 - 5	12
Unidentified 9	2	1 (-)	NA	2
Unidentified 10	69	54 (±116)	1 - 653	3,721
Unidentified 11	1	1 (-)	NA	1
Unidentified 12	1	3 (-)	NA	3
Unidentified 13	6	13 (±20)	1 - 51	78
Unidentified 14	4	5 (±2)	3 - 4	20
Unidentified 15	1	1 (-)	NA	1
Unidentified 16	3	3 (±2)	1 - 4	9

[a] Invasive species

2.6.3 | Germination Experiments

Seed germination experiments were conducted on the five species selected as previously described (Section 2.5) between December 2017 and May 2018. Data from these experiments were used in Chapter 3 and for calculation of the quality component of the SDE framework (Schupp 1993; Schupp et al. 2010) in Chapter 5. During reconnaissance follows with the monkeys, the primary method of dispersal by samango monkeys for *Ficus* spp. and *S. chirindensis* seeds was observed to be via ingestion and defecation. The monkeys were observed to drop partially consumed *Ficus* spp. fruit under the parent tree and spat out *S. chirindensis* seeds either under the parent tree or to a lesser degree, away from it following storage in cheek pouches. The monkeys spat out *S. cordatum* seeds under parent trees as they consumed the fruit, and occasionally away from the parent tree following storage in cheek pouches. Similar seed dispersal methods were observed at the study site during a previous study (Linden et al., 2015).

Germination experiments were conducted *in-situ* in purpose-built seed germination nurseries using an indigenous soil substrate. To avoid raiding from baboons, vervet monkeys, samango monkeys and other granivores, the nurseries were constructed close to human infrastructure. The site was an open area where there would be no shading effect from trees or other structures. Two germination nurseries were constructed by building two wooden frames and covering them with shade cloth. One was covered with 80% shade cloth (shaded) and the second was covered with 40% shade cloth (unshaded) (Fig. 2.6). We use shade cloth to emulate shaded conditions into which samango monkeys deposited seeds under closed (Shaded) and open (Unshaded) canopies. We used 40% shade cloth for the unshaded nursery to prevent the sun drying out and damaging the seeds. Preliminary investigations found that during heavy rainfall seeds were displaced from trays, so temporary rain covers that could be extended and retracted quickly were erected (Fig. 2.6).

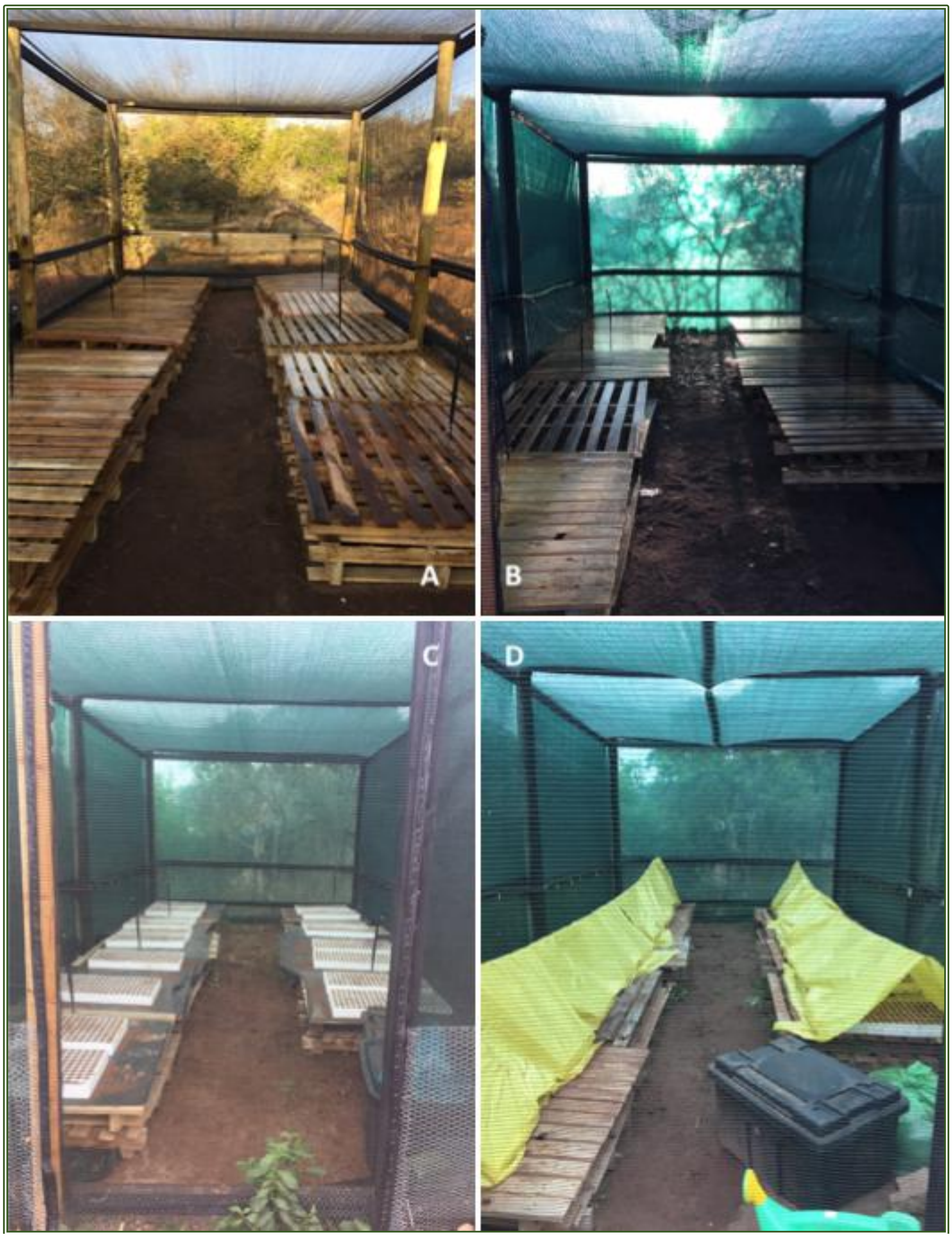


Fig. 2.6 (A) Unshaded and (B) Shaded seed nurseries with (C) seed trays and (D) rain covers used during torrential rainfall to prevent seeds washing away.

Germination trials were conducted with topsoil collected from a transitionary zone between the evergreen forest and semi-deciduous woodland. Sufficient soil was collected for all trials at once, in order to homogenise the substrate and eliminate inconsistencies in soil texture, porosity and chemical composition between trials. Soil was sieved using a

1 mm mesh to remove large particles, seeds and plant matter. The sieved soil was then mixed with quarry sand (5-part soil to 1-part sand) and stored in a covered black plastic container until required. Soil pH was analysed by the Agricultural Research Council, Institute for Soil, Climate and Water, Pretoria, South Africa, and was 6.76 and 6.52 in the shaded and unshaded nursery respectively. Temperature (ºC) and relative humidity (%) were recorded at 30-min intervals using data loggers (see 2.6.1) placed in the centre of each nursery 1 m above ground level (Table 2.3). Seeds were watered evenly every evening using water piped directly from the forest. In the shaded nursery, soil remained permanently moist for the duration of the germination trials. In the unshaded nursery, soil dried out daily between watering. Further methods related to germination experiments are given in detail in Chapter 3.

Table 2.3 Mean (±SD) temperature (ºC) and relative humidity (%) in each seed nursery, shaded (80% shade cloth) and unshaded (40% shade cloth)

Nursery	Mean Temperature (ºC)	Mean Relative humidity (%)
Shaded	19.67 (±5.98)	74.92 (±21.13)
Unshaded	20.72 (±7.66)	81.07 (±17.60)

2.6.4 | Gut Passage Time Trials

Gut passage time trials (Chapter 4) were conducted in February and May 2018 to estimate the time it takes seeds to pass through the gut of samango monkeys after swallowing. Beads made of two different natural materials (coconut shell or wood) were used as artificial digestive markers for this study. Plastic beads typically used in *ex-situ* studies were not used in this study to avoid environmental pollution from beads not recovered during the trials. Distinct marker types differing in material, colour (white, natural or dark) and shape (flat or round edged) were used for each trial. Preliminary trials were conducted in September 2017 to assess the resilience of natural markers to chewing and gut passage.

To avoid over-provisioning and minimise the monkeys' association between humans and food, which could endanger future observers, three preliminary trials were tagged onto giving up density experiments over three consecutive days. During these experiments, bowls filled with a substrate and a limited number of small (< 1 cm) food items were left at different heights within the canopy of the forest (Fig. 2.7); the methodology of which is given in detail by Nowak et al. (2014). Raisins were used as the vessel in which to hide the markers, although bananas were used in the study trials, as detailed in Chapter 4. Forty raisins containing markers were mixed into 30 bowls (3,600 markers in total) containing a sawdust substrate each morning at 07:30 and left until 16:30, when remaining raisins were recovered from the sawdust and counted. The group were followed each day of the preliminary trials and a fourth day following the trials, with as many faecal samples as possible collected. Faecal samples were also collected *ad libitum* from other group members to assess differences in marker resilience between individuals.

Fig. 2.7 Resident male 'Chief' of Barn group foraging at one of the GUD bowls used during the preliminary gut retention trials at Lajuma, South Africa, September 2017.

At the end of the trials, faecal samples were processed as described in section 2.6.2, with recovered markers checked for damage and retention of their colour and shape. The monkeys removed 41% of the raisins from the buckets and assuming each contained a marker that had been swallowed, 1, 478 markers had been ingested. During follows, 68 faecal samples were collected, six of which contained ten markers between them, meaning 0.7% of ingested markers were recovered. All retrieved markers were identifiable as their original colour and shape.

The preliminary trials demonstrated that without targeted provisioning of focal animals, it was impossible to detect which individual monkeys had ingested markers, which probably influenced the low number of recovered markers. It was also impossible to determine the exact time at which the markers were ingested, which is crucial to determining gut retention time. Furthermore, without targeted provisioning and subsequently following an easily recognisable individual, keeping track of the times of marker ingestion and faecal deposition of several monkeys, would require many more observers than were available.

In large groups guenons are difficult to identify (Coleman 2013; Linden et al. 2015; Parker 2018). The gut passage time trials were being conducted in a montane, high-canopy environment, potentially making it more difficult to be able to quickly recognise an individual and not lose sight of them. Therefore, methodology was refined to targeted provisioning of the resident male, 'Chief' from Barn group (Fig. 2.8). The comparatively large body size and sex-specific vocal repertoire (Fuller 2014) of adult males made Chief more distinguishable and easily recognisable than a female (for distinguishing identification features see section 2.6.5.1). The second trial in May 2018 took place during the monkeys' mating season and it became more difficult to quickly identify and keep up with Chief. For this trial, the only female with an ear tag from previous studies (Russell Hill, *pers. comm.*) was selected (Fig. 2.8). In the main gut passage trials (Chapter 4), a banana, which had been used in *ex-situ* studies, replaced the raisins as the marker delivery vessel. It was easier to push the markers into the soft flesh of the banana *in-situ*, ensuring all of the markers were taken into the mouth.

Fig. 2.8 The male monkey 'Chief' (A) and the female monkey 'OB' (B) used for the gut passage time trials (Chapter 4).

2.6.5 | Behavioural Sampling

Two different focal animal sampling (Altman 1974) methods were employed to collect data on specific elements of behaviour related to the SDE framework (Chapter 5); 15-min all occurrence focal animal sampling and 1-min fruit processing focal animal sampling

(Altman 1974). Behavioural data were collected between December 2017 and May 2018. Each samango monkey group was followed from dawn (between 05:30 in December and 06:00 in May) until dusk -1 hr (16:00 - 18:00). The monkeys were left at dusk -1 hr to allow time to water the seeds and assess seed germination in the nurseries before nightfall.

Each group was followed for between four and eight days per month (mean ±SD Barn 6 ±1.41, House 6.17 ±1.72 days) by either SS or a Primate and Predator Project research assistant. Inter-observer reliability was checked prior to the research assistants working alone by simultaneously recording a monkey's behaviour and calculating Cohen's kappa statistic (k), which assesses the chance agreement of two observers (Cohen 1960). Inter-reliability was assessed between SS and each of the research assistants: SS and Observer 1, $k = 0.93$; SS and Observer 2, $k = 0.81$, demonstrating excellent inter-observer reliability of behavioural data recording (Kaufman & Rosenthal 2009). In total, Barn group were followed for 36 days and House group for 37 days. Both groups were followed simultaneously on 20 of these days. During follow days, focal animal sampling (Altmann 1974) was employed to gather detailed information on feeding behaviour. Below are described the methods employed for each of the focal sampling techniques, with further details on how these data were used given in Chapter 5.

2.6.5.1 | All Occurrence Focal Animal Sampling

Behavioural data were collected for time budget analysis and to calculate the quantity component of the SDE framework (Chapter 5). Preliminary observations found that a 15-min sampling time to be the optimal duration in which individuals could be intensely followed without losing them. Behavioural data were collected using two 15-min focal animal time samples with all-occurrence recording (Altmann 1974) per hour. Total focal observation time for each group was 191.92 hrs for Barn group and 200.55 hrs for House group.

Behavioural data were collected only from adult and sub-adult individuals (Table 2.4), as they were more accustomed to observers and easier to observe than juveniles and infants. Sex was determined only for adults. To avoid sampling bias toward certain individuals or proportion of the group, focal individuals were selected farthest away from the previous. Resident males were sampled only once before and after 12:00 to avoid oversampling. On occasions where we lost the focal animal before two thirds (600 secs) of observation time, we discarded the observation data, selected a new individual and began the sampling period again. If the focal individual was lost after 600 secs, observation data were retained, and the observation recorded as successful. In total, 36/1596 observations were discarded on 16 occasions for Barn group and 20 occasions for House group.

Table 2.4 Identifying features of age-sex classes for samango monkeys at Lajuma, South Africa.

Age-Sex Class	Identification Features	
	Physical	Behavioural
Adult Male	Comparatively larger body size than female (~7 kg) with a muscular physique, long canine teeth and prominent genitalia	Low-frequency territorial 'boom' calls and loud repetitive 'pyow' alarm calls[a]
Adult Female	Comparatively smaller body size than male (~4.4 kg) with a slenderer build and prominent mammary glands	Antagonistic towards females in neighbouring groups[b]; often nursing infants or juveniles
Sub-Adult	Smaller in size than adult females, although mature sub-adults can be of similar size to adult females, with less prominent genitalia (males) or undeveloped mammary glands	Often playful, smaller individuals remain outside of antagonistic between-group encounters[c]
Juvenile	Comparatively smaller body size than preceding age-sex classes with no obvious genitalia or mammary glands, fluffy coat and infant-like facial characteristics	Often playful with other juveniles; inquisitive and cautious towards observers
Infant	Comparatively smaller than juveniles, with darker coat	Most often with mother and rarely by itself

[a] Fuller 2014; [b] Butynski 1990; [c] Cords 2002

During each follow day, the location of the group was recorded at 15 min intervals using a GPS and behavioural data were collected on a tablet using the Prim8 mobile behavioural data collection software (section 2.6.1). The Prim8 application enabled continuous time-stamped data collection and recorded the duration of each behaviour at a scale of one second. At the start of each 15-min focal sample, the application recorded the date and time. Prior to the sampling period, the application was set up for recording age-sex class (Table 2.4) and group identity of the focal individual. The application was also set up using an ethogram to record general activities (Table 2.5), followed by categorical information related to items consumed (Table 2.6). In addition, when consuming fruit, the plant species was also recorded.

Table 2.5 Ethogram of general behaviours recorded during 15-min focal samples on samango monkeys at Lajuma, South Africa.

Activity	Definition
Feeding	Actively processing food items in the mouth, handling or transferring from hand to mouth, or removing item from substrate with mouth
Resting	Remaining still lying, sitting or standing not displaying behaviour related to feeding or socialising
Socialising	Engaging in physical contact with another, through grooming, fighting or feeding infant
Travelling	Moving along any surface without behaviours related to feeding or socialising
Lost Group	Entire group out of site due to relocating during the night, entering inaccessible land over, for example, high fencing, or traversing a cliff
Lost Focal Subject	Subject out of site due to traversing a cliff, travelling faster than the observer can keep up with, or with a group indistinguishable.
View Obstructed	Location of subject known but behaviour unreportable due to view being obstructed e.g. branches/leaves, cliffs, or too high in canopy

Table 2.6 Food item categories recorded additional to feeding behaviour during 15-min focal samples on samango monkeys at Lajuma, South Africa.

Food Item	Description
Cheek Pouch	Actively moving stored food items from cheek pouch to mouth, using either the tongue or hands, and processing
Flowers	Consuming inflorescence from trees or shrubs, excluding grasses
Fruit	Consuming fleshy or non-fleshy fruits from trees or shrubs, by placing item into the mouth or cheek pouch; species recorded
Leaves	Consuming greenery from trees or shrubs; excludes any other plant part
Seed Pod	Processing seed pods usually from Acacia trees, includes consuming seeds removed from pods

Table 2.6 Continued

Other	Bark: consuming woody parts of trees or shrubs, excluding removing bark to search for invertebrates
	Fungi: consuming any form of fungi including mushrooms and tree fungi
	Grass: consuming any part of grasses - leaves, stems, flowers or seeds
	Invertebrate: consuming invertebrates off the ground, plants, or under bark
	Tree sap: licking sap or other tree exudates, usually from pre-gouged trees
	Water: drinking water from tree holes, streams or human infrastructures

2.6.5.2 | Fruit Processing Sampling

Data were collected on fruits consumed per minute using 1-min focal animal sampling (Altmann 1974). These data were used to estimate seeds either spat or swallowed per minute as part of the quantitative component of the SDE framework (Chapter 5). Fresh fruit from focal plant species were collected from plants, dissected, and mean seeds per fruit calculated. One-minute focal sampling was undertaken during follow days and in-between the 15-min focal animal sampling. As before, only adult and sub-adult monkeys were targeted, although group identity was not considered. On occasions when the focal animal was lost, or the view of feeding behaviour obstructed, a different individual was selected, and the observation restarted.

During each minute focal sample, the number of *S. chirindensis* and *S. cordatum* fruits taken into the mouth, and the number of seeds expelled from the mouth, were recorded. As *Ficus* spp. and *S. chirindensis* seeds were recovered from samango monkey faeces, it was assumed that seeds not expelled from the mouth during the observation were swallowed. For *S. chirindensis,* seeds swallowed per minute was calculated as fruits consumed minus seeds spat. Broom-cluster figs were too large for the fruits to be consumed whole, and unless they were very ripe, other fig species were also only partially consumed. As such, partially consumed fruit were collected as they were dropped by the monkeys and the proportion of fruit consumed recorded as 25%, 50% or 75% (or 100% if no flesh was expelled), and therefore proportion of dropped (spat) fruit as 100% minus proportion consumed. Mean seeds per minute was calculated as the product of mean seeds per fruit and mean proportion of fruit either dropped or consumed. No *S. cordatum* seeds were recovered from faeces and therefore seed-swallowing was not included for this species, and it was assumed that the difference between the number of fruits consumed and seeds expelled were stored in cheek pouches or spat outside of the observation.

2.7 | Data Analysis

All statistical analyses were conducted using R (R Core Team 2018). All GIS analyses were conducted using QGIS (Version 2.6, QGIS Development Team 2014) and a satellite image base map (Microsoft Corporation 2019). Location data were projected into Universal Transverse Mercator coordinate system (WGS 1984, Zone 35s).

2.7.1 | Seed Germination

Probability of germination and germination latency were analysed using Generalised Liner Mixed-Effect Models (GLMMs) using the lme4 package (Bates et al. 2015). Recent reviews recommend GLMMs as the preferred method of analysis for germination data (Sileshi 2012). The model allows analysis of nested designs such as the dichotomous shading effect, as well as allowing for non-normal distributions of the response variable and random effect specification (Schupp 1993; Bolker et al. 2009). In all cases, the model included seed treatment (four or five levels depending on species) and the interaction between treatment and shading (two levels, shaded and unshaded) as fixed effects. Trial nested in shading (or nursery) was included as a random effect to control for spatiotemporal variation across trials, as trials were sown at different times due to accessible fruit availability. Model parsimony was tested against a reduced model that omitted the interaction term, followed by a null model of the random effect only, using a likelihood ratio test. Optimal model adequacy was assessed by examining standard residuals vs. fitted residuals and graphical distribution of errors. Wald Chi-Square tests were conducted to determine the significance of the fixed effects at $\alpha = 0.05$. To isolate the effects of the different treatments on seed germination, Least-Squares Means analysis of the final model were conducted using the emmeans package (Lenth 2018) and pairwise Tukey' HSD comparisons were conducted using the multcomp package (Hothorn et al. 2008), to compare treatments to control seeds.

2.7.2 | Behaviour

Gut passage time was calculated as time (hh:mm) since ingestion for each recovered faecal sample that contained markers. Feeding behaviour and diet composition were calculated as the mean proportion (%) of time per day focal animals consumed each food type or species over total observation time (feeding) or total feeding time (diet composition) per day.

2.7.3 | Daily Path Length and Home Range

Mean daily path length was estimated by converting locations recorded during each follow day to paths. Home range and daily ranging area were calculated for each group using nearest neighbour (k = 3) minimum concave polygons (MCaP) using the 'ConcaveHull' plugin (Moreira & Santos 2007) in QGIS. Minimum Convex Polygon (MCP) analysis is more frequently used in home range analysis than MCaP (Vieira et al. 2019), however this method has a tendency to over-estimate home range, as it is sensitive to sample size and outliers, assumes the home range is a convex polygon, and therefore includes areas unused by the subjects (Burgman & Fox 2003; Vieira et al. 2019). In contrast, MCaP analysis creates a polygon of concave edges, thereby encompassing fewer unused areas (Marzluff et al. 1997; Fernández et al. 2009). Initial analysis using MCP analysis did in fact include areas that the monkeys did not use during this study (Fig. 2.9) and thus overestimated home range, most notably for House group, and therefore MCaP was deemed most suited for this study.

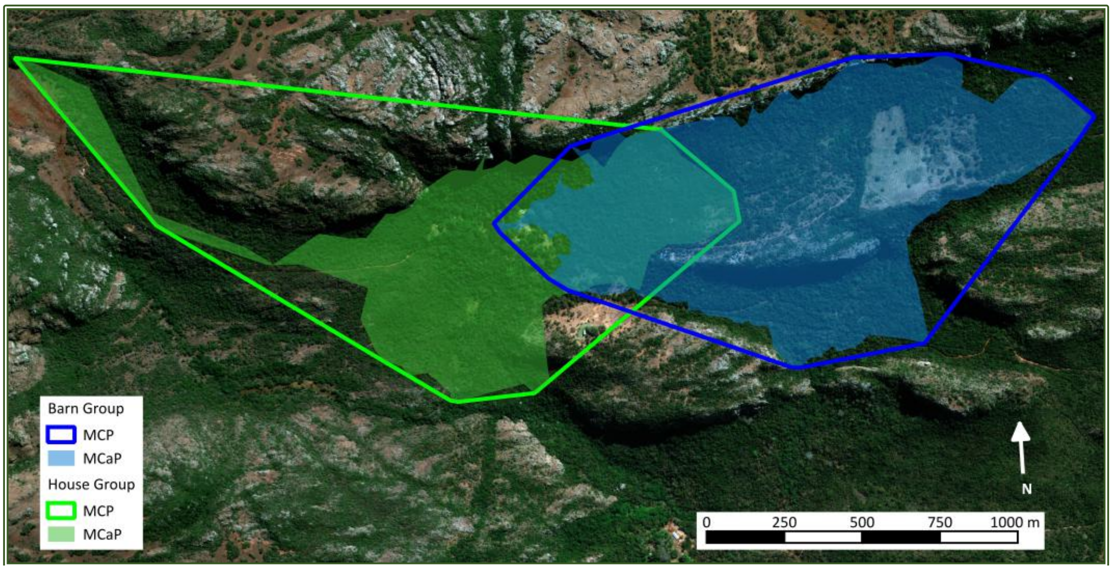


Fig. 2.9 Comparison between Minimum Convex Polygon (MCP, outline) and Minimum Concave Polygon (MCaP, shaded) analyses of home range estimation for two samango monkey groups (Barn, blue and House, green) at Lajuma, South Africa December 2017-May 2018 inclusive.

2.7.4 | Seed Dispersal Effectiveness

The SDE is calculated as the product of the quantity of dispersal and the quality of dispersal (Schupp 1993; Schupp et al. 2010). Dispersal quantity is determined by the number of seeds dispersed per unit of time (Schupp 1993). Dispersal quality is determined by the probability that dispersal produces a new adult (Schupp 1993). Dispersal quality is typically measured as the product of the effect of seed handling on germination and the quality of seed deposition into microsites which favour survival and growth (Schupp 1993; Schupp et al. 2010).

In this study, the dispersal quantity was calculated as mean seeds dispersed per day, as this unit of time was most suited to the data recorded during daily follows. Mean seeds dispersed per day was calculated as the product of mean daily time spent feeding on each fruit species and mean seeds either spat or swallowed per minute (section 2.6.5). Mean daily time spent feeding was calculated as the product of the proportion of time during focal sampling each day consuming each fruit species and the actual day length at the study site (time zone Bravo, UTC+2; Geoscience Australia 2010).

For gut-passed seeds, the qualitative component was calculated as the product of the probability of seed germination from Chapter 3 and proportion of faecal samples deposited on a suitable soil substrate as identified from the photographs taken during faecal sample collection. Each photograph was coded as either soil (soil, leaf litter on soil or in between exposed tree roots), where germinated seeds would be able to establish without additional extraneous factors such as secondary dispersal, or other (rocks, tree branches, leaf litter on rocks, roads or heavily compacted soil on tracks), where seeds would require additional extraneous factors to establish following germination. For spat seeds, the qualitative component was the probability of germination only.

Chapter 3

Interpreting the role of frugivores in seed germination potential depends on study design: A case study from Soutpansberg Mountain, South Africa

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In this chapter, I assess the influence of samango monkey seed processing mechanisms on seed germination, using all ecologically relevant treatments and an appropriate control group of entire fruits. These data will also be used as part of the quality component of the SDE framework in Chapter 5.

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[1] Author contributions: SS, RH, LS, SD and NK conceived and designed the experiments. SS performed the experiments. SS and BL collaborated in seed nursery design, construction, and seed identification; SS, RH, LS and NK designed analyses; SS analysed the data and wrote the manuscript; RH, LS; SD, BL and NK revised manuscript drafts.

Abstract

Frugivory and seed dispersal contribute to the maintenance and regeneration of plant communities through transportation of seeds and enhancing germination through seed processing mechanisms. The effects of frugivore seed processing mechanisms on seed germination are well studied and the potential benefits include disinhibition (pulp removal), scarification (gut passage) and fertilisation (from faecal matrix). Nevertheless, in a review of studies on mammalian seed dispersers we found that there is bias in the experimental treatments included in seed dispersal studies, through exclusion of entire fruit control groups and the fertiliser effect. In this study, we aimed to assess the effect of such bias on the role of a seed disperser by using ecologically relevant experiments to investigate the influence of seed processing mechanisms on germination probability and latency of three locally abundant plant species, common in the diet of samango monkeys (*Cercopithecus albogularis schwarzi*), that are both seed-spitters (disinhibition) and seed-swallowers (gut-passage and fertiliser effects). We designed experiments to isolate the cumulative effects of seed processing mechanisms and tested the effects of five treatments and one control treatment (entire fruit). We further assessed if exclusion of ecologically relevant seed treatments or relevant controls would affect our interpretation of the impact of the disperser on seed germination. Comparing gut passage and disinhibition indicated negative effects, whereas comparing gut passage and entire fruit controls indicated neutral effects in one species. Compared to gut passage alone, the fertiliser effects indicated positive or neutral benefits on germination probability. Our study demonstrates

that the impacts of frugivores on germination may be under- or over-estimated in ecological literature where relevant treatments and meaningful controls are excluded.

3.1 | Introduction

Frugivory and seed dispersal form an important mutualistic relationship (Farwig & Berens 2012). Across many habitats, plants rely on frugivores to disperse seeds away from the parent (Janzen 1970; Connell 1971) and enhance germination and seedling establishment (Terborgh et al. 2002; Traveset et al. 2007). Germination experiments have been vital in understanding the role that vertebrate dispersers play in seed dispersal effectiveness (Schupp et al. 2010) and thus the contribution of frugivory to the maintenance and regeneration of plant communities (Janzen 1970; Howe & Smallwood 1982; Traveset et al. 2007). The effectiveness of a disperser depends on the quality of dispersal (the probability of seed germination and survival to reproduction) and quantity of seeds dispersed (Schupp 1993). The quality of dispersal refers to any potential enhancement of germination through seed processing mechanisms, such as passage through the gut of the disperser (Schupp 1993; Schupp et al. 2010; Traveset 1998), which are extrinsic to deposition into microsites favourable for germination and survival (see Chapter 1, Section 1.3).

The effects of frugivore seed processing mechanisms on seed germination are well studied (Traveset 1998; Traveset et al. 2007; Fuzessy et al. 2016) and directly affect seed germination in three ways (Traveset & Verdú 2002). Firstly, removal of fruit pulp (*the disinhibition effect*) releases seeds from chemicals that inhibit germination and decrease the risk of fungal-mediated mortality (Traveset & Verdú 2002). Secondly, passage through the gut or fine oral processing can enhance germination by breaking seed dormancy through mechanical and chemical scarification of the seed coat (*the scarification effect*) which, in addition to releasing the seed from inhibiting chemicals through pulp, may increase its permeability to water and gases (Traveset & Verdú 2002; Baskin & Baskin 2014). Thirdly, the faecal matrix can enhance seed germination through a fertilising effect, or can have a lethal effect by facilitating the growth of fungus and/or bacteria *(the fertiliser effect)* (Traveset & Verdú 2002; Traveset et al. 2007). The majority of studies focus on the effect of gut passage, reporting an increase in the number of seeds germinating and decrease in latency to germinate (time from seed deposition to germination) (e.g. Petre et al. 2015; Muñoz-Gallego et al. 2019). However, despite previous calls for ecologically valid comparative experiments to ascertain the effect of processing mechanisms and the importance of entire fruits as controls (e.g. Samuels & Levy 2005), there is still a prominent bias in the comparative treatments included in seed dispersal studies (Fuzessy et al. 2016).

It has been 14 years since Samuels and Levey (2005) posed the question *'Do germination experiments answer the questions they ask?*', highlighting the importance of choosing appropriate treatments to answer questions about the effectiveness of gut passage on seed dispersal. At that time 77% of studies used the comparison between germination of gut-passed and manually extracted seeds in their study design. We therefore conducted a review of the literature since 2005, restricting our search to mammals only, to assess whether studies are now appropriately designed to answer such questions. We used the following search terms in a Web of Science topic search (which includes title, abstract and keywords) for the period January 2005 to May 2019: GERMINATION, SEED, EXPERIMENT OR DISPERS*, "GUT PASSAGE" OR "SEED HANDLING" OR SPIT*. The results were then systematically sorted and studies on mammals extracted for analysis. Whilst noting that the review was not exhaustive, the search generated 212 papers in total, 69 of which investigated the likelihood of seed germination following spitting by, or passage through the gut of, mammal seed dispersers (Appendix Table A.1).

Of these 69 studies 62% used the disinhibition effect, rather than entire fruit, as the control treatment. Of the 59 studies investigating dispersal of fleshy-fruit seeds, 76% omitted entire fruit controls. Of the 66 studies investigating dispersal via gut passage 76% excluded the fertiliser effect of faecal matrix. Furthermore, only 9% of studies included manual, chemical and/or mechanical scarification of de-pulped seeds along-side gut-passed seeds, which would isolate the effect of scarification processes. Without differentiating each fundamentally different mechanism, the absolute effect of frugivores on seed germination is confounded (Samuels & Levey 2005; Robertson et al. 2006; Baskin & Baskin 2014) and these studies are weakened in their conclusions.

Therefore, it is important to consider all processes and include entire fruits as a control group to estimate describe the role of frugivores in seed dispersal.

An additional issue in the literature is that many experiments are conducted *ex-situ* in laboratories (e.g. Kankam and Oduro 2012; Lessa et al. 2013), growth chambers and incubators (e.g. De Carvalho-Ricardo et al., 2014; Maldonado et al., 2018), while few studies (e.g. Chen et al., 2016; Sánchez de la Vega and Godínez-Alvarez, 2010) conduct germination experiments in the field where natural environmental conditions fluctuate. Experiments conducted in controlled conditions often report that the effect of gut passage on seed germination is consistently higher than controls, whilst in field experiments, studies most often report no significant difference (Fuzessy et al. 2016), highlighting the importance of well-designed and controlled *in situ* studies.

Therefore, the aim of our study was two-fold. First, we investigate the effect of seed processing mechanisms by a vertebrate disperser on seed germination using all ecologically relevant seed treatments. Secondly, we assess if a biased study design, excluding one or more of those treatments, would under- or over-estimate such a role. Specifically, how would our interpretation of the role of our frugivore in seed dispersal change if we excluded entire fruits as control groups and/or the fertiliser effect from our experiments, as is often the case in the literature.

In this study we focussed on a species of guenon monkey (*Cercopithecus albogularis schwarzi*) as they make an ideal model species for seed dispersal studies for several reasons. First, primates typically comprise a major fraction of the frugivore biomass in the areas in which they are found (Eisenberg & Thorington 1973; Terborgh 1983; Chapman 1995), therefore consuming a large fraction of the fruit biomass (Chapman & Onderdonk 1998; Balcomb & Chapman 2003). Primates process fruit in different ways and can be classified as seed-swallowers, seed-spitters and seed-destroyers (Corlett & Lucas 1990). The majority of primates species are seed swallowers (Lambert 1999; Clark et al. 2002; Dominy & Duncan 2005) typically able to disperse relatively large seeds through ingestion (Fuzessy et al. 2018), however *Cercopithecinae*, or the cheek-pouched monkeys (Grubb 2003), are unique in that they display multiple seed-processing mechanisms. Guenons are seed-swallowers of seeds smaller than 4 mm (on longest axis), seed-spitters of seeds larger than 4 mm (Lambert 1999; Gross-Camp & Kaplin 2011; Linden et al. 2015) and seed destroyers as they can crush seeds during oral processing of fruits and often consume unripe fruits (Wrangham et al. 1998; Lambert 1999). Mechanical and chemical scarification of seeds during oral processing may have similar effects to the scarification effects during gut passage, though to a lesser degree (Anzures-Dadda et al. 2016), or may have only a disinhibitory effect through pulp removal. Cheek pouches are used to store food and contain a high level of α-amylase, a saliva enzyme involved in pre-digestion breakdown of starch (Murray 1975). These cheek pouches can hold the same volume as the stomach when full (Rowell & Mitchell 1991) and therefore allow for the potential transport of twice as many seeds. As such, seed-spitting by guenons may be as important as seed-swallowing in terms of seed dispersal (Corlett & Lucas 1990).

Secondly guenons have a broad distribution from Ethiopia to South Africa (Lawes 1990; Grubb 2003) and are highly frugivorous, with more than 50% of their diet consisting of fruit (Lawes 1991; Chapman et al. 2002). In South Africa, samango monkeys are the only forest-dwelling primate, highly dependent on high-canopy evergreen forest (Linden et al. 2015), and are the only large-bodied arboreal species that feed on medium to large sized fruits in the canopy layer of South Africa's evergreen forests (Coleman & Hill 2014a; Linden et al. 2015, 2016). As such, the loss of samango monkeys could have negative cascading effects on the forests in which they reside.

We designed our germination experiments to isolate the effects of processing mechanisms on germination success. We selected three locally abundant plant species, common in the diet of samango monkeys (Coleman 2013; Linden et al. 2015), that represented different seed processing mechanisms, and tested the effects of five treatments that represented biological processes and one control treatment (entire fruit). The treatments were the disinhibition effect (simulating spitting and isolating pulp removal), scarification effect (simulating gut passage and isolating the mechanical effects of gut passage), gut passage effect (collected from faeces and isolating the chemical effect of gut passage) and the fertiliser effect (sown in faeces and isolating the effect of the faecal matrix). We also tested the added effect of seed desiccation following the disinhibition effect for one species, to simulate dispersal into dry habitat.

3.2 | Methodology

3.2.1 | Field Experiments

3.2.1.1 | Study Area

We conducted germination trials between January and May 2018 at the Lajuma Research Centre (29°26'E, 23°01'S) in the far western Soutpansberg mountain range of South Africa's Limpopo Province. The Soutpansberg has an altitudinal range between 1150 to 1750 m and local climate conditions are mesothermal with distinct cool dry winter (April to September) and warm wet summer (October to March) seasons (Munyati & Kabanda 2009). Vegetation at the study site is characterised by a complex mosaic of vegetation types including Limpopo Mistbelt Forest, Soutpansberg Moist Mountain Thickets and Soutpansberg Mountain Bushveld (Maltitz et al. 2003; Mostert et al. 2008). The south-facing ridges of the mountain range receive orographic and increased localised rainfall (Mostert 2006) which support high-canopy evergreen forests at their base (Linden et al. 2015). Away from the ridges, the evergreen forest transitions into semi-deciduous woodland, thicket, grassland and intersecting riverine forest (Maltitz et al. 2003; Mucina & Rutherford 2006).

3.2.1.2 | Study Species

In this study we followed two groups of well habituated samango monkeys, "Barn" group, comprising approximately 40 individuals and "House" group, comprising approximately 60-70 individuals (Emerson et al. 2011; Coleman & Hill 2014a; Nowak et al. 2014), between December 2016 and May 2017. Both groups comprised one resident male, multiple females, and their sub-adult and infant offspring. Between March and May, four to six bachelor males joined both groups intermittently for the mating season. The monkeys have been studied since 2004 (Ian Gaigher, *pers. comm.*) and we were able to follow them at a minimum distance of five metres, using binoculars when they were high in the canopy.

For germination experiments, we selected fruiting tree species based on samango monkey feeding preferences in the preceding years (2015 – 2017 inclusive). We calculated the annual proportion of fruit species in the diet using data collected by the Primate and Predator Project, as described by Coleman (2013), subsequently selecting the ten most consumed fruit species, in terms of proportion of time spent feeding. We also took into account the ways in which the monkeys disperse the seeds, as well as the fruiting season of the trees, ensuring we were able to collect sufficient quantities of monkey-dispersed seeds and fresh ripe fruits for controls and manipulated treatments. Based on these criteria, we selected three *Ficus* species, *Ficus burkei* (common wild fig), *Ficus craterostoma* (forest fig), *Ficus sur* (broom-cluster fig), and two other species, *Searsia chirindensis* (red currant, formerly *Rhus*) and *Syzygium cordatum* (water berry) (Table 3.1). We observed the primary method of dispersal by samango monkeys for *Ficus* spp. and *S. chirindensis* seeds to be via ingestion and defecation. Monkeys dropped partially consumed fruit under the parent tree and, to a lesser degree, spat out seeds either under the parent tree, or away from it following storage in cheek pouches (Linden et al., 2015). Monkeys spat *S. cordatum* seeds under the parent tree as they consumed the fruit, and occasionally away from the parent tree following storage in cheek pouches. Seeds of *Ficus* spp. and *S. chirindensis* are orthodox and can withstand desiccation whilst *S. cordatum* seeds are recalcitrant and are sensitive to desiccation (Roberts 1973; Royal Botanic Gardens Kew 2017).

Table 3.1 Plant and samango monkey dispersal traits, seed morphology and germination information reported in the literature for species used in our germination experiments.

Species[a]	**Plant & Dispersal Traits**			**Mean Dimensions mm (± SD)**		
Scientific Name (Family) Common Name | Local Venda Name	**Habitat**[b]	**Typical Fruiting Period**[b]	**Samango Dispersal (% Diet)**[c]	**Fruit H x W**	**Seed H x W**	**$\bar{x}$ no. seeds**
Ficus burkei (Miq.) Miq. (Moraceae) common wild fig | Muumo	Woodland / Wooded Grassland	Year Round	Ingest /Spat (9.32%)	12.08 x 10.56 (±1.67 x 1.76)	genus $\bar{x}$ 1.25 x 0.82 (± 0.11 x 0.09)	122 (±44)
Ficus craterostoma Warb. ex Mildbr. & Burret (Moraceae) forest fig | Tshikululu	Evergreen Forest (Strangler Fig)	Aug - Dec (Variable)	Ingest /Spat (8.69%)	14.11 x 12.04 (±0.9 x 1.03)		180 (±59)
Ficus sur Forssk. (Moraceae) broom cluster fig | Muhuyu	Forest / Riverine Fringes / Open Woodland	Sep - Mar (Variable)	Ingest /Spat (9.43%)	29.35 x 33.17 (±4.23 x 6.06)		795 (±319)
Searsia chirindensis[d] (Baker f.) Moffett (Anacardiaceae) red currant | Muvhadela-phanga	Open Woodland to Mountain Scrub & Forest	Nov - Feb	Ingest /Spat (7.13%)	3.8 x 4.07 (±0.42 x 0.45)	3.37 x 3.97 (± 0.45 x 0.44)	1
Syzygium cordatum Hochst. Ex C.Krauss (Myrtaceae) water berry | Mutu	Occurs Near Water in Variety of Habitats	Dec - April	Spat (4.27%)	13 x 9.14 (±1.28 x 1.01)	8.93 x 6.64 (± 1.59 x 1.07)	1

[a] *Ficus* spp. seeds and entire fruit controls were selected randomly from these three species as we were unable to identify seeds retrieved from faecal samples to species

[b] Coates-Palgrave 2002; [c] 2015 – 2017, based on data collected as described in Coleman 2013; [d] Formerly *Rhus chirindensis* Moffett 2007

Table 3.1 Continued

Species[a]	**Published Seed Data**		
Scientific Name (Family) Common Name | Local Venda Name	**Desiccation Tolerance**	**Germination**	
		Time (days)	**Proportion (%)**
Ficus burkei (Miq.) Miq. (Moraceae) common wild fig | Muumo	genus - Orthodox [e]	genus - 42 – 70 [e]	genus - 64 – 100 [e]
Ficus craterostoma Warb. ex Mildbr. & Burret (Moraceae) forest fig | Tshikululu			
Ficus sur Forssk. (Moraceae) broom cluster fig | Muhuyu			
Searsia chirindensis [i] (Baker f.) Moffett (Anacardiaceae) red currant | Muvhadela-phanga	Orthodox [f]	35 – 56 [g]	not available
Syzygium cordatum Hochst. Ex C.Krauss (Myrtaceae) water berry | Mutu	Recalcitrant [h]	18 – 40 [i]	90 - 99 [i]

[d] Formerly *Rhus chirindensis* Moffett 2007; [e] Royal Botanic Gardens Kew 2017 Data only available for *Ficus sur*; 100% of 52 known taxa of genus *Ficus* are Orthodox. [f] Royal Botanic Gardens Kew 2017 Data not available for *S. chirindensis*; 100% of 8 other *Searsia* taxa are Orthodox.; [g] South African National Biodiversity Institute (SANBI) 2008, http://pza.sanbi.org/searsia-chirindensis. Accessed March 2017; [h] Royal Botanic Gardens Kew 2017; [i] Wilson and Downs 2012 Seeds soaked 24hrs prior to sowing

3.2.1.3 | Germination Experiments

Seed Treatments. We applied five seed treatments that isolated specific biological processes, and a control (Control) of entire fruits for each seed species (Table 3.2). The control, in which seeds were left unchanged, allowed us to isolate the effect of the second treatment and fully evaluate the effect of seed handling mechanisms on germination (Samuels & Levey 2005; Baskin & Baskin 2014). The second treatment replicated the disinhibition effect (Disinhibition) of pulp removal either in the mouth or following gut passage, and allowed us to isolate the effects of seed-spitting and the chemical and/or mechanical effects of gut passage in proceeding treatments (Traveset & Verdú 2002; Samuels & Levey 2005; Fuzessy et al. 2016). The third treatment isolated mechanical scarification (Scarification) during oral processing and passage through gut from the first treatment and additional chemical scarification in the third treatment (Baskin & Baskin 2014). The fourth treatment was the gut passage effect (Gut-Passage), which allowed us to isolate the chemical processes that alter the seed during gut passage from the pulp removal and mechanical scarification effects of the second and third treatments respectively (Traveset & Verdú 2002; Samuels & Levey 2005). The fifth treatment was the fertiliser effect (Fertiliser) which allowed us to isolate the effect of the faecal matrix and measure the gut passage effect separately (Traveset & Verdú 2002). We only used the fourth and fifth treatments with *Ficus* spp. *S. chirindensis* seeds, as *S. cordatum* were not swallowed by samango monkeys. Lastly, the sixth treatment measured the added effect of desiccation following disinhibition on *S. cordatum* seeds (Desiccation), which we used to simulate dispersal into unfavourable dry habitats, with a potentially negative effect on germination, as these seeds are recalcitrant (Roberts 1973; Royal Botanic Gardens Kew 2017). Hereafter, we refer to treatments as Control, Disinhibition, Scarification, Gut-Passage, Fertiliser and Desiccation.

Table 3.2 Seed processing treatments of three samango monkey-dispersed fruit species used in our germination experiments, including the number of seeds sown and number and duration of trials.

Treatment / Effect	Description / Seed Source	Species	Trials/Seeds in Each Nursery		
			Number of Trials	Length (days)	Seeds/ Trial[a]
Control	Entire fruit, no treatment. Fresh ripe fruit collected from different trees for each trial.	*Ficus* spp.	5	105	40 fruits
		Searsia chirindensis	5	62	20 fruits
		Syzygium cordatum	4	102	20 fruits
Disinhibition	Manual removal of seed from pulp and sown within 24 hrs / fresh ripe fruit collected from different trees for each trial.	*Ficus* spp.	5	105	40
		Searsia chirindensis	5	62	20
		Syzygium cordatum	4	102	20
Scarification	Manual removal of pulp and seed coat damaged by rubbing once along 100 mm length of medium-coarse sandpaper. Fresh ripe fruit collected from different trees for each trial.	*Ficus* spp.	5	105	40
		Searsia chirindensis	5	62	20
		Syzygium cordatum	4	102	20
Gut-Passage	Seeds collected from fresh faeces after passage through the monkeys' gut and washed in untreated water.	*Ficus* spp.	5	105	40
		Searsia chirindensis	5	62	20
Fertiliser	Seeds left in freshly collected faecal matrix after passage through the monkeys' gut and sown into the soil.	*Ficus* spp.	5	105	20
		Searsia chirindensis	4	62	16 - 20

Table 3.2 Continued

Desiccation	Seeds collected after being spat out by the monkeys and stored for 14 days.	*Syzygium cordatum*	4	102	20

[a] *Ficus* spp. seeds were sown five per cell to control for hollow seeds used by fig wasps and we counted each cell as one seed.

Seed Collection. We collected seeds used for Gut-Passage and Fertiliser treatments from fresh faecal samples and seeds for Desiccation treatment as the monkeys spat them out. To do this, we followed the samango monkey groups two days each week per group from dawn at their sleep site, until dusk when they settled at their sleep site. We collected fresh faecal samples from all age and sex classes *ad libitum* in separate plastic bags, noting the date and time of deposition on the bag. Faecal samples were stored overnight in dark sealed plastic boxes to keep them cool and processed early the following day. When processing the faecal samples, we either checked them for *Ficus* spp. or *S. chirindensis* seeds and sowed Fertiliser treatment seeds as described in *Germination Trials* below, or gently washed them removing digesta and air-drying them in a tent for 48 hours. Once dry, we collected all entire and undamaged seeds from each sample, identified and counted them. We could only identify *Ficus* spp. to genus level, due to the high similarity and very small (< 2 mm) seed size and pooled all *Ficus* spp. seeds together. To avoid potential bias, we also pooled *Ficus* spp. seeds and entire fruits collected from sample trees of the three species for the other treatments. As *Ficus* spp. and *S. chirindensis* seeds are orthodox, we were able to store these seeds in paper bags in a sealed dark plastic box until needed, which we did for a maximum of ten days prior to sowing for the Gut-Passage treatment (Baskin & Baskin 2014).

We collected monkey-dispersed *S. cordatum* seeds immediately after being spat out, storing them for fourteen days also in paper bags in a sealed dark plastic box prior to sowing for the Desiccation treatment. These seeds are recalcitrant, and we stored them prior to sowing to simulate dispersal into dry habitats, which the monkeys did in their cheek pouches. We collected entire fresh mature fruits from monkey feeding trees, which we used for Control, Disinhibition and Scarification treatments, processing them no longer than 24 hrs after collection. We removed seeds from fruit pulp by hand and left seeds to air-dry at room temperature for 24 – 48 hours (Baskin & Baskin 2014), although seeds removed from *S. cordatum* fruit pulp were air-dried for a maximum of 24 hrs to avoid desiccation. We scarified *S. chirindensis* and *S. cordatum* seeds by rubbing them once along a 15 x 15 cm^2 piece of medium-coarse sandpaper (Kimura & Islam 2012). Due to their small size, we scarified *Ficus* spp. seeds by placing all seeds used per trial into a small plastic tub with a piece of the same sandpaper glued to each end and shaking the tub in a circular motion for five minutes.

Germination Trials. We constructed two germination nurseries in an open area where there was no shading effect from trees or other structures. We built a wooden frame and covered one with 80% shade cloth (Shaded) and the other with 20% shade cloth (Unshaded) to simulate the difference in light conditions (hereafter shading) within and outside of continuous canopy cover into which the monkeys may disperse seeds respectively. Within each nursery, we recorded temperature (ºC) and relative humidity (%) at 30-min intervals using Easy-Log USB 2+ data loggers (Lascar Electronics, Salisbury, UK) placed in the centre 1 m above ground level. We collected topsoil from a transitionary zone between the evergreen forest and semi-deciduous woodland. We collected sufficient topsoil for all trials at once, in order to homogenise the substrate between trials and eliminate inconsistencies in soil texture, porosity and chemical composition between trials. Soil pH was analysed by the Agricultural Research Council, Institute for Soil, Climate and Water, Pretoria, South Africa, and was 6.76 and 6.52 in the Shaded and Unshaded nursery respectively. We attribute the small difference in soil pH between the two nurseries to the microscale dynamic soil hydration processes between the shaded and unshaded conditions, which can act as a driver for localised pH zonation (Kim & Or 2019). We sieved the soil using a 1 mm mesh to remove large particles, seeds and plant matter, mixed it with quarry sand (5 parts soil to 1-part sand), and stored it in a covered black plastic container until required.

We sowed seeds in polystyrene germination trays (Plasgrow, Mpumalanga, South Africa), each containing 200 30 x 30 mm cells with a depth of 50 mm. We sowed one seed or entire fruit (Control) per cell at a depth of 15 mm, except *Ficus* spp., for which we sowed five seeds per cell to control for those used by fig wasps (Serio-Silva & Rico-Gray 2002), counting each cell as one seed. We sowed entire *Ficus* spp. fruits at depths according to their individual size (Table 3.1), allowing for a covering of 15 mm of soil. For all species, we marked the placement of the seed with a toothpick and undertook daily removal of seedlings that were not at that location. We left seedlings that emerged next to the toothpick until we could identify them as our focal seed.

We used a nested experimental design whereby trays and cells in each nursery mirrored each other in terms of species, treatments, faecal samples and positioning within the nursery, placing the germination trays on wooden pallets 50 cm above the ground. We used one tray per trial in each nursery, with all seeds used for simulated treatments originating from the same source tree in each trial. Primate-dispersed *Ficus* spp. and *S. chirindensis* seeds came from different faecal samples for each trial, although it was not always possible to use a single faecal sample per trial, as they did not always contain sufficient quantities of seeds. For the Fertiliser treatment, we divided faecal samples used for *Ficus* spp. ensuring identical numbers of sub-samples were used in each nursery. For *S. chirindensis*, we ensured seeds from faecal samples were sown in sufficient faecal matter to bury the seed into. As with the seeds and entire fruits, we sowed faecal sample portions at a depth of 15 mm. We evenly watered trays in both nurseries daily using a hosepipe and water piped directly from a stream in the forest, until the soil was wet to the touch. Soil within the Shaded nursery remained permanently moist for the duration of the germination trials, whilst within the Unshaded nursery, soil dried out daily between watering. We monitored germination daily and considered the seed to have germinated upon first emergence of the cotyledon from the soil. Each trial was terminated after the maximum published germination time (Table 3.1) plus either 10% or 14 days with no new germination (Table 3.2). We did not determine the viability of ungerminated seeds after each trial.

3.2.2 | Data Analysis

We conducted separate analyses for each species using Generalised Linear Mixed-Effects Models (GLMMs) in R version 3.5.1. (R Core Team 2018) using the lme4 package (Bates et al. 2015). Recent reviews recommend GLMMs as the preferred mode of analysis for germination data (Sileshi 2012), as the model allows analysis of nested designs such as our dichotomous shading effect, as well as allowing for non-normal distributions of the response variable and random effect specification (Schupp 1993; Bolker et al. 2009). In all cases, we modelled seed treatment (four or five levels depending on species) and the interaction between treatment and shading (two levels, Shaded and Unshaded) as fixed effects, to evaluate separately the effects of each treatment on the probability of germination (binomial) and germination latency (number of days taken to germinate). We included trial nested in shading (or nursery) as a random effect to control for spatiotemporal variation across trials, as we could not sow all trials at the same time due to accessible fruit availability across the study site. We verified parsimony of the model against a reduced model omitting the interaction term, followed by a null model of the random effect only using a likelihood ratio test. We assessed optimal model adequacy by examining standard residuals vs. fitted residuals and graphical distribution of errors and conducted Wald Chi-Square tests to determine the significance of the fixed effects at $p = 0.05$. To isolate the effects of the different treatments on seed germination, we conducted Least-Squares Means analysis of the final model using the emmeans package (Lenth 2018) and performed pairwise Tukey' HSD comparisons using the multcomp package (Hothorn et al. 2008), to compare between treatments and control seeds.

3.3 | Results

3.3.1 | Probability of Germination

We had a total germination success of 57.1% in *Ficus* spp., 25.3% in *S. chirindensis* and 53.9% in *S. cordatum* seeds. There was no interaction effect between shading and treatment on the probability of germination in all three fruit-tree species (Table 3.3). However, there was a significant effect of seed processing treatment on the probability of germination (Table 3.3) and significant pairwise differences between treatments (Fig. 3.1). All pairwise comparisons with Control were significant except for Fertiliser in *Ficus* spp. and Gut-

Passage and Fertiliser in *S. chirindensis*. Non-significant pairwise comparisons are given in Appendix Table A.2.

Table 3.3 Model output of the GLMM Wald Chi-square test on the effect of treatment and the interactive effect of shading (Shaded/Unshaded) and treatment, with Tukey's HSD pairwise comparison tests on the probability of germination for three samango monkey-dispersed fruit species' seeds. Treatments: Control, entire fruit, no treatment; Disinhibition, effect of pulp removal; Scarification, disinhibition *plus* mechanical scarification of seed coat; Gut-Passage, disinhibition *plus* mechanical and chemical scarification during gut passage (*Ficus* spp. and *S. chirindensis*); Fertiliser, gut passage effect *plus* fertiliser effect of the faecal matrix (*Ficus* spp. and *S. chirindensis*); Desiccation, disinhibition *plus* desiccation (*S. cordatum*).

Species	GLMM Wald Chi-square Test			
	Effect	x^2	df	*p*-value
Ficus spp.				
	Shading : Treatment	10.02	5	0.07
	Treatment	112.14	4	<0.001
Searsia chirindensis				
	Shading : Treatment	2.65	5	0.75
	Treatment	35.49	4	<0.001
Syzygium cordatum				
	Shading : Treatment	2.67	4	0.16
	Treatment	61.88	3	<0.001
	Significant Tukey's HSD Pairwise Comparisons			
	Effect Comparison	Estimate ±SE	*Z*-value	*p*-value
Ficus spp.				
	Control – Disinhibition	-0.7 ±0.17	-4.2	<0.001
	Control – Scarification	-0.52 ±0.16	-3.27	0.009
	Control – Gut-Passage	0.99 ±0.15	6.5	<0.001
	Disinhibition – Gut-Passage	1.7 ±0.16	9.45	<0.001
	Disinhibition – Fertiliser	0.99 ±0.16	6.32	<0.001
	Scarification – Gut-Passage	1.52 ±0.17	8.77	<0.001
	Scarification – Fertiliser	0.81 ±0.15	5.45	<0.001
	Gut-Passage – Fertiliser	-0.71 ±0.14	-4.98	<0.001
Searsia chirindensis				
	Control – Disinhibition	-1.6 ±0.41	-3.86	<0.001
	Control – Scarification	-1.66 ±0.42	-3.98	<0.001

Table 3.3 Continued

	Disinhibition – Gut-Passage	1.14 ±0.31	3.65	0.002
	Disinhibition – Fertiliser	0.92 ±0.31	2.96	0.02
	Scarification – Gut-Passage	1.2 ±0.32	3.8	0.001
	Scarification – Fertiliser	0.99 ±0.32	3.12	0.01
Syzygium cordatum				
	Control – Disinhibition	-7.2 ±1.52	-4.75	<0.001
	Control – Scarification	-3.75 ±0.68	-5.54	<0.001
	Control – Desiccation	-2.06 ±0.65	-3.17	0.007
	Disinhibition – Desiccation	5.25 ±1.38	3.72	<0.001
	Scarification – Desiccation	1.69 ±0.28	5.94	<0.001

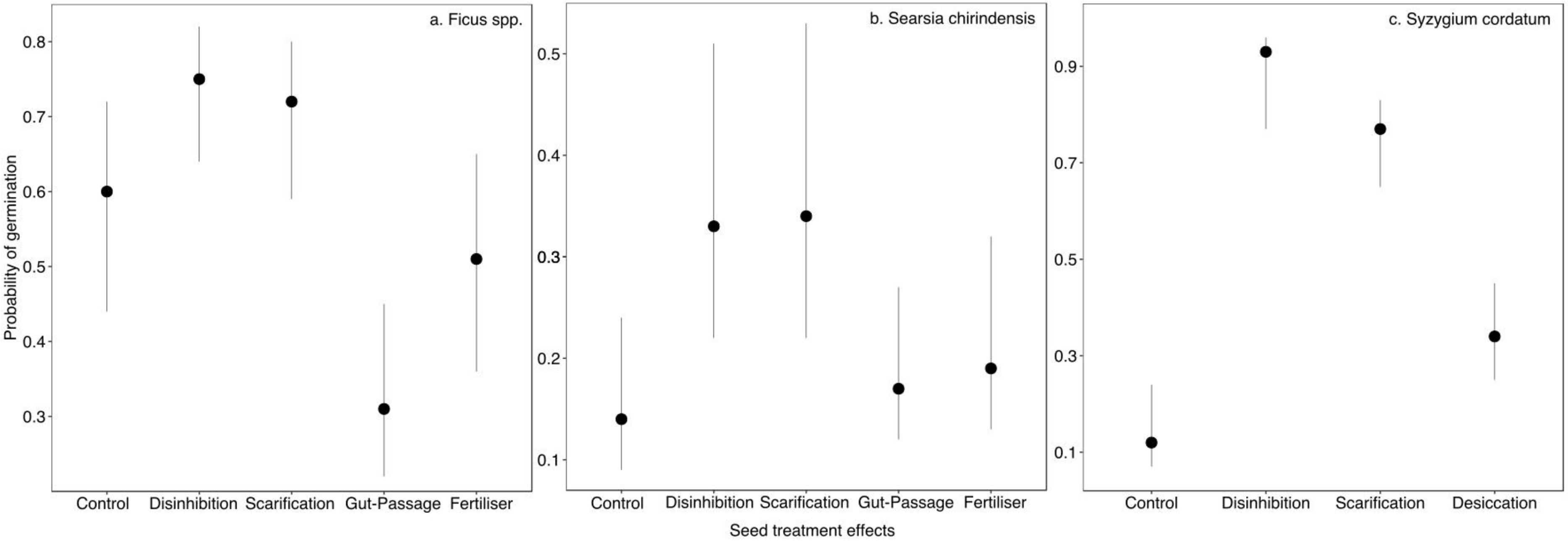

Fig. 3.1 Least squares means probability of germination (± 95% CI) of three samango monkey-dispersed fruit species' seeds subject to different processing treatments. Treatments: Control, entire fruit, no treatment; Disinhibition, effect of pulp removal; Scarification, disinhibition *plus* mechanical scarification of seed coat; Gut-Passage, disinhibition *plus* mechanical *and* chemical scarification during gut passage (*Ficus* spp. and *S. chirindensis*); Fertiliser, gut passage effect *plus* fertiliser effect of the faecal matrix (*Ficus* spp. and *S. chirindensis*); Desiccation, disinhibition *plus* desiccation (*S. cordatum*).

For both *Ficus* spp. and *S. chirindensis* seeds, our analysis indicated Disinhibition and Scarification treatments had the highest probability of germination, both of which were significantly higher than Controls, but not different from each other (Tukey's HSD test $Z = 1.091$, $p = 0.81$ and $Z = -3.03$, $p = 0.99$, respectively). In *Ficus* spp. seeds, Gut-Passage significantly reduced the probability of germination from Controls, and Fertiliser significantly increased the probability of gut passed seeds germinating, however our analysis indicated this was not significantly different from Controls (Tukey's HSD test $Z = 2.12$, $p = 0.21$). For *S. chirindensis*, we found neither Gut-Passage nor Fertiliser significantly affected the probability of seeds germinating compared to Controls (Tukey's HSD test $Z = -0.95$, $p = 0.87$ and $Z = -1.42$, $p = 0.6$ respectively), and Fertiliser had no additional benefits to Gut-Passage (Tukey's HSD test $Z = -0.56$, $p = 0.98$). In *S. cordatum,* our analysis indicated Disinhibition significantly increased the probability of germination compared to Controls, although our analysis also indicated a considerable reduction in the benefit of Disinhibition following Desiccation. Compared to Disinhibition, Scarification reduced the probability of germination, although not significantly (Tukey's HSD test $Z = 2.48$, $p = 0.05$).

3.3.2 | Germination Latency

We observed similar germination patterns between all treatments in *Ficus* spp. and *S. chirindensis* seeds, with 50% germination occurring between 25 – 30 days and 18 – 20 days respectively (Fig. 3.2). We observed similar patterns in germination between two pairs of treatments in *S. cordatum*, with 50% germination occurring after 21 and 16 days in Disinhibition and Scarification treatments respectively, and after 57 and 45 days in Controls and Desiccation treatments respectively (Fig. 3.2).

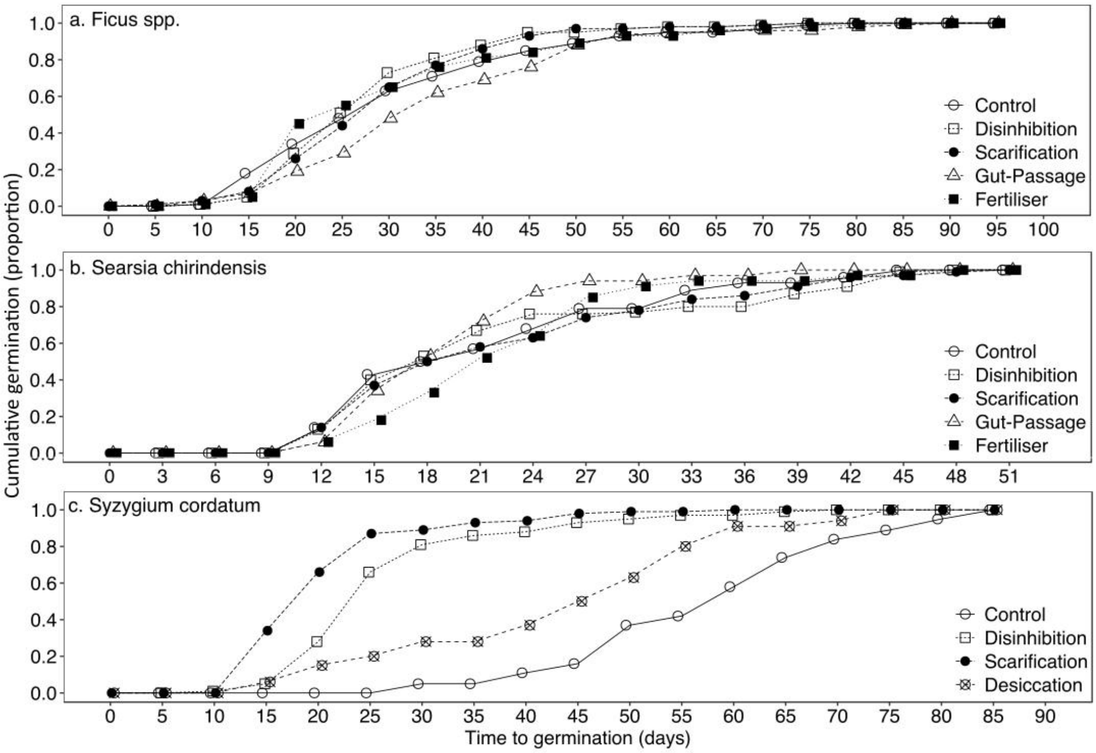

Fig 3.2 Cumulative germination (proportion) of three samango monkey-dispersed fruit species' seeds subject to different processing treatments. Treatments: Control, entire fruit, no treatment; Disinhibition, effect of pulp removal; Scarification, disinhibition *plus* mechanical scarification of seed coat; Gut-Passage, disinhibition *plus* mechanical and chemical scarification during gut passage (*Ficus* spp. and *S. chirindensis*); Fertiliser, gut passage effect *plus* fertiliser effect of the faecal matrix (*Ficus* spp. and *S. chirindensis*); Desiccation, disinhibition *plus* desiccation (*S. cordatum*).

Our analyses indicated significant interaction effects between treatment and shading on germination latency for *Ficus* spp. and *S. cordatum* seeds (Table 3.4); however, we found no significant effect of shading on germination latency within treatments in either of these species (Fig. 3.3). There was no significant interaction effect between shading and treatment in *S. chirindensis*. Non-significant pairwise comparisons are given in Appendix Table A.2.

Table 3.4 Model output of the GLMM Wald Chi-square test on the effect of treatment and the interactive effect of shading (Shaded/Unshaded) and treatment, with significant Tukey's HSD pairwise comparison tests on germination latency for three samango monkey-dispersed fruit species' seeds. Treatments: Control, entire fruit, no treatment; Disinhibition, effect of pulp removal; Scarification, disinhibition *plus* mechanical scarification of seed coat; Gut-Passage, disinhibition *plus* mechanical and chemical scarification during gut passage (*Ficus* spp. and *S. chirindensis*); Fertiliser, gut passage effect *plus* fertiliser effect of the faecal matrix (*Ficus* spp. and *S. chirindensis*); Desiccation, disinhibition *plus* desiccation (*S. cordatum*).

Species	GLMM Wald Chi-square Test			
	Effect	x^2	df	*p*-value
Ficus spp.				
	Shading : Treatment	2192.6	5	<0.001
	Treatment	3376.8	5	<0.001
Searsia chirindensis				
	Shading : Treatment	9.22	5	0.1
	Treatment	12.38	4	0.01
Syzygium cordatum				
	Shading : Treatment	12.3	4	0.02
	Treatment	142.521	3	<0.001

		Significant Tukey's HSD Pairwise Comparisons			
	Shading	Effect Comparison	Estimate ±SE	*Z*-value	*p*-value
Ficus spp.					
	Shaded	Control – Gut-Passage	-8.35 ±1.97	-4.23	<0.001
		Disinhibition – Gut-Passage	-6.51 ±1.91	-3.42	0.02
		Gut-Passage – Fertiliser	6.4 ±2.05	3.12	0.04
	Unshaded	Control – Disinhibition	5.81 ±1.61	3.62	0.008
		Control – Scarification	6.79 ±1.61	4.23	<0.001
		Disinhibition – Gut-Passage	-7.61 ±1.96	-3.9	0.003
		Scarification – Gut-Passage	-8.62 ±1.96	-4.4	<0.001

Table 3.4 Continued

Unshaded : Shaded[a]	Not Significant			
Searsia chirindensis				
	Shading not significant			
	Control – Gut-Passage	0.32 ±0.09	3.35	0.007
Syzygium cordatum				
Shaded	Control – Disinhibition	32.63 ±7.37	4.57	<0.001
	Control – Scarification	41.97 ±7.35	7.71	<0.001
	Disinhibition – Scarification	8.35 ±1.23	6.81	<0.001
	Disinhibition – Desiccation	-14.2 ±7.35	2.68	<0.001
	Scarification – Desiccation	-22.55 ±7.35	2.6	<0.001
Unshaded	Control – Disinhibition	32.07 ±5.75	5.57	<0.001
	Control – Scarification	36.63 ±5.74	6.38	<0.001
	Disinhibition – Scarification	4.56 ±1.45	3.12	0.03
	Disinhibition – Desiccation	-18.95 ±3.43	-5.53	<0.001
	Scarification – Desiccation	-23.5 ±3.43	-6.86	<0.001
Unshaded : Shaded[a]	Control – Disinhibition	34.6 ±6.06	5.71	<0.001
	Control – Scarification	42.95 ±6.03	7.12	<0.001
	Control – Desiccation	20.4 ±6.48	3.15	0.03
	Disinhibition – Control	-31.1 ±7.63	-4.08	<0.001
	Disinhibition – Scarification	10.87 ±2.35	4.64	<0.001
	Disinhibition – Desiccation	-11.67 ±3.34	-3.5	0.008
	Scarification – Control	-35.65 ±7.61	-4.68	<0.001
	Scarification – Desiccation	-16.23 ±3.31	-4.9	<0.001
	Desiccation – Disinhibition	21.48 ±3.92	5.48	<0.001
	Desiccation – Scarification	29.82 ±3.87	7.71	<0.001

[a] The first treatment listed was in Unshaded conditions

In Shade, our analyses indicated that in *Ficus* spp., Gut-Passage significantly increased germination latency compared to Disinhibition and Fertiliser treatments and Controls. Unshaded, our analyses indicated that both Disinhibition and Scarification significantly reduced germination latency compared to the other treatments and Controls. We found no significant interacting effects between treatment and shading for *S. chirindensis* seeds, and our analyses indicated a significant difference in germination latency between Controls and Gut-Passage, the latter of which germinated fastest (Table 3.4). All three treatments reduced germination latency of *S. cordatum* seeds compared to Controls, which we found took the longest to germinate. Our analyses indicated that Scarification significantly reduced germination latency compared to all other treatments, with those sown in shade germinating fastest.

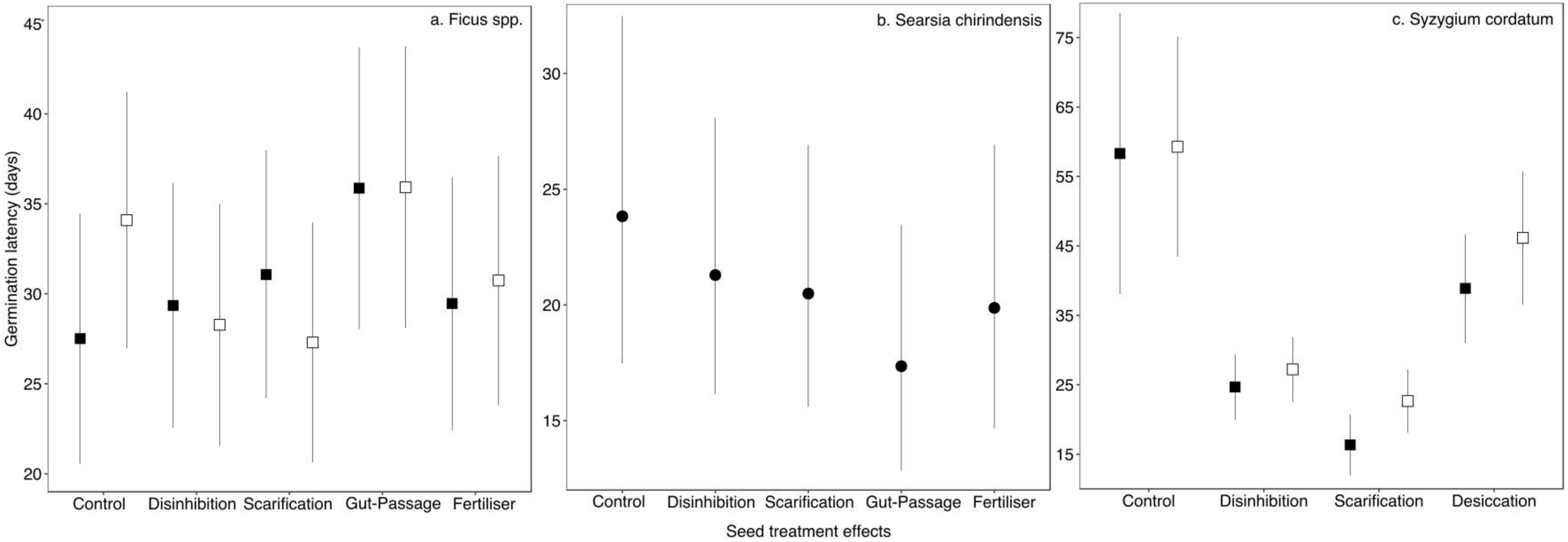

Fig. 3.3 Least squares means germination latency (± 95% CI) of three samango monkey-dispersed fruit species' seeds subject to different processing treatments. Treatments: Control, entire fruit, no treatment; Disinhibition, effect of pulp removal; Scarification, disinhibition *plus* mechanical scarification of seed coat; Gut-Passage, disinhibition *plus* mechanical and chemical scarification during gut passage (*Ficus* spp. and *S. chirindensis*); Fertiliser, gut passage effect *plus* fertiliser effect of the faecal matrix (*Ficus* spp. and *S. chirindensis*); Desiccation, disinhibition *plus* desiccation (*S. cordatum*). Shape indicates interactive effect of treatment & shading, (black circles – no significant interacting effect; squares – significant interactive effect, filled – Shaded, open – Unshaded).

3.3.3 | Exclusion of Ecologically Relevant Seed Treatments

To identify if exclusion of ecologically relevant seed treatments or relevant controls would affect our interpretations of the impact of the disperser on seed germination, we considered the positive, negative or neutral effects our disperser had on the probability of seed germination (Table 3.5). Firstly, we considered exclusion of entire fruit control groups (Controls), instead assessing the difference in probability of germination between manual removal of seeds from mature fruits (Disinhibition) and seeds either removed from faecal samples (Gut-Passage, *Ficus* spp. and *S. chirindensis*), or collected after being spat out (Desiccation, *S. cordatum*). Our analysis indicated negative disperser effects in each of these comparisons as compared to Disinhibition the probability of germination in seeds from Gut-Passage and Desiccation treatments was significantly lower. When we included Controls, disperser effects were positive (Disinhibition and Desiccation) for *S. cordatum*, positive (Disinhibition) and neutral (Gut-Passage) for *S. chirindensis*, and positive (Disinhibition) and negative (Gut-Passage) for *Ficus* spp. seeds. Secondly, we considered the disperser effect when we include the effect of the faecal matrix (Fertiliser) in species with gut-passed seeds. Our analysis indicated neutral effects when compared to both Controls and Gut-Passage in *S. chirindensis*, and neutral and positive effects when compared to Controls and Gut-Passage respectively in *Ficus* spp. seeds.

Table 3.5 Comparison between exclusion/inclusion of entire fruit control groups and/or the fertiliser effect, using model output of the GLMM Tukey's HSD pairwise comparison tests on the probability of germination for three samango monkey-dispersed fruit species' seeds. Treatments: Control, entire fruit no treatment; Disinhibition, effect of pulp removal; Gut-Passage, disinhibition *plus* mechanical and chemical scarification during gut passage (*Ficus* spp. and *S. chirindensis*); Fertiliser, gut passage effect *plus* fertiliser effect of the faecal matrix (*Ficus* spp. and *S. chirindensis*); Desiccation, disinhibition *plus* desiccation (*S. cordatum*).

Species	Comparison	GLMM Tukey's HSD Pairwise Comparisons			Impact on Germination
		Z-Value	*p*-Value	Difference	
Exclusion of Entire Fruit Control and Fertiliser Effect					
Ficus spp.	Disinhibition – Gut-Passage	9.45	<0.001	- 44.28 %	Negative
Searsia chirindensis	Disinhibition – Gut-Passage	3.65	0.002	- 16.2 %	Negative
Syzygium cordatum	Disinhibition – Desiccation	3.72	<0.001	- 59.46 %	Negative
Inclusion of Entire Fruit Control					
Ficus spp.	Control – Disinhibition	-4.2	<0.001	+ 15.57 %	Positive
	Control – Gut-Passage	6.5	<0.001	- 28.71 %	Negative
Searsia chirindensis	Control – Disinhibition	-3.86	<0.001	+ 19.22 %	Positive
	Control – Gut-Passage	-0.95	0.87	+ 3.02 %	Neutral [a]
Syzygium cordatum	Control – Disinhibition	-4.75	<0.001	+ 81.59 %	Positive
	Control – Desiccation	-3.17	0.007	+ 22.1 %	Positive
Inclusion of Fertiliser Effect					
Ficus spp.	Control – Fertiliser	2.12	0.21	- 8.84 %	Neutral [a]
	Gut-Passage – Fertiliser	-4.98	<0.001	+ 19.87	Positive
Searsia chirindensis	Control – Fertiliser	-1.42	0.6	+ 4.9 %	Neutral [a]
	Gut-Passage – Fertiliser	-0.56	0.98	+ 1.88 %	Neutral [a]

[a] Non-significant difference

3.4 | Discussion

In a review conducted in 2005, 77% of studies omitted using entire fruits as controls in experiments assessing the effect of gut passage on seed germination (Samuels & Levey 2005). In our review, 76% of studies used manually extracted seeds as controls demonstrating a lack of progression. Furthermore, 76% of studies excluded the fertiliser effect and 9% included mechanical scarification of de-pulped seeds along-side gut-passed seeds. Without isolating each fundamentally different mechanism, the absolute effect of frugivores on seed germination is confounded (Samuels & Levey 2005; Robertson et al. 2006; Baskin & Baskin 2014) and these studies are weakened in their conclusions. Our analyses indicated that samango monkeys are effective in the qualitative side of seed dispersal, as seed processing mechanisms had a positive and/or neutral influence on germination potential of seeds compared to entire fruits where seeds were untreated. As is widely reported (Robertson et al. 2006), removal of seeds from fruit pulp (*the disinhibition effect*) had the greatest positive effect on the probability of germination in each of the three fruit species we assessed. Excluding entire fruit as control groups from our analyses altered the conclusions drawn from our data, thus underestimating the influence seed handling by samango monkeys has on seed germination. As such, our results concur with others, and reiterate the need for inclusion of all ecologically relevant treatments that simulate dispersal modes of frugivores, to estimate accurately their role in seed dispersal (Samuels & Levey 2005; Baskin & Baskin 2014; Fuzessy et al. 2016).

3.4.1 | Effect of samango monkeys on seed germination

The disinhibition effect had a significant positive influence on the probability of germination compared to control groups of entire fruits in each of the fruit species we assessed, suggesting that as seed-spitters samango monkeys have an important role in their dispersal. This was most noticeable in *S. cordatum* where we observed samango monkeys to disperse seeds via spitting as they were consuming fruits in the parent tree or following storage in cheek pouches. Our results are similar to previous research conducted on *Syzygium legatii* (mountain water-berry) seeds spat out by samango monkeys (B. Linden, unpublished data), as well as studies on *Syzygium* spp. in other taxa (e.g. Albert et al., 2013; Gross-Camp and Kaplin, 2005; Sengupta et al., 2014). The role of samango monkeys in *S. cordatum* seed dispersal may also be greatly dependent on where they deposit seeds, as shown by the significant reduction in the probability of germination of seeds we subjected to desiccation, compared to freshly de-pulped seeds. As recalcitrant seeds are sensitive to desiccation (Roberts 1973), it may be that *S. cordatum* relies on seed-spitters to remove pulp and that germination must occur soon after before seeds desiccate. Mature *S. cordatum* trees are typically located close to water and dispersal under or close to parent trees, where the environment can slow the desiccation process, may confer an advantage to seeds. Compared to the disinhibition effect, we found scarification to have a non-significant negative effect on the probability of germination and a significant reduction on germination latency in *S. cordatum*. Damage to the protective seed coat through scarification or removal has been shown to reduce cumulative germination in *S. cordatum* (Prins & Maghembe 1994). Guenon cheek pouches contain a high level of α-amylase, a saliva enzyme involved in pre-digestion breakdown of starch (Murray 1975), which may reduce the need for high-molar mastication and therefore scarification damage to seeds in soft-pulped fruits. The significant benefits in increased germination and reduced latency to *S. cordatum* seeds through pulp removal are likely to help these seeds germinate and establish during the wet season. This is further evident in the significantly reduced benefits we observed when we dried spat seeds prior to sowing

While the disinhibition effect had positive effects on germination in each of the species we assessed, the gut passage effect was negative in *Ficus* spp. and neutral in *S. chirindensis*. In *Ficus* spp., the gut passage effect significantly reduced the probability of germination, and increased germination latency, more than every other treatment. The effect of gut passage on *Ficus* spp. seeds reported in the literature are highly variable, with positive (e.g. Chen et al., 2017; Figueiredo, 1993; Mosallam, 1996; Oleksy et al., 2017), negative (e.g. Chang et al., 2016; Compton et al., 1996; Tsuji et al., 2017) and neutral (e.g. Heer et al., 2010; Maccarini et al., 2018; Stevenson et al. 2002) effects reported from a wide range of frugivorous mammals. Previous research on samango monkeys found the gut passage effect significantly reduced germination of *Ficus* spp. seeds compared to the disinhibition effect but had no significant effect on *Keetia gueinzii* (climbing turkey-berry) seeds (B.

Linden, unpublished data). In *S. chirindensis*, we found the gut passage effect on seed germination was neutral compared to entire fruit controls, although the gut passage effect significantly reduced germination latency. Again, results reported in the literature for *Searsia* spp. are variable (e.g. Foord et al., 1994; Mosallam, 1996).

The highly variable results reported for these species suggest there are likely to be species- and/or site-specific variables not typically measured in germination experiments that influence seed germination following gut passage. These may include chemicals in the gastrointestinal (GI) tract that may vary in respect to dietary intake of dispersers, as well as anatomical differences of the GI tract that may increase the passage time of seeds and therefore time available for chemical and mechanical scarification (Traveset et al. 2007). However, while germination latency increased in *Ficus* spp., seeds were still viable following passage through the gut, and in *S. chirindensis*, gut-passage significantly reduced germination latency.

More surprisingly, in *Ficus* spp.**,** the fertiliser effect increased germination success and reduced germination latency compared to gut passage alone, and this effect was neutral compared to entire fruit controls. We observed a similar neutral effect in *S. chirindensis*. The majority of studies remove seeds from faecal samples to test the gut passage effect and the literature including the fertiliser effect is scarce. In our literature search, 76% of studies omitted the fertiliser effect. Where the effect is included, results are again variable (Heer et al., 2010; Rojas-Martinez et al., 2015; Tutin et al., 1991; Valenta and Fedigan, 2009). Lethal effects reported in some studies (e.g. Anzures-Dadda et al., 2016) may result from seeds being removed from faecal samples and washed prior to re-covering with fresh faeces, increasing susceptibility to fungal attack (Wang & Smith 2002).

Our *in-situ* germination experiments were subject to natural variation of abiotic factors: temperature, humidity and sunlight levels and are in contrast to *ex-situ* studies conducted under controlled conditions (e.g. Anto et al., 2018; Figueiredo, 1993; Kankam and Oduro, 2012). Significant differences between the gut passage and disinhibition effects in field experiments are rarely reported, with the majority of positive influences coming from studies conducted in laboratory settings (Fuzessy et al. 2016). The significant decrease in the probability of germination we report from gut passed *Ficus* spp. seeds requires further investigation. We had pooled together *Ficus* spp. seeds retrieved from faecal samples as we could not identify them to species level. We also pooled together seeds collected from ripe fruits for the other treatments and entire fruit for the controls. Whilst we acknowledge that this may have introduced bias into the germination experiments of *Ficus* spp. seeds, we took care to assign seeds randomly to each treatment and each trial to minimise such bias.

Ficus spp. fruits are considered keystone resources for many animal species including primates (Estrada & Coates-Estrada 1984), as their typical asynchronous year-round fruiting can be a reliable food source (Bleher et al. 2003). Figs are synconium (Galil 1977) containing hundreds of small (<2 mm) imbedded seeds (Lambert 1999). The lengthy processing time it would take to orally remove the seeds means samango monkeys are likely to swallow more than they spit out (Lambert 1999). As such, *Ficus* spp. may trade reduced quality of dispersal of gut-passed seeds for quantity, relying instead on the unpredictable heterogeneity of the environment into which samango monkeys disperse seeds (Chang et al. 2016). Similarly, *S. chirindensis* may rely on the reduced germination latency of gut-passed seeds to help them establish. Like other Cercopithecines, samango monkeys consume unripe fruit (Lawes 1991; Linden et al. 2015) acting as seed predators (Wrangham et al. 1998). As such, low germination of seeds we collected from samango monkey faeces may be because they came from unripe fruit. Alternatively, the chemical and/or mechanical scarification in the gut may damage the embryo (Samuels & Levey 2005). Embryos inside the *Ficus* spp. seeds may also have been destroyed by fig wasps (Figueiredo 1993; Righini et al. 2004).

3.4.2 | Exclusion of ecologically relevant seed treatments

The majority of studies generated from our literature search exclude ecologically relevant treatments from their study design. More than three-quarters of studies did not use entire fruits as control groups in germination studies, instead comparing germination of gut passed seeds removed from faeces to seeds manually removed from fruit pulp. This approach has several issues. Firstly, as discussed by Samuels and Levey (2005), removal of fruit pulp is already a mechanism that can induce germination by removing chemicals within fruit pulp that act as germination inhibitors (the *disinhibition effect*). Therefore the effect of gut passage being assessed is the mechanical and/or chemical alteration (scarification) of the seed coat, and not the combined effect of disinhibition *plus* gut passage, which is important as each of these mechanisms can influence germination independently (e.g. Baskin and Baskin, 2014). Secondly, in this approach there are no other treatment against which the mechanical and chemical scarification of the seed coat can be assessed, further weakening interpretation of the effect of frugivores on seed germination, extending to their role in seed dispersal.

In the current study, excluding entire fruit control groups, instead comparing germination response of seeds subject to the disinhibition effect and gut passage (*Ficus* spp. and *S. chirindensis*) or desiccation (*S. cordatum*) effect, influenced the interpretation of our analyses: we interpreted the disperser as having a negative impact on seed dispersal, as the probability of germination was significantly lower for the gut passage and desiccation effects than for the disinhibition effect. On the other hand, our analyses, which included entire fruit as the control group, indicated that samango monkeys are effective in the qualitative side of seed dispersal, as seed processing mechanisms had positive and/or neutral effects on the germination potential of seeds. Including entire fruits in the analysis meant that we isolated scarification in the gut from disinhibition and were able to include an assessment of the ecological role seed spitting plays on seed germination.

In addition to the gut passage effect, we included a separate treatment in our germination experiments to isolate the chemical and mechanical effects of gut passage. The term 'scarification effect' is used ambiguously in the current literature to describe the chemical and mechanical alteration of the seed coat during gut-passage (Samuels & Levey 2005; Traveset et al. 2007). However, it does not distinguish chemical treatments, which can alter and soften the seed coat, from mechanical action, which can physically damage it (Baskin & Baskin 2014). Instead, each dispersal mechanism should be assessed against a control whereby the disperser has no influence on seed fate, as well as identifying a positive or negative cumulative effect from the previous treatment (Traveset & Verdú 2002; Samuels & Levey 2005; Robertson et al. 2006). Only 9% of studies generated from our literature search included manual chemical and/or mechanical scarification of de-pulped seeds alongside gut-passed seeds, thereby isolating scarification processes. In the current study, we found the probability of manually scarified seeds germinating was significantly higher than gut passed *Ficus* spp. and *S. chirindensis* seeds. It may be that the methods we employed to scarify seeds were insufficient to damage the seed coat to the same extent as passage through the gut, or it may be that chemical scarification in samango monkey's gut reduces the germination potential of seeds.

We found that in Ficus spp., the faecal matrix significantly increased the probability of gut-passed seeds germinating. We found a similar, albeit negligible, effect in *S. chirindensis*, and it may be that digestive acids contained within the faecal matrix continue to alter the seed coat after defaecation. Alternatively, the embryo may be able to extract nutrients from the faeces, which were no longer available once we had removed seeds from faeces. Either way, inclusion of the fertiliser effect has significant consequences on our interpretation of the influence seed handling by samango monkeys has in seed germination. Without it, especially in Ficus spp., the role of samango monkeys would have been significantly underestimated.

3.4.3 | Implications for future studies

The results we obtained in *Ficus* spp. require further investigation, not least, as they are in contrast to results reported in other studies. We suggest that germination experiments investigating the effect of gut passage on *Ficus* spp. seeds should share seeds from faecal samples between the gut passage and fertiliser effect treatments. The seeds we used for each of these treatments came from different faecal samples and as a result, we did not isolate the fertiliser effect using seeds from the same faecal sample. Furthermore, we could not control for individual variation of digestive enzyme activity, which can vary as a function of biotic and abiotic conditions (Hani et al. 2018), gut microbiome, which can vary as a function of social interaction and social stress (Tung et al. 2015; Trosvik et al. 2018) and gut-passage time, which can vary as a function of diet and health (Lambert 1998). The dispersal mode of seed swallowing may be a precursor for secondary dispersers, such as dung beetles (Culot et al. 2018), and longitudinal studies incorporating secondary dispersal may elucidate to this. Our treatments for *S. cordatum* isolated the disinhibition effect and the effect of desiccation; however, we did not isolate the potential effects of individual variation in salivary alpha-Amylase activity, which can vary as a function of stress (Behringer et al. 2012), on seed germination. We suggest that future studies should aim to use freshly de-pulped and spat out seeds in both the disinhibition and desiccation treatments.

3.4 | Conclusion

Samango monkeys are South Africa's only forest-dwelling primate and are highly dependent on high-canopy evergreen forest (Linden et al. 2015). As both seed-spitters and seed-swallowers, samango monkeys have multiple and important roles in seed dispersal by influencing the germination probability and latency of seeds contained with the fruits they consume. Our study addressed these roles by including in our germination experiments fruit species whose seeds they disperse through both roles. Our study also demonstrated that to understand the role of frugivores in vegetation dynamics, experiments that assess the influence of seed handling on seed germination should include ecologically relevant treatments that isolate each handling mechanisms' cumulative effect, as well as a meaningful control. Germination is only one component of successful establishment of a plant in a suitable microsite, the others being the method of transport and successful arrival in that site, and the continued delivery of niche space to maintain a plant throughout its life cycle. However, our study demonstrates that the impacts of frugivores on germination may be under- or over-estimated in ecological literature where ecologically relevant treatments and meaningful controls are excluded. There is, therefore, a distinct gap in the literature aimed at understanding the substantial role frugivores have in maintaining the resilience of ecosystems exposed to continued degradation.

Chapter 3 summary

In this Chapter, the role of samango monkeys in seed dispersal was considered as I investigated the effect several samango monkey seed processing mechanisms had on the germination of seeds. I did this through germination experiments using ecologically relevant seed treatments and an appropriate *control. The results indicate that samango monkeys have a positive influence on seed germination through processing mechanisms that release the seed from germination inhibiting fruit pulp. These results will form part of the qualitative component of the SDE framework in Chapter 5. These results also highlight the importance of including ecologically relevant treatments alongside meaningful controls, which for primates are entire fruits, in order to appropriately assess the role of frugivores in seed dispersal.*

In the next Chapter, I will investigate the gut passage time of wild samango monkeys in-situ and assess if experimental methods used on captive cercopithecines in ex-situ studies of gut passage can be adapted for use in the field.

Chapter 4

Developing an *in-situ* method for calculating gut passage time in samango monkeys (*Cercopithecus albogularis schwarzi*)

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In Chapter 3, samango monkeys had the greatest positive influence on seed germination through processing mechanisms that release the seed from germination inhibiting fruit pulp. The germination experiments indicated that gut passage through the gut of the monkeys had either a negative or neutral influence on seed germination. Gut passage of seeds is thought to have a positive influence on seeds in many primate species (Chapman 1989; Fuzessy et al. 2016), although longer retention times may have negative consequence for germination potential by damaging seeds (Kunz & Linsenmair 2008; Petre et al. 2015a). Research has previously demonstrated that cercopithecines

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[2] SS, RH and NK conceived and designed the experiments. SS performed the experiments. SS analyzed the data and wrote the manuscript; RH, LS and NK revised manuscript drafts.

exhibit extended retention times, which may be an adaptation for diets high in fibrous matter (Lambert 1998, 2002).

In this chapter, I adapt an experimental method previously used on captive cercopithecines (Lambert 2002) for use in the field to investigate the gut passage time of samango monkeys in the wild and further extend our understanding of cercopithecine digestive strategy.

Abstract

Gut passage time of food has consequences for primate digestive strategies, which subsequently affect seed dispersal. Seed dispersal models are critical in understanding plant population and community dynamics through estimation of seed dispersal distances, combining movement data with gut passage times. Thus, developing field methods *in-situ* to collect data on gut passage time are of great importance. Here we present a first attempt to develop an *in-situ* study of gut passage time in an arboreal forest guenon, samango monkey (*Cercopithecus albogularis schwarzi*) in the Soutpansberg Mountain, South Africa. *Cercopithecus* spp. consume large proportions of fruit and are important seed dispersers. However, previous studies on gut passage times have been conducted only on captive *Cercopithecus* spp. subjects, where movement is restricted, and diets are generally dissimilar to those observed in the wild. Using artificial digestive markers, we targeted provisioning of a male and a female samango monkey four times over three and four days respectively.

We followed focal subjects from dawn until dusk following each feeding event, collecting faecal samples, and recording the date and time of deposition and the number of markers found in each faecal sample. We recovered 6.61% ± 4% and 13% ± 9% of markers from the male and the female respectively and were able to estimate a gut passage window of 16.63 – 25.12 hrs from three of the eight trials. We discuss methodological issues to help future researchers to develop *in-situ* studies on gut passage times.

4.1 | Introduction

The length of time food remains in the gastrointestinal (GI) tract (gut passage time) of animals has consequences for digestive strategies and how animals access energy and nutrients from the food they consume (Blaxter et al. 1956; Lambert 2002). In frugivores, gut passage time influences seed dispersal distance (Link & Di Fiore 2006) which has important ecological implications for the recruitment, range expansion, genetic structure and gene flow in plant populations (Traveset 1998; Nathan & Muller-Landau 2000), as well as affecting germination success (Robertson et al. 2006) (Chapter 1, section 1.1). Among primates, frugivorous species play an important role in seed dispersal in many communities (Andresen et al. 2018; Razafindratsima et al. 2018). In seed dispersal models, dispersal kernels combine movement data with gut passage time to infer the statistical distribution of post-dispersal locations relative to the seeds' point of origin (Nathan et al. 2012). These data allow for predictions of seed dispersal, whilst removing the effort required in measuring actual dispersal distances in the field (Bullock et al. 2006). Therefore, reliable estimates of gut passage time from animals *in-situ* are critical in estimating dispersal kernels (Chapman & Onderdonk 1998; Lambert & Chapman 2005). Nevertheless, studies measuring gut passage time in wild animals are scarce.

Gut passage time is a measure of gut function and reflects the length of time food items are retained in the GI tract, subject to mechanical and chemical digestive processes such as the breakdown of food, microbial fermentation and absorption, before undigested matter is eliminated through faeces (Cabre-Vert & Feistner 1995). Several indices are used to calculate gut passage times including Transit Time (TT), defined as the time of the first appearance of the focal elements in faeces, Time of Last Appearance (TLA), defined as the time of the last appearance of the focal elements in faeces and Mean Retention Time (MRT) defined as the mean gut passage time of the focal elements from ingestion to excretion (Blaxter et al. 1956; Warner 1981).

Gut passage time has been widely studied in primates (Cabre-Vert & Feistner 1995; Lambert 1998; Norconk et al. 2002; Remis & Dierenfeld 2004; Tsuji et al. 2015; Bai et al. 2019) and can vary considerably (Lambert 1998). It is thought that both body size and digestive strategy can explain the large variation observed in primates (Lambert 1998; Clauss et al. 2008; Blaine & Lambert 2012). There is a general trend of increasing gut passage time observed between the smallest and the largest sized primates (Lambert 1998). There is also a general pattern for frugivorous primates, whose diets contain greater quantities of simple carbohydrate such as glucose and fructose, to display reduced gut passage times compared with folivorous and exudativorous primates, whose diets consist of greater quantities of complex structural carbohydrates such as cellulose (Lambert 2002; Clauss et al. 2008; Cabana et al. 2017). Cellulose is a major constituent of plant cell walls and many primates rely on non-fruit plant matter as a major source of energy. Unlike simple carbohydrates, digestion of cellulose depends on fermentation which, like in other herbivorous vertebrates, occurs through fermentation in the primate GI tract and can increase gut passage time (Chivers & Hladik 1980).

Within primates, *Cercopithecus* spp. show increased gut passage time compared to similar sized primate species (Lambert 1998, 2002), with studies reporting gut passage times between 21.4 hrs in *C. mona mona* (crested Mona monkey) (Poulsen et al. 2001) and 40.6 hrs in *C. mitis* (blue monkey) (Clemens & Phillips 1980) (Table 1). Cercopithecines exhibit considerable feeding flexibility with consistently large proportions of both fruit and non-fruit plant parts in their diets (Blaine & Lambert 2012). It is suggested that *Cercopithecus* spp. digestive strategies include extended retention time of food for fermentation and extraction of nutrients from a diet high in fibrous material (Lambert 1998, 2002).

Table 4.1 Mean marker transit time (TT), time of last appearance (TLA) and gut retention time (± SD) (MRT) of Cercopithecus spp. reported in ex-situ studies (NA - not reported), presented with study sample size/sex and body mass; marker type, size (mm) and recovery (%); faecal collection method (Continuous Collection – samples collected as time of deposition; Estimated by Appearance – samples collected in the morning and then time of deposition estimated by degree of desiccation); subjects' diet (CFP Commercial and Fresh produce; CFCP Commercial and Fresh and Cooked Produce; C Commercial only; NFP Natural fruits and Fresh Produce) and location.

Sample				Measures of Gut Passage			Marker Information		
Species	Trials per Subject	n / Sex	Body Mass (kg)	TT	TLA	MRT	Type	Size (mm)	Recovery (%)
Cercopithecus ascanius [a]	4	1 M	5.7	19.9 (4.6)	35.6 (9.3)	24.9 (6.6)	Plastic Beads	4 x 2 x 1	90
	4	1 F	4.7	19.4 (0.1)	42.1 (5.7)	29.4 (9.8)			
Cercopithecus ascanius [b]	2	1 M	4.2	20.6 (0.5)	48.7 (6.7)	26.7 (3.7)	Plastic Ribbon	5 x 0.09	NA
Cercopithecus erythrotis [b]	2	1 M	4.2	20.6 (0.5)	48.7 (6.7)	26.7 (3.7)	Plastic Ribbon	5 x 0.09	NA
Cercopithecus l'hoesti [c]	3	1 M	3.6	23.3 (0.4)	41.05 (7)	26.6 (3.14)	Plastic Beads	1 x 2 x 1	5 – 45
	3	1 F		23.9 (1.5)	33 (9.19)	25.43 (0.81)			5 – 20
Cercopithecus mitis [d]	1	3 NA	6.2	NA	NA	40.6	Plastic Tube	2 x 2	NA
Cercopithecus mitis stuhlmanni [a]	4	1 M	9.8	17.2 (2.9)	54.8 (12.7	29.7 (14.6)	Plastic Beads	4 x 2 x 1	80
	4	1 F	7.4	16.5 (3.4)	42.8 (19.8)	20.6 (12.8)			
Cercopithecus mona mona [e]	1	1 M	5.1	NA	NA	21.4 (6.9)	Seeds / Food	NA	NA
	1	1 F	NA	NA	NA	21.7 (7.4)			
Cercopithecus mona pogonias [b]	2	2 M	4.5	16.6 (2.6)	43.7 (6)	26.6 (6.7)	Plastic Ribbon	5 x 0.09	NA
Cercopithecus neglectus [a]	4	1 M	6.9	21.7 (2.5)	56 (12.7)	33.9 (10.8)	Plastic Beads	4 x 2 x 1	78
	4	1 F	6.1	19.1 (3.4)	63.1 (10)	34.4 (16.6)			
Cercopithecus nictitans nictitans [e]	1	1 M	6.7	NA	NA	23.8 (4.8)	Seeds / Food	NA	NA
	1	1 F		NA	NA	22.8 (2.4)			

[a] Lambert (2002), [b] Maisels (1994), [c] Blaine and Lambert (2012), [d] Clemens and Phillips (1980), [e] Poulsen et al. (2001)

Table 4.1 Continued

Sample	Study details	
Species	Faecal Collection	Diet / Location
Cercopithecus ascanius [a]	Day: Continuous Collection Night: Estimated by Appearance	CFP / Zoo
Cercopithecus ascanius [b]	Continuous Collection	CFCP / Research Colony
Cercopithecus erythrotis [b]	Continuous Collection	CFCP / Research Colony
Cercopithecus l'hoesti [c]	Day: Continuous Collection Night: Estimated by Appearance	CFP / Zoo
Cercopithecus mitis [d]	Every 12 Hours	C / Not Reported
Cercopithecus mitis stuhlmanni [a]	Day: Continuous Collection Night: Estimated by Appearance	CFP / Zoo
Cercopithecus mona mona [e]	Continuous Collection	NFP / Zoo
Cercopithecus mona pogonias [b]	Continuous Collection	CFCP / Research Colony
Cercopithecus neglectus [a]	Day: Continuous Collection Night: Estimated by Appearance	CFP / Zoo
Cercopithecus nictitans nictitans [e]	Continuous Collection	NFP / Zoo

[a] Lambert (2002), [b] Maisels (1994), [c] Blaine and Lambert (2012), [d] Clemens and Phillips (1980), [e] Poulsen et al. (2001)

Prior research on *Cercopithecus* spp. gut passage times have all been conducted in captivity, predominantly in zoos, where subjects' diets consist of commercial food pellets supplemented with domestic fruits and vegetables, and where movement is limited (Table 1). However, wild animals are generally more active than captive animals, and energy expenditure can also influence gut passage times (Blaine & Lambert 2012). Captive diets are also not necessarily representative of the diets of wild counterparts. For example, in slow loris (*Nycticebus* spp.), subjects fed a natural wild diet had significantly longer gut passage rates than those fed a captive diet (Cabana et al. 2017). Furthermore, the 'captivity effect' (Martin et al. 1985), whereby the GI tract can become reduced in captivity, can reduce gut passage rates (Milton 1984; Martin et al. 1985; Blaine & Lambert 2012). As such, captive studies may paint a misleading picture of gut passage time in primates adapted to high-fibrous and considerably flexible diets.

Several different insoluble particulate markers have been used for gut retention studies. The majority of cercopithecine studies have used artificial markers such as such as 2-3 mm plastic beads and plastic ribbon (Table 1) (e.g. Maisels 1994; Lambert 2002). Of the ten studies conducted on cercopithecines so far, six did not report the percentage of markers recovered (Table 1). Where reported recovery of these markers from faeces following ingestion is highly variable. For example, Blaine and Lambert (2012) reported marker recovery between 5 - 20% and 5 – 45% in *C. l'hoesti* (L'Hoest's monkey), and

Lambert (2002) reported 80% marker recovery in C. mitis (blue monkey), 78% in C. neglectus (De Brazza's monkey) and 90% in *C. ascanius* (red-tailed monkey) (Lambert 2002). Low marker recovery in *Cercopithecus* spp. has been attributed to oral processing in which markers may have been crushed by high-crowned molars (Lambert 2001). In other animals, particulate markers associated with food particles, such as chromium oxide (e.g. Cabre-Vert and Feistner 1995) have been used. Other particulate markers have included glitter (Cabana et al. 2017) and polystyrene and cellulose acetate beads (Power & Oftedal 1996). Such markers are not biodegradable, and their use *in-situ* presents environmental concerns such as plastic pollution from uncollected markers. Enrichment of seed coats during the developmental phase with stable isotope ^{15}N-urea has been used to identify parent plants of dispersed seeds (Carlo et al. 2009), which could be used to estimate gut retention time of seeds *in-situ,* although this would require several months preparation between application and ingestion. Several *in-situ* studies in other primates, for example, bonobo *(Pan paniscus)* (Beaune et al. 2013b), spider monkeys *(Ateles belzebuth)* (Link & Di Fiore 2006), woolly monkeys *(Lagothrix lagothricha)* (Stevenson 2000) and white-faced capuchins (*Cebus capucinus*) (Valenta & Fedigan 2010), have used seeds from infrequently ingested fruit items to estimate gut retention times. For species of which gut retention time is relatively short, such as capuchins (Valenta & Fedigan 2010) and tamarins (*Saginus* spp.) (Oliveira & Ferrari 2000), DNA fingerprinting of dispersed seeds has shown this method to be highly reliable (Heymann et al. 2012). However, for species of which gut retention time is longer, such as guenons, this observation-based method can be extremely difficult and much less reliable (Heymann et al. 2012). Relying on infrequently ingested fruit means ensuring continuous observation of the focal animal for the entire sampling period to avoid replicated feeding on focal tree species (Stevenson 2000). Depending on the number of fruits consumed, as well as the number of seeds actually swallowed, this method also has a high risk of missing the collection of faeces containing the focal seeds.

Our aim was to test, for the first time, gut retention experimental methods developed in captivity, in the field. We measured the gut passage rate of samango monkey (*Cercopithecus albogularis schwarzi*) *in-situ* following published methodology used *ex-situ* (Lambert 2002), but using a novel marker made from natural material and with lower environmental impact than previous plastic markers. Specifically, our study aimed to determine a gut passage time window that could be used to estimate TT, TLA and MRT in a wild primate. Samango monkeys are South Africa's only true forest primate and are restricted to pockets of indigenous forest (Linden et al. 2016; Nowak et al. 2017a). The sub-species at Lajuma, *C. a. schwarzi* (Dalton et al. 2015), is classified endangered as indigenous forests are being converted for agriculture and other human activities (Linden et al. 2016). Investigations into the relationship between samango monkeys and indigenous forests may be vital in decisions regarding forest protection and therefore samango monkey survival.

4.2 | Methods

We conducted trials at Lajuma (29°26'E, 23°01'S) in the western Soutpansberg Mountain, Limpopo Province, South Africa. The study site is a mountainous environment with an altitudinal range of between 1100 and 1747 metres above sea level. Local vegetation is characterised by a complex mosaic of vegetative and structural elements of forest, thicket, grassland and savannah biomes (Maltitz et al. 2003; Mucina & Rutherford 2006). We conducted gut retention trials on two well-habituated, easily recognisable wild samango monkeys (Fig. 4.1) from Barn Group (Coleman and Hill 2014a; Nowak et al. 2014), one male and one female, during February and May 2018 respectively. We used 2 x 3 mm beads made from natural materials (Fig. 4.1) as artificial digestive markers for these experiments. Similar sized plastic markers have been used in *ex-situ* studies on *Cercopithecus* spp. (Table 4.1) and previous research reported that samango monkeys swallowed seeds between <1 x <1 mm and 6 x 10mm (Linden et al. 2015). We used distinct marker types differing in material (coconut shell or wood), colour (white, natural or dark) and shape (flat or round edged) for each trial. The average (mean ± SD) mass of the coconut shell markers was 0.019 ± 0.002 g and wooden markers weighed 0.014 ± 0.0003 g on average. We tested the resilience of the markers to chewing and gut passage in a preliminary study in September 2017, and successfully collected and identified different coloured intact markers from faecal samples. We did not find any partial segments of damaged beads in faecal samples. We conducted four trials on each subject using 50 markers per trial, totalling 200 markers for each subject.

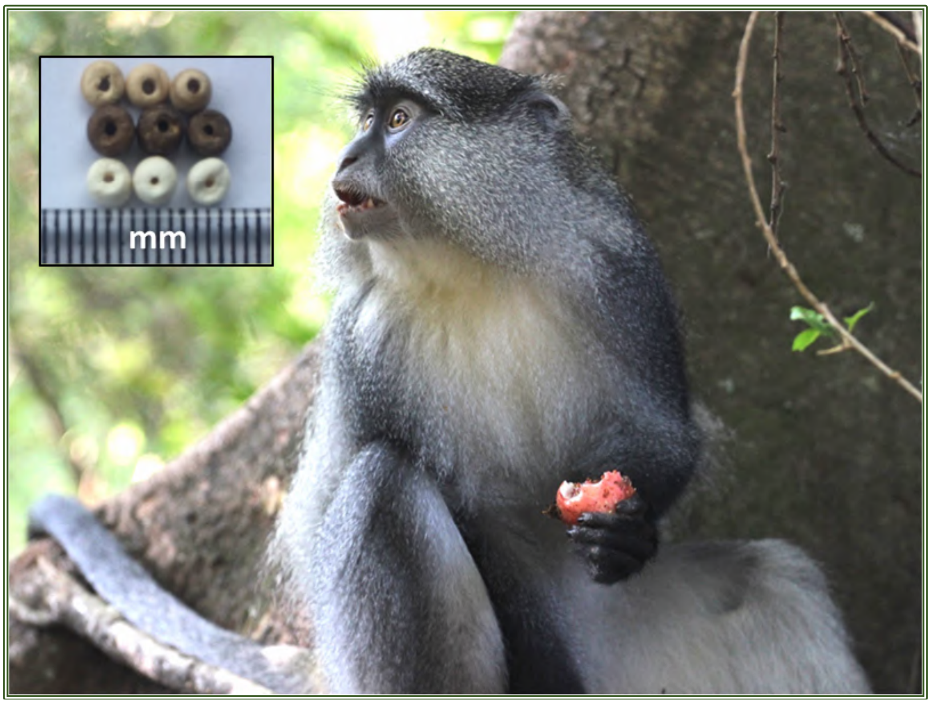


Fig. 4.1 Samango monkey *Cercopithecus albogularis schwarzi* feeding on ripe broom cluster fig (*Ficus sur*) fruit at Lajuma, South Africa, with examples of the beads used as artificial digestive markers for gut retention time experiments.

For each trial, we split a firm peeled yellow banana into five pieces, inserted 10 markers into each piece and positioned the pieces in the path of the approaching target subject (feeding event). We either left pieces on the floor or dropped them from an upside-down container upon the approach of the target individual by means of a pulley. We timed each feeding event, to occur when the target subject was not in close proximity to other individuals in the group, nor human observers, to facilitate targeted provisioning and minimise the association between humans and food. During the experiment with the male, feeding events occurred once on Day 1 at 16:30, twice on Day 2 at 06:20 and 13:00 and once on Day 3 at 07:00. During the experiment with the female, feeding events occurred once per day between 12:00 and 15:00 over four days. The timing of feeding events were coordinated to control for the natural daily variation in food items, which might affect gut passage time. We also wanted to ensure that following each feeding event, we had sufficient time (from 16 hrs after ingestion) to collect markers from faecal samples within the passage times reported in *ex-situ* studies (Table 4.1). We recorded the time of ingestion as the time when the monkey placed the final banana piece into the mouth. We followed focal subjects from dawn until dusk following each feeding event, with the male subject being followed for four successive days and the female subject for five successive days. If the target individual was briefly lost during a follow day, we continued to search until they had been relocated.

During daily follows we collected faecal samples from observed defaecation events and recorded the date and time of deposition. We could not collect samples at night. We washed samples using a sieve with 0.5mm diameter mesh at the end of each follow day and recorded the number and type of each marker that we removed from the remaining undigested matter. We recorded the times at which we located the troop each morning and left them each evening, as well as the times and duration of periods during which the focal subject was out of view. We used these data to identify estimates of TT and TLA if we could be confident that we collected all possible faecal samples, because we had successfully followed the subject continuously at least within the potential TT window of 16 – 24 hours reported in *ex-situ* studies (Table 4.1), and if we retrieved clear faecal samples (containing no markers) immediately before (TT) or after (TLA) samples with markers. We set out to measure MRT (Blaxter et al. 1956; Warner 1981), which is the standard measure of gut passage times, but low marker return meant we did not have sufficient data to calculate this index.

4.3 | Results

4.3.1 | Marker Ingestion and Focal Animal Observation

In the first trial with each subject, a non-target individual consumed one of the five pieces of banana, reducing the number of available markers to 40 for that trial. Both the male and female subjects placed the remaining banana into their mouths within 30 seconds. During five out of eight trials, we observed the focal animals spitting markers directly in the location of the feeding event and attempted to collect all of these markers (Table 4.2).

Table 4.2 Reliable (*) estimates of Transit Time (TT) and Time to Last Appearance (TLA) of markers (hrs), of the male and female *Cercopithecus albogularis schwarzi subjects* at Lajuma, Soutpansberg Mountain, South Africa, presented with the number of markers spat out, recovered from faeces and unaccounted for. Remaining values are not definitive first and last appearance but presented for information as potential TT and TLA.

	Marker Recovery			Gut Passage Times (hrs)	
Subject/Trial	Collected Spat	Recovered from Faeces	Unaccounted	TT	TLA
Male					
1	4	0	36	-	-
2	6	2	42	24.88*	25.48
3	32	2	16	16.73*	23.18
4	26	1	23	-	27.92
Female					
1	0	6[a]	34	21.37	26.73
2	0	4	46	18.73	25.12*
3	6	2[b]	42	-	27.27
4	0	12	38	16.63*	23.43
Species	74	28[a]	277	16.63	27.92

[a] Excluding an anomaly retrieved at 4.25 hrs after ingestion

[b] Both markers retrieved from one faecal sample

Due to difficulties in following arboreal animals in undulating, natural environments, especially high canopy forests and semi-deciduous woodlands with thick understoreys, the time that the focal animal was followed after each feeding event differed between subjects. On average (mean ± SD), the male was lost 2.5 ± 1.7 times per day and the female 2.2 ± 1.9 times per day. The average (mean ± SD) time to relocation was 55 ± 49 mins for the male subject and 49 ± 48 mins for the female subject, with a maximum time to relocation for each sex of three hours (only recorded once for each sex). Total focal observation time was 30.25 hrs for the male (3 full days) and 37.92 hrs for the female (4 full days) and mean (± SD) daily observation time was 9.95 hrs (± 1.56) and 9.48 hrs (± 1.58) respectively. On the fifth day of the experiment with the female, the group slept on land that we were not permitted to enter and so data collection ended. The group could not be found on the fifth day during the experiment with the male; hence, we terminated the experiment at the end of the fourth day. Although finishing earlier than planned the staggered nature of the trials meant that we followed both individuals for at least three days from the initial feeding trial.

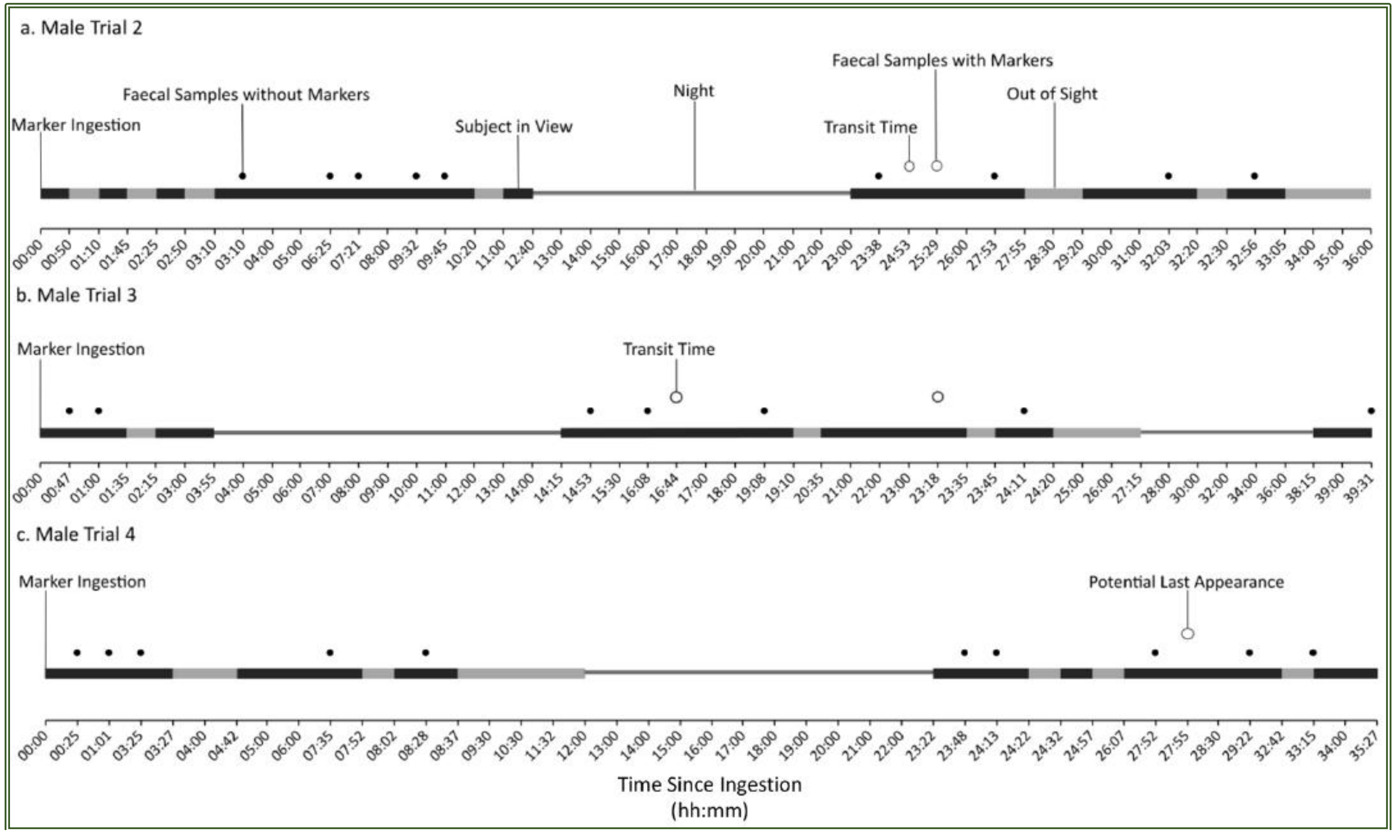
4.3.2 | Marker Recovery and Gut Passage Time

On average (mean ± SD), we observed the male defecating 6 ± 1 times per day, with an average defaecation rate of 1 hr 45 mins during daily follow time. We observed the female defecating 10 ± 3.46 times per day, with an average defaecation rate of 46 mins during daily follow time. Overall, we collected 18 faecal samples from the male and 45 faecal samples from the female. Of these, 5 (27.8%) male faecal samples and 15 (33.33%) female faecal samples contained markers.

We recovered no markers from the first trial with the male and on average (mean ± SD), we recovered 6.61% ± 4% of markers from three trials with the male and 13% ± 9% of markers from four trials with the female (Table 4.2). We recovered one marker after 4.25 hrs from the female subject during an aggressive between-troop encounter. As we encountered this TT on just one occasion, we regarded it as an anomaly. Two trials out of four for each subject provided reliable estimates of either TT or TLA (Table 4.2) and we were therefore able to estimate a preliminary gut passage time window of between 16.63 – 25.12 hrs. We were unable to reliably estimate TT and TLA from a single trial, nor were we able to reliably estimate an overall MRT. This was due to potentially missing faecal samples when each subject was out of sight and the low number of returned markers was insufficient to calculate average passage times; however, we are confident in our estimation of a gut passage time window for the following reasons.

From the male subject, we were able to confidently estimate a TT of between 16.73 - 24.88 hrs from the third and second trials respectively (Table 4.2; Fig. 4.2). In the second trial, we successfully followed the male from 3.17 – 12.65 hrs following ingestion of the markers, except for a 40 min period between 10.34 – 11 hrs after ingestion, collecting five clear faecal samples. We left him at the groups' sleep site over-night, relocating him 23hrs after marker ingestion and collecting a clear sample at 05:58, 23.63 hrs after ingestion. The peak time of defaecation in other *Cercopithecus* spp. has been documented as 06:00 – 09:00 (Lambert 2002; Blaine & Lambert 2012), and we are confident that this was the first defaecation after waking. We successfully followed him and collected a further three faecal samples without losing him from sight. The first of these contained markers from the second trial at 24.88 hrs, which we can be confident was the TT of these markers. As we lost him for 1.42 hrs after collecting the third of these samples, we could not be confident that the second marker retrieved at 25.48 hrs after ingestion was the TLA of markers from this trial. In the third trial with the male subject, we collected two clear faecal samples at 14.88 and 16.13 hrs after marker ingestion and retrieved the first marker from this trial at 16.73 hrs after ingestion.

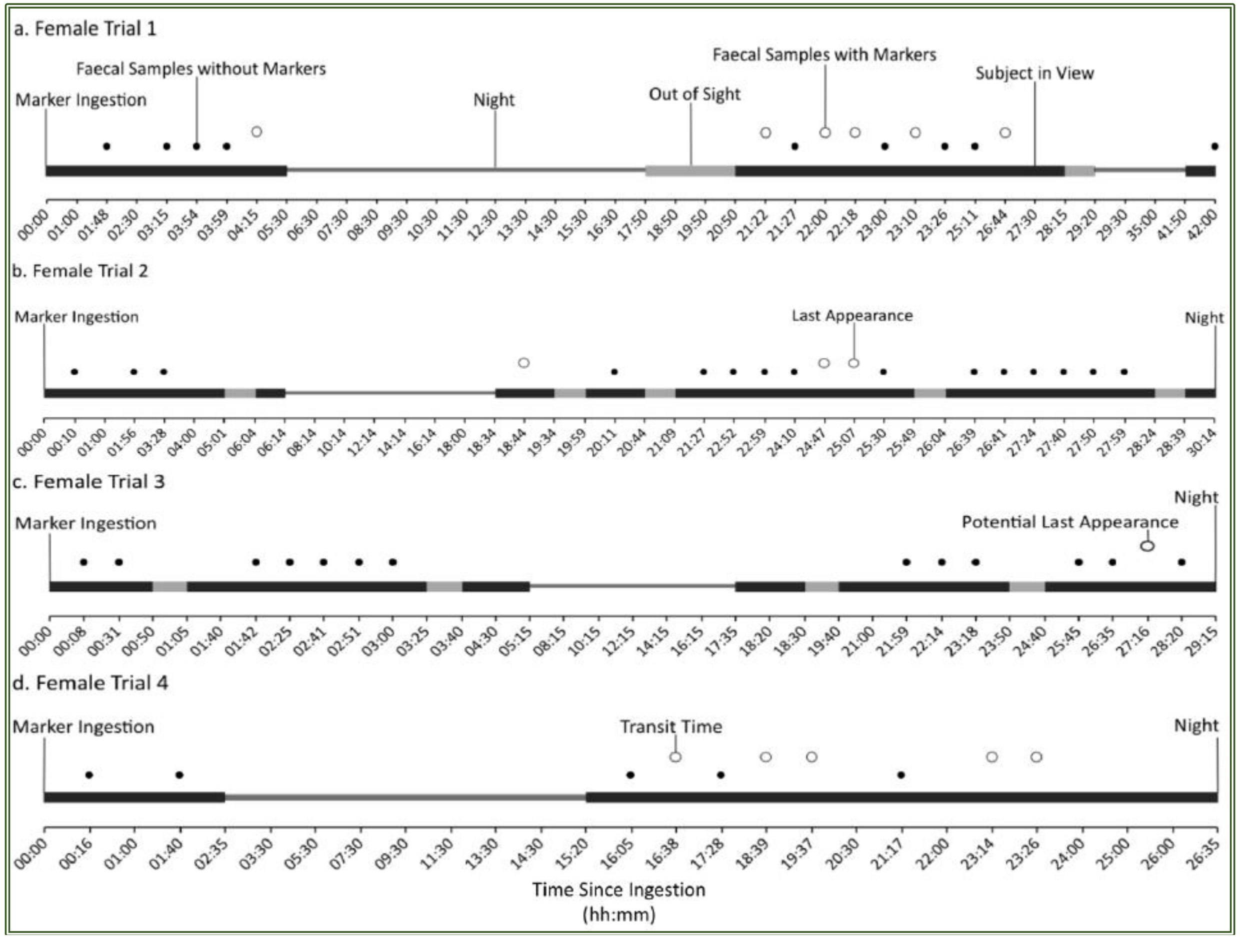
Fig. 4.2 Timelines of three gut passage time trials conducted on a male *Cercopithecus albogularis schwarzi* subjects at Lajuma, Soutpansberg Mountain, South Africa, presenting times since ingestion of times subject was in view, out of view and night hours, faecal samples collected with and without markers, and indication of reliable estimates of either Transit Time or Time of Last Marker Appearance. Note the x-axis time since ingestion is not to scale.



In the fourth trial, we were unable to locate the male between 22.53 – 23.37 hrs following ingestion the morning after marker delivery and could not be certain that we collected the first faecal sample defecated by the male that day. As we also lost him between 24.95 – 26.12 hrs and 32.7 – 33.2 hrs after marker ingestion, we have not included the marker we recovered at 27.92 hrs after ingestion as a reliable TT, including it instead as a potential TLA because it indicates markers were retained in the gut for at least this period of time.

From the female subject, we were able to confidently estimate a TT of 16.63 hrs and TLA of 25.12 hrs from the fourth and second trial respectively (Table 4.2; Fig. 4.3). Following ingestion of the markers in the fourth trial, we relocated the group at the sleep site 14.92 hrs after marker ingestion and collected a clear sample at 16.08 hrs and a sample containing three markers 16.63 hrs after ingestion. Both of these faecal samples were collected before 09:00 and we are confident they were the first samples defecated by the female that day. We are confident in our estimate of the 25.12 hrs TLA of markers from the second trial with the female, as we retrieved a further seven clear faecal samples between 25.5 – 30.23 hrs after marker ingestion. We are confident that these seven faecal samples represented all of the samples deposited by the female during this time as we followed her continuously during the collection period, with only two 15 min periods in which we could identify her as being in a small group of travelling monkeys, but could not identify her individually. We were away from the female between 5.5 – 20.83 hrs after ingestion of the markers in the first trial, which included the peak defaecation period between 06:00 – 09:00, and lost her between 28.25 – 29.33 hrs after marker ingestion.

Fig. 4.3 Timelines of three gut passage time trials conducted on a female *Cercopithecus albogularis schwarzi* subjects at Lajuma, Soutpansberg Mountain, South Africa, presenting times since ingestion of times subject was in view, out of view and night hours, faecal samples collected with and without markers, and indication of reliable estimates of either Transit Time or Time of Last Marker Appearance. Note the x-axis time since ingestion is not to scale.



As such, although we collected six faecal samples collectively containing seven markers between 20.83 hrs and 28.25 hrs after ingestion, we were unable to use these data to reliably estimate TT or TLA. Likewise, we lost the female several times between 17.58 – 24.67 hrs after ingestion of the markers in the third trial and, even though we collected five clear samples between 21.98 – 26.58 hrs after ingestion, we have included the 27.27 gut passage time as a potential, but not reliable, estimate of TLA (Table 4.2).

4.4 | Discussion

To our knowledge, our study is the first to present data on the gut passage time of *Cercopithecus* spp. *in-situ* using artificial digestive markers. We were able to confidently estimate a gut passage time window of between 16.63 – 25.12 hrs, which provides valuable data for future studies to compare *in-situ* estimates of *Cercopithecus* spp. gut passage times. Our results concur with other published studies that indicate an extended gut passage rate in *Cercopithecus* spp. (Maisels 1994; Lambert 1998), which is indicative of digestive adaptation for fermentation of plant parts (Lambert 2002). It has previously been reported that forest cercopithecines exhibit considerable feeding flexibility (Blaine & Lambert 2012) and previous studies using time budget analysis have reported samango monkeys to spend 51.7% - 72% of feeding time consuming fruit, 17% - 52% of feeding time consuming leaves and 4.4% - 11% of feeding time consuming other items (Coleman and Hill 2014a, 2014b; Linden et al. 2015).

In captive studies, TT for *Cercopithecus* spp. is estimated to be between 16.05 – 23.95 hrs after marker ingestion (Table 1). Our finding of 16.63 – 25.12 hrs TT for samango monkeys, is remarkably consistent with results from captivity and as such, provides an important ecological validation. Whilst captivity can reduce gut passage rates (Milton 1984; Martin et al. 1985; Blaine & Lambert 2012) through the 'captivity effect' (Martin et al. 1985) and invariable diets (Cabana et al. 2017), our results suggest that other factors, such as site-specific behaviours, may influence gut passage time in wild subjects. For example, aggressive between-troop encounters may influence gut passage time, as observed from the retrieval of one of our markers 4.25 hrs after ingestion. Additionally, daily and seasonal changes in diet can also influence gut passage times (Lambert 1998; Tsuji et al. 2015). These behavioural traits and changes in diet can only be observed *in-situ*, are likely to be site specific, and may differ to behaviours displayed in captive subjects. Hence, whilst our results obtained *in-situ* are consistent with those obtained in captivity, our results demonstrate the importance of *in-situ* measures of gut passage time where behaviours linked to the social and physical environment may influence gut passage times. For species of which gut retention time is relatively short, methods described in this study may not be applicable as using seeds from infrequently ingested fruit items has been shown to be a reliable method of estimating gut passage times (Heymann et al. 2012). For species of which gut retention time is longer, observation-based methods can be much less reliable (Heymann et al. 2012) and our study provides valuable data on which to build more efficient techniques *in-situ*.

In this regard, we highlight some caveats to our study. First, as is typical of gut retention studies, we had a low sample size (one animal of each sex), although this is in line with other published studies (Table 1) (Maisels 1994; Poulsen et al. 2001; Lambert 2002; Blaine & Lambert 2012). Secondly, we had low faecal marker recovery. Low faecal marker recovery has been previously documented in *Cercopithecus* spp. studies, and has been attributed to cercopithecine use of cheek pouches and oral processing, which includes seed predation through crushing by high-crowned molars (Lambert 2001). For example, Blaine & Lambert (2012) reported 5% - 45% marker recovery from a male *C. l'hoesti* (L'Hoest's monkey) subject and 5% - 20% marker recovery from a female subject. With our markers being made of natural materials, it may be that some markers were crushed prior to swallowing, although we did not find fragments of markers in any of the faecal samples we collected. Although we watched each subject closely following each feeding event, it is possible that more markers were spat out following feeding events than we observed. Alternatively, we could have waited for the ingestion of infrequently consumed food items, a practice adopted in a few seed dispersal studies (e.g. Stevenson 2000; Link and Di Fiore 2006; Beaune et al. 2013a). However, this may happen rarely across species and is not predictable. Such practice relies on either locally scarce or clumped food resources that minimise replicated feeding on focal tree species (Stevenson 2000). Depending on the number of fruits consumed, as well as the number of seeds actually swallowed, this method also has a high risk of missing the collection of faeces containing the focal seeds. As such, the use of artificial markers may reduce the error and loss of data potentially associated with this method. Finally, we were only able to conduct one set of trials in our study and so our results only reflect the various food items that were present during that season. As the degree of frugivory may be both seasonal and individual, future studies should aim to capture data that spans the spectrum of variation in frugivory and therefore the range of gut passage times within their study systems.

Adapting a methodology such as we have, from a captive to an *in-situ* setting, was partially successful in estimating a gut passage time window, although we were not able to calculate MRT. There is currently no minimum for the number of retrieved markers required to estimate MRT, however such calculations require reliable and consistent collection of faeces clear of markers before and after the first and last marker respectively. Given the challenges in the study of wild animals, especially those associated with arboreal primates and the level of habituation required for such intense focal observations (e.g. Souza-Alves and Ferrari 2010), it would be near impossible to expect to collect all of the markers spat out or defecated following ingestion, as well as being entirely sure that all faecal samples during the night were collected. However, as we have shown, as long as the first and last appearance of markers in faeces can be captured from across trials, researchers should be encouraged to develop and refine methods which prevent markers being spat out and that will allow for the identification of faecal samples deposited at night from focal individuals.

We can make several recommendations for future *in-situ* gut retention studies. Firstly, as a novel and potentially high value food item, the banana we used for the delivery of the markers may have elicited retrieve-and-retreat behaviour in response to feeding competition (Smith et al. 2008), especially in the female who may have stored the banana in her cheek pouches temporarily. In cercopithecines, adult males dominate other group members, whereas subordinates use cheek pouches to store high value contestable food items (Smith et al. 2008). Ideally, replacing the banana with a native locally available fruit would be preferable to such a high value food item, although we note that high value items may increase the probability of marker delivery compared with low value readily available items that are commonly available in the surrounding environment. In addition, local fruits must be soft enough to allow removal of the seed and/or large enough to accommodate markers, neither of which were available at our study site.

Secondly, following arboreal animals in natural environments is intrinsically difficult, especially in high canopy forests and semi-deciduous woodlands with thick understoreys, and we lost the male and female subjects occasionally, which could account for the low marker recovery. Although we collected an average of ten faecal samples per day from the female subject, faecal sample collection was considerably lower for the male subject, from whom we collected six per day on average. There is a possibility that the male subject especially, defecated out of sight of the observer. Future studies should be optimised to maximise the likelihood of continuous observation through careful planning of the timing and location of their experiments. This should include additional observers strategically placed to monitor established travel paths during experiments.

Thirdly, we could not collect faecal samples at night and markers excreted at night have not been included in our analyses. However, a first step should be the identification of the gut passage time window by establishing reliable estimates of TT and TLA, followed by repeated trials designed to maximise faecal sample collection within this target window. Future studies should aim to stagger the delivery of different marker types, as we did throughout the day to increase the likelihood of marker retrieval within a day's follow. Traps underneath sleeping sites, such as fine mesh cloth, may aid in collection of faecal samples in locations during the night to capture samples with markers. Time of deposition can then be read from a camera trap or estimated by appearance (Lambert 2002). Notwithstanding, the staggered nature of our trials enabled us to follow both individuals for at least four days from the initial feeding trial. We collected clear faecal samples, and successfully followed each subject sufficiently to obtain estimates of TT and TLA for samango monkeys in our study system.

Our results indicate a wide range in gut passage times for samango monkeys which may also have consequences for models of primate seed dispersal distances. Dispersing seeds away from parent plants can reduce the negative effects of conspecific density-dependent competition and natural enemies (Janzen 1970; Connell 1971; Comita et al. 2014) and can influence range expansion (Howe & Smallwood 1982). However, this would be dependent on mean annual home range (HR), daily path length (DPL), direction and speed of travel, and tortuosity. For example, longer retention times of seeds in the digestive tract may mean that although seeds are transported over the DPL, they may be deposited close to the original source, depending on HR size and tree re-visitation rates. For samango monkeys at our study site, mean (± SE) annual HR has been estimated to be between 0.56 km^2 (± 0.07 km^2) and 0.60 km^2 (± 0.13 km^2) from 2012 to 2016 (Parker 2018), and between 0.67 km^2 and 0.97 km^2 in 2018 (Stringer *unpub. data*). Whilst samango monkeys may therefore be able to cover a wide area of their home range per day, they often utilise different locations for sleeping sites which may increase variability in dispersal distance. Dispersal kernels can be used to infer the statistical distribution of seed dispersal distances by combining gut passage time with movement data (Nathan et al. 2012; Fuzessy et al. 2017). Inaccurate estimation of gut passage time could thus produce dispersal kernel models that over- or underestimate dispersal distances (Côrtes and Uriarte 2013) and studies such as ours that aim to ascertain retention times *in-situ*, provide valuable data from which to estimate dispersal kernels, especially where the use of captive animals for estimating gut passage time is restricted.

In conclusion, *C. a. schwarzi* follow the general trend in cercopithecines of a relatively long gut retention time. This can be attributed to the inclusion of large proportions of non-fruit plant parts in their diet and the need for longer fermentation of these food items. Our study is the first to report a gut passage time window of a *Cercopithecus* species *in-situ*. Whilst our study goes some way to validate similar results reported from *ex-situ* studies, we encountered methodological issues in retrieving all of the markers following ingestion by the monkeys and were unable to estimate MRT. However, *in-situ* studies are critical to providing ecologically valid estimates of gut passage times requisite in models of seed dispersal distances and which may be necessary when the use of captive animals is restricted. Therefore, moving forward, we highlight the need for discussion in implementing a standardised protocol for future studies investigating gut retention time *in-situ* and hope that our study encourages similar attempts to study gut passage rates on naturally foraging primates.

Chapter Summary

In this chapter the gut retention time of wild samango monkeys was investigated in-situ by adapting experimental methods used on captive cercopithecines for a field setting. I demonstrated that C. a. schwarzi follow the general trend of a relatively long retention time, as has been observed in ex-situ studies on gut retention time in cercopithecines. I was able to reliably estimate a gut passage time window of between 16.63 – 25.12 hrs, although within this window, gut passage is variable. Extrinsic factors such as intragroup aggression, as well as intrinsic factors such as the composition of the diet, may alter gut passage time, which have important consequences for seed dispersal, and which cannot be captured in captive studies. Methodological issues meant I was unable to estimate mean retention time, and this chapter highlights the need for a reliable standardised protocol for future studies.

In the next chapter, results from Chapter 3 and additional data on the behaviour of samango monkeys is used to assess SDE and addresses the behavioural and ecological drivers of intergroup SDE variability.

Chapter 5

Intergroup variability in seed dispersal effectiveness of samango monkeys (*Cercopithecus albogularis schwarzi*) in a mixed-forest landscape

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In Chapter 3, samango monkeys had the greatest positive influence on seed germination through processing mechanisms that release the seed from germination inhibiting fruit pulp. However, within the SDE framework, germination is only one measure of an effective disperser (Schupp 1993; Schupp et al. 2010). In Chapter 4, extrinsic factors such as intragroup aggression influenced the gut passage time of artificial digestive markers, highlighting that an animal's behaviour can have consequences for seed dispersal.

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[3] SS, RH and NK conceived and designed the experiments. SS performed the experiments. SS analyzed the data and wrote the manuscript; RH, LS and NK revised manuscript drafts.

In this chapter, I use the results from Chapter 3 and additional data on monkeys behaviour to assess the SDE of samango monkeys, the behavioural and ecological drivers of intergroup SDE variability (John et al. 2016) and the impact such variation could have on plant fitness.

Abstract

Frugivory and seed dispersal are interactions critical for maintaining forest dynamics by moving seeds away from the parent and enhancing seed germination and seedling establishment. Animal-mediated seed dispersal is a complex process in which behaviour of the disperser determines the spatiotemporal distribution of fruiting plants. In social foraging animals, such as primates, behaviour can be constrained by, and vary as a consequence of, the social, environmental and physical environments they inhabit. The effectiveness of a disperser is dependent on the impact it has on plant fitness, which can be quantified as a product of the quantity and quality components of the Seed Dispersal Effectiveness (SDE) framework. The aim of this study was to investigate how seed dispersal effectiveness differed between two groups of samango monkeys (*Cercopithecus albogularis schwarzi*) within the same population, and inhabiting home ranges in close proximity to each other. We identified the movement and feeding behaviour of the two groups and combined these data with results from published germination studies (Chapter 3) to model SDE for three fruit species common in the diet of each group. We found that variability in time budgets influenced group differences in the quantity of dispersal.

Variability in ranging behaviour influenced group differences in the quality of dispersal, through differences in the time groups spent in habitats in which they deposit seeds. These differences seem largely driven by group-specific behavioural and ecological attributes. Our findings highlight the need for intergroup variation to be included in models of seed dispersal effectiveness.

5.1 | Introduction

Frugivory and seed dispersal are mutualistic interactions between animals and plants (Farwig & Berens 2012; Eriksson 2016). This mutualistic relationship is critical in maintaining forest dynamics (Terborgh et al. 2002) and plants rely on dispersers that are effective in moving seeds away from the parent (Janzen 1970; Connell 1971) and enhancing seed germination and establishment (Terborgh et al. 2002; Traveset et al. 2007). The effectiveness of a disperser is dependent on the impact it has on plant fitness (Schupp 1993), which can be quantified using the quantity and quality components of the Seed Dispersal Effectiveness (SDE) framework (Schupp et al. 2010). Within the SDE framework, the dispersal quantity component is determined by the number of seeds dispersed per unit of time, typically measured as the product of the number of seeds dispersed per visit and the number of visits (Schupp 1993). The dispersal quality component describes the probability that dispersal produces a new adult, typically measured as the product of the effect of seed handling on germination and the quality of seed deposition into microsites which favour seed and seedling survival and subsequent growth (Schupp 1993; Schupp et al. 2010).

Recent studies emphasise the need to adopt inter- and intraspecific comparisons in seed dispersal models to better understand seed dispersal from the population, community, network and landscape levels (Russo et al. 2006; Strier 2009; Matías et al. 2010; McConkey et al. 2014; Heymann et al. 2017; Andresen et al. 2018; Fricke et al. 2019). The SDE framework offers a flexible tool with which to quantify the degree of variation at a specific level of comparison (Schupp et al. 2017). Thus the framework can be used for comparisons within and between populations of dispersers (e.g. McConkey et al. 2018) and provide insights into their relative contribution to the maintenance and regeneration of plant communities (Zwolak 2018). However, as research encompassing interspecific variation in seed dispersal populations, communities and networks steadily increases (e.g. Poulsen et al. 2001; Czarnecka 2005; Dennis & Westcott 2006; McConkey et al. 2014; 2015, Heymann et al. 2017; Mokotjomela et al. 2016; Nakabayashi et al. 2019, Nogales et al. 2017; Fricke et al. 2019), our understanding of intraspecific variability in seed dispersal at the local scale is lacking. To date, much of the work investigating variation in seed dispersal at the local scale has been focussed on interspecific variability in dispersal of several plant species (e.g. Yumoto et al. 1999; Culot et al. 2010; Gross-Camp & Kaplin 2011), dispersal of a single plant species by several dispersers (e.g. Figueroa-Esquivel et al. 2009; Mokotjomela et al. 2015; Niederhauser & Matlack 2015), or by assessing functional groups of dispersers with common traits (e.g.Dennis & Westcott 2007) and dispersers of functional plant groups (Aslan et al. 2019).

Animal-mediated seed dispersal is a complex process in which the behaviour of the disperser determines the spatiotemporal distribution of fruiting plants (Russo et al. 2006; Karubian & Durães 2009; John et al. 2016; Zwolak 2018; Aslan et al. 2019). Studies on intraspecific variability in seed dispersal will broaden our understanding of how seed dispersal can be influenced by individual and group behaviour and the impacts such variation may have on plant fitness (Westcott & Graham 2000; Russo et al. 2006; Robledo-Arnuncio et al. 2014; Zwolak 2018; Snell et al. 2019). Movement behaviour associated with intersex differences in reproduction strategy can influence dispersal distance and seed deposition patterns (Tarszisz et al. 2018). Dispersal by female orangutans (*Pongo pygmaeus wurmbii*) centres around a predictable and stable core range, while dispersal by mate-seeking males is less predictable (Tarszisz et al. 2018). Sex-related seasonal differences in diet, whereby males of three *Cercopithecus* species consume more fruit and females consume more protein-rich foods during birthing and nursing periods (Gautier-Hion 1980), may also impact sex-related seed dispersal differences. Sex-specific reproductive strategies in multi-female, single-male primate social systems may also influence sex-related differences in seed dispersal, whereby small groups of bachelor males move between several groups of females during mating seasons, potentially creating larger seed shadows than females. Courtship behaviour in lek mating systems facilitates intersex differences in seed deposition patterns (Krijger et al. 1997; Karubian et al. 2012). The aggregation of male birds around lekking sites facilitates clumped dispersal patterns of seeds, whereas solitary females disperse seeds more evenly across their home range (Krijger et al. 1997; Karubian et al. 2012). Environmentally driven behaviour can influence seed dispersal (Nathan et al. 2012; Robledo-Arnuncio et al. 2014). Seasonal movement patterns of elephants (*Elephas maximus*) within two ecologically distinct habitats facilitated seasonal variation in seed dispersal distance, as in seasonally dry habitat, elephants travelled further to locate water sources (Campos-Arceiz et al. 2008). Habitat selection and preference can have direct impacts on seed deposition quality and the spatial distribution of plants (Rodríguez-Pérez et al. 2012; Arroyo-Rodríguez & Fahrig 2014; Snell et al. 2019). Habitat preference of Balearic lizards (*Podarcis lilfordi*) and thrushes (*Turdus* sp.) may determine seed dispersal patterns and the spatial aggregation of seed deposition sites (Rodríguez-Pérez et al. 2012; Morales et al. 2013).

Intraspecific behavioural patterns are a response to fluctuating ecological conditions, predation pressure, physiological differences associated with sex and age, and the spatiotemporal distribution of resources (Clutton-Brock 1977; Cords 1986; Strier 2009; Sasaki et al. 2016). In social foraging animals, such as primates, decisions regarding when, where and for how long to forage are influenced by the decisions of others, and can vary as a consequence of the social, environmental and physical environments (Chapman & Chapman 2000a; Galef & Giraldeau 2001; Marshall et al. 2012). As such, the degree of sociality can influence the effectiveness of a disperser (Karubian & Durães 2009) and dispersers from neighbouring groups of primates and even within the same population, may differ in their SDE (Razafindratsima et al. 2014; Phiphatsuwannachai et al. 2018). Intergroup variation in seed dispersal can include the number of seeds dispersed, treatment of seeds during fruit processing and transit through the gut, dispersal distance and the quality of the microhabitat into which they are deposited (Phiphatsuwannachai et al. 2018; Zwolak 2018; Snell et al. 2019). Variation in dispersal quantity may not necessarily imply poor dispersal, as the total effect of SDE means that variation in dispersal quality can influence the probability of seed germination and the spatial distribution of dispersed seeds (Schupp et al. 2017). Therefore, population and/or species estimates of SDE, while important, may overlook the inherent variation of the components of SDE in social foraging animals (Zwolak 2018). While interspecific variation in primate seed dispersal is well documented (e.g. Muller-Landau et al. 2008, Traveset et al. 2007), intergroup variability in SDE is still poorly understood.

Primates are particularly useful for intergroup comparisons of SDE for several reasons. Firstly, group size among primate populations are highly variable and an adaptation of sociality, often constrained by ecological properties of their environment (Chapman & Chapman 2000b; Grove 2012). Under these ecological constraints, it is proposed that larger groups experience increased intragroup feeding competition from other group members (Janson & van Schaik 1988) and rapid depletion of resources forces foraging across greater areas than smaller groups (Chapman & Chapman 2000b). Increased foraging area can increase seed dispersal distance away from the parent (Chapman & Russo 2006), however, can also result in reduced feeding time and therefore lower quantities of dispersed seeds (Karubian & Durães 2009). Secondly, primates are regarded as important seed dispersers (Andresen et al. 2018), can consume larger fruits and seeds than most birds (Chapman & Onderdonk 1998; Balcomb & Chapman 2003) and can process fruit in different ways resulting in spitting, swallowing or predation of seeds (Corlett & Lucas 1990), such that the quality of dispersal may differ even for the same plant species (Chapter 3). Lastly, primates inhabit many ecosystems and have a broad distribution across habitats under threat from anthropogenic disturbance (Estrada et al. 2017). Thus, understanding the role primate populations have in the habitats in which they live can inform landscape conservation efforts (Arroyo-Rodríguez & Fahrig 2014).

In this study, we selected an arboreal forest guenon, samango monkey (*Cercopithecus albogularis schwarzi*) as the model species to test intergroup variability of SDE. Guenons make an ideal model species for seed dispersal studies as firstly, they are highly frugivorous, with their diets often consisting of more than 50% fruit (Lawes 1991; Chapman et al. 2002). Secondly, while the majority of primate species are seed-swallowers, guenons are unique in that they exhibit multiple seed handling mechanisms. They typically swallow seeds smaller than 4 mm (on longest axis) and spit out seeds larger seeds (Lambert 1999; Gross-Camp & Kaplin 2011; Linden et al. 2015). Guenons also utilise cheek pouches to store food (Lambert 2005a; Linden et al. 2015), which can hold as much volume as the stomach and present a further mechanism for seed dispersal (Chapter 1, section 1.4.3) (Corlett & Lucas 1990; Rowell & Mitchell 1991). Thirdly, guenons are highly gregarious and exhibit territorial behaviour between groups of varying sizes (Lawes 1990; Cords 2002). They are dependent on high-canopy evergreen forest (Cords & Chowdhury 2010; Linden et al. 2015; Parker 2018) and thus, groups living within close proximity may demonstrate variation in resource use that could influence their SDE.

In South Africa, samango monkeys are the only forest-dwelling primate and are highly dependent on samango monkeys are also the only large-bodied arboreal species that feed on medium to large sized fruits in the canopy layer of South Africa's evergreen forests (Coleman & Hill 2014, Linden et al. 2015, 2016). They are tolerant of disturbance and may be important seed dispersers in degraded habitats (Kaplin & Lambert 2002; Albert et al. 2014). As such, the loss of samango monkeys could have negative cascading effects on the forests in which they reside.

The aim of this study was therefore to investigate the effect of variation in group foraging behaviour and spatial ecology on SDE. To achieve this, we first identified the movement and feeding behaviour of the two samango monkey groups. Secondly, we used these data and data from germination experiments of samango monkeys dispersed seeds (Chapter 3), to model SDE of each group for three locally abundant fruit species that are common in the diet of each group. We hypothesized that intergroup variability in group size, activity patterns and diet composition would drive SDE intergroup variability, as the larger of the two groups would require a larger home range and would, on average, spend more time travelling and less time feeding each day (Janson & van Schaik 1988; Chapman & Chapman 2000b).

5.2 | Materials and Methods

5.2.1 | Data Collection

5.2.1.1 | Study Site

We conducted the study between August 2017 and May 2018 at the Lajuma Research Centre (29°26'E, 23°01'S) in the far western Soutpansberg Mountain Range of South Africa's Limpopo Province. The altitudinal range across the study is between 1150 to 1750 m, with a mesothermal climate of dry cool winters between April and September and wet warm summers between October and March (Munyati & Kabanda 2009). The study site is mountainous and contained within a complex mosaic of vegetation types including Limpopo Mistbelt Forest, Soutpansberg Moist Mountain Thickets and Soutpansberg Mountain Bushveld (Maltitz et al. 2003; Mostert et al. 2008). High-canopy evergreen forests at the base of south-facing mountain ridges are supported by orographic and increased localised rainfall (Mostert 2006). These tall evergreen forests transition into semi-deciduous woodland, thicket and dense bush, and grasslands intersected with riverine mixed-forests (Maltitz et al. 2003, Mucina & Rutherford 2006). We focussed this study on three locally abundant plant species that are common in the diet of each samango monkey group (Chapter 3, section 3.2.1.2): *Ficus* spp. (figs), *Searsia chirindensis* (red currant) and *Syzygium cordatum* (water berry). During the study period, *Ficus* spp. fruited year-round due to the asynchronous nature of the genera (Compton et al. 1996b; Bleher et al. 2003). For the other species, the fruiting season occurred between December 2017 and February 2018 for *S. chirindensis* and between December 2017 and April 2018 for *S. cordatum*.

5.2.1.2 | Study Groups

In this study we followed two groups of samango monkeys, "Barn" group, comprising approximately 40 individuals and "House" group, comprising approximately 70 individuals (Coleman & Hill 2014, Nowak et al. 2014; Parker 2018). Both groups comprised one resident male, multiple females, and their sub-adult, juvenile and infant offspring. Four to six bachelor males joined both groups intermittently during the mating season between March and May 2018. The samango monkeys have been studies continuously at the study site since 2007 (Bibi Linden *pers. comm.*) and were fully habituated to observers.

5.2.1.3 | Behaviour Observation

We followed each samango group from dawn until dusk, between four and eight days per month (mean ±SD Barn 6 ±1.41, House 6.17 ±1.72 days), between December 2017 and May 2018. We collected data on feeding behaviour using two 15-min focal animal time sampling with all-occurrence recording per hour. We selected only adult and sub-adult individuals as they were more accustomed to observers and easier to observe than juveniles and infants (Chapter 2, section 2.6.5). To avoid sampling bias toward the same individual or proportion of the group, we selected focal individuals farthest away from the previous individual.

We recorded behaviour data using Prim8 mobile application (McDonald & Johnson 2014) on a handheld tablet (Yoga Tab 3, Lenovo Group Ltd., Beijing, China) powered by Android 5.1 OS (Google Inc., Mountain View, CA, USA). The Prim8 application enabled continuous data collection and recorded the time duration of each behaviour at a scale of one second. During observations we recorded if the individual was resting, travelling, socialising or feeding in the first instance (Table 5.1) (Dunbar 1992; Chapter 2, section 2.6.5). If feeding, we recorded if the monkey was feeding from its cheek pouches, or if feeding on a food item, we recorded food type as either flowers, fruit, leaves, seed pod or 'other' for all other food items (Chapter 2, section 2.6.5). If fruit was being consumed, we recorded the plant species.

Table 5.1 Ethogram of general behaviours and feeding behaviour categories recorded during 15-min focal animal samples of samango monkeys at Lajuma, South Africa.

Activity	Definition
General Behaviour	
Feeding	Actively processing food items in the mouth, handling or transferring from hand to mouth, or removing item from substrate with mouth.
Resting	Remaining still lying, sitting or standing, not displaying behaviour related to feeding or socialising.
Socialising	Engaging in physical contact with another, through grooming, fighting or feeding infant.
Travelling	Moving along any surface without behaviours related to feeding or socialising.
Lost Group	Entire group out of site due to relocating during the night, entering inaccessible land over or traversing a cliff.
Lost Focal Subject	Subject out of site due to traversing a cliff, travelling faster than the observer can keep up with, or indistinguishable within a subgroup.
View Obstructed	Location of subject known but behaviour unrecordable due to view being obstructed e.g. branches/leaves, cliffs, or too high in canopy.
Feeding Behaviour	
Cheek Pouch	Actively moving stored food items from cheek pouch to mouth using either the tongue or hands and processing food item.
Flowers	Consuming inflorescence from trees or shrubs, excluding grasses.
Fruit	Consuming fleshy or non-fleshy fruits from trees or shrubs, by placing item into the mouth or cheek pouch; species recorded.
Leaves	Consuming greenery from trees or shrubs, excluding any other part of the plant.
Seed Pod	Processing seed pods typically from acacia trees, and consuming seeds removed from them.
Other	Consuming bark, fungi, grass, invertebrate, tree sap or water.

If we lost sight of the subject because of obstructions, we recorded 'view obstructed' and if the group was lost at the time of sampling, we recorded 'lost group'. If we lost the focal subject, we recorded 'lost focal subject' (Table 5.1). On occasions where we lost the focal animal before two thirds (600 secs) of observation time, we discarded the observation data, selected a new individual and began the sampling period again. If the focal individual was lost after 600 secs, observation data were retained, and the observation recorded as successful. We kept 36 observations in which the focal subject was lost after 600 secs, 16 observations for Barn group and 20 observations for House group. We discarded follow days that were incomplete because we lost the focal group and could not locate them.

In total, we were able to collect 36 full follow days for Barn group (191.92 hrs) and 37 full follow days for House group (200.55 hrs). We followed both groups simultaneously on 20 of these days using two observers (Cohen's kappa inter-observer reliability $k = 0.93$ and $k = 0.81$; Chapter 2, section 2.6.5). Diet composition was calculated as the mean percentage of time all animals consumed each food type or species per day over the total time spent feeding per day. We recorded the location of the focal animal's group at 15 min intervals using GPS (eTrex10, Garmin International Inc., Olathe, KS, USA) and integrated locations into GIS software (QGIS ver. 2.6).

We also collected feeding behaviour data on fruits consumed per minute using 1-min focal animal time sampling with all-occurrence recording (Altmann 1974) during follow days, in-between the 15-min focal animal sampling. As before, we only targeted adult and sub-adult monkeys, although we did not distinguish between the two groups. For each minute, we recorded the number of *S. chirindensis* and *S. cordatum* fruits taken into the mouth of the monkey and the number of seeds expelled from the mouth. As we observed *S. chirindensis* seeds in samango monkey faeces, for this species, we assumed that seeds that we did not see spat out during the minute observation were swallowed. We did not observe any *S. cordatum* seeds in faeces and therefore did not include seed-swallowing for this species. We assumed the difference between the number of *S. cordatum* fruits consumed and seeds we saw spat out were stored in cheek pouches and did not include this difference in any further analyses. We applied slightly different methodology to *Ficus* spp. observations. This was because the monkeys partially consumed *Ficus* spp. fruits (Fig. 4.1) and unconsumed fruit was dropped to the floor. We collected partially consumed fruit as they were dropped by the monkeys and estimated the proportion of consumed fruit as either 0.25, 0.5, 0.75, or 1 if no flesh was expelled. We then estimated the proportion of consumed fruit as 1 minus the proportion of dropped fruit. If we lost sight of the focal animal during the observation, we selected a different individual and began the observation again, discarding the previous observation data. In total, we recorded 96 *Ficus* spp., 38 *S. chirindensis* and 7 *S. cordatum* 1-min observation samples of fruit processing behaviour. The low number of samples for *S. cordatum* was down to the monkeys not consuming this fruit on 1-min focal sampling days.

5.2.2 | Seed Dispersal Effectiveness

5.2.2.1 | Quantitative Component

For the quantitative component of the SDE framework, we calculated mean seeds dispersed per day as the product of mean daily time spent feeding on each fruit species and the number of seeds either spat or swallowed per minute. Firstly, we calculated the proportion of time spent consuming each fruit species during our focal sampling days. We then multiplied this by the actual day length at the study site (Geoscience Australia 2010) which gave us minutes feeding per day for each fruit species. Secondly, we collected fresh ripe fruits from samango monkey feeding trees and calculated average (mean ±SD) seeds per fruit. We were unable to identify *Ficus* spp. seeds to species, so calculated mean (±SD) seeds per fruit in the three *Ficus* spp. combined. Lastly, for each fruit species, we calculated seeds dispersed per minute via spitting or swallowing (Table 5.2) and multiplied these results by minutes feeding per day.

Table 5.2 Calculation of seeds dispersed per minute through seed-spitting or seed-swallowing by samango monkeys at Lajuma, South Africa.

Plant Species	Samango Monkey Seed Handling Mechanism	
	Seed-Spitting	Seed-Swallowing
Ficus spp.	Mean seeds per fruit multiplied by mean proportion of fruit dropped per minute.	Mean seeds per fruit multiplied by mean proportion of fruit consumed per minute.
Searsia chirindensis	Mean seeds spat out per minute	Mean fruits consumed per minute minus mean seeds spat out per minute
Syzygium cordatum	Mean seeds spat out per minute	NA

5.2.2.2 | Qualitative Component

For the qualitative component of the SDE framework, we calculated the product of the probability of seed germination (all plant species) and the proportion of faecal samples (gut-passed seeds, *Ficus* spp. and *S. chirindensis* only) deposited on a substrate suitable for seedling establishment. The probability of germination was determined in germination trials that isolated specific biological processes that seeds are subjected to during dispersal by samango monkeys (Traveset & Verdú 2002; Samuels & Levey 2005; Fuzessy et al. 2016). The methods and results from these experiments are described in Chapter 3, from which we used results for spat-out seeds (disinhibition effect, all plant species, desiccation effect, *S. cordatum* only) and gut-passed seeds (gut-passage and fertiliser effects, *Ficus* spp. and *S. chirindensis* only). We did not distinguish between groups for seed germination experiments.

We calculated the proportion of faecal samples containing *Ficus* spp. and/or *S. chirindensis* seeds that were deposited onto a substrate suitable for seedling establishment from photographs taken of fresh faecal samples. We collected fresh faecal samples from adult and sub-adult age classes (Chapter 2, section 2.6.5.1) *ad libitum* during daily follows in separate plastic bags, noting the date and time of deposition, group and age-sex class of the individual on the bag. Prior to collection, we marked the location of the faecal sample using GPS and took a photograph of the faecal sample from waist height (approximately

1.2 m), noting the photograph number and GPS data on the collection bag. Each photograph was coded in terms of the substrate onto which the faecal sample had been deposited. We classified the substrate as suitable if seeds would be able to establish following germinating without additional extraneous factors such as secondary dispersal via other fauna or rain (Fig. 5.1). Suitable substrates were soil, leaf litter on soil or in between exposed tree roots. We classified the substrate as unsuitable if seeds would require additional extraneous factors to establish following germination. Unsuitable substrates were rocks, tree branches, leaf litter on rocks, roads or heavily compacted soil on tracks (Fig. 5.1).

Fig. 5.1 Examples of suitable (a-b) and unsuitable (c-d) substrates onto which samango monkey faecal samples (highlighted in red boxes) were deposited at Lajuma, South Africa.

5.2.3 | Data Analysis

Due to the non-independent nature of the data, we used randomisation tests (Manly 1997) with 10,000 permutations to compare the behaviour of the two groups, using code from Kuiper & Sklar (2011) in R statistical software (R Core Team 2018) and $\alpha = 0.05$. We compared mean percentage of time per day spent performing general behaviours (Table 5.1), feeding on food items (Table 5.1) and feeding on the fruit of each of the focal fruit species (*Ficus* spp., *S. chirindensis* and *S. cordatum*). The fruiting seasons of *S. chirindensis* and *S. cordatum* occurred only during the wet season and we collected data on *Ficus* spp. for only six weeks during the dry season. For this reason, we did not include seasonal effects of behaviour in any analyses. We constructed two SDE landscapes for each of the plant species in R using the 'effect.lndscp' package (Jordano 2014). In the SDE landscape, isoclines connect values of the quantity and quality components of SDE, giving an overall value of SDE (Schupp 1993; Schupp et al. 2010). The first SDE landscape compared the effectiveness of seed-spitting and seed-swallowing samango monkey dispersal mechanisms. The second SDE landscape compared seed handling mechanisms between the two groups of samango monkeys. We calculated home range and daily ranging area for each group from location data, using nearest neighbour (k = 3) minimum concave polygons (MCaP) in the 'ConcaveHull' QGIS plugin (Moreira & Santos 2007). We estimated mean daily path lengths by converting locations to paths and calculating total path length. We used location data to estimate the time each group spent in either forest, thicket and dense bush, or open (open woodland, grassland or low shrubland) habitats, by calculating the proportion of locations occurring in each habitat type. Habitat type was taken from the South African National Land-Cover dataset, with a spatial resolution of 30 x 30 m (GeoTerra 2015). We used the same habitat dataset to calculate the proportion of faecal samples deposited on suitable substrates per habitat type. Finally, we compared the quantity of dispersal and daily home range and daily path length (Solow 1989) between the two groups, again using randomization tests in R.

5.3 | Results

5.3.1 | Samango Behaviour and Diet

During a total sampling effort of 73 follow days, the monkeys spent 42.58% of total observation time feeding, 26.82% of time resting, 5.73% of time socialising, 24.58% of time travelling, and were out of sight for 0.29% of observation time. The monkeys spent 39.36% of observed feeding time on fruit, 35.37% feeding on leaves, 10.15% consuming food from cheek pouches, 6.08% feeding on flowers, 5.09% feeding on seed pods and 3.81% feeding on all other food items.

We found a significant difference (p = 0.01) in mean percentage of daily time spent feeding between groups, where House group spent a significantly higher percentage of time feeding (Table 5.3). Similarly, we found a significant difference (p = <0.01) in mean percentage of daily time spent in social interactions between groups, where Barn group spent a significantly higher percentage of time in social interactions than House group (Table 5.3).

Table 5.3 Mean daily activity budget, diet composition (% mean ±SD time spent feeding per day) and statistical significance (randomisation tests with 10,000 permutations) between two groups of samango monkey (Barn group and House group) at Lajuma, Soutpansberg Mountain, South Africa between December 2017 and May 2018, including mean (±SD) proportion of time spent feeding per day for three focal fruit species.

Activity	Behaviour and Diet Composition (mean % of time per day ±SD)		Comparison *p*-value (α = 0.05)
	Barn	House	
Feeding	41.66 (±9.56)	46.85 (±8.66)	0.01
Socialising	7.58 (±6.28)	4.17 (±2.97)	<0.01
Travelling	24.88 (±8.64)	22.76 (±6.58)	0.11
Food Item [a]			
Cheek Pouch	11.61 (±8.78)	9.39 (±7.79)	0.14
Flowers	9.08 (±10.96)	5.56 (±6.89)	0.08
Fruit	35.64 (±18.44)	42.88 (±16.32)	0.04
Leaves	35.92 (±20.29)	34.29 (±15.71)	0.35
Seed Pod	15.01 (±6.96)	13.22 (±6.71)	0.23
Other	4.71 (±5.11)	3.93 (±3.65)	0.23
Fruit [a]			
Ficus spp.	12.76 (±9.5)	16.97 (±8.82)	0.04
Searsia chirindensis	20.91 (±19.74)	26.27 (±15.22)	0.25
Syzygium cordatum	10.06 (±14.65)	6.22 (±7.63)	0.21

[a] mean percentage of time feeding daily

We found a significant difference in mean percentage of daily feeding time spent feeding on fruit ($p = 0.04$) and *Ficus* spp. ($p = 0.04$), where House group spent a significantly higher percentage of daily feeding time on fruit and *Ficus* spp. than Barn group (Table

5.3). We found no significant differences in mean percentage of daily time spent resting or travelling between the two groups, nor did we find any significant differences feeding time spent feeding on any other food item, including *S. chirindensis* or *S. cordatum* (Table 5.3). A comprehensive list of fruit species consumed by samango monkeys during this study is given in Appendix Table A3.

5.3.2 | Seed Dispersal Effectiveness

5.3.2.1 | Quantitative Component

Ficus spp. fruit contained, on average, (mean ±SD) 341 ±347 seeds and *S. chirindensis* and *S. cordatum* fruits each contained one seed. We recorded House group feeding on each species on more days than Barn group (Table 5.4). We found a significant difference (p = <0.01) in the daily number of *Ficus* spp. seeds dispersed per day between the two groups, where House group dispersed greater quantities of seeds than Barn group (Table 5.4). We found no significant difference in the daily number of *S. chirindensis* and *S. cordatum* seeds dispersed between the two groups (Table 5.4).

Table 5.4 The quantity component of SDE and number of days we observed feeding, for three fruit-species dispersed by samango monkeys at Lajuma, Soutpansberg Mountain, South Africa. We calculated quantity as the product of mean (±SD) time spent feeding per day (mins) and mean (±SD) seeds consumed per minute.

Species	Group	№ Days Feeding	Mean (±SD) Seeds Consumed / Min (C)		Time Feeding mins/day (±SD) (T)	Quantity of Dispersal (±SD): (C x T)	
			Spitting	Swallowing/ Cheek Pouch [a]		Spitting	Swallowing/ Cheek Pouch [a]
Ficus spp.							
	Barn	26	No group distinction		24.08 (±18.96)	8393.79 (±6609.132)	45602.87 (±35906.93)
	House	36	No group distinction		56.38 (±32.8)	19777.26 (±11579.54)	107448.39 (±62910.79)
	Combined	62	348.65 (±276.87)	1894.19 (±1212.82)	42.83 (±31.98)	14925.29 (±11242.82)	81088 (±61081.41)
Searsia chirindensis							
	Barn	10	No group distinction		68.64 (±67.73)	167.49 (±165.27)	834.72 (±823.63)
	House	11	No group distinction		72.73 (±41.93)	174.77 (±107.43)	870.98 (±535.37)
	Combined	21	2.44 (±1.94)	12.16 (±6.19)	70.78 (±54.29)	171.13 (±135.71)	852.85 (±676.35)
Syzygium cordatum							
	Barn	6	No group distinction		31.27 (±44.26)	93.81 (±132.78)	46.9 (±66.39)
	House	13	No group distinction		20.66 (±29.21)	65.04 (±90.79)	30.99 (±43.81)
	Combined	19	3 (±1)	1.5 (±1)	24.01 (±33.74)	74.63 (±103.51)	36.02 (±50.61)

[a] Swallowing in *Ficus* spp. and *S. chirindensis*; Cheek Pouch in *S. cordatum*

5.3.2.2 | Qualitative Component

Probability of germination data from Chapter 3 (section 3.3) indicated that seeds spat out by samango monkeys (DI) were more likely to germinate than gut-passed seeds (GP and FE) for *Ficus* spp. and *S. chirindensis* (Table 5.5). In *Ficus* spp., seeds sown in the faecal matrix (FE) were more likely to germinate than gut-passed seeds removed from the faecal matrix (GP) (Table 5.5; Chapter 3, section 3). Similarly, freshly de-pulped (DI) *S. cordatum* seeds were more likely to germinate than seeds subjected to desiccation (DE) (Table 5.5; Chapter 3, section 3). These treatments simulated seed-spitting (DI) in moist habitat directly underneath the parent and seed-spitting in dry habitat following storage in cheek pouches.

We collected 364 faecal samples from Barn group and 370 from House group, with an average (mean ±SD) of 6.39 ±5.09 and 6.17 ±4.3 faecal samples collected per day from each group respectively. Of these, 343 faecal samples from Barn group and 323 from House group contained *Ficus* spp. seeds, and 91 samples from Barn group and 111 from House group contained *S. chirindensis* seeds. A high percentage of recovered faecal samples from both groups (Barn 77.19% and House 85%) were deposited on a substrate suitable for seedling establishment. House group deposited more faecal samples containing *Ficus* spp. or *S. chirindensis* seeds on a suitable substrate than Barn group (Table 5.5). Barn group deposited 73.86% of faecal samples on a suitable substrates in forest habitat, 24.62% in thicket and dense bush and 1.52% in open habitat. House group deposited 92.73% of faecal samples on a suitable substrate in forest habitat and 7.27% in thicket and dense bush. No faecal samples recovered from House group were deposited on a suitable substrate in open habitats. In terms of gut-passed seeds, House group had a higher quality of dispersal than Barn group (Table 5.5). A comprehensive list of seeds recovered from samango monkey faecal samples during this study is given in Chapter 2.

Table 5.5 The quality component of SDE for three fruit-species dispersed by samango monkeys at Lajuma, Soutpansberg Mountain, South Africa. For spat seeds (DI Disinhibition Effects of pulp removal through seed-spitting; DE disinhibition *plus* Desiccation (*S. cordatum* only)), defined quality as the probability of seed germination (±SE) from Chapter 3 (P). For swallowed seeds (*Ficus* spp. and *S. chirindensis* only: GP mechanical and chemical scarification effects during Gut-Passage; FE gut-passage *plus* Fertilizer effects of faecal matrix), we calculated quality as the product of the probability of germination (±SE) from Chapter 3 (P) and the proportion of faecal samples deposited on a substrate suitable for seedling establishment (S).

Species	Group	Probability of Germination (±SE) (P)[a]				Proportion of Faecal Samples Deposited on Suitable Substrate (S)	Quality of Dispersal (±SE) (P x S)			
		DI	DE	GP	FE		DI	DE	GP	FE
Ficus spp.										
	Barn	No group distinction				0.77	No group distinction		0.24 (±0.03)	0.39 (±0.05)
	House	No group distinction				0.85	No group distinction		0.26 (±0.03)	0.43 (±0.05)
	Combined	0.75 (±0.03)	NA	0.31 (±0.04)	0.51 (±0.06)	0.81	0.75 (±0.02)	NA	0.25 (±0.03)	0.41 (±0.05)
Searsia chirindensis										
	Barn	No group distinction				0.71	No group distinction		0.12 (±0.02)	0.13 (±0.02)
	House	No group distinction				0.89	No group distinction		0.15 (±0.03)	0.17 (±0.03)
	Combined	0.33 (±0.06)	NA	0.17 (±0.03)	0.19 (±0.03)	0.81	0.33 (±0.05)	NA	0.14 (±0.02)	0.15 (±0.02)
Syzygium cordatum										
	Combined	0.93 (±0.02)	0.34 (±0.04)	NA	NA	NA	0.93 (±0.02)	0.34 (±0.04)	NA	NA

[a] Results from germination experiments detailed in Chapter 3

5.3.3 | SDE Landscapes.

5.3.3.1 | SDE of Samango Monkeys

The SDE landscape (Fig. 5.2) indicated that samango monkeys were more effective in dispersing *Ficus* spp. and *S. chirindensis.* seeds via seed-swallowing (GP, FE) than seed-spitting (DI). The SDE landscape further indicated that samango monkeys were more effective in dispersal of *S. cordatum* when seeds were spat-out under the parent and were not subject to desiccation (DE) (Fig. 5.2). The SDE landscape indicated that the fertilizer effect of the faecal matrix increased the effectiveness of seed-swallowing by samango monkeys for *Ficus* spp. compared to gut-passage alone (Fig. 5.2). In contrast, the fertilizer effect was no more effective than gut-passage for *S. chirindensis* (Fig. 5.2).

5.3.3.2 | Intergroup Variability in SDE

The SDE landscape (Fig. 5.3) indicated that House group were more effective in dispersing *Ficus* spp. seeds than Barn group through either seed-spitting (DI) or seed-swallowing (GP, FE). Barn group were as effective in dispersing *Ficus* spp. seeds through seed-swallowing as House group were through seed-spitting (Fig. 5.3). The SDE landscape indicated that House group were also more effective in dispersing *S. chirindensis* seeds than Barn group through seed-swallowing (Fig 5.3). House group and Barn group were equally effective in dispersing *S. chirindensis* seeds through seed-spitting (Fig. 5.3). In contrast, the SDE landscape indicated that Barn group were more effective in dispersing *S. cordatum* seeds than House group (Fig. 5.3).

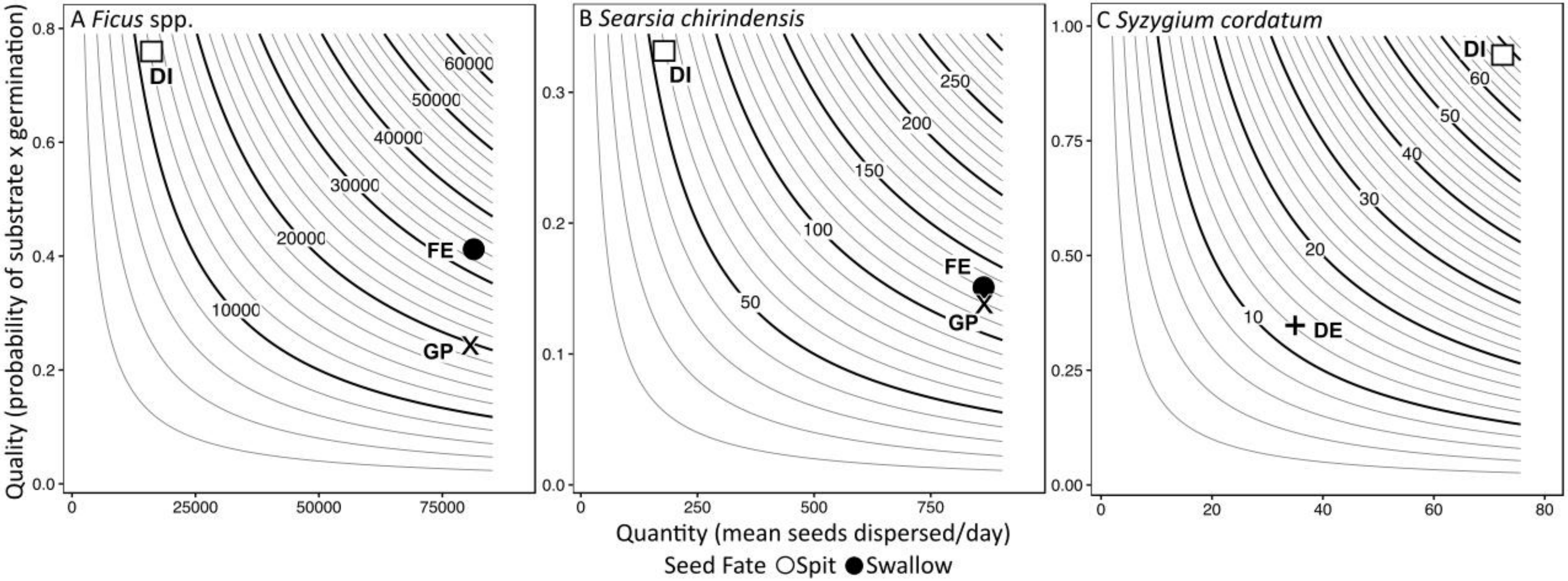

Fig. 5.2 Seed Dispersal Effectiveness landscape of three fruit-species seeds dispersed by samango monkeys through spitting and swallowing at Lajuma, Soutpansberg Mountain, South Africa. Isoclines denote all combinations of quantity and quality components of dispersal that generate the same effectiveness. Seed Treatments: DI Disinhibition Effects of pulp removal through seed-spitting; DE disinhibition *plus* Desiccation (*S. cordatum* only); GP mechanical and chemical scarification effects during Gut-Passage through seed-swallowing (*Ficus* spp. and *S. chirindensis* only); FE gut-passage *plus* Fertilizer effects of faecal matrix (*Ficus* spp. and *S. chirindensis* only).

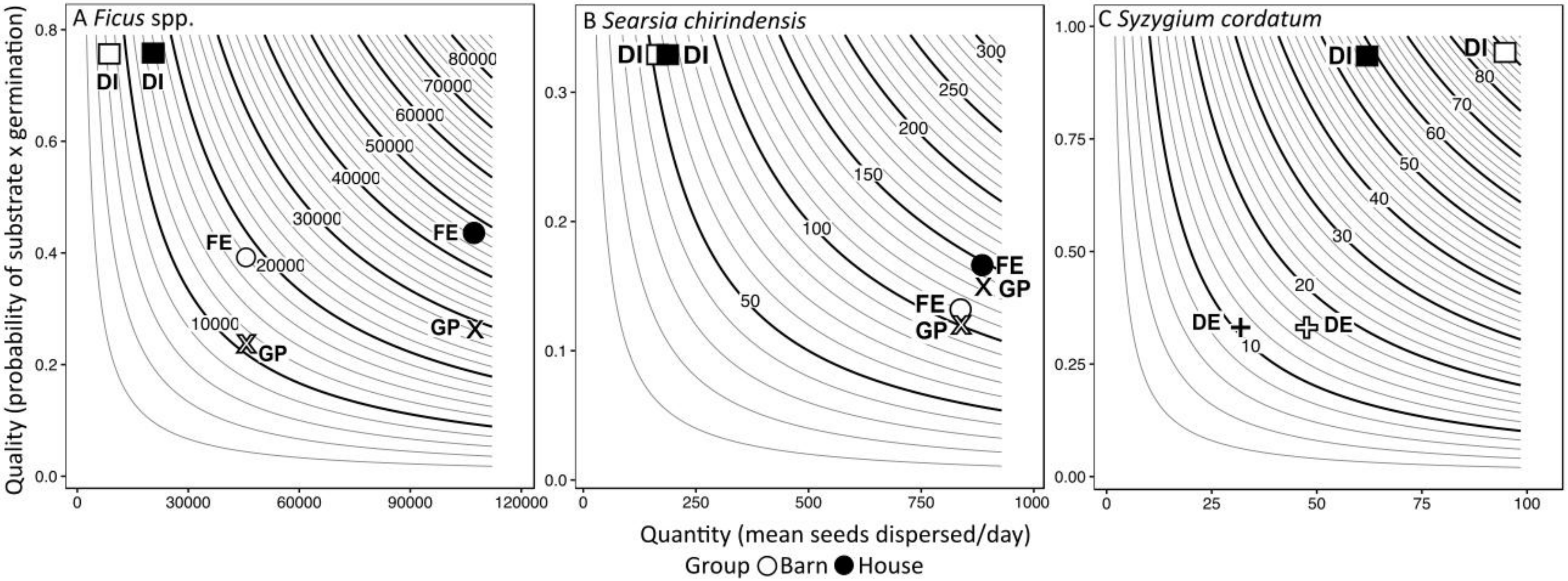

Fig. 5.3 Seed Dispersal Effectiveness landscape of three fruit-species seeds dispersed by two samango monkey groups (Barn and House) through spitting and swallowing at Lajuma, Soutpansberg Mountain, South Africa. Isoclines denote all combinations of quantity and quality components of dispersal that generate the same effectiveness. Seed Treatments: DI Disinhibition Effects of pulp removal through seed-spitting; DE disinhibition *plus* Desiccation (*S. cordatum* only); GP mechanical and chemical scarification effects during Gut-Passage through seed-swallowing (*Ficus* spp. and *S. chirindensis* only); FE gut-passage *plus* Fertilizer effects of faecal matrix (*Ficus* spp. and *S. chirindensis* only).

5.3.4 | Home Range and Daily Movement Behaviour

Minimum concave polygon analysis indicated the home range of the two samango groups during the study were 97 ha for Barn and 67 ha for House (Fig. 5.4). There was 20 ha of home range overlap between the two groups. We found a significant difference (p = <0.001) in mean (±SD) daily ranging area between the two groups, where on average (mean ±SD) Barn group (10 ±7 ha) covered a larger area each day than House group (7 ±4 ha). Similarly, we found a significant difference (p = 0.04) in mean (±SD) daily path length between the two groups, where Barn group (1951 ±448 m) travelled further each day then House group (1817 ±427 m). Barn group spent 59.03% of total focal observation time in forest habitat, 25% in thicket and dense bush habitat, and 15.07% of time in open habitat, including forest fragments within agricultural land. House group spent 83.17% of total focal observation time in forest habitat, 10.65% of time in thicket and dense bush habitat and 6.18% of time in open habitat.

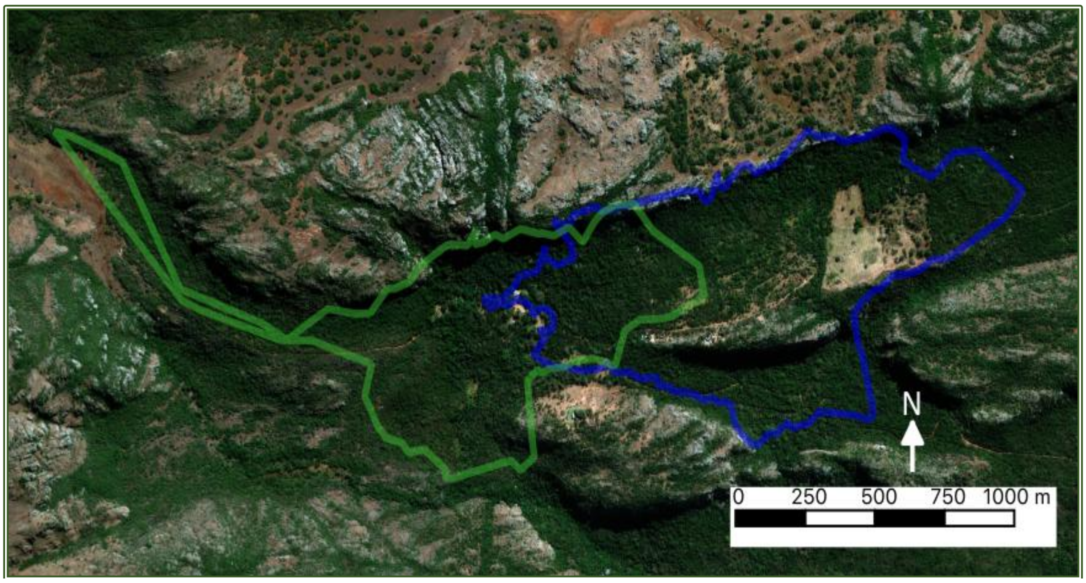

Fig. 5.4 Home range of two samango monkey groups, 'Barn' (blue) and 'House' (green) at Lajuma, Soutpansberg Mountain, South Africa, calculated using minimum concave polygon analyses. The patch of bare ground within Barn groups' home range is the location of macadamia nut agricultural land.
(Base map: Microsoft Corporation 2019).

5.4 | Discussion

This study reports for the first time in South Africa the SDE of a mammalian frugivore. Our study demonstrates that two groups of individuals of the same species, within the same population and inhabiting partially overlapping home ranges, are distinctly different in SDE for several plant species. Intergroup variation in SDE seems largely driven by group-specific behavioural and ecological attributes. Specifically, intergroup variability in time budgets drove group differences in the quantity of dispersal, while differences in the habitats in which the monkeys travel and deposit seeds drove group differences in the quality of dispersal. We propose that these differences may manifest as a consequence of intragroup competition for resources, which arise from ecological constraints associated with group size and the distribution of resources (Chapman & Chapman 2000b). Such competition can be diminished through optimal foraging strategies (Krebs 1980) by selecting habitats of high productivity, travelling further between smaller resource patches (Grove 2012), or fission-fusion grouping dynamics during feeding (Strier 2009). For example, forests are highly productive habitats on which samango monkeys rely for safety (Coleman & Hill 2014), reproduction (Linden et al. 2016) and access to preferred foods such as *Ficus* spp. (Coleman 2013, Linden et al. 2015). Previous research has found that inclusion of a greater proportion of indigenous forest within samango monkey home range, significantly reduced monthly and core home ranges (Parker 2018). This is likely because the availability of preferred food items is greater within indigenous forest (Linden et al. 2015; Parker 2018). Thus, socially driven foraging behaviour can have important influences on the SDE of a disperser. Such behaviour may influence intergroup variability in habitat maintenance, forest regeneration and recruitment.

We found a difference in the quantity of dispersal between the two groups of samango monkeys. Individuals in the larger group (House) dispersed significantly more *Ficus* spp. seeds than the smaller group (Barn). There is evidence in the literature that individuals within population differ in the quantity of seeds they disperse (Côrtes & Uriarte 2013; Zwolak 2018). Adult males in groups of blue monkeys (*Cercopithecus mitis*) and red-tailed monkeys (*Cercopithecus ascanius*), have been shown to be more frugivorous than adult females (Cords 1986), thereby dispersing a greater quantity of seeds (Zwolak 2018). In this study, intergroup differences in quantity of dispersal arose from variation in mean daily time budgets. The larger group spent more time feeding, less time socialising, and had a shorter daily path length than the smaller group. This was in contrast to the ecological constraints hypothesis (Chapman & Chapman 2000b), which proposes that increased intragroup scramble competition in larger groups facilitates foraging across a greater area, compared to smaller groups (Janson & van Schaik 1988; Chapman & Chapman 2000b). Increased foraging area can increase the time spent travelling (Chapman & Chapman 2000a, b; Avgar et al. 2013), thus reducing time available for feeding and therefore lowering the quantities of dispersed seeds (Karubian & Durães 2009). Intragroup feeding competition may become weaker in habitats of high productivity, where depletable resources such as fruit are abundant (Korstjens et al. 2018). Furthermore, greater-than-expected group size may be a function of high predation risk (Wrangham et al. 1993). Variability in the quantity of dispersal may mean that within a disperser population, individuals or groups contribute disproportionately to seed dispersal (Zwolak 2018).

There were marked differences in group size between the two groups of samango monkeys, which may have driven behavioural attributes of the variation we observed in dispersal quantity. Travelling distance between resources is expected to increase with group size (Chapman & Chapman 2000b). Once group size is no longer optimal for the individuals within the group, a smaller group size proffers an advantage for efficient foraging (Chapman & Chapman 2000b). This has been demonstrated in red colobus monkeys (*Procolobus pennantii*) and red-tailed monkeys, where group size increased with resource density (Chapman & Chapman 2000a). In this respect, it may be that the habitat in which House group foraged was sufficient for maintaining such a markedly larger group (Chapman & Chapman 2000a). Barn group potentially depleted their resources at a faster rate, thus necessitating greater travelling distances between patches of lower quality. Alternatively, the size of Barn group was optimal for the habitats in which they forage (Chapman & Chapman 2000a).

In social foraging animals such as samango monkeys, trade-offs associated with group size and foraging performance may have important implications for seed dispersal and plant fitness (Karubian & Durães 2009). Specifically, intraspecific and intergroup variation in SDE can have consequences on plant community demography, genetic variability and plant population dynamics (Snell et al. 2019). Movement and foraging patterns determine deposition sites and the spatial distribution of dispersed seeds (Karubian & Durães 2009). Sites frequently used for foraging, resting and sleeping can be areas of high seed deposition, as observed in woolly monkeys (*Lagothrix lagothricha,* Stevenson 2000), spider monkeys (*Ateles geoffroyi,* Russo & Augspurger 2004) and tamarins (*Saguinus* spp., Muñoz

Lazo et al. 2011). As the larger group, we expected House group to require more food resources, thus spending less time feeding, and encompassing a larger daily range and longer daily travel paths than Barn group (Janson & van Schaik 1988; Chapman & Chapman 2000b). Feeding time was significantly longer for House group and as such, deposition of seeds under feeding trees may result in a more clumped distribution, potentially increasing conspecific density-dependent competition for seedlings (Janzen 1970; Connell 1971). On the other hand, the longer travelling distances and time spent outside of the forest we observed in Barn group, could result in longer dispersal distances and less clumped deposition patterns, thereby reducing conspecific competition.

We found intergroup differences in the quality of seed deposition (deposition onto a substrate suitable for seedling establishment following germination). The habitat matrix in which frugivores feed can influence seed dispersal services beyond fruit consumption (Phiphatsuwannachai et al. 2018). In white-handed gibbons (*Hylobates lar*), the time groups spent in habitats within a mosaic forest influenced seed deposition sites and dispersal of seeds between forest types (Phiphatsuwannachai et al. 2018). In our study, House group deposited more faecal samples on suitable substrates in forest habitat, while Barn group deposited more faecal samples on suitable substrates in thicket and dense bush habitat, as well as depositing faecal samples on suitable substrates in open areas. Intergroup differences in deposition in the different habitats followed a pattern similar to the time that each group spent in each habitat. Thus, intergroup variability in ranging behaviour can have consequences for maintaining forests through plant recruitment, as well as expanding forests through range expansion, forest regeneration and colonisation of novel habitats (Howe & Smallwood 1982; Terborgh et al. 2002; Howe & Miriti 2004). This suggests that House group are potentially more effective in forest maintenance (Terborgh et al. 2002), while Barn group are potentially more effective at forest regeneration and recruitment (Howe & Smallwood 1982).

Amongst primates, cercopithecines are relatively unique as they disperse seeds via seed-spitting and seed-swallowing (Corlett & Lucas 1990) and use their cheek pouches to store food and transport seeds away from parent plants (Lambert 1999; Linden et al. 2015). Cheek-pouch use by cercopithecines has been attributed to predation risk in more open habitats (Lambert 2005a) and intragroup competition (Lambert 2005a; Smith et al. 2008). Thus, the time Barn group spend in more open habitats where high-quality food resources may be of a more clumped distribution, may make them effective at dispersing seeds in their cheek pouches. Alternatively, cheek-pouch use may be quite prevalent in House group, as there may be a high number of low-ranking subordinates in such a large group (Lambert 2005a). That being said, our findings suggest that the intergroup differences in SDE are down primarily to differences in the quantity component of seed dispersal. Nonetheless, samango monkeys deposited seeds in various habitats and the high proportion of faecal samples deposited on soil that contained *Ficus* spp. and *S. chirindensis* seeds demonstrate that samango monkeys disperse seeds into potentially suitable microhabitats that may facilitate seedling survival and growth (Schupp et al. 2010).

In this study, while our findings demonstrate intergroup differences in SDE manifest through differences in ranging behaviour and time budgets, we address limitations of our study. Firstly, our study is based on data collected over one fruiting season and hence, we could not include seasonal (Clutton-Brock 1977; Culot et al. 2010) or inter-annual (Chapman et al. 2002; Tsuji 2014) variation in diet between the two groups. For comparison, we included daily intergroup variation in time budget and diet composition (Chapman et al. 2002). As such, longitudinal studies on SDE that include frugivore behaviour and spatiotemporal variation in resources availability, would extend our understanding of the complex mechanisms that underpin dispersal patterns (Karubian & Durães 2009). Secondly, we do not account for short-term post-dispersal seed fate, such as seed predation or removal of seeds by granivores or dung beetles (Vander Wall et al. 2005b; Culot et al. 2015, 2018). To quantify quality of deposition, we assume that deposition of faeces onto a suitable substrate implies a greater survival rate for seeds. It was not within the scope of this study to include secondary dispersal or seed predation, deposition microsite analysis or demographic parameters seedling survival. Lastly, we did not differentiate fruit handling behaviour (number of fruits consumed per minute) between the two samango monkey groups. Social foraging behaviour at the individual level can be influenced by the behaviour of others within a group, which itself is influenced by, and a function of, group size (Marshall et al. 2012). Thus, the quantity of fruits consumed per minute may be influenced by group size, as well as individual dynamics associated with within-group competition in terms of the use of cheek pouches in cercopithecines (Lambert 2005b). However, we sampled the behaviour of the two groups over the same time period and for similar amounts of time (± 8.63 hrs). We are therefore confident that our results are an accurate reflection of intergroup differences in SDE of two groups of monkeys.

Our findings stress the importance of including representative groups within target disperser populations when assessing SDE. Population estimates may overlook the inherent variation in the components of SDE, especially in social foraging primates, where the ecology of the disperser drives group-specific behavioural variation within the population. Our findings also confer that for effective seed dispersal, plants may not rely on a trade-off between lower quality dispersal (germination following gut-passage) for higher quantity dispersal (the number of seeds dispersed). Within the SDE framework, if dispersal quality is low, a large increase in dispersal quantity would not substantially increase overall SDE (Schupp et al. 2010). In our study, a three-fold increase in the quantity of *Ficus* spp. seeds dispersed by House group increased SDE by a ratio of approximately 1:3. Dispersing seeds away from parent trees may reduce natural enemy predation and conspecific competition (Terborgh 2012; Comita et al. 2014).

Dispersal distance and the microhabitats into which seeds are dispersed, are influenced by gut passage time and the path length and the path curvature during that time (Link & Di Fiore 2006; Fuzessy et al. 2017; Phiphatsuwannachai et al. 2018). Therefore, combining daily travel path length with gut passage time could highlight the role both groups play in forest maintenance, regeneration and recruitment (Howe & Smallwood 1982; Terborgh et al. 2002) through estimation of dispersal kernels and mean dispersal distances (Dennis & Westcott 2007; Nathan et al. 2012).

5.5 | Conclusion

Although germination of gut-passed seeds was much lower than manually de-pulped seeds, our study suggests that the effectiveness of samango monkeys as seed dispersers, increased, albeit a relatively small increase, with the quantity of seeds they swallowed rather than spat out. However, we are unable to suggest that either dispersal mechanism is more effective than the other, as SDE remained low in both seed species, *Ficus* spp. and *S. chirindensis*, which were dispersed via gut passage. Our study also suggests that two groups of samango monkeys within the same population, and inhabiting partially overlapping home ranges, are distinctly different in their effectiveness in seed dispersal for several plant species. As predicted, there was variation in the quantity component of SDE between the two groups, although contrary to our prediction, the larger group were more effective in seed dispersal for two plant species. Intergroup variation in SDE arose as a consequence of intergroup variability in activity patterns, daily diet composition and the quality of the habitats in which the groups forage, which probably manifest from ecological constraints associated with group size and habitat quality. Variation in SDE within animal populations can have important implications for plant communities through, for example, spatial-genetic structure, persistence and recruitment and studies such as ours highlight the need for this variation to be included in models of SDE.

Chapter 5 summary

In this final data Chapter, I assessed the SDE samango monkeys and the behavioural and ecological drivers of intergroup SDE variability and the impact such variation could have on plant fitness. I found that although germination of gut passed seed was lower than entire fruit controls and the Disinhibition effect, samango monkeys were more effective in seed dispersal through seed-swallowing because of the quantities of seed they consume daily. I also found intergroup variability in SDE between the two groups of monkeys, which is a consequence of variability in activity patterns, diet composition and foraging habitats. These results highlight how intergroup variability in behaviour could impact plant fitness as the quantity and quality components of seed dispersal can be influenced through feeding and movement behaviour associated with group size and habitat quality.

Chapter 6

General Discussion

The preceding three data chapters deconstructed the components of the SDE framework to and investigated how the behaviour of samango monkeys influence the quality and quantity of dispersal. This chapter serves to evaluate the findings of the research and integrate the main findings of the preceding Chapters in the context of the research aims set out in chapter 1. I elucidate as to how the research presented contributes knowledge to, and furthers the understanding of, the role of animal-mediated seed dispersal on plant fitness. I conclude this thesis by addressing limitations of the study and make recommendations for developing this research in the future.

6.1 | Seed Dispersal Effectiveness of African Mammalian Frugivores

Research focussing on seed dispersal by mammalian frugivores is, in general, lacking in South Africa and thus this thesis is a first step towards filling this gap. This is despite the country harbouring 8% of the world's plant species and 7% of the world's bird, mammal and reptile species (Cherry 2005). Previous studies on seed dispersal by frugivorous mammals in South Africa have been focussed on bats (Voigt et al. 2011; Bonaccorso et al. 2014), primates (Foord et al. 1994; Slater & du Toit 2002; Linden et al. 2015; Tew et al. 2018; Kiepiel & Johnson 2019) and rodents (White & Midgley 2017). However, none of these studies utilised the SDE framework, instead investigating subcomponents of seed dispersal services (see Chapter 1, section 1.3, Fig. 1.2) provided by the focal frugivore. In respect of the limited research on mammalian frugivores in South Africa, results from each of the preceding chapters in this thesis represent an important foundation on which future SDE studies in South Africa can be established.

As discussed by Schupp et al. (1993, 2010), the SDE framework was introduced to standardise terminology in seed dispersal studies and to develop a framework for quantifying dispersal services by individual dispersal agents. My study empirically estimates the contribution of samango monkeys in South Africa by utilising the SDE framework in its entirety. To my knowledge, this study is the first to quantify SDE of a mammalian frugivore in South Africa. The SDE framework has previously only been applied to South African frugivores in one other study that quantified the SDE of four bird species for an invasive plant, *Acacia cyclops* (western coastal wattle; Mokotjomela et al. 2016). My study compared the SDE of different seed handling mechanisms utilised by one frugivorous species and intergroup variability of these mechanisms. In contrast, Mokotjomela and colleagues were comparing SDE between different species of two functional groups of dispersers, frugivorous and granivorous birds (Mokotjomela et al. 2016). The different questions being answered through the SDE framework by these two studies, clearly demonstrates the flexibility of the framework for research investigating the contribution of frugivores to seed dispersal.

My study was focussed on an Afrotemperate forest within the Afromontane archipelago in southern Africa (see Chapter 2; section 2.3.3). The Afromontane archipelago stretches from Sierra Leone across to southern Sudan and down to South Africa (White 1978). The archipelago is made up of isolated mountains and mountain ranges (Grimshaw 2001). The lack of connectivity between mountains and mountain ranges means Afromontane forests require consistent and reliable seed dispersal services (McKey 1975; Heymann et al. 2017; Culot et al. 2018). My study builds on one preliminary study conducted in Afromontane habitats in South Africa (Linden et al. 2015) that assessed the role of samango monkeys as seed dispersers by describing percentages of seeds predated, spat, consumed and detected in faeces. Results from my study support and extend results from previous work, in that samango monkeys have an important and effective role in the maintenance of Afromontane forests in South Africa through seed dispersal (Linden et al. 2015; see Chapter 5).

The SDE framework has previously been applied in its entirety to frugivores across sub-Saharan Africa in only one other study that quantified SDE of western lowland gorilla (*Gorilla gorilla gorilla*) in Gabon (Haurez et al. 2018). Similar to the methods I employed for this thesis (Chapter 3), Haurez and colleagues investigated the quality of dispersal by conducting germination experiments to assess the impact of gut passage on seeds from two plant species ingested by gorillas, including entire fruits as the control group (Haurez et al. 2018). Unlike seeds ingested by samango monkeys (Chapter 3), both species ingested by gorillas exhibited higher germination success following gut passage, although the faecal matrix had an inhibiting effect on germination (Haurez et al. 2018). Haurez and colleagues took a different approach to me in calculating the quantity of dispersal, however, were able to use these data to quantify the SDE of gorillas and construct an SDE landscape as I did in Chapter 5.

Other studies have previously investigated the quantity and/or quality components of SDE in African mammalian frugivores. Such studies include evaluating seed dispersal services by bonobo (*Pan paniscus;* Beaune et al. 2013), chimpanzee (*Pan troglodyte;* Gross-Camp & Kaplin 2005), western lowland gorilla (Petre et al. 2015b), guenons (Kaplin & Lambert 2002) and elephants (*Loxodonta africana;* Cochrane 2003), as well as comparing seed dispersal services of mammalian and avian frugivore species (Cordeiro et al. 2004; Voigt et al. 2011). The authors describe their studies as 'disperser' (Schupp et al. 1993) or 'dispersal' (Schupp et al. 2010) effectiveness, however, fail to combine the two components to approximate SDE. That is not to say that these studies are not important for advancing our knowledge of seed dispersal; quite the opposite is true. However, for

SDE studies to be comparable, adoption of an equally relevant and transferable framework across habitats will enable us to link together the understanding of the complex processes and consequences of mammalian seed dispersal (Schupp et al. 2010). My study therefore begins to fill the gap within existing literature on mammalian frugivores in Africa, South Africa and Afromontane habitats. My study provides a framework from which future studies in these areas can begin to link together the effectiveness of mammalian frugivores in seed dispersal and plant demography (Schupp et al. 2010).

My study contributes to a growing body of research on how the behaviour of socially gregarious animals influences seed dispersal (Karubian & Durães 2009; Wehncke & Reyes-Amaya 2019). Previous studies have tended to incorporate the effect of social animal behaviour into dispersal distances (Westcott et al. 2005; Russo et al. 2006) or the spatial distribution of defaecated (Gonzalez-Zamora et al. 2012; Karubian et al. 2012; Petre et al. 2015b). For social foraging primates, the degree of sociality can influence the effectiveness of a disperser in more ways than seed movement and deposition patterns (Karubian & Durães 2009). In this study, I assessed how fruit processing, feeding and movement behaviour influenced SDE of a highly social frugivorous primate. I achieved this by deconstructing the quantity (Chapter 5) and quality (Chapters 3, 4 and 5) components of seed dispersal (Schupp 1993; Schupp et al. 2010) and investigated how the behaviour of samango monkeys influence each component.

6.2 | Seed Dispersal in Frugivorous Primates

My results demonstrated that samango monkeys were more effective dispersers through seed-swallowing than they were for seed-spitting, although I acknowledge that these results were based on a limited number of plant species. Increasing the number of focal plant species would broaden the breadth of the findings in terms of the overall SDE of samango monkeys at Lajuma. I also acknowledge that these results are based on a limited sample size of 1-min focal animal behavioural samples which did not include following monkeys that utilised cheek pouches for food storage (Linden et al. 2015). The use of the SDE framework for quantifying SDE in studies of primate seed dispersal is relatively lacking (see Chapter 1, section 1.4.2). In the Web of Science literature review I conducted in Chapter 3 (section 1.3; Appendix Table A.1), 21 studies were conducted on primates. Of these 21 studies, 4 considered the 'effectiveness' of their focal species (Chaves et al. 2011; Albert et al. 2013; Sengupta et al. 2014; Petre et al. 2015b), although none of them quantified SDE as a product of the quantity and quality components (Schupp et al. 1993). A similar pattern is observed in other primates studies that did not appear in the literature search from Chapter 3 (e.g. Wehncke et al. 2004; Aguado et al. 2019).

In the limited primate seed dispersal studies that do use the SDE framework in its entirety, the SDE framework was used to compare seed dispersal by either several dispersers of one plant species (McConkey et al. 2014, 2015; Hai et al. 2018; Nakabayashi et al. 2019), or one disperser of several plant species (Haurez et al. 2018). In contrast, my study stands alone in comparing SDE of different seed handling mechanisms of several fruit species by one seed disperser (Chapters 3 and 5). In each of the aforementioned studies, the measures of each of the SDE components differ, although the use of the SDE landscape remains consistent.

Within the large body of research on primate seed dispersal, many studies focus on one or more of the variables and/or demographic parameters that the SDE framework encompasses (see Chapter 1, section 1.3; Schupp et al. 1993, 2010). Such studies include seed dispersal patterns (e.g. Yumoto et al. 1999; Petre et al. 2015b; Kalbitzer et al. 2019), the effect of gut passage on seed germination (e.g. Knogge et al. 2003; Valenta & Fedigan 2009), the quantity of seeds dispersed (Slater & du Toit 2002; Linden et al. 2015), or a combination of variables (Petre et al. 2015b; Tsuji et al. 2017) (see also Chapter 1, section 1.4.2). As such, my study is one of a few primate seed dispersal studies to utilise the SDE framework. My study enhances the knowledge of primate seed dispersal by incorporating fruit processing behaviour into the SDE framework and comparing different seed handling mechanisms (seed-spitting and seed-swallowing) of several plant species.

My findings from Chapter 3 suggested that samango monkeys are most effective as seed dispersers through seed-spitting, as the disinhibitory action of separating the seed from fruit pulp had the greatest significant effect on the probability of germination. In contrast, the SDE framework and SDE landscapes (Schupp 1993; Schupp et al. 2010) in Chapter 5, suggested that in species for which dispersal occurs via seed-spitting and seed-swallowing (*Ficus* spp. and *S. chirindensis*), samango monkeys were at least twice as effective as dispersers when they swallowed seeds than when they spat them out. This was because of the number of seeds that the monkeys dispersed via swallowing. Vice-versa, estimating just the number of seeds dispersed, either through seed-spitting or by counting seeds recovered from faecal samples, could give the illusion of effective or efficient seed dispersal. For example, in my study, I collected an average (mean ±SD) 592.63 ±855.23 *Ficus* spp. seeds from 718 samango monkey faecal samples (see Chapter 2, section 2.6.2), which could be interpreted as potentially efficient dispersal. The germination experiments (Chapter 3) showed that gut passed *Ficus* spp. seeds had the lowest probability of germination, which could be interpreted as poor quality and therefore inefficient dispersal. Separately these two different measures of seed dispersal could give contrasting interpretations of the role of samango monkeys in *Ficus* spp. seed dispersal and demonstrate the importance of capturing the different stages of seed dispersal and assessing both quantity and quality components (Chapman 1989).

The quality of dispersal typically includes the effect of seed handling on germination (Schupp 1993; Schupp et al. 2010). Currently, the literature describes the treatment of seeds by frugivores as either 'disinhibition' or 'scarification' (Chapter 1, section 1.2; Traveset & Verdú 2002; Samuels & Levey 2005; Baskin & Baskin 2014; Fuzessy et al. 2017). This dichotomous view of seed treatment relates to all of the ecologically relevant seed handling mechanisms afforded to seeds through fruit processing by frugivores (Chapter 3).

Isolation of the specific actions each seed handling mechanism has on seeds is rarely achieved in germination studies investigating mammalian seed dispersal (Chapter 3; Appendix Table A.1). In Chapter 3, I deconstructed the dichotomy of disinhibition and scarification into ecologically relevant treatments that isolated each fundamentally different mechanism (disinhibition, mechanical scarification, chemical scarification, fertilisation). I then assessed the effect of each treatment on the germination potential of seeds against an appropriate control group of intact seeds in entire fruits (Samuels & Levey 2005). Results demonstrated that interpretations of the results of germination experiments are reliant on appropriate study design and reinforced the need for appropriate controls in germination experiments (Samuels & Levey 2005; Fuzessy et al. 2016).

Typically (76%), studies investigating the effect of mammalian seed treatments on germination compare gut-passed seeds with manually de-pulped seeds (Samuels & Levey 2005; Appendix Table A.1). Within the literature review I conducted in Chapter 3, 19 of the 21 studies focussed on primates omitted ecologically relevant treatments from their germination experiments (Appendix Table A.1), including all four studies on primates that considered the 'effectiveness' of their focal species (Chaves et al. 2011; Albert et al. 2013; Sengupta et al. 2014; Petre et al. 2015b). The SDE framework is not reliant on the use of ecologically relevant control treatments and requires only the germination success of the seed handling mechanism being considered (Schupp 1993). However, as those studies did not include SDE, it may be that the 'effectiveness', as they describe it, of their focal species in seed dispersal is under- or over-estimated. The remaining 11 of the 19 studies omitted entire fruit controls and therefore may also be under- or over-estimating the role of their focal species. My findings indicate that the potential for such a high number of primate seed dispersal studies that omit ecologically relevant treatments from germination studies requires attention. While recent studies include all ecologically relevant treatments (e.g. Haurez et al. 2018), despite repeated calls for the inclusion of entire fruit control groups, studies still omit entire fruit controls (e.g. Aguado et al. 2019).

My study is one of a few studies to explore study design in germination experiments (Kelly et al. 2004; Robertson et al. 2006), although the issue of appropriate study design has also been discussed in several review papers (Traveset 1998; Samuels & Levey 2005; Fuzessey et al. 2016). Yet my review of literature on seed germination studies found that the issues highlighted in the previous papers not only remain the same, interpretations drawn on results that omit ecologically relevant treatments may be confounded (Chapter 3). There is clearly a need for studies to adopt a more thorough approach to germination experiments that aim to elucidate to the role of seed handling mechanisms on germination potential. Future studies should aim to consider all of the potential ways in which fruit processing by focal frugivore species may alter the seed and influence germination.

Like all guenons (Lambert 1999; Gross-Camp & Kaplin 2011; Linden et al. 2015), samango monkeys in this study exhibited multiple seed handling mechanisms, dispersing seeds either through seed-spitting or seed-swallowing. My findings concur with previous studies that guenon monkeys are effective seed dispersers and have an important ecological role within their habitat (see Chapter 1, section 1.4.3). However, my findings demonstrate effective seed dispersal in a different way to the previous studies as my study is the first to quantify SDE of a guenon monkey.

Previously, studies have found guenons to be important seed dispersers as spat seeds (Lambert 2001; Gross-Camp & Kaplin 2011) and defaecated seeds (Foord et al. 1994; Poulsen et al. 2001; Chapman et al. 2010) exhibited greater germination than control seeds. My results for spat seeds concur with those from previous studies but my results for defecated seeds do not. Of the 8 studies that included germination experiments, 5 did not use entire fruit controls, instead assessing the focal treatments against seeds removed from fruit pulp (Foord et al. 1994; Kaplin et al. 1998b; Poulsen et al. 2001; Righini et al. 2004; Chapman et al. 2010b). Whilst this does not detract from the important knowledge these studies add to understanding guenon seed dispersal, it makes comparisons difficult. For example, Chapman et al. (2010) found that gut passed seeds showed enhanced germination potential compared to de-pulped seeds, whereas spat seeds showed reduced germination potential. Alternatively, I found that gut passed seeds showed reduced germination potential compared to de-pulped seeds, whereas in *S. chirindensis*, gut passed seeds showed neutral germination potential compared to entire fruits. Compared to entire fruits, I found that manually de-pulped seeds showed enhanced germination potential. I did not include seeds spat out by the monkeys in my germination experiments and it might be that germination is enhanced through chemical scarification from saliva enzymes involved in pre-digestion breakdown of starch (Murray 1975). Notwithstanding the above, through inclusion of ecologically relevant treatments in germination experiments, as well as quantification of SDE for those treatments, my study enhances and extends the knowledge of the role guenon monkeys have in seed dispersal.

My study is also the first to attempt to identify the gut passage time of a guenon monkey using artificial digestive markers *in-situ* (Chapter 4). Gut passage times of guenons *in-situ* is currently lacking, as all previous studies have been conducted on captive subjects. Nonetheless, captive studies have demonstrated an increased gut passage time in guenons compared to similar sized primate species (Lambert 1998, 2002) and my study goes some way in validating an extended gut passage time in guenons. The considerable dietary flexibility exhibited by cercopithecines (Blaine & Lambert 2012) suggests extended retention time of food for fermentation and extraction of nutrients from a diet high in fibrous material (Lambert 1998, 2002). My findings from Chapter 5 indicated that the samango monkeys were more omnivorous than specifically frugivorous. Whilst the monkeys spent the most feeding time on fruit (see Chapter 5, section 5.3), the monkeys spent a considerable amount of time feeding on leaves. These findings concur with previous studies in that guenons would require extended gut passage time for fermentation of plant matter (Lambert 1998, 2002).

As well as increasing the time seeds are subject to mechanical and chemical scarification, gut passage time can influence the distribution of internally-dispersed seeds (Lambert & Chapman 2005; Traveset et al. 2014; Rehm et al. 2019). The element of dispersal distance is not included within the SDE framework (Schupp et al. 1993, 2010), however can be an important measure of 'effective' seed dispersal (Lambert & Chapman 2005; Heymann et al. 2017). In the future, I aim to incorporate the gut passage times from Chapter 4 with daily path lengths from Chapter 5 to estimate dispersal distances of fruits consumed by samango monkeys.

6.3 | Intergroup Variability in Seed Dispersal

Recent studies emphasise the need to adopt inter- and intraspecific comparisons in seed dispersal models to better understand seed dispersal from the population, community, network and landscape levels (Russo et al. 2006; Strier 2009; Matías et al. 2010; McConkey et al. 2014; Heymann et al. 2017; Andresen et al. 2018; Fricke et al. 2019). In social foraging animals such as birds and primates, time budget decisions regarding when, where and for how long to forage are influenced by the decisions of others and can vary as a consequence of the social and physical environments (Krebs 1980; van Schaik 1983; Marshall et al. 2012). The foraging behaviour, time budgets and movement behaviour of the two groups of samango monkeys influenced the SDE of each group (Chapter 5). My results demonstrated that population estimates of SDE may overlook variation in behaviour that influences SDE in social foraging animals. As such, population estimates, while important, may represent incomplete descriptions of seed dispersal (Zwolak 2018).

Variation in the behaviour of sympatric species has been shown to influence the relative contribution of sympatric species to seed dispersal. Foraging behaviour influenced SDE of two sympatric primate species, selective foraging by white-handed gibbons (*Hylobates* *lar*) and opportunistic foraging by northern pig-tailed macaques (*Macaca leonina*), as macaques utilised a wider range of habitat types and deposited seeds farther and into a greater variety of habitats than gibbons (McConkey et al. 2014). Three dispersers of hemi-epiphytic figs, binturongs (*Arctictis binturong*), Mueller's gibbons (*Hylobates muelleri*) and helmeted hornbills (*Rhinoplax vigil*), demonstrated SDE variability in terms of the quantity of seeds dispersed the likelihood of seeds arriving at microsites suitable for establishment (Nakabayashi et al. 2019). Binturongs exhibited behavioural and physiological that favoured consumption of greater numbers of seeds, movement into suitable microsites, and faecal matter that acted as a glue-like substrate to hold seeds in place (Nakabayashi et al. 2019). My study expands on previous studies of interspecific variability in seed dispersal by investigating the complex link between animal behaviour and seed dispersal (Wehncke & Reyes-Amaya 2019). While interspecific studies are well represented in the literature, our understanding of intraspecific variability in seed dispersal at the local scale is limited (Andresen et al. 2018).

My study is one of a limited pool of literature that aims to broaden our understanding of how seed dispersal can be influenced by individual and group behaviour (see Chapter 5, section 5.1; Westcott & Graham 2000; Russo et al. 2006; Robledo-Arnuncio et al. 2014; Phiphatsuwannachai et al. 2018; Zwolak 2018; Snell et al. 2019). My findings concurs with others in that seed dispersal can be influenced by the social context of behaviour

(Karubian & Durães 2009; Phiphatsuwannachai et al. 2018). My study identifies important functional traits of social foraging primates, such as time budgets and movement behaviour that can influence seed dispersal (Zwolak 2018). Intergroup variability in seed dispersal services may have important implications for plant fitness (Zwolak 2018; Snell et al. 2019) such as non-random dispersal under latrines or sleeping sites (Wenny & Levey 1998; Wenny 2001; Gonzalez-Zamora et al. 2012), which could limit the spatial structure of plant populations at the local scale (Russo & Augspurger 2004).

The findings of this thesis do not implicate either of the samango groups in 'poor' dispersal. In fact, each group exhibited traits that conferred potentially positive influences on plant fitness. Barn group could play an important role in recruitment and colonization of open habitats, while House group could play an important role in forest maintenance (Chapter 5). These differences translate the intergroup variability into alternative characteristics intrinsic to effective dispersal, the results of which will only become apparent once seeds that they disperse now, become reproducing adults in 20-100 generations (Herrera 1985). If members of a population are disproportionally more or less effective in seed dispersal, they are likely to be under- or over-represented when intraspecific variability is excluded in study design. Similarly, species estimates of dispersal services may conceal unique or disproportionately different effectiveness of particular groups within the population, such as age or sex classes, the loss of which could significantly alter seed dispersal within a given area (Zwolak 2018).

6.4 | Primate Seed Dispersal in a Changing World

In my study, SDE of samango monkeys was influenced by intergroup variability in foraging behaviour (Chapter 5). I propose that such differences are a consequence of intragroup competition for resources, resulting from ecological constraints associated with group size and the distribution of resources (Chapman & Chapman 2000b). Across their broad distribution, many primate species face increasing threats because from anthropogenic disturbance and habitat destruction (e.g. Myers et al. 2000; Rovero et al. 2012; Wich et al. 2014; Linder and Palkovitz 2016; Estrada et al. 2017; Strona et al. 2018). Primates are highly vulnerable to such threats because of their slow life histories and high infant mortality rates (Chapman et al. 2010a; Van Allen et al. 2012). Indeed, while 60% of primate species are threatened with extinction, 76% of these are threatened due to the conversion of land to agriculture (Estrada et al. 2017).

As anthropogenic activities continue to alter the landscape, most notably for agriculture (Flinn & Velland 2005; Kissinger et al. 2012; Estrada et al. 2017), mutualistic relationships such as seed dispersal become more important for maintaining the pockets of remaining forest and the integrity of terrestrial ecosystems (McConkey et al. 2012; Arroyo-Rodríguez et al. 2017; Andresen et al. 2018). Variability in the components of seed dispersal within populations will, as habitat productivity declines, have important consequences on mutualistic relationships on which both groups of organisms rely (Markl et al. 2012; Andresen et al. 2018). The contraction of forests and suitable foraging habitat may impact on the behaviour of social foraging frugivores, perhaps removing opportunities for long-distance seed dispersal (Bohrer et al. 2005; McConkey & O'Farrill 2016). In the long-term this is likely to have a cascading effect on the landscape as opportunities for gene flow between plant populations decrease (Bohrer et al. 2005; Hardesty et al. 2006; Gelmi-Candusso et al. 2017).

Sustained pressure on disperser populations through, for example, habitat contraction and habitat degradation, may have evolutionary consequences on plant fitness. Declines in disperser populations, as a consequence of reduced habitat quality, may significantly decrease the number of interactions between dispersers and the plants they consume (McConkey et al. 2012; McConkey & O'Farrill 2016). While the quantity of food individuals of each disperser generation requires remains constant, the sustained loss of individuals from each disperser generation may thereby reduce the overall quantity of seeds dispersed by the population (McConkey & O'Farrill 2016). Over time, and when coupled with the potential reduction in quality habitat available to each disperser generation, the dispersal ability of each disperser generation may also decline, thereby reducing the contribution of each generation to plant recruitment. On an evolutionary timescale, the reduction in plant recruitment may limit range expansion, reduce plant community genetic diversity, or may impact the population viability of plants through greater kin competition from increased spatial aggregation (Caughlin et al. 2015).

Of particular concern for primates are the threats facing extant species in Africa (Chapman et al. 2006), where species are under threat from deforestation, hunting, disease and climate change (Chapman et al. 2006; Watson et al. 2016; Estrada et al. 2017; Strona et al. 2018). Conversion of relatively undisturbed land for use to support human population growth encourages immigration, increasing pressure on natural resources already heavily impacted, and further increasing hunting, disease and deforestation (Chapman et al. 2006; Laurance et al. 2008, 2014). The ability of primates to disperse seeds between habitats and into previously degraded habitats (Oliveira & Ferrari 2000; Culot et al. 2010; Razafindratsima & Martinez 2012; Albert et al. 2014), is therefore of high conservation value in the restoration of African forests (Chapman & Dunham 2018). Cercopithecines have a broad distribution throughout sub-Saharan Africa (Lawes 1990; Grubb 2003). Currently, 48% of cercopithecine species including 39% of African species, are listed by IUCN as threatened (Albert et al. 2014). Many (~80%) cercopithecine species can successfully inhabit disturbed habitats including secondary forest, heavily disturbed areas such as pasture, plantations, rural gardens and urban environments (Albert et al.

2014) and could, therefore, be a useful taxa for forest restoration throughout their range (Kaplin & Lambert 2002; Albert et al. 2014). The sub-species of samango monkey in this study is classified locally as endangered, primarily because of habitat fragmentation from expanding agriculture (see Chapter 2, section 2.2.4; Linden et al. 2016). The positive influence of seed processing mechanisms on seed germination (Chapter 3), the relatively long retention times of seeds (Chapter 4) and their ability to travel relatively long distances (Chapter 5), should make conservation of the areas in which samango monkeys live a priority, not least because of the valuable contribution they could have in seed dispersal.

6.5 | Limitations of the Research

6.5.1 | Quality of Dispersal: Germination of Seeds

The germination experiments in Chapter 3 were designed to isolate the fundamentally different effects of seed handling mechanisms on seed germination (Samuels & Levey 2005). I included the Fertiliser effect alongside the Gut Passage effect to assess the impact of the faecal matrix on seeds sown within it. To be more confident of the effect of the faecal matrix, it would have been more appropriate to have used seeds from each faecal sample for both of these treatments instead of seeds from different samples for each treatment. This limitation does not invalidate the findings of Chapter 3 but may have altered the size of the effect. Mixing seeds recovered from the same faecal sample into these two treatments would have further isolated the effect of each treatment, as they would have been exposed to similar mechanical treatment within the gut.

I could not include the effect of saliva enzymes on seed germination. Oral processing can have a disinhibitory effect through pulp removal (Traveset & Verdú 2002), or it can have a disinhibitory effect *plus* a mechanical scarifying effect from teeth scraping the seed coat (Janzen 1981; Anzures-Dadda et al. 2016). Furthermore, guenon cheek pouches may have a chemical scarifying effect from saliva enzymes involved in pre-digestion breakdown of starch (Murray 1975). Cheek pouch use is an important tool in which cercopithecines can disperse large quantities of seeds (Corlett & Lucas 1990; Rowell & Mitchell 1991), and which they can use as a result of intragroup competition (Lambert & Whitham 2001; Lambert 2005a; Hannibal 2008; Smith et al. 2008). Moving forward, collecting seeds spat out by monkeys and sowing them without cleaning them, would enable the effect of saliva enzymes on seed germination to be assessed. Separating faecal and cheek pouch dispersal modes into different studies may help future research where time and resources are limited.

I could not include repetitions with seeds from identical trees and monkeys across several fruiting seasons in the germination experiments. Temporal variation in fruit availability may have influenced the viability and germination of seeds for two reasons. Firstly, fluctuations in the environmental conditions in which seeds develop, such as temperature and drought, can influence seed germinability (Fenner 1991; Penfield & MacGregor 2017). Secondly, the diets of frugivores are not constant (Suwanvecho et al. 2018). Interannual variation in fruit production (Chapman et al. 2005) and fruit quality (O'Driscoll Worman & Chapman 2005) could alter the quality of treatment the seeds are subject to within the gut. As well as temporal variation in fruit quality, studies have demonstrated vertical stratification of within-tree variation in fruit quality (Schaefer et al. 2002; Houle et al. 2010, 2014). Higher quality fruits tend to found within the upper-crown of trees (Houle et al. 2010, 2014), fuelling within-group frugivore feeding competition (Houle et al. 2010) and which may have also influenced the viability and germination potential of seeds in Chapter 3.

6.5.2 | Quality of Dispersal: Gut Passage Time

To investigate the gut passage time of seeds, in Chapter 4 I adapted experimental methodology previously used on captive cercopithecines (Lambert 2002) for use in the field on wild samango monkeys. Adapting such a methodology proved difficult and while I discuss inadequacies of the study in Chapter 4, there are important limitations to investigating gut passage time *in-situ*. Firstly, I did not test the natural markers in a captive setting prior to using them *in-situ* and make the assumption that plastic and natural markers give similar results, which was also not tested. Ideally these two markers should be tested in a captive setting to make sure there are no differences in passage time or recovery rate and to set a standard for which natural markers to use.

Secondly, the data required to estimate mean retention time (Blaxter et al. 1956) - reliable and consistent collection of faeces clear of markers before and after the first and last marker respectively, can be more reliably collected within a captive setting, as movement of the focal subject is limited by the size of its enclosure. Furthermore, the observer is limited only by (a) the number of cameras available to capture marker ingestion and defaecation events and (b) the treatment of markers during oral processing. Feeding events can be repeated with minimal intrusion or impacts on the safety of observers. On the other hand, in the field the observer is limited by (a) ensuring monopolisation of the marker delivery resource, (b) treatment of the markers in the mouth, (c) collecting all faecal depositions (most notably at night), (d) the structure of the habitat in which the subjects reside, (e) the ability of arboreal animals to avoid regular contact with observers, (e) the need for rest, and (f) the unpredictable behaviour of wild animals. And yet it is this last point that means *in-situ* studies that capture the unpredictable nature of wild animals are necessary for accurately determining the gut passage time of seeds.

6.5.3 | Quality of Dispersal

As with the germination experiments, data were only collected on the behaviour of the monkeys (Chapter 5) during one six-month period and, as such, did not capture seasonal variation in behaviour typically associated with seasonal and inter-annual time periods (Gautier-Hion 1980; Wrangham et al. 1998; Campos-Arceiz et al. 2008; Culot et al. 2010; Tsuji 2014; Heymann et al. 2017; Suwanvecho et al. 2018). Frugivore seed dispersal has been shown to exhibit seasonal fluctuations associated with, for example, the availability of fruit (Wrangham et al. 1998; González-Varo et al. 2019) and environmental conditions (de A. Moura & McConkey 2007; Campos-Arceiz et al. 2008). It was also not feasible to include demographic parameters of seed and seedling survival beyond germination. These limitations are constrained by time constraints and longer field studies, or collation of data acquired through several studies, could address this limitation.

6.5.4 | Quantity of Dispersal: 1-min Focal Animal Sampling

During the 1-min focal animal sampling in which I collected data on the number of seeds processed by the monkeys (Chapter 5), I did not differentiate between the two groups, as I did not expect the groups to process fruits at different rates. In hindsight, differentiating between the groups would have given greater weight to the how intergroup variability in foraging behaviour influences the quantity of dispersal. Furthermore, data on the habitat type, number of animals in each tree and nearest neighbour distances would have helped contextualise those data further.

6.6 | Future Research

6.6.1 | Dispersal Kernels

For plants, seed dispersal represents the only mobile life stage and therefore its outcome is highly influential in determining plant fitness (Nathan & Muller-Landau 2000; Vander Wall et al. 2005a; Snell et al. 2019). Seed shadows represent the spatial distribution of seeds during the mobile life stage, typically from an individual plant or disperser, that shape the structure and dynamics of plant populations and communities (Howe & Smallwood 1982; Nathan & Muller-Landau 2000; Gelmi-Candusso et al. 2017). Dispersing seeds away from parent trees may reduce natural enemy predation (Janzen 1970; Terborgh 2012) and conspecific density-dependent competition (Janzen 1970; Connell 1971; Terborgh 2012; Comita et al. 2014). Describing patterns of seed movement by frugivores may also provide an understanding of their role in recruitment and colonisation of habitats in response to future global change (Clark et al. 1999, 2002).

Dispersal distance and the microhabitats into which seeds are dispersed, are influenced by gut passage time and the distance travelled during that time (Link & Di Fiore 2006; Fuzessy et al. 2017; Rehm et al. 2019). In Chapter 4, I was able to reliably estimate a gut passage time window of between 16.63 – 25.12 hrs for samango monkeys at the field site which, when combined with daily travel path length could offer further insights of the role both groups play in forest maintenance, regeneration and recruitment (Howe &

Smallwood 1982; Terborgh et al. 2002) through estimation of dispersal kernels and mean dispersal distances from feeding trees (Dennis & Westcott 2007; Nathan et al. 2012).

6.6.2 | Secondary Seed Dispersal

Primary seed deposition (Phase I: *sensu* Culot et al. 2015) is rarely the final stage of seed movement as secondary dispersal (diplochory) (Phase II: *sensu* Culot et al. 2015) by seed predators, seed hoarders and dung beetles is a widespread phenomenon in dispersal networks (Levey & Byrne 1993; Andresen 2001; Lambert & Chapman 2005; Vander Wall et al. 2005b; Chapman et al. 2010b; Seufert et al. 2010; Culot et al. 2018; Ocampo-Castillo & Andresen 2018). Without secondary dispersal services, the seed may be predated on by seed consumers such as granivores and pathogens (Vander Wall et al. 2005b). In primate dispersal networks more than half of seeds dispersed by primates are removed by seed predators and seed hoarders (Lambert & Chapman 2005). Previous research at the field site demonstrated a variety of Phase II fruit and seed removers captured through camera trapping (Seufert et al. 2010), the consequence of which can modify the primary deposition patterns generated by primates (Chapman & Dunham 2018).

As with the SDE framework for primary seed dispersal, Phase II SDE can assess the role of diplochory through quantitative evaluation of the quantity and quality component effects on plant fitness (Culot et al. 2015). Through comparisons between the fate of seeds within a Phase I SDE landscape (Chapter 5) and Phase I SDE *plus* the positive or negative effects of Phase II SDE, it is suggested that the relative contribution of each Phase to the SDE of a given plant species can be identified (Culot et al. 2015). The Phase I and II SDE framework has found positive cumulative contributions of bird followed by ant dispersal (Camargo et al. 2016), primate followed by dung beetle dispersal (Culot et al. 2018), and a wider study assessing the effect of the loss of large bodied mammals on dung beetles (Raine et al. 2018). Phase II SDE will aid in increasing our understanding of the complex dispersal networks at the local and landscape scale, which could be vital in (a) predicting, and (b) mitigating, the effects of anthropogenic-induced global change (Arroyo-Rodríguez & Fahrig 2014; Griffiths et al. 2016; Razafindratsima et al. 2018).

6.6.3 | Individual Variation in SDE

This thesis has gone some way in assessing intraspecific variation in SDE, using samango monkeys as the model species. This is important as population and/or species estimates of SDE, may overlook the inherent variation of the components of SDE in social foraging primates (Zwolak 2018). In animals where the monopolisation of resources can occur, socially-driven behaviour may limit the quantity of seeds dispersed (Zwolak 2018), spatial seed deposition patterns (Karubian et al. 2012) and the quality of the habitat into which seeds are dispersed (Beckman & Rogers 2013; Snell et al. 2019). Guenons live in multi-female, single-male groups of typically up to ~45 individuals (Skinner & Chimimba 2005).

Future research is to determine the potentially unique seed dispersal services performed by classes of individuals within the population such as age- or sex-class groups or particular life stages, such as lactating females or bachelor males (Zwolak 2018; Snell et al. 2019).

Individual variation in SDE may be significant if the loss or decline of individuals that confer disproportionately greater dispersal services has the potential to considerably alter seed dispersal (McConkey & O'Farrill 2016; Zwolak 2018). For example, in multi-male multi-female social systems, bachelor males may exhibit lower quantity but higher quality dispersal functions during mating seasons, by moving between groups of females. In structured social systems, subordinate members may exhibit greater use of cheek pouches than more dominant members because of intragroup competition (Lambert & Whitham 2001; Lambert 2005a; Hannibal 2008; Smith et al. 2008). Increased cheek pouch use may lead to greater quantities of seeds being moved away from the parent plant, reducing density dependent competition and increasing the likelihood of germination.

6.7 | Conclusion

This thesis set out to investigate intergroup variability in SDE between two neighbouring groups of samango monkeys, through quantification of the quality and quantity components of seed dispersal (Schupp 1993). Germination experiments demonstrated that the disinhibition effect of pulp removal confers the most influence on seed germination. Further analysis demonstrated that when germination potential of gut passed seeds is integrated into the SDE framework, the quantity of seeds dispersed through swallowing increased the effectiveness of samango monkeys when they disperse seeds via swallowing. These findings demonstrate that plants may trade negative or neutral effects of germination with the quantity of seeds dispersed and the likelihood of seeds being transported into microsites suitable for seedling establishment.

Intergroup variability in foraging behaviour influenced the quantity of seeds dispersed by each group per day, and the movement behaviour of each group influenced the quality of dispersal into microsites suitable for seedling establishment. One group spent longer in forest habitat and are potentially more influential in forest maintenance. The other group spent less time in forest habitat and more time in open habitat and are potentially more influential for recruitment into gaps and novel habitats. These results indicate groups within the same population, inhabiting partially overlapping home ranges, are distinctly different in their effectiveness in seed dispersal for several plant species. Intergroup variability in SDE arose as a consequence of variation in activity patterns, daily diet composition and the quality of the habitats in which the groups forage, which probably manifest from ecological constraints associated with group size and habitat quality. These findings highlight the need for inclusion of intraspecific variability into seed dispersal models, as species-level analysis may fail to account for individual or group-level variability (Russo et al. 2006; Strier 2009; Matías et al. 2010; McConkey et al. 2014; Heymann et al. 2017; Andresen et al. 2018; Fricke et al. 2019). The SDE framework provides a suitable tool for comparisons within and between populations of dispersers (e.g. McConkey et al. 2018) to provide insights into their relative contribution to the maintenance and regeneration of plant communities (Zwolak 2018). Future studies should aim to incorporate the framework into models of seed dispersal to further increase our understanding of the complex mechanisms that underpin the dynamics of animal-plant mutualisms.

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Appendices

Appendix 1.

Table A.1 Literature review of 69 studies published between 2005 and 2019 that aimed to assess the effects of either seed-spitting or seed-swallowing on germination, that excluded (Y) or included (N) Entire Fruit Control groups or the Fertiliser Effect. NA - treatment not required.

Study Details		Included Treatments					Excluded Treatments	
Reference	Study Aim	Control	1	2	3	4	Entire Fruit Controls	Fertiliser Effect
Abbas et al. 2018	Effect of gut passage on seed germination	Manual extracted seeds	Chemical scarification of manually extracted seeds	Gut passed seeds 24-48 hr	Gut passed seeds 48-72 hr		Y	Y
Albert et al. 2013	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Spat seeds	Dropped seeds		Y	Y
Anzures-Dadda et al. 2016	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Chemical scarification of manually extracted seeds	Mechanical scarification of manually extracted seeds		Y	Y
Baldwin & Whitehead 2015	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces				Y	Y
Beaune et al. 2013	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces - animal	Seeds removed from faeces - human	Mechanical scarification of manually extracted seeds	Animal scarified seeds	Y	Y
Boone et al. 2015	Effect of Pleistocene gut passage on seed germination using extant analogues	Entire Fruits (2/3 species) Manual extracted seeds (1/3 species)	Seeds sown in faeces (2/3 species)	Seeds removed from faeces	Mechanical scarification of manually extracted seeds (1/3 species)		Y (1/3 species)	Y (1/3 species)

Bourgeois et al. 2005	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Bravo 2009	Effect of gut passage on seed dispersal quality	Manual extracted seeds	Seeds removed from faeces		Y	Y
Cáceres & Monteiro-Filho 2007	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Carvalho et al. 2017	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Castro et al. 2008	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Chapman et al. 2010	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Spat seeds	Y	Y
Chaves et al. 2011	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Chen et al. 2016	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Chen et al. 2017	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Regurgitated seeds	Y	Y
Colon & Campos-Arceiz 2013	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y

Cosyns et al. 2005	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Seeds sown in faeces		NA	N
Carvalho-Ricardo et al. 2014	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Sánchez de la Vega & Godínez-Alvarez 2010	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Seeds sown in faeces		Y	N
Dellafiore et al. 2007	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Fedriani & Delibes 2009	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Giordani et al. 2015	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
González-Di Pierro et al. 2011	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Grande et al. 2013	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Grande et al. 2016	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Gross-Camp & Kaplin 2005	Effect of regurgitation on seed germination	Entire fruit	Regurgitated seeds			N	NA
Gross-Camp & Kaplin 2011	Effect of regurgitation and gut passage on seed germination	Entire fruit	Regurgitated seeds	Seeds sown in faeces	Manual extracted seeds	N	N

Harich et al. 2016	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Heer et al. 2010	Effect of gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces	Seeds sown in faeces	N	N
Jara-Guerrero et al. 2018	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Kankam & Oduro 2012	Effect of spitting on seed germination	Entire fruit	Manual extracted seeds	Spat seeds		N	NA
Kunz & Linsenmair 2008	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Lessa et al. 2013	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Levi & Peres 2013	Effect of simulated gut passage (pulp removal) on seed germination	Entire fruit	Manual extracted seeds			N	Y
Maldonado et al. 2018	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Mancilla-Leytón et al. 2012	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces			Y	Y
Mancilla-Leytón et al. 2011	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Seeds sown in faeces		NA	N

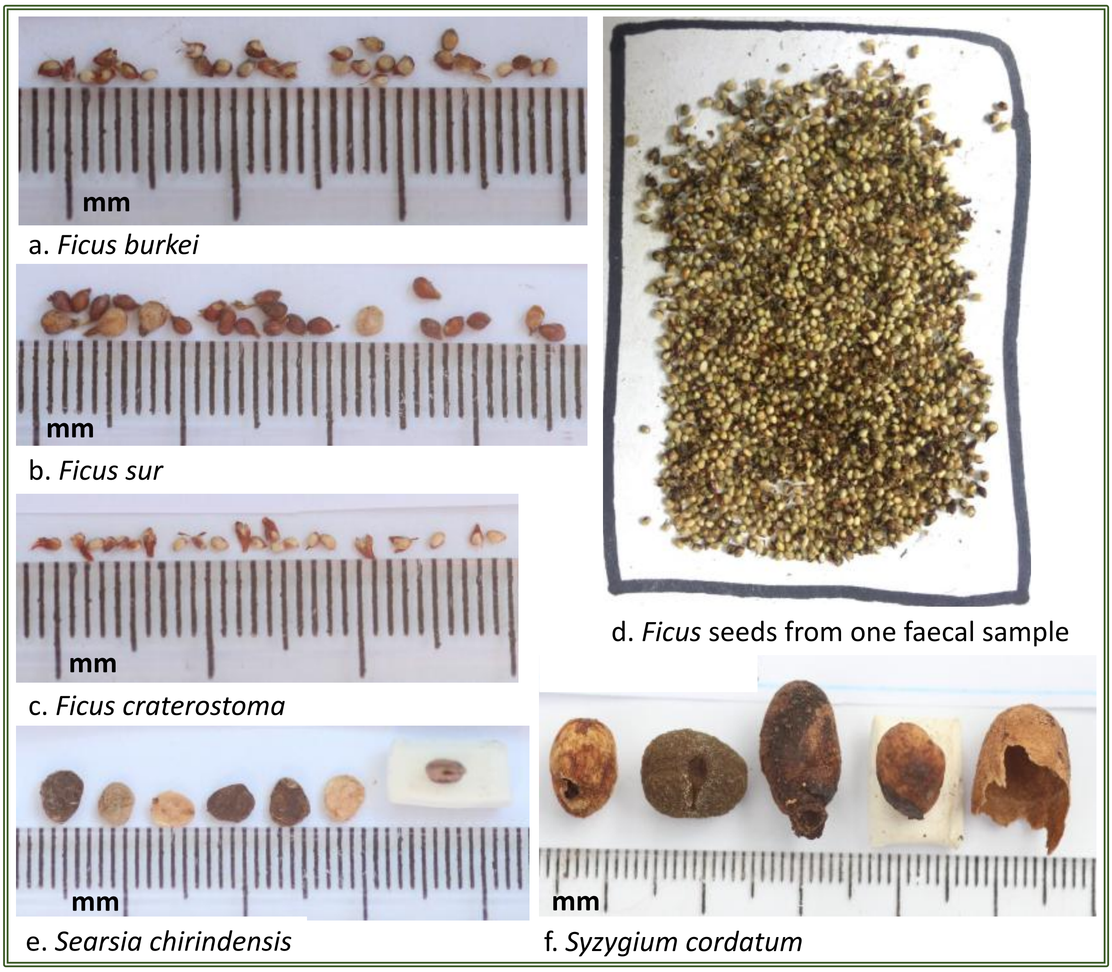
Mancilla-Leytón et al. 2013	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces				Y	Y
Manzano et al. 2005	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces				NA	Y
Michael et al. 2006	Effect of mastication and digestion on seed germination	Mechanical scarification of manually extracted seeds	Manual extracted seeds				NA	N
Milotić & Hoffmann 2016a	Effect of faeces on grassland plants	Manual extracted seeds	Seeds sown in faeces				NA	N
Milotić & Hoffmann 2016b	Effect of gut passage on seed germination	Manual extracted seeds	Chemical scarification of manually extracted seeds	Mechanical scarification of manually extracted seeds	Heat treated manually scarified seeds	Combination of treatments 1-3	NA	N
Milotić & Hoffmann 2016c	Effect of faeces on grassland seeds	Manual extracted seeds	Seeds sown in faeces	Mechanical scarification of manually extracted seeds			NA	N
Moses & Semple 2011	Effect of gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces			N	Y
Muñoz-Gallego et al. 2019	Effect of regurgitation and gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds sown in faeces	Regurgitated seeds		N	Y

Nowak & Crone 2012	Effect of gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces			N	Y
O'Connor & Kelly 2012	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces				Y	Y
Padrón et al. 2011	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces				Y	Y
Pakeman & Small 2009	Effect of faeces on grassland seeds	Manual extracted seeds	Seeds sown in faeces				N	N
Peco et al. 2006	Effect of mastication and digestion on seed germination	Manual extracted seeds	Mechanical scarification of manually extracted seeds	Chemical scarification of manually extracted seeds			NA	N
Pegg 2014	Effect of gut passage and/or fire on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces	Manual extracted and burnt seeds	Entire fruit burnt	N	Y
Peguero & Espelta 2014	Effect of gut passage and/or fire on seed germination	Manual extracted seeds	Mechanical scarification of manually extracted seeds	Heat-shocked seeds			Y	Y
Petre et al. 2015a	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces				Y	Y
Petre et al. 2015b	Effect of gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces			N	Y

Ramos et al. 2006	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Seeds sown in faeces	Mechanical scarification of manually extracted seeds		Y	N
Ramos et al. 2010	Using sheep to introduce fodder species to fallow	Seeds sown in faeces					NA	N
Razafindratsima & Martinez 2012	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces				Y	Y
Rebein et al. 2017	Effect of gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces			N	Y
Roehm & Moran 2013	Effect of gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces			N	Y
Rojas-Martinez et al. 2015	Effect of gut passage on seed germination	Manual extracted seeds	Seeds sown in faeces	Chemical scarification of manually extracted seeds			Y	N
Rost et al. 2012	Effect of gut passage on seed germination	Entire fruit	Manual extracted seeds	Seeds removed from faeces			N	Y
Sengupta et al. 2014	Effect of spitting and gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Spat seeds			Y	Y
Tjelele et al. 2015	Effect of livestock and fire on woody plant species	Manual extracted seeds	Seeds removed from faeces	Seeds sown in faeces			NA	N

Tsuji et al. 2017	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Valenta & Fedigan 2009	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces	Seeds sown in faeces	Y	N
Varela & Bucher 2006	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Vergara-Tabares et al. 2018	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y
Voigt et al. 2011	Effect of spitting on seed germination	Entire fruit	Manual extracted seeds	Spat seeds	N	NA
Yang et al. 2019	Effect of gut passage on seed germination	Manual extracted seeds	Seeds removed from faeces		Y	Y

Appendix 2.



a. *Ficus burkei*

b. *Ficus sur*

c. *Ficus craterostoma*

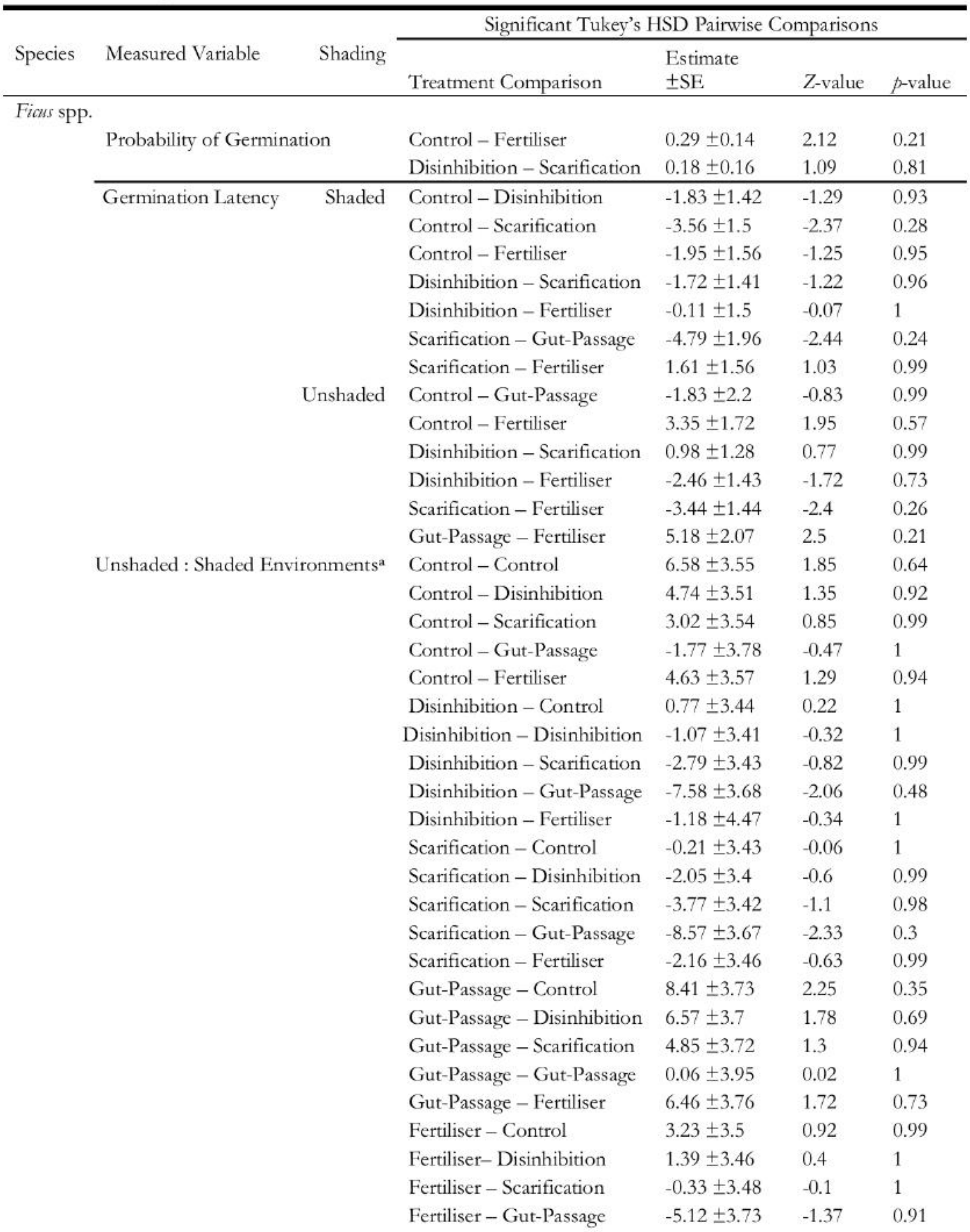
d. *Ficus* seeds from one faecal sample

e. *Searsia chirindensis*

f. *Syzygium cordatum*

Fig. A.1 (a - c) *Ficus* spp. seeds removed from ripe fruit and (d) from a samango monkey faecal sample, (e) *Searsia chirindensis* and (f) *Syzygium cordatum* seeds removed from ripe fruit.

Appendix 3. Table A.2 None-significant Tukey HSD pairwise comparison tests conducted following GLMM Wald Chi-square test of the effect of treatment, and the interactive effect of shade (Shaded and Unshaded) and treatment, on the germination latency for three samango monkey dispersed fruit species' seeds. Treatments: Control, entire fruits, no treatment; Disinhibition, effect of pulp removal; Scarification, mechanical damage to the protective seed coat; Gut-Passage, disinhibition *plus* mechanical *and* chemical scarification during gut passage (*Ficus* spp. and *S. chirindensis* only); Fertiliser, gut passage effect *plus* fertiliser effect of the faecal matrix (*Ficus* spp. and *S. chirindensis* only); Desiccation, disinhibition *plus* desiccation (*S. cordatum* only).



Species	Measured Variable	Shading	Significant Tukey's HSD Pairwise Comparisons			
			Treatment Comparison	Estimate ±SE	*Z*-value	*p*-value
Ficus spp.						
	Probability of Germination		Control – Fertiliser	0.29 ±0.14	2.12	0.21
			Disinhibition – Scarification	0.18 ±0.16	1.09	0.81
	Germination Latency	Shaded	Control – Disinhibition	-1.83 ±1.42	-1.29	0.93
			Control – Scarification	-3.56 ±1.5	-2.37	0.28
			Control – Fertiliser	-1.95 ±1.56	-1.25	0.95
			Disinhibition – Scarification	-1.72 ±1.41	-1.22	0.96
			Disinhibition – Fertiliser	-0.11 ±1.5	-0.07	1
			Scarification – Gut-Passage	-4.79 ±1.96	-2.44	0.24
			Scarification – Fertiliser	1.61 ±1.56	1.03	0.99
		Unshaded	Control – Gut-Passage	-1.83 ±2.2	-0.83	0.99
			Control – Fertiliser	3.35 ±1.72	1.95	0.57
			Disinhibition – Scarification	0.98 ±1.28	0.77	0.99
			Disinhibition – Fertiliser	-2.46 ±1.43	-1.72	0.73
			Scarification – Fertiliser	-3.44 ±1.44	-2.4	0.26
			Gut-Passage – Fertiliser	5.18 ±2.07	2.5	0.21
	Unshaded : Shaded Environments[a]		Control – Control	6.58 ±3.55	1.85	0.64
			Control – Disinhibition	4.74 ±3.51	1.35	0.92
			Control – Scarification	3.02 ±3.54	0.85	0.99
			Control – Gut-Passage	-1.77 ±3.78	-0.47	1
			Control – Fertiliser	4.63 ±3.57	1.29	0.94
			Disinhibition – Control	0.77 ±3.44	0.22	1
			Disinhibition – Disinhibition	-1.07 ±3.41	-0.32	1
			Disinhibition – Scarification	-2.79 ±3.43	-0.82	0.99
			Disinhibition – Gut-Passage	-7.58 ±3.68	-2.06	0.48
			Disinhibition – Fertiliser	-1.18 ±4.47	-0.34	1
			Scarification – Control	-0.21 ±3.43	-0.06	1
			Scarification – Disinhibition	-2.05 ±3.4	-0.6	0.99
			Scarification – Scarification	-3.77 ±3.42	-1.1	0.98
			Scarification – Gut-Passage	-8.57 ±3.67	-2.33	0.3
			Scarification – Fertiliser	-2.16 ±3.46	-0.63	0.99
			Gut-Passage – Control	8.41 ±3.73	2.25	0.35
			Gut-Passage – Disinhibition	6.57 ±3.7	1.78	0.69
			Gut-Passage – Scarification	4.85 ±3.72	1.3	0.94
			Gut-Passage – Gut-Passage	0.06 ±3.95	0.02	1
			Gut-Passage – Fertiliser	6.46 ±3.76	1.72	0.73
			Fertiliser – Control	3.23 ±3.5	0.92	0.99
			Fertiliser– Disinhibition	1.39 ±3.46	0.4	1
			Fertiliser – Scarification	-0.33 ±3.48	-0.1	1
			Fertiliser – Gut-Passage	-5.12 ±3.73	-1.37	0.91

Table A.2 continued

	Fertiliser – Fertiliser	1.28 ±3.52	0.36	1
Searsia chirindensis				
Probability of Germination	Control – Gut-Passage	-0.46 ±0.48	-0.95	0.87
	Control – Fertiliser	-0.67 ±0.48	-1.42	0.6
	Disinhibition – Scarification	-0.06 ±0.21	-0.3	0.99
	Gut-Passage – Fertiliser	-0.22 ±0.39	-0.56	0.98
Germination Latency	Control – Disinhibition	0.11 ±0.08	1.39	0.62
	Control – Scarification	0.15 ±0.0.08	1.85	0.34
	Control – Fertiliser	0.18 ±0.1	1.82	0.36
	Disinhibition – Scarification	0.04 ±0.06	0.65	0.96
	Disinhibition – Gut-Passage	0.2 ±0.08	2.7	0.05
	Disinhibition – Fertiliser	0.07 ±0.08	0.84	0.92
	Scarification – Gut-Passage	0.17 ±0.07	2.22	0.17
	Scarification – Fertiliser	0.03 ±0.08	0.38	0.99
	Gut-Passage – Fertiliser	-0.14 ±0.09	-1.44	0.59
Syzygium cordatum				
Probability of Germination	Disinhibition – Scarification	3.46 ±1.39	2.5	0.05
Germination Latency Shaded	Control – Desiccation	19.43 ±7.75	2.51	0.15
Unshaded	Control – Desiccation	13.12 ±6.56	2	0.41
Unshaded : Shaded Environments[a]	Control – Control	0.98 ±9.43	0.1	1
	Disinhibition – Disinhibition	2.53 ±2.43	1.04	0.95
	Scarification – Disinhibition	-2.03 ±2.4	-0.85	0.99
	Scarification – Scarification	6.32 ±2.31	2.73	0.08
	Desiccation – Control	-12.15 ±8.23	-1.48	0.77
	Desiccation – Desiccation	7.28 ±4.53	1.61	0.69

[a] The first treatment listed was in unshaded conditions

Appendix 4. Table A.3 A comprehensive list of diet composition (proportion of time per day feeding) of two groups of samango monkeys (Barn and House) at Lajuma, South Africa between December 2017 and May 2018.

Feeding / Fruit Species	Diet Composition (% time/day ±SD)	
	Barn	House
Non-Fruit		
Bark	1.07 ±1.3	1.43 ±2.08
Cheek Pouch	11.61 ±8.78	9.39 ±7.79
Flowers	9.08 ±10.96	5.56 ±6.89
Fungi	3.72 ±4.12	1.73 ±2.71
Grass Seed/Flower	2.17 ±3.05	3.16 ±3.59
Invertebrate	1.11 ±2.23	0.83 ±0.7
Leaves	35.92±20.29	34.29±15.71
Sap	2.16 (-)	0.33 ±0.38
Seed Pod	15.01 ±6.96	13.22 ±6.71
Water	1.6 ±2.15	1.25 ±1.6
Unknown	1.57 ±2.15	0.63 ±0.7
Fruit	35.64±18.44	42.88±16.32
Family *Species* (common name)		
Anacardiaceae (sumac)		
Searsia chirindensis (red currant)	20.91 ±19.74	26.27 ±15.22
Searsia pentheri (crowberry)	16.21 ±22.63	18.59 ±14.23
Searsia lancea (karee)	2.82 (-)	
Apocynaceae (dogbane)		
Carissa bispinosa (forest num-num)	1.72 (-)	0.89 ±0.94
Carissa edulis (climbing num-num)	2.47 ±2.05	7.11 ±5.83
Rauvolfia caffra (quinine tree)	0.68 ±0.68	5.79 ±3.47
Brassicaceae (mustards)		
Maerua cafra (common bush-cherry)	3.8 (-)	
Cannabaceae (hemp)		
Celtis africana (white stinkwood)	7.43 ±8.84	5.4 ±5.38
Capparaceae (caper)		
Capparis fascicularis var. *fascicularis* (caper-bush)	3.36 ±3.92	
Celastraceae (staff-vine)		
Elaeodendron transvaalense (bushveld saffron)	8.58 (-)	
Euphorbiaceae (spurge)		
Croton sylvaticus (forest fever-berry)	7.36 ±6.8	6.65 ±6.99
Fabaceae (legume)		
Senegalia ataxacantha (flame thorn)	11.94 ±6.05	7.87 ±7.78
Vachellia karroo (sweet thorn)	5.45 ±3.81	5.04 ±4.04
Vachellia sieberiana var. *woodii* (paper thorn)	1.61 ±1.4	1.43 ±1.85

Table A.3 Continued

Juglandaceae (hickory)		
Carya illinoinensis (pecan nut)[a]		6.81 (-)
Lauraceae (laurels)		
Ocotea kenyensis (bastard stinkwood)		5.24 ±3.15
Meliaceae (mahogany)		
Ekebergia capensis (cape ash)	6.4 ±4.89	7.28 ±6.94
Trichillia dregeana (forest mahogany)		4.57 ±4.37
Moraceae (mulberry)		
Ficus spp. (fig)	12.76 ±9.5	16.08 ±9.4
Myrtaceae (myrtle)		
Psidium guajuava (common guava)[a]	9.15 ±11.96	8.97 ±11.01
Syzygium cordatum (water berry)	10.06 ±14.65	6.55 ±7.63
Oleaceae (olive)		
Chioanthus foveolatus subsp. *foveolatus* (pock-ironwood)	5.86 (-)	
Olea capensis (black ironwood)	7.72 ±7.07	1.02 (-)
Olea europaea subsp. *africana* (wild olive)	5.2 ±5.13	5.2 ±4.33
Passifloraceae (passionflower)		
Adenia gummifera var. *gummifera* (monkey rope)	1.91 ±2.37	
Putranjivaceae (rosid) formerly Euphorbiaceae		
Drypetes gerrardii (forest iron plum)	0.61 (-)	
Rhamnaceae (buckthorn)		
Ziziphus mucronata subsp. *mucronata* (buffalo thorn)	2.49 ±3.23	4.3 ±3.66
Rubiaceae (coffee)		
Canthium mundianum (rock alder)		8.87 (-)
Hyperacanthus amoenus (thorny gardenia)	0.55 (-)	
Salicaceae (willow)		
Dovyalis zeyheri (wild apricot)	6.84 (-)	
Sapotaceae (sapodilla)		
Englerophytum magalismontanum (Transvaal milk plum)	4.29 ±1.84	13.15 (-)
Mimusops zeyheri (Transvaal red milkwood)	2.81 ±2.83	
Vitaceae (grapevine)		
Rhoicissus rhomboidea (bastard forest grape)	12.45 ±8.13	7.62 ±4.97
Rhoicissus tomentosa (wild grape)	5.89 ±6.27	5.99 ±5.35
Unidentified	6.06 ±9.04	4.67 ±3.78

[a] invasive species