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Dispersion of large-seeded tree species by two forest primates: primate seed handling, microhabitat variability, and post-dispersal seed fate

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DISPERSION OF LARGE-SEEDED TREE SPECIES BY TWO FOREST PRIMATES:

PRIMATE SEED HANDLING, MICROHABITAT VARIABILITY, AND POST-DISPERSAL SEED FATE

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DISPERSION OF LARGE-SEEDED TREE SPECIES BY TWO FOREST PRIMATES:

PRIMATE SEED HANDLING, MICROHABITAT VARIABILITY, AND POST-DISPERSAL SEED FATE

by

Nicole D. Gross-Camp

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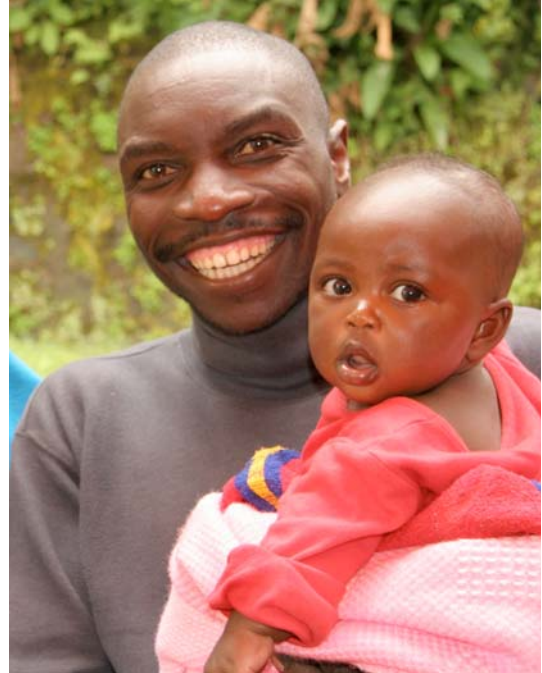
Innocent with Senna (top left),
Theoneste and his daughter
(top right) and Donati and
Felicee (bottom)

Martin and Senna (top)

Martin, Cesar, Fidele with Senna, and Nicole (bottom)

Abrahim, Nicole and
Gratien in pine buffer
near Banda (top)

Stella, Beth and Senna
in Butare (bottom)

Dedication

The efforts of many Rwandans made my dissertation possible and for this I am deeply grateful. My life and graduate research was enriched by our interactions and I am humbled by their strength and tenacity. They have given me the gift of perspective and taught me that generosity extends far beyond the material world. Murakoze cyane cyane.

Abrahim Ngiruwonsanga

Fidèle Muhayeyezu

Theonèste Nzabonimana

Innocent Semahoro

Martin Mudaheranwa

Donat Murwanashyaka

Gratien Gatorano

I also dedicate my dissertation to Anastase Benimana who taught me so much about the forest and the chimpanzees. His delightful sense of humor warmed my heart on many a cold day in the forest. May he be able to return to his work with the chimpanzees someday.

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In addition to Beth, my other committee members, Peter Palmiotto and Joanna Lambert nurtured my formation into a scholar. Peter's expertise in forest ecosystems kept me to task ensuring that my dissertation adequately addressed the plant perspective. His critical insights into my work helped to expand my perspectives and ability to discuss my work with scientists from varying backgrounds. Joanna's work was an inspiration to the formation of my dissertation proposal. She gave me the gift of the unknown providing fodder for what became my doctoral research. Joanna, too, has helped me grow as a scholar. I am deeply indebted to all of my committee members for their diligence in reading through my dissertation and providing me with critical feedback.

Many individuals in Rwanda where my research was based welcomed me (and my family) into their homes and provided a solid foundation from which to conduct my research. I am grateful for the friendship and professional support of Michel Masozera, Ian Munanura, Nsengi Barakabuye, Felix Mulindahabi, and Francois Bizimungu. My

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Abstract

I describe the relative effectiveness of two primates in dispersing large-seeded tree seeds

(> 0.5 cm) in the Nyungwe National Park (NNP), Rwanda. My objectives are three-fold:

(1) to describe the relative effectiveness of primates in dispersing the seeds of five large-

seeded tree species, (2) to evaluate the influence of primate seed-handling method on

seed fate, and (3) to determine the influence of deposition site on seed fate. I employed

focal tree observations, day-follows of habituated primate groups, *in situ* monitoring of

primate-dispersed seeds, and experimental plots to achieve these objectives. Data were

collected over the course of one year (April 2006 – April 2007).

Frugivore assemblages dispersed the seeds of four of the five focal tree species.

Chimpanzees and cercopithecines spent the most time in trees and had the largest group

size. Large-bodied birds (LB) and chimpanzees dispersed the highest number of seeds per

minute. LB and cercopithecines potentially disperse the greatest number of seeds for

Ekebergia capensis, and chimpanzees for *Syzygium guineense*. My study highlights the

complexities of determining a disperser's effectiveness and suggests that large-bodied

birds and primates are relatively important dispersers of large-seeded trees.

Primates deposit seeds most often in open forest where seeds experience the highest

establishment. In addition primates deposit seeds in five habitats that are likely dispersal-

limited suggesting that primates contribute to the regeneration processes of otherwise

dispersal-limited areas. My results suggest that the former emphasis of seed dispersal

studies on defecations is not representative and should be expanded to include orally-discarded seeds. Furthermore my study highlights that primates do not deposit seeds randomly and that the characteristics of the deposition site are a reflection of primate seed handling.

I found no relationship between the top five fruiting tree species found in chimpanzee feces and fruit availability suggesting that chimpanzees do not choose fruits solely based on their availability. In contrast the wadged fruits of *Syzygium guineense* are positively correlated to fruit availability. A closer examination of the relationship between chimpanzees and *S. guineense* may provide insight into potential repercussions on the regeneration of *S. guineense* if the chimpanzee were to be extirpated. I compare the relationship of seed presence in the NNP chimpanzees' feces and wadges and forest-wide fruit availability with two other chimpanzee communities in the Albertine Rift.

Finally I organized a workshop for educators living in communities on the NNP's periphery in an effort to disseminate my results to a broader community. Pre- and post-workshop questionnaires completed by workshop participants suggest that this kind of interaction between researchers, management authorities and local peoples helps to build trust as well as identify areas where sensitization of the population may be needed.

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Introduction

Seed dispersal links an individual plant's reproductive cycle with the distribution of its offspring and is widely recognized as having a significant influence on vegetation patterns (Stiles & White 1986; Estrada *et al.* 1993; Schupp 1993; Hubbell 2001; Jordano & Godoy 2002; Wang & Smith 2002). In tropical communities up to 90% of fruiting tree species are adapted for vertebrate dispersal (Frankie *et al.* 1974; Janson 1983; Gautier-Hion *et al.* 1985; Jordano 1992) suggesting an ecological advantage to vertebrate dispersal (Howe & Miriti 2004). Although most studies that examine vertebrate seed dispersal have investigated aspects of avian seed dispersal, primates comprise the largest percentage of the frugivore biomass in many tropical communities and disperse large quantities of viable seeds (Eisenberg & Thorington 1973; Estrada & Coates-Estrada 1984, 1986; Terborgh 1986; Julliot 1996).

In order to evaluate the contribution of a frugivore species to forest processes, Schupp (1993) developed a framework to determine frugivore effectiveness that is defined according to aspects of *quantity*, involving the number of seeds dispersed, and *quality*, the probability that seeds are deposited unharmed in a site where they may germinate and establish. More recently studies have focused on understanding the broader mechanisms driving vegetation patterns, namely recruitment limitation, including dispersal and establishment limitation (Hurtt & Pacala 1995; Harms et al. 2000; Nathan & Muller-Landau 2000; Muller-Landau et al. 2002; Schupp et al. 2002). Dispersal limitation is broadly defined as the failure of seeds to reach all available microhabitats, whereas establishment limitation is the inability of a seed to establish at its site of deposition (Jordano & Godoy 2002; Schupp *et al.* 2002). Dispersal limitation may arise

as a consequence of insufficient seed production ('source limitation' in Clark *et al.* 1999) as well as a result of distance-restricted seed delivery due to territory defense and/ or spatially aggregated seed delivery (e.g. near an adult conspecific, latrines, or roosts; Snow & Snow 1988; Guindon 1997; Julliot 1997; Mcconkey 2000; Wenny 2001).

Primate seed handling has important implications for where a seed will be deposited and its subsequent survival probability (Kaplin & Moermond 1998; Lambert 1999, 2002; Gross-Camp & Kaplin 2005). Frugivore movement away from the fruit source after swallowing or cheek pouching a fruit increases the likelihood that seeds will be deposited away from underneath an adult conspecific thereby 'escaping' the associated density-dependent mortality (Janzen 1970; Connell 1971; Harms et al. 2000). Primate seed handling behaviors have been described in three ways: (1) *seed predators*, in which seeds are masticated or rendered unviable through digestion, (2) *seed swallowers*, in which seeds are swallowed whole, intact and passed in viable condition in the fecal material, and (3) *seed spitters*, in which seeds are orally-processed and discarded (Corlett & Lucas 1990). Most primates employ some combination of these seed-handling techniques depending on species, sex and age of the animal, habitat, fruit species consumed, or fruit availability (Gautier-Hion 1980; Rowell & Mitchell 1991; Kaplin & Moermond 1998; McConkey 2000). My study shows that each of these handling methods has profound implications for seed fate.

Primate seed dispersal studies have predominantly focused on seeds dispersed through defecations and largely ignored seeds dispersed via spitting behavior (Corlett & Lucas 1990; Wrangham *et al.* 1994; Julliot 1996). However, recent studies on *Cercopithecus* monkeys and chimpanzees have demonstrated the significance of seed

spitting on seed persistence and germination (Lambert 2001; Kaplin & Lambert 2002; Gross-Camp & Kaplin 2005). Lambert (2001) demonstrated that the seeds of the tree species *Strychnos mitis* had a significantly higher probability of germinating under the parent tree when spit by *Cercopithecus ascanius* compared to simply falling unprocessed to the forest floor from the tree canopy. Lambert hypothesized that the seed spitting reduces attack by fungal pathogens by removing pulp surrounding the seed. Seeds orally-discarded by chimpanzees also experience a reduction in pathogen attack (Gross-Camp & Kaplin 2005) but differ from the seeds spit by *Cercopithecines* in two ways: (1) seeds are deposited in a clump by chimpanzees versus singly and (2) fruit pulp and skin are deposited with seeds by the chimpanzees versus as a bare seed. My study is one of the first to examine the affect of primate seed handling, namely methods of oral-discarding, on seed fate.

Few studies have examined the microhabitat where seeds are dispersed and their subsequent survival probabilities (but see Schupp 1988; Forget 1997; Wenny 2000; Gross-Camp & Kaplin 2005; Russo 2005) yet this is a significant aspect in our ability to describe primates' effectiveness as dispersal agents (Schupp 1993). Once a seed is deposited it becomes subject to a host of post-dispersal processes including abiotic and biotic. The impact of these processes on primate-dispersed seeds was given relatively little attention until recent studies indicated that post dispersal processes can extensively alter initial dispersal patterns (Herrera et al. 1994; Rey & Alcantra 2000; Balcomb & Chapman 2003; Lambert & Chapman 2005). My study describes microhabitat characteristics where primate-dispersed seeds are deposited, following seeds through time to determine the influence of such characteristics on seed fate.

Several recent publications have suggested that because primate seed dispersal plays such a significant role in forest dynamics, the loss of frugivorous primate populations will alter vegetation patterns and result in a reduction of plant diversity (Kaplin & Lambert 2002; Lambert 2002; Balcomb & Chapman 2003). The loss of primates may disproportionately affect large-seeded plant species (≥ 0.5 cm; Yumoto et al. 1998; Lambert 2002; Nunez-Iturri & Howe 2007; Stoner et al. 2007; Wang et al. 2007). This hypothesis is based on the correlation between frugivore body size and the fruit and seed size consumed (Janson 1983; Howe 1986). In general, fleshy-fruited species are dispersed by a suite of dispersers (Jordano 1992) but as seed size increases the number of dispersal vectors predictably decreases (Peres & Van Roosmalen 2002). Chapman & Onderdonk (1998) found a reduction in the number of large-seeded sapling species in fragments where only the smallest-bodied frugivorous primate, *Cercopithecus ascanius*, remained, suggesting that large-bodied frugivorous primates play an important role in the recruitment of large-seeded trees. Wang *et al.* (2007) found that the extermination of large primates in a Cameroonian forest altered seed deposition patterns for the large-seeded tree species *Antocaryon klaineanum* resulting in most seeds falling directly beneath the parent tree, where they are more likely to be killed by host-specific pathogens and a higher density of seed predators.

My dissertation describes the seed dispersal patterns created by two semi-terrestrial primates, the mountain monkey (*Cercopithecus lhoesti*) and the common chimpanzee (*Pan troglodytes schweinfurthii*), in an effort to understand the influence of their seed dispersal behaviors on tropical forest regeneration processes. I selected primate species based on their relatively large body size, endangered or threatened status, known

frugivory, and ease of observation in the study area. This work is an extension of my

master's research (Gross-Camp & Kaplin 2005) that described chimpanzee seed dispersal

patterns and post-dispersal seed fate of large seeds. My dissertation is comprised of three

main chapters describing the experimental design and major findings, and a fourth

chapter describing an outreach workshop aimed at extending my research and its

significance to the human communities living in close proximity to the study site. My

first chapter explores the relative effectiveness of primate seed dispersal to large-seeded

mature forest trees by documenting all diurnal frugivore visitation to five tree species

known to occur in the focal primates' diets. The second chapter describes the influence

of primate seed-handling treatment and characteristics of the deposition site on post-

dispersal seed fate. In the third chapter, I focus on chimpanzee seed dispersal examining

the influence of fruiting phenology on chimpanzee seed dispersal, comparing my findings

with other chimpanzee communities.

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CHAPTER 1

COMPARING THE DISPERSAL OF LARGE-SEEDED TREE SPECIES

BY FRUGIVORE ASSEMBLAGES IN TROPICAL MONTANE FOREST

Abstract

We examined frugivore visitation and seed dispersal of five large-seeded ($\geq$ 5 mm) tree species in tropical montane forest based on their occurrence in frugivorous primate diets: *Ekebergia capensis, Olea capensis, Parinari excelsa, Prunus africana,* and *Syzygium guineense.* A total of 21 frugivores in five assemblages (*i.e.* chimpanzees, cercopithecines, large-bodied birds, small-bodied birds, and squirrels) were observed over the study period (August 2006 and October – April 2007). We observed seed dispersal in four of five tree species studied; no dispersal was observed for *P. excelsa*. Frugivore assemblages did not visit tree species equally. Primates spent the most time in trees and had the largest group size. Large-bodied birds (LB) and chimpanzees dispersed the highest number of seeds per minute. LB and cercopithecines potentially dispersed the greatest number of seeds for *E. capensis,* and chimpanzees for *S. guineense*. Our analyses indicated that the mean fruiting duration of the focal tree, time in tree and number of species present are significant predictor variables for small- and large-bodied birds and cercopithecines seed dispersal. The fruiting trees surrounding the focal tree further predicted seed dispersal for small-bodied birds (SB). LB seed dispersal also was predicted by time in tree by SB and the number of individuals for SB and cercopithecines. Cercopithecines were further explained by the time in tree and number of species (SB & LB), and number of individuals for cercopithecines. Our study highlights the complexity of describing the relative effectiveness of a frugivore assemblage to the dispersal of a tree species seeds.

Introduction

Fleshy-fruited tree species are generally dispersed by multiple frugivores (Howe & Vande Kerckhove 1981, Jordano 1992); however, as seed size increases the number of dispersal vectors predictably decreases (Janzen 1982, Leighton & Leighton 1983, Wheelwright 1985, Chapman *et al.* 1992). Recent research has explored how the loss of large-bodied frugivores may alter forest structure and composition (Peres & Palacios 2007, Stoner *et al.* 2007, Wright *et al.* 2007) or the impact of dispersal recruitment of large-seeded plants (Cochrane 2003, Galetti *et al.* 2006). Nunez-Iturri & Howe (2007) showed how the loss of large- and medium-bodied frugivorous primates has changed forest composition and altered the spatial distribution of large-seeded tree species in a Peruvian forest. Similarly, Wang *et al.* (2007) demonstrated that the extermination of large primates changed seed deposition patterns for a large-seeded canopy tree, resulting in the majority of seeds falling beneath the parent crown where they are subject to higher rates of mortality.

In African forests, hunters often target large-bodied mammals, many of which are important seed dispersers (Alexandre 1978, Yumoto *et al.* 1995, Poulsen *et al.* 2002). These practices result in what scientists have called "empty forests" in which the flora remains relatively intact but the fauna is seriously reduced (Redford 1992, Fa *et al.* 2005). Beyond the aesthetic loss of these species, the loss of seed-dispersing frugivores impacts the ability of forests to maintain their current populations of fruiting plant species – particularly large-seeded tree species that tend to be canopy, mature or primary forest species (Kitamura *et al.* 2002). Furthermore, the evolutionary relationship between certain large-bodied fruit-eating mammals and frugivore-dependent large-seeded tree

species in tropical forests, whether extinct megafauna in the neotropics (Guimarães et al.
2008) or the large paleotropical mammals such as elephants (Cochrane 2003), suggests
that loss of large-bodied frugivores in these forests will have significant impacts on forest
structure and composition. An important step in understanding the consequences of
frugivore loss on forest structure and composition is determining the relative
effectiveness of different frugivore assemblages (*e.g.* birds vs. primates, large- vs. small-
bodied frugivores) to the dispersal of a given tree species.

In this study, we examined the effectiveness of five frugivore assemblages in
dispersing the seeds of five large-seeded mature forest tree species in a tropical montane
forest community. Frugivore assemblages included large-bodied birds, small-bodied
birds, cercopithecines, and squirrels, as well as a single species category of chimpanzees.
While we acknowledge that chimpanzees are not technically a frugivore assemblage, we
were particularly interested in documenting their role in the dispersal of large-seeded tree
species and as such refer to them as an assemblage in our data analyses. Frugivores were
placed in assemblages according to body-size (*i.e.* small and large) and type (*i.e.* bird,
primate, squirrel). Large-bodied birds (*i.e.* hornbills and turacos) were defined based on
their body-size, predominantly frugivorous diet, and demonstrated dispersal of many
fruiting plant seeds (Sun & Moermond 1997; Poulsen et al. 2002). We conducted focal
tree watches to determine qualitative and quantitative aspects of frugivore effectiveness
(Schupp 1993). Quality includes aspects of seed-handling (whether seeds are destroyed,
swallowed and defecated intact, or spit) and suitability of the deposition site, whereas
quantity pertains to the number of seeds processed, group size, and the time spent in a
fruiting tree. Presumably as aspects of quantity increase, i.e. time in tree, group size, and

number of seeds processed, so does the overall number of seeds dispersed. Combining such data with the additional detail of qualitative seed-handling aspects lends a clearer picture of a frugivore's seed dispersal potential, the likelihood that dispersed seeds will survive and establish. We focused on large-seeded ($\geq$ 5 mm) species based on the correlation of frugivore body- and seed-size (Janson 1983, Gautier-Hion *et al.* 1985, Howe 1989), the role of larger frugivores in the dispersal of large-seeded tropical trees (Wrangham *et al.* 1994, Chapman 1995), the tendency for hunters to target large-bodied species, and the subsequent ecological impacts that large-frugivore loss could have in tropical forests (Redford 1992). We were particularly interested in the role of primates in dispersing the seeds of the selected tree species given they are the largest frugivores in our study area. We hypothesized that large-seeded tree species rely proportionally more on the dispersal services of large-bodied frugivores like primates. Specifically, we asked the following questions: (1) Are some frugivore assemblages more effective in dispersing the seeds of large-seeded tree species than other frugivore assemblages? (2) What factors predict frugivore visitation and seed dispersal?

Methods

Study Site

We present 8 months of data (August 2006 and October – April 2007) of frugivore visitation to five large-seeded mature forest tree species in the Nyungwe National Park (NNP; 2°17'-2°50'S and 29°07'-29°26'E) in southwestern Rwanda. The 1,013 km^2 park adjoins the Kibira National Park, Burundi, forming one of the largest

contiguous blocks of montane forest on the African continent (Vedder *et al.* 1992). Daily

temperatures vary little throughout the year with average maximum and minimum

temperatures of 19.6° and 10.9°, respectively (Sun *et al.* 1996). The average annual

rainfall is 1744 mm (Kaplin & Moermond 1998). The forest experiences a major dry

period between July and August, and a minor dry season in December to February,

lasting two to five weeks. Sun *et al.* (1996) describe a reduction in fruit production during

the beginning of the minor dry season and a fruiting peak during the major dry period.

NNP contains one of the most species rich montane primate communities in

Africa (Vedder 1988) including thirteen species with two Albertine Rift endemics,

lhoest's monkey (*Cercopithecus lhoesti*) and the owl faced monkey (*C. hamlynii*).

Nyungwe is considered an Important Bird Area with a total of 275 identified species, 25

of which are endemic to the Albertine Rift (Bennun & Fishpool 2000; Fishpool & Evans

2001). Nyungwe was gazetted as a National Park in 2004, but has had some level of

protection since 1933 when it was first gazetted a forest reserve. Rwanda is one of the

most densely populated countries on the African continent with an estimated 350

people/km^2 (Barakabuye 2001). As such the NNP experiences a variety of human

pressures including mining, honey collection, wood cutting, hunting of animals, and

small scale agriculture (Plumptre *et al.* 2002). Hunting pressure on the NNP frugivore

community is not well documented, though a biodiversity study conducted in 1999

suggests that targeted species (*i.e.* bushpigs, duikers, porcupines, and Gambian rats) are

not considered seed dispersers.

Focal tree observations

We selected focal tree species based on their occurrence in the diet of two frugivorous primates (*i.e.* chimpanzee, *Pan troglodytes,* 30-35 kg, and lhoest's monkey, *Cercopithecus lhoesti*, 3-10 kg). In addition, focal tree species had a minimum seed size of 5 mm and were in fruiting phenophase during the course of our study (Table 1). Our focus on these two primate species is an effort to evaluate the seed-dispersing services of semi-terrestrial primates, both of which have been observed to use degraded or regenerating forest and may subsequently facilitate the transportation of seeds into these areas (Gross-Camp & Kaplin 2005, Kaplin 1998).

We selected a minimum of ten individuals of each tree species (10-14 individuals per species, except *Prunus africana N* = 4*;* following Gathua 2000, Clark *et al.* 2001, Cordeiro *et al.* 2004) off of research trails that overlap with the territories of primate groups including habituated lhoests's and chimpanzee groups. Focal trees were located a minimum of 70 m (Saracco *et al.* 2005) from another focal tree to increase the likelihood of statistical independence and were observed as their fruits ripened. Although we could locate only four individuals of *Prunus africana* this species was included based on its endangered status and rapid decline in other forests due to anthropogenic harvesting for medicinal and timber uses (Cunningham & Mbenkum 1993, Schippmann 2001, Fashing 2004). In the NNP, populations of *P. africana* are not under direct threat and may lend insight into the management of this species in other forest communities.

We observed trees for frugivore activity during two 4 ½ hour time periods, morning (0630-1100 h) and afternoon (1200-1630 h). Individuals were observed a

minimum of 27 times in each period. Following Sun *et al.* (1996) we estimated the

percent of the crown occupied with fruit at the beginning of each observation period

assigning a score between zero and four (0 = 0%, 1 = 1-25%, 2= 26-50%, 3 = 51-75%,

and 4 = 76-100%). The DBH (diameter at breast height; 1.4 m) of each tree was also

recorded to help weight the fruiting score of an individual based on its correlation with

crown size and canopy volume (Leighton & Leighton 1982, Gentry & Terborgh 1990).

We always made frugivore observations from the same location (*ca.* 20-30 m

from the bole of the focal tree) where canopy visibility was good (≥ 80% of canopy in

view) using a stopwatch and binoculars. We were often able to position ourselves at eye

level with the canopy as a result of the park's landscape, greatly enhancing our ability to

observe small frugivorous birds and squirrels. We employed two methods to collect

frugivore visitation: scan and focal sampling.

Scan sampling

 Every 30 minutes we scanned the tree canopy for a one-minute period and recorded all

frugivores present. These observations were used to determine the number of individuals

and species visiting a given tree.

Focal sampling

We employed focal observations to determine the quantity of fruits and seeds handled by

different dispersers, and to characterize the quality of frugivore seed-handling. Focal

sampling occurred continuously with the exception of the interruption for a scan sample

on the half-hour. When a frugivore entered the tree, we recorded the time of arrival and

departure, species, the number of fruits removed and their corresponding seed treatment.

We defined the focal animal's seed treatment as follows: (1) seed dispersal (*i.e.* seed was

carried away from the parent tree) and (2) dropped seed (*i.e.* a fruit/ seed was processed

but dropped beneath the parent crown). If more than one individual of the same species

entered the tree, the group size was recorded and a focal animal chosen based on

proximity to an observer and ease of observation. In the case of primates, we chose adults

or sub-adults over juveniles for observations.

A focal observation began when the focal individual touched or placed a fruit in

its mouth and terminated when the animal exited the tree, moved out of the observer's

view, or at the onset of the next scan sample. In addition to the total time a frugivore

spent in a tree, focal observations were timed to calculate a fruit-processing rate (fruits

per minute). We estimated the number of fruits ingested and seeds processed by other

individuals in a group based on the behaviors of the focal individual of the same species

in a given group. We assumed that fruits swallowed by the focal animal, placed into its

cheek pouch (primates), or carried out of the tree in its beak (birds) were deposited away

from the parent crown unless otherwise observed.

We categorized frugivores into one of five frugivore assemblages (i.e. large-

bodied birds (LB), small-bodied birds (SB), chimpanzees or *Pan troglodytes* (PT),

cercopithecines (CS), and squirrels (SQ); Appendix 2) to evaluate the relative

effectiveness of different frugivore assemblages to a given tree species. Small-bodied

birds were between 10-24 cm, whereas large-bodied birds varied from 40-75 cm

(Stevenson & Fanshawe 2002). Small-bodied primates included cercopithecines and were between 45-70 cm, whereas large-bodied primates were represented by a single species, chimpanzees, 70-179 cm in size (Kingdon 1997). Distinctions in frugivore body-size have been similarly made in other studies (Clark *et al.* 2001, Poulsen *et al.* 2002) and facilitate comparisons across studies.

Fruiting neighborhood of focal tree

We described the fruiting neighborhood immediately surrounding a focal tree to examine the potential influence of this variable on frugivore visitation and seed dispersal. Fruiting neighborhood has been demonstrated to enhance frugivore visitation and thus seed dispersal in previous studies (Garcia *et al.* 2001, van Ommeren & Whitham 2002, Saracco *et al.* 2005). All individual trees $\geq$ 10 cm DBH within a 30 m radius (2827 m^2) of the focal tree with fruit presence $\geq$ 1 (between 1-25% of canopy in fruit) were recorded. Saracco *et al.* (2004) determined this distance to be consistent with the spatial scale at which avian frugivores perceive fruit patches. We described the fruiting neighborhood a single time over the course of the fruiting period of a focal tree corresponding to its fruiting peak (phenology = 4).

Phenological data collection

In addition to the proximate fruiting community surrounding a focal tree, we collected data on the phenological patterns of 66 fruit-producing tree species on a

monthly basis from April 2006 – April 2007 to evaluate the influence of forest-wide fruit

availability on frugivore seed dispersal. This sample is a subset of a larger phenological

study initiated in 1991 as part of a forest-wide frugivore-seed dispersal study (Sun *et al.*

1996, Sun *et al.* 1997, Sun & Moermond 1997, Kaplin & Moermond 1998, Kaplin *et al.*

1998, Kaplin 2001). The sample tree species were located along 25 phenology trails in

the study area. We sampled reproductively mature, adult trees whose crowns were easily

observed from trails. Adult trees were defined as individuals with > 20 cm DBH except

for species that begin to reproduce at DBH < 20 cm; adults for these species were defined

as individuals with a DBH $\geq$ 15 cm (Appendix S1). The phenological patterns of the

sampled trees were assumed to be representative of the tree species located in the vicinity

of the focal trees. The mean sample size was 12.6 $\pm$ 8.6 (mean $\pm$ SD) trees per species (*N*

= 909 total individuals). Sampling took place over 2–3 days at the same time each month.

The percentages of fruit in a given tree canopy were estimated using the 0-4 scale

described for focal tree phenology.

Data Analysis

We used chi-square test of independence to determine if there was a significant

difference in frugivore assemblage visitation of the five large-seeded tree species. Chi-

square was also employed to examine whether frugivore assemblages significantly differ

in the number of seeds dispersed per visit by tree species.

We calculated the similarity of the frugivore assemblage visiting a given tree

species using the Morisita's index (Morisita 1959). This index is the probability that

individuals randomly drawn from the two communities will belong to the same species, relative to the probability of randomly selecting two individuals of the same species from one of the communities. It considers relative abundance of the species visiting a tree and is little affected by the sizes and diversities of the community samples (Morisita 1959, Wolda 1981).

To determine the relative effectiveness of a frugivore assemblage to a focal tree species we calculated the potential number of seeds dispersed (PSD) per visit by a frugivore assemblage. We first determined the seed dispersal rate (seeds processed/ minute) for each focal animal. We then multiplied the seed dispersal rate by the number of individuals in the group and the time spent in the tree for a given observation. Values for each frugivore assemblage were then averaged to obtain the PSD. Calculating the PSD in this way as opposed to the multiplication of mean values for group size, seed dispersal rate, and time in tree, lends more weight to the individual observation. Furthermore PSD is a more accurate reflection of a frugivore's relative effectiveness by calculating the overall number of seeds dispersed by a given frugivore assemblage based on several behavioral characteristics (*i.e.* time in tree, number of individuals in the group, seeds dispersed/ minute). The number of seeds processed per minute was calculated by subtracting the number of seeds dropped beneath the parent crown from the total number of fruits/ seeds processed (*i.e.* swallowed or placed in the cheek pouch). We used ANOVA to determine difference in frugivore assemblages and group size, time in tree, and seed dispersed/ minute. Our sample size for these analyses are large enough to make the means normally-behaved and thereby achieves the required assumptions of normality (Hoaglin *et al.* 1977, Mosteller 1991).

We used a generalized linear model (GLM) with a negative binomial error and log-link distribution to determine which variables best described frugivore seed dispersal away from the parent tree for each frugivore assemblage using the following predictor variables: (1) mean fruiting duration for focal tree species (months); (2) the number of trees with fruit (within 30 m of the focal tree and a DBH $\geq$ 10 cm); and, for each frugivore assemblage, (3) the number of frugivore species; (4) the number of individuals; and (5) the time spent in a tree. We chose a GLM with a negative binomial error distribution based on its ability to deal with overdispersion common to count data (Hilbe 2007). Three separate models were created using the number of seeds dispersed per visit by (1) large-bodied birds (LB), (2) small-bodied birds (SB), and (3) cercopithecines (CS); chimpanzees (PT) and squirrels (SQ) did not have enough data to perform regression analysis. We used STATA v.9 (StataCorp LP) for the GLMs and JMP v.7 (SAS) for all other analyses.

Results

Focal trees were observed for a total of 1,552.5 hours (mean = 310.5 h/ species but see *P. africana* in Table 1).

Overall frugivore assemblage visitation

Twenty-one frugivore species were observed in the five tree species during scan sampling including 15 bird, 3 primate, and 3 squirrel species (Table 2; Appendix S2).

Syzygium guineense had the greatest diversity of frugivore species visitations ($N = 16$

species) whereas *Parinari excelsa* experienced the lowest diversity ($N = 8$; Table 2).

Frugivore visitation did not correspond to fruit consumption. Although chimpanzees were

observed in *P. africana* and *S. guineense* during the study period, they were not observed

to eat *P. africana* fruit while they were in the fruiting canopy.

    Ekebergia capensis experienced the greatest number of visits by all frugivore

assemblages ($N = 788$) in contrast to *P. excelsa* that experienced the least number of

visits ($N = 69$). Frugivore assemblages did not visit tree species equally ($\chi^2 = 338.1$, df =

16, p = <.0001). The chi-square values for three cells explained 88% of the total chi-

square value including squirrels in *Olea capensis*, small-bodied birds in *P. africana*, and

chimpanzees in *S. guineense* (Cell $\chi^2 = 134.5$, 43.41, and 121.5, respectively). Squirrels

and cercopithecines visited *O. capensis* and *P. africana* more than other frugivore

assemblages suggesting that these assemblages are more important to the seed dispersal

of these tree species. Chimpanzees appeared more than expected by chance at *S.

guineense,* but were only the third most common visitor. The large cell chi-square value

for chimpanzees may be due to their absence from all other tree species during our study.

    We found considerable variation in the frugivore assemblage responsible for

dispersing the most seeds per visit by tree species. Cercopithecines dispersed

significantly more seeds per visit for *E. capensis* ($F_{3,785} = 54.9$, p = <0.0001), whereas

chimpanzees dispersed the highest number of seeds per visit for *S. guineense* ($F_{4,213} =

35.4$, p = <0.0001). Large-bodied birds and cercopithecines dispersed the greatest number

of *P. africana* seeds per visit ($F_{4,303} = 7.2$, p = <0.0001), whereas small-bodied birds

dispersed the greatest number of seeds per visit for *O. capensis* ($F_{3,211} = 9.72$, p =

<0.0001). *P. excelsa* had no dispersal events during the study period.

Likelihood of dispersal

Frugivore assemblages had significantly different seed dispersal treatment for all

five tree species ($\chi^2 = 317.1$, df = 8, p = <0.0001). Dispersal was the most common seed

dispersal treatment for cercopithecines (63%, $N = 171$) followed by large-bodied birds

(54%, $N = 562$), and small-bodied birds (35%, $N = 711$). Ninety-nine percent of the

observations of squirrels ($N = 139$) resulted in no dispersal or a dropped seed. Additional

chi-squares of individual tree species revealed significant differences in frugivore

assemblage seed dispersal treatment (*E. capensis* $\chi^2 = 211.7$, df = 6, p = <0.0001, *O.*

capensis $\chi^2 = 76.1$, df = 3, p = <0.0001, *P. excelsa* $\chi^2 = 16.4$, df = 3, p = .001, *P. africana*

$\chi^2 = 40.2$, df = 4, p = <0.0001, *S. guineense* $\chi^2 = 87.0$, df = 8, p = <0.0001; Figure 1). CS

dropped seeds more than expected by chance accounting for 33.6% of the total chi-square

value for *E. capensis*. For *O. capensis*, SB dispersed seeds more than expected by chance

(29% total chi-square value). CS dispersed seeds and SQ dropped seeds more than

expected by chance for *S. guineense*, accounting for 60% of the total chi-square value. *P.*

excelsa and *P. africana* did not have any cells with high chi-square values (> 16).

Community similarity

The Morisita index showed an average overlap of 50.4 $\pm$ 0.93% (mean $\pm$ SD) of the frugivore assemblage visiting two tree species for all pairwise comparisons. *P. africana* and *P. excelsa* were the least similar, and *O. capensis* and *S. guineense* were the most similar in their frugivore communities at 33.9% and 63.9%, respectively.

Effectiveness of frugivore assemblages

We found a significant difference in the PSD for frugivore assemblages in two of the five tree species, *E. capensis* and *S. guineense* ($F_{3,443}$ = 10.2, p = <0.0001 and $F_{4,87}$ = 29.42, p = < 0.0001, respectively). Large-bodied birds and cercopithecines had the highest PSD rate for *E. capensis* and chimpanzees for *S. guineense* (Figure 2; mean: LB = 231.2 and CS = 205.1, and PT = 1684.4). There were significant differences between frugivore assemblages and the time spent in a tree by a focal animal, group size, and seeds dispersed per minute (ANOVA: $F_{4,1586}$ = 40.39 p = <0.0001, $F_{4,1585}$ = 32.91 p = <0.0001, and $F_{4,748}$ = 37.24 p = <0.0001, respectively; Table 3). Chimpanzees and cercopithecines spent significantly more time in trees than other frugivore assemblages and had the largest group size (mean = 28.3 and 13.8 minutes and 2.75 and 2.89 individuals, respectively). Large-bodied birds and chimpanzees had the highest number of seeds dispersed per minute (mean = 9.2 and 11.6, respectively). Chimpanzees potentially dispersed the greatest number of seeds per visit (mean = 1684.4; Figure 2), more than all other frugivores combined.

Our method of calculating the PSD resulted in some frugivore assemblages receiving a negative value. Specifically, squirrels were "negative dispersers," dropping seeds beneath the parent crown or dropping more seeds than were carried out of the tree. Squirrels were observed to process the fruits of two focal tree species, *E. capensis* and *S. guineense* (mean PSD = -11.3 and -14.4, respectively) by cleaning the seeds of fruit pulp before dropping them beneath the parent canopy. Similarly, the cercopithecine assemblage (CS), and specifically the species *Cercopithecus mitis*, were the only frugivore assemblage and species observed to process the fruits of *P. excelsa*, dropping cleaned seeds *beneath* the parent crown (mean PSD = -24.6).

Predicting seed dispersal by frugivores

Small birds dispersed more seeds from trees that had a longer mean fruiting duration, more fruiting trees in the vicinity, more species of small birds, and where small birds spent more time (GLM: Log likelihood = -529.9, AIC = 3.11; Table 4); whereas large birds dispersed more seeds from trees that had a longer mean fruiting duration, more large bird species, more individuals of small birds and cercopithecines, and large birds and cercopithecines spent more time in the tree (GLM: Log likelihood = -523.5, AIC = 3.08). Finally, we found that cercopithecine seed dispersal was predicted by a longer mean fruiting duration, the number of species and the time spent in the focal tree (LB, SB, and CS), and the number of individuals for cercopithecines (GLM: Log likelihood = -229.9, AIC = 1.39).

Discussion

Our study highlights the complexities of determining the effectiveness of a frugivore assemblage and thus relative effectiveness to a given tree species. We found that of the five large-seeded tree species, only four were observed to be dispersed during our study, and the frugivore assemblages dispersing the most seeds per visit varied by tree species. Furthermore, our attempt to evaluate the relative effectiveness of frugivore assemblages by incorporating additional factors (potential seed dispersal value or PSD), showed only two tree species with frugivore assemblages that dispersed significantly more seeds than other assemblages (*i.e.* chimpanzees dispersed more *S. guineense* and CS and LB assemblages dispersed more *E. capensis*).

Likelihood of dispersal

Our results highlight variable seed dispersal treatment by frugivore assemblages and tree species (Figures 1A-E). Seed dispersal treatment (*i.e.* dispersed, dropped, no dispersal) is in part a reflection of how a frugivore handles a fruit (*i.e.* spit or defecated), which is likely influenced by fruit characteristics and availability (Chapman & Chapman 1996; Kaplin & Moermond 1998; Yumoto et al. 1998). Gross-Camp and Kaplin (2005) speculated that a change in chimpanzee seed handling of two tree species was a result of pulp adherence to the seed. Chimpanzees swallowed the seeds of *O. capensis*, which has a very hard flesh that is difficult to remove from the seed. In contrast, *S. guineense* has fleshy pulp that is easily removed from the seed, and was predominantly spit. Our study shows similar differences in frugivore assemblage seed treatment by tree species. Small

birds mainly operated as seed dispersers with the exception of *S. guineense* that was more often dropped beneath the parent crown. The large seeds of *S. guineese* may be difficult, if not impossible, for the majority of small birds to swallow due to a limited gape-width (Wheelwright 1985; Levey 1987). Small birds were often observed to peck at the soft flesh of the fruits, knocking them to the ground. Similarly, cercopithecines predominantly swallowed the seeds of the focal tree species but dropped all *P. excelsa* seeds. *P. excelsa* had the largest fruit/ seed size with a hard adhering pulp. Squirrels never operated as seed dispersers but dropped *E. capensis* and *S. guineense* seeds cleaned of fruit pulp beneath the parent tree.

Effectiveness of frugivore assemblages

The differences in the PSD values are largely explained by the behaviors exhibited by frugivore assemblages. Cercopithecines and chimpanzees were observed less at focal trees than other frugivore assemblages (11% of 1587 total visits), accounted for 16% of the dispersal events recorded ($N = 109$ of 657 dispersal events), and yet had two of the highest PSD values. In contrast, large birds accounted for the majority of visits to focal trees (80.1%) and had one of the highest seed processing rates at 9.20-seeds/ minute. Primates were rarely observed alone, moving into a focal tree as a group and spending several minutes to several hours processing fruits with interspersed resting and grooming behavior. We often observed cercopithecines to quickly collect fruits in their cheek pouches while in a fruiting tree canopy and then descend the tree where they would process fruits one at a time, dropping the cleaned seeds, as they moved through the forest

understory. Cheek pouching enables an individual to quickly gather fruits in contrast to

birds that are limited to processing a single seed at a time. Furthermore birds, especially

small-bodied birds, were often observed alone or in small groups (<3 individuals) flying

into the tree and processing a single fruit before leaving. Some species (*e.g. Andropaedus*

spp. and *Pycnonotus barbatus*) would remove a fruit and then fly elsewhere to consume

it. Large-bodied birds such as the social *Corythaeola cristata* were the exception,

tending to travel in small flocks (6-20 individuals) and spending several minutes moving

about the canopy swallowing fruits in their entirety.

The case of chimpanzees

Chimpanzees were only observed on a handful of occasions to enter focal trees

and in even fewer observations to actually consume fruits of only *S. guineense* ($N = 4$ and

2, respectively). The lack of chimpanzee observation at focal trees is likely due to a

combination of observer detection, general wariness of humans, and relatively lower

population densities to that of other frugivores, although we do not have comparative data

on population densities for these frugivore species. Furthermore, *S. guineense* has

regularly occurred in the chimpanzee's diet for the past several years (M. Masozera,

unpublished data). So consistent is the chimpanzee's consumption of *S. guineese* that the

movements of the group are often predicted based on the location of fruiting *Syzygium*

trees.

Chimpanzees were observed in *S. guineense* focal trees on three occasions, only

two of which resulted in seed dispersal. However, we regularly observed *S. guineense*

wadges containing up to a few hundred of seeds around or en route to focal trees. This additional information suggests that these animals play a more significant role than our focal tree watch data indicate. On several opportunistic observations of chimpanzees feeding on *S. guineense,* they would stuff handfuls of fruits into their large lower lip maneuvering the fruits against their teeth and extracting the juice. Gross-Camp has observed on three separate occasions a small group of chimpanzees strip a *S. guineense* tree of its ripe fruit over the course of several hours.

<div align="center">

Parinari excelsa*: frugivores lost?*

</div>

P. excelsa was poorly visited by frugivores during the course of our study (6% of all visits). Frugivores rarely consumed fruits prior to their departure from the tree and those fruit-eating events that were observed resulted in non-dispersal, *e.g.* cleaned seeds were dropped beneath the parent tree. Chimpanzees and hornbills (in the large-bodied bird or LB assemblage) have been observed to consume the fruits of *P. excelsa* (N. Gross-Camp, pers. obs.) though not during this study. In the Neotropics, *P. excelsa* is dispersed by muriquis (*Brachyteles arachnoides*) and tapirs (*Tapirus terrestris*; R. Bueno, pers. com.). The lack of seed dispersal observations in *P. excelsa* may be an indicator of potential change for the species and begs the question of how well *Parinari excelsa* is reproducing. Elephants have been observed to disperse the fruits of *P. excelsa* elsewhere (Lieberman & Lieberman 1987, Chapman & Chapman 1996, Primack & Corlett 2005) but were extirpated from the NNP in 1999 (Plumptre et al. 2002). The relatively recent absence of elephants from Nyungwe National Park may lead to dramatic changes in the

regeneration of primary forest species like *Parinari* as it has in other areas (see Alexandre 1978, Ivory Coast).

<p style="text-align:center">Predicting seed dispersal by frugivores</p>

The results of our generalized linear models of the three frugivore assemblages highlights the importance of mean fruiting duration of the focal tree, time spent in the tree and number of species of the frugivore assemblage and were significant variables in all models (Table 4; large- and small-bodied birds and cercopithecines; insufficient data for GLMs on chimpanzees and squirrels). Small bird seed dispersal was best predicted with the least number of variables including mean fruiting duration, time in tree and number of species of small birds, and the corresponding fruiting population surrounding the focal tree. The influence of the fruiting tree community in attracting frugivores has been recognized in other studies. Garcia (2001) and Laska (1994) demonstrated an increase in avian frugivores' visitation to plants with large crop sizes. We posit that the immediate fruiting community may not be as important to larger-bodied frugivores because of their tendency to have large, defended home ranges within which they track availability of specific food resources. On the other hand, sampling the fruiting community at a larger spatial scale (> 30 m) may have resulted in this being an important predictor for other larger-bodied frugivore assemblages. Cercopithecines had the most significant variables in predicting seed dispersal. We consider two possible explanations in interpreting this model. It is possible that because cercopithecines spend so much time in focal trees that they tend to overlap with the greatest number of species across all frugivore assemblages.

Thus the significance of the variables in explaining cercopithecine seed dispersal is simply a reflection of the time that they spend in a tree. Alternatively, cercopithecines may be using the presence of other frugivore assemblages as an indication of fruit presence, *i.e.* cercopithecine foraging patterns are influenced by the presence of other frugivores. Finally, large-bodied bird seed dispersal was best described by the mean fruiting duration, the number of individuals (SB & CS), species (LB), and time spent in tree (SB & LB) suggesting that, like cercopithecines, large-bodied birds are influenced by the presence of frugivores in other assemblages or that the explanatory variables are simply a reflection of the time that large birds spend in the focal tree.

Understanding the variables that help to predict seed dispersal by different frugivore assemblages may also improve our ability to predict where seeds will be deposited (i.e. seed shadow) and their subsequent fate (Wheelwright & Orians 1982, Kaplin & Moermond 1998, Lambert 1999, Jordano & Godoy 2002, Kaplin & Lambert 2002, (Clark et al. 2005). Previous studies comparing bird and primate seed dispersal patterns indicate that birds disperse seeds farther from the parent tree and in a more contagious pattern than primates (Holbrook & Smith 2000; Poulsen et al. 2001; Clark et al. 2004). Our results suggest a similar pattern with small-bodied birds dispersing large seeds away from under the parent tree in small numbers in contrast to primates that tend to remain in the tree for longer periods of time dropping several seeds directly beneath the parent canopy and depositing the majority of seeds they handle in large clumps (*i.e.* in a defecation or wadge, composed of discarded fruit pulp, skin, and seeds) or singly (in the case of cheek pouching) away from the parent canopy.

Acknowledgements

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Tables

Table 1: *Focal tree species (N = number of individuals) and their respective seed size, fruiting duration, number of observations for each period, and percent of observations with no frugivore visitation. Each observation period was 4.5 hour in duration (AM = 0630-1100 h and PM = 1200-1630 h).*

Tree species	Seed size (mm)*	Fruiting duration mo. (SD)*	Number of observation periods		Percent of observations with no frugivore activity
			AM	PM	
Ekebergia capensis (Meliaceae; n=12)	8.7	6.1 (1.6)	41	37	1.3%
Olea capensis (Oleaceae; n=14)	7.3	unknown	56	53	38.5%
Parinari excelsa (Chrysobalanaceae; n=10)	25.0	11.4 (9.3)	32	27	50.8%
Prunus africana (Roseaceae; n=4)	9.3	4.0 (1.1)	9	7	0.0%
Syzygium guineense (Myrtaceae; n=14)	13.0	3.7 (1.3)	41	42	25.3%

* Data from Sun *et al.* (1996)

Table 2. *Number of frugivorous species in each assemblage observed during focal tree watches (scan sampling). N is the maximum number of species in an assemblage.*

Tree species	Large-bodied Birds (n=5)	Small-bodied Birds (n=10)	Chimpanzee (n=1)	Cercopithecines (n=2)	Squirrels (n=3)	Total no. of frugivores observed (n=21)
Ekebergia capensis	4	6	0	2	2	14
Olea capensis	3	5	0	1	3	12
Parinari excelsa	2	3	0	2	1	8
Prunus africana	3	8	1	1	1	14
Syzygium guineense	3	7	1	2	3	16

Table 3: *Mean values ($\pm$ SE) for each frugivore assemblage for all five tree species. Superscript indicates results of Tukey HSD; values with the same letter are not significantly different.*

Frugivore assemblage (N=total no. of individuals observed)	Group size (SE)	Time in tree (min) (SE)	Seeds dispersed/ minute (SE)
Large-bodied birds (558)	1.75 [B] (0.05)	9.91 [B] (0.57)	9.20 [A] (0.36)
Chimpanzees (4)	2.75 [A,B,C] (1.11)	28.25 [A] (11.81)	11.64 [A,B] (5.74)
Small-bodied birds (713)	1.58 [B] (0.06)	3.69 [C] (0.16)	5.73 [B] (0.30)
Cercopithecines (172)	2.89 [A] (0.20)	13.75 [A] (1.78)	4.91 [B] (0.34)
Squirrels (140)	1.11 [C] (0.03)	9.65 [B] (0.83)	-1.51 [C] (0.25)

Table 4. *Significant variables from the GLM models predicting seed dispersal by small-bodied birds, large-bodied birds, and cercopithecines.*

Variable	Small-bodied birds (SB)	Large-bodied birds (LB)	Cercopithecines (CS)
Mean fruiting duration of focal tree (months)	X	X	X
Immediate fruiting vicinity (Trees with fruit presence > 1 within 30 m of the focal tree and ≥ 10 cm DBH)	X		
Time in focal tree:			
SB	X	X	X
LB		X	X
CS			X
Number of species:			
SB	X		X
LB		X	X
CS			X
Number of individuals:			
SB		X	
LB			
CS		X	X

Figure 1. The proportion of visits by frugivore assemblages in which no dispersal occurred (white), seeds were dropped beneath the parent crown (grey), and seeds were dispersed away from the parent tree (black). All were significantly different ($\chi^2 = 317.1$, df = 8, $P = <0.0001$). LB = large-bodied bird, SB = small-bodied bird, PT = *Pan troglodytes* or chimpanzee, CS = Cercopithecines, and SQ = squirrels
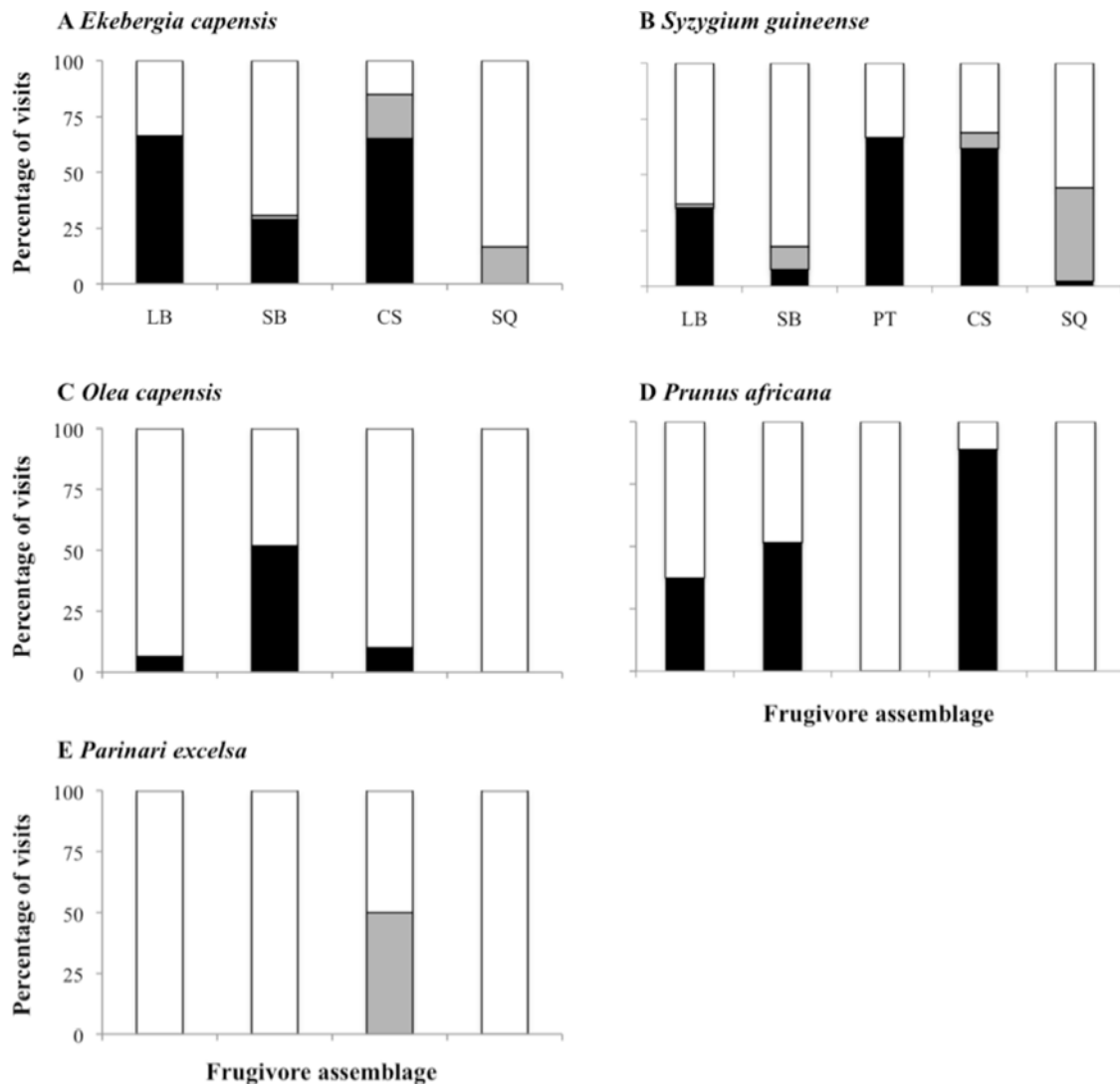
Figure 2. The potential number of seeds dispersed per visit (PSD) by each frugivore assemblage. Positive values indicate seeds dispersed away from underneath the parent canopy whereas negative values indicate seeds dropped under the parent tree. Chimpanzees had the highest seed dispersal potential of any frugivore assemblage ($N = 1684.4$ seeds/visit).

Frugivore assemblage
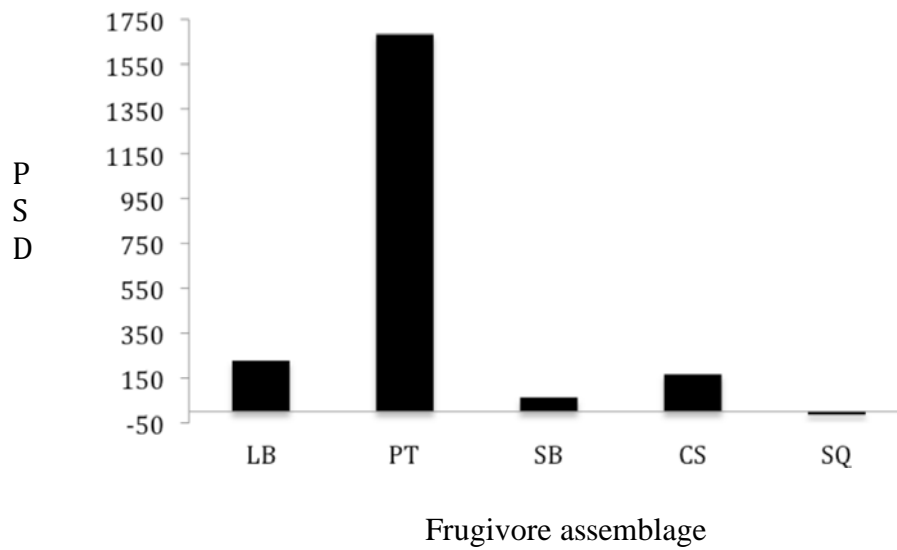
Appendix S1. *Plant species sampled in the phenology survey, and information for each species including the number of trees sampled and seed size. * = species with reproductively mature adults defined as DBH ≥ 15 cm.*

Species	No. sampled	Seed size (mm)
Alangium chinense	19	4.5
Albizia gummifera	19	10
Allophylus kiwuensis	1	-
Antidesma membranaceum	7	-
Apodytes dimidiata	10	3
Aulacocalyx diervilleoides	1	-
Balthasarea schliebenii	15	1.5
Beilschmiedia rwandensis	15	14.7
*Bersama abyssinica**	19	5
Bridelia brideliifolia	19	6
Carapa grandiflora	24	30
Casearia engleri	1	-
Casearia runssorica	17	4
Cassipourea gummiflua	1	-
*Cassipourea ruwenzoriensis**	11	3
Chionanthus africanus	11	-
Chrysophyllum gorungosanum	20	10.4
Chrysophyllum rwandense	10	13.2
Cleistanthus polystachyus	8	-
Croton macrostachys	7	-
Croton megalocarpus	11	6
Dichaetanthera corymbosa	4	-
Dombeya goetzenii	13	4

Drypetes occidentalis	1	-
Ekebergia capensis	9	8.8
Entandrophragma excelsum	18	12.5
Erica kingaensis	3	-
Ficalhoa laurifolia	21	0.5
Ficus oreodryadum	26	1
Ficus spp	2	-
*Galiniera coffeoides**	16	3.4
Garcinia volkensii	1	-
Grewia mildibraedii	7	-
Harungana montana	11	2
*Ilex mitis**	19	5
*Ixora burundensis**	10	11
Macaranga kilimandschalica	23	-
*Macaranga neomildbraediana**	1	3.7
*Maesa lanceolata**	22	0.5
Magnistipura butayei	15	25
*Maytenus acuminata**	17	2.8
Memecylon walikalense	18*	12.8
Milletia dura	4	-
Musanga leo-errerae	7	-
Myrianthus holstii	20	8
Neoboutonia macrocalyx	12	5.4
Newtonia buchananii	14	-
Ochna afzelii	15	2.5
Ocotea usambarensis	20	3.5
Olea capensis	19	7.3

Olea spp	1	-
Olinia rochetiana	29	2
Parinari excelsa	21	25
Pentadesma reyndersii	16	-
Podocarpus falcatus	4	-
Podocarpus latifolius	42	9.4
Polyscias fulva	17	1.5
Prunus africana	16	10.9
Psychotria mahonii *	37	3.5
Psydrax subcordatum	1	-
Rapanea melanophloeios*	33	4.4
Rytiginia kigeziensis*	16	5.1
Sapium ellipticum	2	-
Schefflera goetzenii	23	3
Strombosia scheffleri	32	18.9
Symphonia globulifera	18	26.9
Syzygium guineense	42	13
Tabernaemontana stapfiana	7	-
Vepris stolzii	4	5.5
Xymalos monspora	3	-
Zanthxylum gillettii	3	6
Zeyerhele rwandense	1	-

Appendix S2. *List of frugivore species observed in the five focal tree species.*

Big birds:	MUSOPHAGIDAE	*Corythaeola cristata*
		Tauraco johnstoni
		Tauraco schuetti
	BUCEROTIDAE	*Bycanistes subcylindricus*
		Tockus alboterminatus

Small birds:	CAPITONIDAE	*Pogonilius bilineatus*
	ORIOLIDAE	*Oriolus percivali*
	PYCNONOTIDAE	*Andropadus latirostris*
		Andropadus nigriceps
		Andropadus gracilirostris
		Phyllastrephus flavostriatus
		Pycnonotus barbatus
	STURNIDAE	*Onychognathus tenuirostris*
		Onychognathus walleri
	TURDIDAE	*Turdus olivaceus*

Big primates:	HOMINIDAE	*Pan troglodytes*

Small primates:	CERCOPITHECOIDEA	*Cercopithecus lhoesti*
		Cercopithecus mitis

Squirrels:	SCIURIDAE	*Heliosciurus rufobrachium*
		Paraxerus boehmi
		Unknown sp. 1

CHAPTER 2

DIFFERENTIAL SEED HANDLING BY TWO AFRICAN PRIMATES AFFECTS SEED FATE AND

ESTABLISHMENT OF LARGE-SEEDED TREES

Abstract

We examined the influence of seed handling of two African primates, chimpanzees (*Pan troglodytes*) and mountain monkeys (*Cercopithecus lhoesti*), on the fate of large seeded tree species in an afromontane forest in Rwanda. Primates dispersed the seeds of eleven species over a period of one year, though dispersal varied through time. Primates differed in their seed handling behaviors with chimpanzees defecating large seeds (> 0.5 cm) significantly more than mountain monkeys. Furthermore, primates exhibited different oral processing techniques with chimpanzees discarding large quantities of seeds in wadges and mountain monkeys spitting single seeds cleaned of fruit pulp. The first two components of a PCA of eight microhabitat characteristics describing the site where primates deposited seeds explained 46.7% of the variance. When plotted, microhabitat characteristics of defecations and spit seeds have little overlap suggesting that seed handling influences the deposition site. We monitored a total of 552 primate seed dispersal samples through time at their site of deposition for seed persistence, germination, and establishment. Defecations were deposited significantly farther from an adult conspecific where they experienced the greatest persistence but poorest establishment. In contrast, spit seeds were deposited closest to an adult conspecific but experienced the highest seed establishment rates. We used experimental plots to further examine the relationship of seed handling, deposition site, and seed fate. Plot results revealed a significant difference in seed handling and fate, with undispersed seeds in whole fruits experiencing the lowest establishment rates. Seed germination differed by habitat type with open forest experiencing the highest rates of germination. Our results highlight the importance of primate seed handling on the deposition site and seed fate,

and may be helpful in the development of models to predict seed shadows and recruitment patterns of large seeded trees.

Introduction

Primates take up a large percentage of the frugivore biomass in tropical forests and are demonstrated dispersers of large quantities of viable seeds (Estrada & Coates-Estrada 1986; Terborgh 1986). Corlett & Lucas (1990) described three generic fruit-processing strategies employed by primates including spitting, defecation, and predation. Most primates employ some combination of these seed handling techniques depending on species, sex and age of the animal, habitat, fruit species consumed, or fruit availability (Gautier-Hion 1980; Kaplin & Moermond 1998; Mcconkey 2000). Previous studies have focused on seed dispersal via defecation (Lambert 1998; Kaplin & Moermond 2000; Gross-Camp & Kaplin 2005), largely ignoring seeds dispersed via spitting behavior. In African primates spit seeds may be ejected singly as observed in many Ceropithecine species (Corlett & Lucas 1990; Lambert 1999) or as a wadge (Goodall 1986), consisting of a dense aggregate of seeds, fruit pulp and skin. Chimpanzee wadging is an intriguing and poorly studied method of seed dispersal.

Seed handling differs between frugivore species and has important consequences on both seed deposition and establishment (Jordano et al. 2007). For example, seeds swallowed versus spit by a primate tend to be deposited further from the parent tree (Rowell & Mitchell 1991; Lambert 1999). Being deposited farther from the parent tree has been demonstrated to reduce seed mortality and is attributed to a decrease in intraspecific competition for spatially-restricted resources (Stiles 1989) and the potential

escape from host-specific pathogens and seed predators that tend to congregate under the canopy of a parent tree (Augspurger 1983).

Removal of the pulp surrounding a seed has been demonstrated to incur an advantage to seed persistence and establishment for some species (Lambert 2001; Wenny 2001; Gross-Camp & Kaplin 2005). Lambert (2001) demonstrated that the seeds of *Strychnos mitis* had a significantly higher probability of germinating under the parent tree when spit by *Cercopithecus ascanius*, compared to falling unprocessed to the forest floor from the parent canopy. Lambert hypothesized that the seed spitting behavior reduces fungal pathogen attack by removing pulp surrounding the seed. The fate of spit seeds is critical to our ability to evaluate the ecological role of primate seed dispersal on forest dynamics such as regeneration and species diversity.

This paper explores the seed dispersal behaviors of two primate species, the common chimpanzee (*Pan troglodytes schweinfurthii*) and the mountain monkey (*Cercopithecus lhoesti*), in an afromontane forest in southwestern Rwanda. Primate species were selected based on their relatively large-body size, known frugivory (Wrangham et al. 1994; Kaplin & Moermond 2000; Gross-Camp & Kaplin 2005), and ease of observation in the study area. We were interested in the influence of primate seed handling behaviors on where seeds are deposited and subsequent seed fate at the site of deposition. We focused on large-seeded tree species (> 0.5 cm; Lambert 2002; Gross-Camp & Kaplin 2005) based on the likelihood that such species will be disproportionately affected by the loss of large-bodied frugivores (i.e. primates), the predominant dispersers of large-seeded plants (Chapman & Onderdonk 1998; Peres & Van Roosmalen 2002). We addressed the following questions: 1) Does method of seed

handling affect where seeds are deposited, i.e. the microhabitat, 2) What microhabitat variables best predict the probability of seed survival, and 3) What is the relationship between seed handling, microhabitat, and seed fate.

Methods

Study Site

Our data were collected from April 2006 to April 2007 in the Nyungwe National Park (NNP) in southwestern Rwanda. The 1,013 km^2 park connects with the Kibira National Park, Burundi, forming one of the largest contiguous blocks of montane forest on the African continent (Plumptre et al. 2002). The NNP is home to 13 species of primates including a unique high elevation population of chimpanzees traveling up to 2750 m (ASL; Gross-Camp & Kaplin 2005). Daily temperatures vary little throughout the year with average maximum and minimum temperatures of 19.6° and 10.9°, respectively (Sun *et al.* 1996). The average annual rainfall is 1744 mm (Kaplin & Moermond 1998). The forest experiences a major dry period between July and August, and a minor dry season in December to February, lasting two to five weeks.

Study species

We followed a habituated chimpanzee group and a mountain monkey group five days a week every other week for a period of one year (April 2006 - March 2007). Follows lasted from 7 to 12 hours per day with variable contact hours. Habituation of the mountain monkey group began in December 2005, whereas the chimpanzee community, Mayebe group, has been undergoing habituation since 1998. Mountain monkeys have a

home-range of 2 km^2 and consume 31 different fruit species (25% of diet; Kaplin &

Moermond 1998). The largest proportion of plant species consumed by mountain

monkeys were from canopy trees (34%) suggesting the potential role of the species in the

dispersal of such tree species. Chimpanzees have a larger home-range, 7-15 km^2

(Newton-Fisher 2003), and higher percentage of frugivory, consuming approximately 66

different fruiting species (M. Masozera, unpublished data).

We located primates in the morning at their sleeping sites or by vocalization and

followed them until dusk. Our proximity to the mountain monkey group was < 1 m and >

20 m to the chimpanzees. Once the animals left the area, we searched the forest floor for

primate-dispersed seeds. The mountain monkey group's tendency to move through thick

understory obscured our view and likely resulted in our missing defecations that

potentially contained seeds.

Seed dispersal

When a chimpanzee or mountain monkey feces or orally-discarded seed (i.e. spit

or wadge) was located it was marked with fluorescent tape, and the following data

recorded at the site of deposition: 1) identification of large seeds (> 0.5 cm) to family and

species, 2) number of seeds per tree species, and 3) seed handling methodology (i.e.

defecated, spit, or wadged). Fecal and orally-processed samples were dissected at the site

of deposition, reformed to reflect the original state of the sample, and monitored for seed

fate (i.e. persistence, germination, and establishment) on a weekly basis for the first six

weeks, then every two weeks every six weeks, then monthly thereafter for the duration of

the study (Rogers *et al.* 1990).

We defined germination as the production of a radicle and establishment as the emergence of two leaflets and being rooted firmly in the soil. In order to determine the ultimate post-dispersal fate of seeds, we marked a sub-sample of *Syzygium guineense* seeds with a 50-cm white nylon thread to facilitate their recovery if moved (Wenny 2000; Andresen & Feer 2005). Only one seed per primate seed dispersal sample was tagged to increase statistical independence of the sub-sample. Based on the finding that seed removal is highest during the first few days after deposition (Forget et al. 1998; Andresen & Feer 2005), the sub-sample was monitored daily for the first two days and then as described above for unmarked seeds. For individually marked seeds moved from their original site of deposition we recorded: the distance of movement (m), fate of the removed seed, and the secondary disperser or seed predator.

Characterizing the microhabitat

To determine whether the focal primates deposit seeds into specific microhabitats where they may experience different rates of survivorship, we measured the following variables around primate depositions: 1) degree of canopy closure using a densiometer, 2) herbaceous vegetation cover in a 1-m^3 area surrounding the deposition, 3) distance to nearest fallen log ($\geq$ 10-cm in diameter) within a 30-m distance, 4) distance to the nearest adult conspecific ($\geq$ 10-cm dbh) of each tree species found in a given deposition within 30-m, 5) slope measured over a 4-m distance in the north-south and east-west directions using the primate seed deposition as a central point, and 6) elevation using a Thommen© altimeter (accuracy $\pm$ 10 m). We also included 7) the number of woody stems (> 1-cm circumference) and 8) woody leaf coverage in a 1-m^3 area based on the finding that

woody plants and herbs create different microhabitats and influence a seed's ability to germinate (Harms et al. 2004; Benitez-Malvido 2006). The larger habitat surrounding a primate seed deposition was defined on a gross scale based on a modification of habitat categories used in a survey of NNP biodiversity including clearing, burned, closed forest, open forest, buffer zone, secondary, and roadside (Table 1; Plumptre et al. 2002).

Experimental seed fate studies

We used seeds of *Syzygium guineense* in experimental plots and marked individual seeds in primate seed dispersal samples to evaluate the influence of seed handling on post-dispersal seed fate. *S. guineense* was the only species to fruit in large enough quantities during our study to permit its use in experimental plots. The species is dispersed by a variety of frugivorous birds, primates (N. Gross-Camp, unpublished data), and possibly bats (N. Cordeiro, pers. comm.). *S. guineense* is one of the top two most common tree species in the NNP accounting for 35.7% of the large ($\geq$ 30-cm dbh) trees (Plumptre *et al.* 2002) and has fruited annually the past eight years (M. Masozera, unpublished data). The species is commonly dispersed by chimpanzees in wadges (Gross-Camp & Kaplin 2005) and spit by mountain monkeys (B. Kaplin, pers. obs.). *S. guineense* has a circular fruit deep purple in color when ripe containing a single seed (13 mm; Kaplin *et al.* 1998) and is used by local people to treat dysentery (Hines & Eckman 1993).

We established experimental plots in four habitat types where primate-dispersed seeds were found including: 1) open forest (primary forest where > 50% of the canopy is open), 2) closed forest (primary forest where < 50% of the forest is open), 3) burned

forest (burned < 10 years ago), and 4) clearings (predominantly open areas with a single

species of fern, *Pteridium aquilinum,* and secondary growth trees including *Macaranga*

kilimandscharica, Maesa lanceolata, and *Polyscias fulva*). We established two transects

of 100 m in each of the four habitat types (except open forest) along which seed

treatments were placed at right angles 5-m off a transect and at 5-m intervals alternating

sides and treatments following Lambert (2002). Four transects of 50 m were placed in

open forest due to relatively smaller stretches of this habitat type. All transects were

located within a 2-km^2 area with the exception of one of the burned forest transects,

located approximately 2-km west.

    S. guineense seeds were subjected to six different treatments in each of the four

habitats based on chimpanzee and mountain monkey seed handling methods: 1) 10

dispersed seeds in wadge material, 2) 10 dispersed seeds in primate feces, 3) 10

undispersed seeds cleaned of fruit pulp, 4) 10 seeds contained in their fruit, 5) a single

dispersed seed, and 6) a single seed contained in its fruit. Seeds were placed in fecal

material to distinguish the influence of primate seed handling method from that of

individual tree species fruit and/ or seed characteristics on seed fate. Experimental plots

included groups of 10 seeds and solitary seeds to test density effects on the probability of

survival. Clusters of ten seeds simulated wadged or defecated seeds by chimpanzees and

single seeds simulated spit seeds of the mountain monkey.

    Seed treatments were replicated 10 times (N = 40 samples/ treatment) in each of

the four habitat types with the exception of defecated seeds in burned and open forest (N

= 5 and 6 samples) because we were unable to obtain sufficient primate fecal material.

Seeds were monitored for persistence, germination, and establishment at their placement

sites after one week and then every two weeks for a period of 4 ½ months (Andresen &

Levey 2004).

Data Analysis

We report the principal component loadings of the microhabitat variables based

on the significance rules described by Hair *et al.* (1987) in which loadings greater than

0.30 or less than -0.30 are considered significant. Only those samples containing seeds

were included in the analyses. Due to the large representation of *S. guineense* seeds in the

primates' seed depositions and almost exclusive oral-discarding methods employed, we

determined whether this species was driving the variability in the PCA described above.

We performed two additional PCAs on samples containing only *S. guineense*, and all

other species. One-way ANOVAs between a single microhabitat variable and the method

of dispersal were conducted to determine which microhabitat variables best describe the

microhabitats into which seeds are dispersed via defecation, wadging, and spitting

behaviors. Due to collinearity between the microhabitat variables as well as the

complexity of interpreting a regression of the principal components and the probability

that a seed persisted, germinated, or became established, we performed regressions

between a single microhabitat variable and the proportion of seeds persisting, germinated,

or established helped to determine which variables are good predictors of seed fate. To

determine whether the pattern of seed fate was driven by *S. guineense* and its high (>

50% of samples) representation, ANOVAs between a single microhabitat variable and the

proportion of seeds persisting, germinated, or established for *S. guineense* samples were

done. For ANOVAs and regressions we applied a Bonferroni correction to account for

type I errors in multiple testing (Quinn & Keough 2002). All statistical analyses were performed using JMP v.7.0.2.

Results

Seed dispersal

We located 227 chimpanzee fecal samples and 82 wadges containing a total of 1100 and 3120 large seeds, respectively. The highest number of seeds found in a single feces and wadge was 130 and 280, respectively. Approximately 28 % (n = 64) of the fecal samples contained large seeds from seven fruiting tree species (Table 2). Defecated seeds were rarely found in combination of more than a single tree species (n = 14 samples; 8 with two and 6 with three tree species). Eighty-six percent (n = 82) of the wadges contained large seeds from a single tree species, *Syzygium guineense*. *S. guineense* seeds occurred in only two fecal samples (n = 1 and 9 seeds) suggesting that the fruits are primarily dispersed in wadges. Chimpanzee defecations containing large seeds were found only during the first 4 months of our study (May – August 2006). Wadges began to appear in September 2006 and by November 2007 no more defecations were located, only wadges.

We sampled 180 mountain monkey fecal samples and 63 spitting events containing a total of 22 and 310 large seeds, respectively. Five fecal samples were found that contained large seeds from three tree species though never in combination of more than a single large-seeded tree species. Spit seeds were organized into 63 events (1-23 seeds/ event); an event involved the total number of seeds spit by a single animal during a period of observation beginning when a seed was ejected from the mouth of the focal

animal and terminating when the animal moved off and/ or stopped spitting seeds for more than 2 minutes. Spit seeds were grouped into events to increase the likelihood of statistical independence among sampling units.

The two primate species differed significantly in their seed handling method ($\chi^2 =$ 241.1, df = 2, P = <0.0001) with chimpanzees being more likely to defecate large seeds than mountain monkeys. Primates displayed different oral-processing behaviors with mountain monkeys predominantly spitting seeds and chimpanzees wadging them. Seed handling methods varied significantly by tree species ($\chi^2 = 244.3$, df = 12, P = 0.0001) with certain species being exclusively defecated, spit or wadged. *S. guineense* was the only species to be spit, wadged, and defecated (Table 2) and was the single most common species found in both primates' seed depositions, 61.5% of all samples and 91.6% of spit and wadged samples.

Characterizing the microhabitat

The first two components of the PCA of microhabitat characteristics associated with seeds deposited by chimpanzees and mountain monkeys in feces, wadges, and spit seeds explained 46.7% of the total variance. The first multivariate axis (PC1) was characterized by positive loadings for slope and distance to a fallen tree, and a negative loading for elevation and distance to an adult conspecific. The second principal component (PC2) was characterized by positive loadings for canopy cover, the number of woody stems, and woody leaf coverage.

No distinct clumping patterns were apparent when mean loadings for PC1 and PC2 were plotted, suggesting that chimpanzees and mountain monkeys did not disperse

seeds into different microhabitats. When the three seed handling methods (i.e. defecation, wadge, and spit) are examined on a plot of the same principle components, a pattern emerged (Figure 1). Mean loadings of seed locations differed significantly among the seed handling methods for PC1 and PC2 ($F_{2,114}$ = 36.9, P = <0.0001 and 21.5, <0.0001, respectively). All microhabitat variables differed significantly among the seed handling methods (except the number of woody stems) with Tukey HSD tests describing how seed handling methods differed (Table 3). Defecations were characterized by the greatest distance from an adult conspecific and fallen log, highest woody leaf cover, and the lowest herbaceous vegetation and canopy coverage. Spit seeds, exclusive to the mountain monkeys, had the highest canopy and herbaceous vegetation coverage, and were closest to an adult conspecific and fallen log. Chimpanzee wadges had the lowest woody leaf coverage. Additional PCAs on samples containing only *S. guineense* seeds and all other species showed similar variations to the PCA containing all species (47.6% and 48.6% of variation explained by the first two components) suggesting that *S. guineense* and its method of dispersal is not solely responsible for the variation.

Primates deposited seeds into seven gross habitats including open forest, clearing, burned forest, buffer zone, closed forest, roadside, and secondary growth forest (for habitat definitions see Table 1). Chimpanzees and mountain monkeys deposited seeds into significantly different habitats (χ^2 = 24.5, df = 6, P = 0.0004) although the majority of seeds from both species were deposited into open forest (80.5% and 73.8%, respectively). Chimpanzees deposited seeds in three habitat types where mountain monkey seed dispersal was not documented including burned forest, buffer zone, and

secondary growth forests. Only mountain monkeys were found to disperse seeds in the roadside habitat.

Post-dispersal seed fate

Seed fate was analyzed 144 days or approximately five months post-dispersal. We found significant differences in the proportion of seeds persisting, germinated, and established at the site of deposition by seed handling method (one-way ANOVA: $F_{2,116} =$ 8.8, P = 0.0003; 6.1, 0.003; and 30.3, <0.0001, respectively). Additional analysis (Tukey HSD, P ≤ 0.05) showed that defecated seeds persisted at the site of deposition significantly longer than spit or wadged seeds and that significantly more spit and wadged seeds germinated than defecated seeds. Furthermore spit seeds experienced the highest establishment rates followed by wadged and then defecated seeds.

Linear regressions between each microhabitat variable and the percentage of seeds persisting were significant only for distance to an adult conspecific ($F_{1,116} = 13.3$, $R^2 = 0.10$, P = 0.0004; Table 4). No microhabitat variables were significant in explaining the proportion of germinated seeds. Five microhabitat variables including elevation, distance to an adult conspecific, distance to a fallen log, herbaceous vegetation cover, and slope were significant variables in explaining the percentage of established seeds at five months ($F_{1,116} = 9.5$, $R^2 = 0.08$, P = 0.003; 24.9, 0.18, <0.0001; 8.5, 0.07, 0.004; 26.5, 0.19, <0.0001; and 12.6, 0.10, 0.0006, respectively). There were positive trends between the distance to a conspecific and seeds persisting, and elevation and herbaceous vegetation cover and seeds established. In contrast, the distance to an adult conspecific, distance to a fallen log, and slope had negative trends with the proportion of established

seeds. When we examined seed fate in relation to the microhabitat variables for *S. guineense* samples, there was a single significant positive trend between the proportion of seeds established and slope ($F_{1,58} = 8.1$, $R^2 = 0.12$, $P = 0.006$) suggesting that wadging does not drive the trends we see in analyzing all tree species together.

We marked and monitored 58 *S. guineense* seeds including 34 in chimpanzee wadges and 24 spit by a mountain monkey. More than half of the marked seeds (53.4%) had established into seedlings approximately 6 months post-dispersal. The remaining twenty-six seeds (44.8%) were consumed with six seeds moved from their original placement site (range: 0.6 – 5.3 m; Table 5). We opportunistically determined the fate of 66 seeds based on their inspection at allotted seed monitoring intervals. The seeds were from three tree species including *Grewia mildbraedii*, *Myrianthus holstii,* and *Syzygium guineense* (N = 23, 10, and 33 seeds). Forty-one percent of these seeds (n = 27) were removed due to human activities and presumed dead. An additional 24% showed evidence of a boring insect that eventually led to the seed's death. Seventeen percent of the monitored seeds rotted due to excessive moisture, becoming covered in a white fungal pathogen. The remaining seeds were not viable due to desiccation or rodent activity.

Experimental seed fate studies

Eighty-two percent of all seeds (N = 1590 seeds) placed in experimental plots were removed or died by the termination of our study at 4 ½ months with the remaining 18% of seeds germinated or established (n = 48 and 237, respectively). No seeds persisted at the site of deposition but were removed, germinated, or established. The proportion of seeds established differed significantly by treatment type, but not for

germinated seeds (one-way ANOVA: $F_{5,231}$ = 5.0, P = 0.0002 and 0.50, 0.81,

respectively). The ten seeds in whole fruits experienced the lowest establishment rates

suggesting that primate seed dispersal incurs an advantage to seed fate (Table 6). We

performed additional analysis on the four seed treatments containing ten seeds to further

examine the influence of chimpanzee seed handling on seed fate (one-way ANOVA:

$F_{3,151}$ = 6.3, P = 0.0005). Seeds placed in primate feces and undispersed experienced

significantly higher establishment and were distinct from seeds remaining in whole fruits

(Table 6). Seeds with wadge material did not significantly differ from the three other

treatment types.

We found a significant difference in the proportion of seeds germinated by habitat

type (one-way ANOVA: $F_{3, 231}$ = 16.9, P = < 0.0001; Table 7). Open forest had

significantly higher germination than all other habitat types. There was no difference in

the number of seeds removed or established by habitat type (one-way ANOVA: $F_{3, 231}$ =

1.4, P = 0.3 and $F_{3, 231}$ = 2.0, P = 0.12).

Discussion

Chimpanzees and mountain monkeys dispersed the seeds of eleven large-seeded

tree species although dispersal varied through time. Primates shifted their seed handling

techniques depending on the tree species being dispersed. Chimpanzees shifted from

seed-swallowers to seed-wadgers with the onset of *Syzygium guineense* fruiting. Such a

shift in seed handling method is consistent with prior research conducted on the Mayebe

chimpanzees in which the group changed from predominantly seed-defecators of *Olea*

capensis to seed-wadgers of *Syzygium guineense* (Gross-Camp & Kaplin 2005), and is

likely due to a change in fruit availability and seeds and/ or fruit characteristics such as seed size (Chapman & Chapman 1996; Kaplin & Moermond 1998; Lambert & Garber 1998).

Spit seeds showed the greatest likelihood of establishment at the site of deposition for some tree species. Although mountain monkeys spit the seeds of three large-seeded tree species (Table 2), seeds were predominantly from a single species, *S. guineense* (82.5%, n = 51 of 63 spitting events). Chimpanzees wadged the fruits of the same species, *S. guineense.* Results from our experimental plots suggest that the difference in seed handling and establishment is likely due to more than seed handling.

Most microhabitat variables with the exception of woody stem count significantly differed based on primate seed handling method. Of these variables, five were helped seed persistence and/ or establishment (Table 4). Spit seeds were deposited the closest to an adult conspecific (Table 3) and experienced the highest rates of establishment. In contrast, seed persistence increased with distance from an adult conspecific. Our findings are supported by a meta-analysis (Hyatt et al. 2003) that found seed predation was likely to be higher farther from, as nearer to, parent plants. This tendency may in part be explained through an examination of the microhabitat trends.

Seed handling may incur an advantage to seed survivorship that operates as a tradeoff with microhabitat characteristics of the deposition site, namely distance to an adult conspecific. Although spit seeds were deposited close to an adult conspecific, their seed handling method in which fruit pulp was removed increased their chances of establishment. In contrast, seed persistence was positively correlated with distance from an adult conspecific. The majority of persisting seeds had been swallowed and defecated,

whereas the established seeds were spit or wadged and of completely different tree species. Our results suggest that the differences in microhabitat and subsequent seed fate are in part due to seed handling. Our study demonstrates a connection between seed handling, the ability to describe the site where a seed is deposited (microhabitat), and its subsequent fate and has the potential to improve models predicting seed shadows and recruitment patterns (Russo *et al.* 2006).

We found an increase in seed establishment at sites with increasing elevation and decreasing slopes. Slope may negatively affect a seed's ability to establish by creating a difficult environment. The increase in the proportion of seeds established at higher elevation may be a result of a decrease in seed predators (Janzen *et al.* 1976) or secondary dispersers at higher altitudes. Spit and wadged seeds were deposited at slightly higher elevations than defecated seeds and may help explain why spit seeds experienced higher establishment rates. Alternatively, altitudinal differences where tree species are found may influence the elevation at which primates deposit seeds, and subsequently seed fate. Finally, spit seeds were deposited in microhabitats with the highest herbaceous vegetation cover (25%) where we found a positive trend with seed establishment. Our finding was contradictory to previous studies that describe the tendency for small mammals, that often operate as seed predators, to occur in greater densities in areas with increasing herbaceous cover (Hulme 1993). We infer that initial seed predation rates in areas with high herbaceous cover may be offset by protection from other abiotic factors such as excess isolation or movement due to intense rain and a lack of vegetation cover.

Both species of primates predominantly deposited seeds into open forest habitats where they experienced high germination and establishment rates (Table 7). We

documented chimpanzee and mountain monkey seed dispersal into five additional habitat types. *S. guineense* had the second highest seed establishment rates in clearings and burned areas. We speculate that despite being a proportionally smaller number of seeds than are dispersed into open forest, primates' dispersal into these potentially dispersal-limited habitats may be relatively more than the seeds dispersed by other vertebrates suggesting that primates' seed dispersal behaviors play a critical role in the regeneration of dispersal-limited habitats (Duncan & Chapman 1999; Holl 1999). Furthermore, our observation of primate seed dispersal in degraded habitats can direct management decisions in the NNP. Clearing of terrestrial herbaceous vegetation in burned forests releases the growth of mostly secondary tree species (R. Fimbel, unpublished data). We propose planting focal trees, like *S. guineense*, in burned areas to encourage primate seed dispersers and increase the likelihood of seed deposition into these otherwise frugivore-limited areas. Prior research has demonstrated success in the manipulation of habitat features to increase seed arrival into degraded habitats (Mcclanahan & Wolfe 1993; Holl 1998). The addition of a fruiting tree may operate as a 'perch' bringing primates and other frugivores into degraded habitats (Clark et al. 2004). In addition to the transportation of seeds into seed-limited areas, we have noticed that chimpanzees moving through fern clearings creates a series of flattened pathways that alters the characteristics of the microhabitat (i.e. increased insolation and reduced distance of seed to soil), thereby increasing the likelihood of germination and establishment.

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TABLES

TABLE 1. *The percentage (N) of primate dispersed large-seeded samples by gross habitat and habitat description (see Plumptre et al. 2002 for additional detail). Percentages are based on the number of seed dispersal samples by primate species.*

Habitat	% samples (N)	
	Chimpanzee (133)	Mountain (65)
Clearing (*open areas of at least 30 m long dominated by* Pteridium aquilinum *ferns and few if any trees)*	8.3% (11)	1.5% (1)
Burned (*regions of the forest that were recently burned, 2-10 years, and are beginning to regenerate)*	1.5% (2)	-
Closed forest (*50% or more of the forest canopy is closed)*	5.3% (7)	23.1% (15)
Open forest (*less than 50% of the forest canopy is closed)*	80.5% (107)	73.8% (48)
Buffer zone (*Pine and eucalyptus tree plantations established in the mid 1970s as a buffer zone along the National Park's edge)*	2.3% (3)	-
Secondary (*Characterized by secondary growth tree species and a lower canopy)*	2.3% (3)	-
Roadside (*Within 5-m of the main road that cuts through the NNP)*	-	1.5% (1)

TABLE 2. *The ten large-seeded tree species found in chimpanzee and mountain monkey feces, wadge, and spit samples.*

Tree species	Primate species	Method of dispersal	% samples containing seeds (N)	Mean no. of seeds per sample + SE (max)
Chrysophyllum rwandense	CL	S	10.3% (7)	3.9 $\pm$ 1.1 (10)
Ekebergia capensis	PT	D	0.6% (1)	9 $\pm$ 4 (13)
Galineria coffeoides	CL	D	4.4% (3)	19.3 $\pm$ 2.3 (12)
Grewia mildibraedii	PT	D	4.1% (6)	24 $\pm$ 12.7 (74)
Myrianthus holstii	PT	D	11.0% (16)	7.3 $\pm$ 3.3 (60)
Olea capensis	PT	D	0.7% (1)	. (1)
Olinia rochetiana	PT	D	17.9% (26)	15.8 $\pm$ 3.3 (73)
Parinari excelsa	CL	S	7.4% (5)	4.4 $\pm$ 1.0 (7)
Prunus africana	PT	D	9.0% (13)	33.5 $\pm$ 11.2 (130)
Sericanthe leonardii	CL	D	0.1% (1)	. (1)
Syzygium guineense	PT / CL	W, D/ S, D	56.6% (82)/ 76.5% (52)	42.6 $\pm$ 7.3 (280)/ 5.03 $\pm$ 0.64 (23)

D = defecated; W = wadged; S = spit

TABLE 3. *Summary of one-way analysis of variance tests for each microhabitat variable compared among samples dispersed via feces, wadge, and spit events. Superscript indicates results of Tukey HSD pairwise comparison in which values with the same letter are not significantly different.*

Microhabitat variable	Defecation	Spit (Mountain)	Wadge (Chimp)	$F_{2,183}$
Canopy cover (%)	79.1 (1.9)[B]	90.3 (1.7)[A]	83.9 (1.7)[B]	10.0*
Distance to adult conspecific (m)	25.4 (1.3)[A]	5.3 (1.2)[C]	17.3 (1.1)[B]	71.5*
Distance to fallen log (m)	16.4 (1.3)[A]	2.6 (1.2)[B]	13.9 (1.2)[A]	35.7*
Elevation (m)	2216.7 (13.3)[B]	2364.1 (12.0)[A]	2362.1 (11.7)[A]	43.5*
Herbaceous vegetation coverage (%)	7.1 (2.7)[B]	25.0 (2.5)[A]	14.6 (2.4)[B]	12.2*
Slope	17.8 (0.9)[A]	12.2 (0.8)[B]	14.5 (0.8)[B]	10.9*
Woody leaf cover (%)	9.4 (1.5)[A]	8.7 (1.3)[A]	3.1 (1.3)[B]	6.6*
Woody stem count	3.6 (0.6)	2.3 (0.6)	1.4 (0.5)	3.6

Mean values are shown for each microhabitat variable with corresponding standard error in parentheses. * Significance with Bonferonni correction, $P \leq 0.006$.

TABLE 4. *Summary of linear regressions between microhabitat variables and the proportion of seeds persisted, germinated, and established at five months post-dispersal.*

Microhabitat variable	Proportion of seeds $F_{1,116}$ (R^2, if significant)		
	Persisted	Germinated	Established
Elevation (m)	1.1	6.4	9.5* (0.08)
Canopy cover (%)	0.56	2.9	0.43
Distance to adult conspecific (m)	13.3* (0.10)	5.1	24.9* (0.18)
Distance to fallen log (m)	1.3	0.15	8.5* (0.07)
Herbaceous vegetation cover (%)	5.4	3.4	26.5* (0.19)
Slope	1.6	0.01	12.6* (0.10)
Woody leaf cover (%)	0.01	1.1	0.24
Woody stem count	0.32	0.36	0.32

* significance with Bonferroni correction, $P \leq 0.006$.

TABLE 5. *Summary of the fate of marked* **Syzygium** *seeds (N = 58) and opportunistically monitored seeds (N = 66).*

Seed fate	Marked seeds	Opportunistic
Established	32	0
Desiccation	6	8
Insect hole & desiccation	7	16
Rodent predation	7	4
Rotted	3	11
Unknown	3	0
Human activity	-	27

TABLE 6. *Summary of treatments and the mean percent of seeds established by treatment at 4.5 months. Levels connected by the same letter are not significantly different for Tukey HSD (P ≤ 0.05; single seeded samples were excluded from this test).*

Treatment	N	Mean (SE)
Ten dispersed in feces	31	24.8 (5.1) [A]
Single dispersed (spit)	40	20.0 (6.4)
Ten undispersed, but cleaned of fruit	40	18.3 (3.7) [A]
Single undispersed in fruit	40	17.5 (6.1)
Ten dispersed in wadge (wadge)	40	14.8 (3.7) [A,B]
Ten undispersed in fruit	40	3.2 (1.6) [B]

TABLE 7. *The mean number (SE) of* S. guineense *seeds removed, germinated, and established in experimental plots by habitat type. Refer to Table 1 for definitions of habitat types. * indicates significance.*

Habitat type	Removed	Germinated,*but not established	Established
Open forest	4.8 (0.5)	8.9 (2.4)[A]	20.9 (4.2)
Clearing	5.6 (0.5)	0.2 (0.2)[B]	17.8 (4.1)
Burned	6.2 (0.6)	0 (0)[B]	14.3 (4.0)
Closed forest	6.1 (0.5)	2.5 (1.7)[B]	11.3 (3.3)

Levels not connected by the same letter are significantly different for Tukey HSD (P $\leq$ 0.05).

Figure 1. Plot of microhabitats on the first two axes determined by principal components analysis of the microhabitat variables (fecal = filled circles, wadge = grey squares, and spit = empty circles). Axis 1 was characterized by positive loadings for slope and distance to a fallen tree, and a negative loading for elevation and distance to an adult conspecific, whereas axis 2 was characterized by positive loadings for canopy cover, the number of woody stems, and woody leaf coverage.
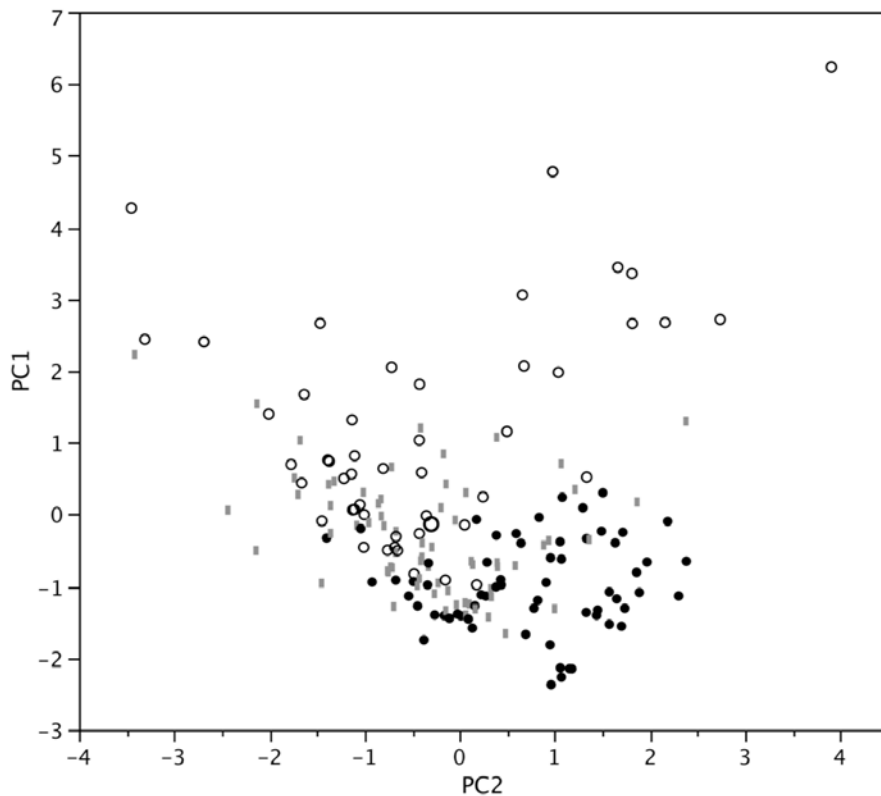
CHAPTER 3

CHIMPANZEE SEED DISPERSAL IN A

TROPICAL MONTANE FOREST OF RWANDA

(in review American Journal of Primatology)

Abstract

We describe chimpanzee seed dispersal in the tropical montane forest of Nyungwe National Park (NNP), Rwanda, for a total of three years from January 1998 through May 2000 and September 2006 through March 2007. Relatively few studies have examined chimpanzee seed dispersal in montane communities where there are generally fewer fruiting tree species than in lowland forests, and may reveal differences in chimpanzee seed dispersal behaviors and the role that they play in forest regeneration processes. Chimpanzees large-body size, high rate of frugivory, and tendency to deposit seeds of the fruits they consume in a viable state indicates their role in the dispersal of large-seeded fruiting tree species. We found that chimpanzees dispersed a total of 37 fruiting species (20 families) in their feces, 35% of which were large-seeded trees (≥ 0.5 cm). A single large-seeded tree species, *Syzygium guineense,* was dispersed in wadges. Our results indicate that chimpanzees do not choose fruits based on their availability for the top five large-seeded tree species found in chimpanzee feces. There was, however, a positive relationship between chimpanzee seed dispersal of *S. guineense* in wadges and *S. guineense* fruit availability. Our data reveal proportionately less seed dispersal by the NNP chimpanzees than in two other communities in the Albertine Rift including one mid-elevation and montane forest. Despite appearing proportionately less often in the NNP chimpanzee feces than in other communities, *Ficus spp.* were the most common genera in their feces. Our data do not support previous studies that describe *Ficus spp.* as a fallback food for chimpanzees and highlights an intriguing relationship between chimpanzees and the large-seeded tree species, *S. guineense.*

Introduction

Chimpanzees (*Pan troglodytes*) are one of the largest-bodied forest-dwelling primates in Africa (Oates 2006). Studies on the four subspecies describe chimpanzees as predominantly frugivorous spending at least 50% of their feeding time eating fruit (Reynolds & Reynolds 1965; Goodall 1968; Nishida & Uehara 1974; Wrangham et al. 1991). Chimpanzees process fruits and their seeds in three ways: (1) by swallowing fruits and later defecating the seeds, (2) spitting, in which a fruit is consumed and its seeds are immediately ejected from the mouth, and (3) wadging, a method in which fruit is placed in the lower lip where the juice is extracted and the remaining pulp, skin, and seeds are eventually discarded in a large ball (Goodall 1986). Seeds processed by chimpanzees are known to maintain or even improve viability for some plant species (Wrangham et al. 1994; Gross-Camp & Kaplin 2005). In addition, chimpanzees' large size and long-gut retention time (Lambert 1999) increases the likelihood that seeds that are swallowed will be defecated away from the parent tree, where they may avoid the increased mortality associated with high densities of seed predators (Augspurger 1983) and spatially-restricted resources (Stiles 1989) that tend to be more limited under the parent crown.

Studies describing chimpanzee frugivory are almost exclusively in lowland to mid-elevation forests (Reynolds & Reynolds 1965; Nishida & Uehara 1974; Wrangham 1977; Ghiglieri 1984; Mcgrew et al. 1988; Suzuki & Nishiara 1992; Wrangham et al. 1994; Lambert 1997; Conklin-Brittain et al. 1998; Newton-Fisher et al. 2000; Furuichi et al. 2001; Marshall & Wrangham 2007) where there is generally an abundance of pulp-fruit species that form the bulk of chimpanzees' diet (Yamagiwa et al. 1996). Lowland forests tend to occur below 1000 m and contain distinct vegetation with a greater number of species than compared to tropical montane forests (2000+ m ASL; White 1978; White 1983). Mid-elevation forests like that of the Kibale

National Park (1500 – 1700 m) and parts of Mahale Mountains National Park (780 – 2300 m), are sometimes referred to as transitional forests, containing a blend of lowland and montane species (White 1983). Studies of montane communities of chimpanzees are less common, yet they may illustrate differences between lowland, mid-elevation, and montane chimpanzee seed dispersal behaviors and the critical role these animals play in forest regeneration.

We present data collected on a chimpanzee community located in the tropical montane forest of the Nyungwe National Park (NNP), Rwanda. The NNP chimpanzee community can travel as high as 2790 m ASL, representing the highest altitudinal limit of their distribution [N. Gross-Camp, pers. obs.]. We describe the fruiting species consumed by chimpanzees using fecal and wadge analysis, and discuss our findings in light of two other studies on chimpanzee frugivory and seed dispersal behaviors in the Kibale National Park, Uganda (Wrangham et al. 1994; Lambert 1999; Balcomb & Chapman 2000) and Kahuzi-Biega National Park, Democratic Republic of Congo (Yamagiwa et al. 1996; Basabose 2002, 2004; Yamagiwa & Basabose 2006). We focused on these studies based on their emphasis on chimpanzee frugivory and seed dispersal, and location in the Albertine Rift, an area widely recognized for its high biodiversity.

In addition to general comparison, we were interested in examining the relationship between chimpanzee seed dispersal and phenological data on fruit availability. Wrangham *et al.* [1994] found that the presence of seeds in chimpanzee feces was a reflection of fruit availability in the forest, in contrast to Basabose [2002] who found no such correlation for the top ten fruit species found in chimpanzee feces. Furthermore we focused our analyses on large-seeded tree species (≥ 0.5 cm) dispersed by chimpanzees based on the finding that these species disproportionately depend on large-bodied frugivores for the dispersal of their seeds and are more likely to be negatively impacted by a reduction in or extirpation of large-bodied frugivores,

like the chimpanzee (Peres & Palacios 2007; Wang et al. 2007). We also include an examination

of the relationship between chimpanzee seed dispersal of *Ficus spp.* and fruit availability based

on the significance of this genera to other chimpanzee communities (Wrangham et al. 1993;

Basabose 2002; Stanford & Nkurunungi 2003).

Methods

Study Area and Species

Data were collected in the Nyungwe National Park (1,013 km^2; 2°17'-2°50'S and 29°07'-29°26'E) located in southwestern Rwanda. The NNP is part of the Albertine Rift and represents

one of the largest contiguous blocks of montane forest on the African continent adjacent to the

Kibira National Park, Burundi on its southern border (Vedder et al. 1992; Plumptre et al. 2007).

The Park is characterized by steep slopes (1600 – 2950 m ASL) containing forested areas and

interspersed open regions often dominated by a single species of fern *Pteridium aquilinum*

(Dennstaedtiaceae) or fast-growing liana *Sericostachys scandens* (Amarantaceae). Daily

temperatures fluctuate little throughout the year with an average maximum and minimum

temperatures of 19.6°C and 10.9°C, respectively (Sun et al. 1996). The average annual rainfall is

1744 mm (Kaplin & Moermond 1998). Sun *et al*. (1996) described a fruiting peak during the

major wet season (March-May), with fruits remaining high through the major dry season (July-

August). The Nyungwe National Park is less species rich than other forests in the Albertine Rift

(Omari et al. 1999) but still sustains over 260 tree and shrub species, 260 bird species, and 13

species of primates.

Our observations on chimpanzee frugivory were made on the semi-habituated Mayebe

group of chimpanzees located approximately two kilometers east of the Uwinka Visitor Center.

The group is estimated to consist of 50 individuals and lives sympatrically with at least ten other

primate species including: *Cercopithecus ascanius, C. hamlynii, C. l'hoesti, C. mitis doggetti, C.*

mona, Colobus angolensis ruwenzorii, Galago demidovi, Galago sp., Lophocebus albigena, and

Papio anubis. Though the home range of the Mayebe community is not well defined, our

observations suggest that the chimpanzees spend the bulk of their time above 2000 m ASL.

Chimpanzee seed dispersal data were predominantly at elevations of $\geq$ 2140 m (97.4%, n = 304

of 312 defecations or wadges). The lowest elevation that the Maybe group was recorded was

1840 m ASL.

Chimpanzee frugivory

We followed the Mayebe chimpanzee group from dawn to dusk five days a week every

other week for a total of three years though not consecutively (from January 1998 through May

2000 and September 2006 through March 2007). Follows usually lasted from 7 to 12 hours per

day with actual contact hours varying greatly. Habituation of the chimpanzee community was

initiated in 1997 by the *in situ* conservation organization (Conservation Project of Nyungwe

Forest, PCFN/ WCS) and governmental management organization (Rwandan Office of Tourism

and National Parks, ORTPN) and is ongoing. We entered the forest early in the morning to locate

the chimpanzees either in their sleeping sites from the night before or by vocalization, and

followed them until dusk when the animals would settle down for the night. We observed the

chimpanzees from a distance ($\geq$ 30-m) and only searched the forest floor for feces or wadges

once the animals had left the area. We included fecal samples deposited within 24 hours

following White and Edwards (2000). Wadge samples were included unless visibly disturbed or

notably discolored, i.e. disintegrating or fading in color. We were able to distinguish chimpanzee

wadges from other potentially wadging species (i.e. bush pigs, baboons, bats, and humans) based on the size of and palette indentation on the wadges.

In the initial phase of our study (January 1998 – May 2000), chimpanzee feces were collected and brought back to our field site where they were weighed and then sieved to determine contents (e.g. meat, mushroom, terrestrial herbaceous vegetation, wood, leaves, fruit pulp). We counted the number of seeds for each plant species in a defecation including small-seeded (< 1 mm) species like *Ficus spp.* We did not sample wadges during this period. The sampling in September 2006 to March 2007 was part of a larger project to examine post-dispersal seed fate of primate dispersed large-seeded tree species. When a chimpanzee feces or wadge was found we identified seeds to species and family, and counted the number of large seeds ($\geq$ 5 mm) at the site of deposition. For plant species with seeds < 5 mm, we estimated the total number in a fecal sample following Kaplin & Moermond (1998): 1 = rare (1-10 seeds), 2 = few (11-20 seeds), 3 = common (20-40 seeds), 4 = abundant (40 to hundreds).

Fruit availability

We collected data on the phenological patterns of 64 fruit-producing tree species (N = 907 trees; mean = 14.2 $\pm$ 1.04 individuals per species) on a monthly basis for the duration of the study period to evaluate the relationship between fruit availability and chimpanzee frugivory. Forty-four percent (28 species) of the monitored tree species' seeds were dispersed by chimpanzees (Appendix 1). The phenology data were extracted from a larger data set initiated in 1991 as part of a forest-wide frugivore seed dispersal study (Sun et al. 1996; Sun & Moermond 1997; Kaplin & Moermond 1998; Kaplin et al. 1998; Kaplin 2001). The sample tree species were located along 25 phenology trails in the study area. We sampled reproductively mature, adult

trees whose crowns were easily observed from trails. Adult trees were defined as individuals

with a diameter at breast height (DBH: 1.4 m) of $\geq$ 15 cm. The phenological patterns of the

sampled trees were assumed to be representative of the tree species forest-wide and specifically,

fruit availability within the home range of the Mayebe chimpanzee community. Sampling took

place over 2-3 days at the same time each month. We estimated the percentage of the crown

occupied with fruit each month by assigning a fruiting score between zero and four (0 = 0%, 1 =

1-25%, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%; Sun et al. 1996).

A fruit availability index (FAI) was calculated for the top five large-seeded tree species

based on the number of chimpanzee defecations in which the species' seeds were found. We

focused on large-seeded tree species based on prior research that indicates the importance of

large-bodied frugivores like chimpanzees to the dispersal of these species (Chapman &

Onderdonk 1998; Peres & Van Roosmalen 2002). Following Basabose (2002) and Holbrook *et

al.* (2002), we calculated a FAI for each tree species by multiplying density (individuals/ ha) by

basal area by the proportion of individuals in fruit for each month. Density was taken from Sun

et al. (1996). We calculated the basal area $[(1/2DBH)^2 \times \pi]$ using the mean DBH of all

individuals of a given species that were monitored along phenology transects. Individuals were

considered in fruit if they had a fruit value $\geq$ 1 (1-25% of the canopy in fruit).

Data analysis

We performed a one-way ANOVA on seed dispersal method (defecation and wadge) and

the number of seeds in a sample to determine if there was a significant difference in the number

of seeds dispersed by either seed dispersal method. Non-parametric Wilcoxon tests were utilized

to assess annual and monthly variation in the number of seeds in chimpanzee feces. We used

linear regressions to determine the relationship between fruit availability and the number of

seeds in chimpanzee defecations for the top five large-seeded tree species found in defecations

during the study period. Regressions were run individually on each of the five species as well as

together to determine whether fruit availability is a good indicator of chimpanzee seed dispersal.

We also ran a regression on the FAI for the wadged tree species, *S. guineense,* and the mean

number of seeds per wadge. We evaluated whether *Ficus spp.* may operate as a fallback food for

the Mayebe chimpanzees through a series of two regressions. The first regression determined the

relationship of fig fruit availability to forest-wide fruit availability, whereas the second

regression examined fig fruit availability in relation to fig seed presence in chimpanzee feces.

We use the proportion of chimpanzee feces containing fig seeds in lieu of mean number of seeds

per feces due to different methods of quantifying the number of seeds in a defecation for small-

versus large-seeded plant species. JMP 7.0.2 was used for all statistics.

Results

Fecal and wadge analysis

We found a total of 975 samples (mean 13.2 ± 0.4 samples per month) including 882

defecations and 93 wadges containing 18,499 and 3122 seeds, respectively. Defecations

weighed an average of 106.1 ± 2.0 grams (N = 639, range 2.7 – 330, median 100 g). We

excluded seeds from *Ficus spp.* and *Urera spp* as species from these two genera were only found

in defecations and were calculated separately due to their small size and occurrence in the

thousands. Excluding *Ficus spp.* and *Urera spp.,* we counted an average of 40.6 ± 4.8 seeds per

defecation (including *Ficus spp.* and *Urera spp.:* 3045.9 ± 194.9, maximum 70,168) and $35.4 \pm$

6.0 seeds per wadge (maximum 280). Defecations contained significantly more seeds per sample

than seeds dispersed in wadges ($F_{1,782} = 46.0$, P <0.0001) when we included *Ficus spp.* and *Urera spp.,* but there was no significant difference when these genera were excluded ($F_{1,540} = 0.0001$, P = 1.0).

We found seeds from a total of 37 fruiting species and 20 families in chimpanzee defecations (mean 1.7 ± 0.03 species/ defecation, maximum 6 species; Table 1), but only the seeds of a single species *Syzygium guineense,* in wadges. Over half of the species (n = 21) occurred in less than 1% of defecations and wadges combined. Fifty-one percent of the species were trees (n = 19; including 9 understory and 10 canopy tree species), 18.9% lianas, 8.1% shrubs, 2.7% herbs, and the remaining 18.9% unknown. Trees were predominantly from species with large seeds (≥ 5 mm, n = 13). Ten species including two lianas, five understory trees, and four canopy trees, accounted for 89.8% of all seeds found in chimpanzee feces (n = 1,906,260 seeds). At least one of the ten species was present in all fecal samples: *Cleistanthus polystachyus, Ekebergia capensis, Ficus oreodryadum, Ficus spp., Grewia mildbraedii, Maesa lanceolata, Myrianthus holstii, Prunus africana, Olinia rochetiana, Syzygium guineense,* and *Vepris stolzii.*

Fruit availability and seed presence

We found a significant difference in the number of seeds dispersed in chimpanzee feces by month and year (Wilcoxon: $\chi^2 = 107.6$, df = 31, P = <0.0001 and $\chi^2 = 14.5$, df = 6, 0.02, respectively). We were unable to examine the variation in number of seeds in wadges per month due to small sample size.

There was a significant relationship between the mean number of seeds per wadge and the fruit availability index for *S. guineense* ($F_{1,10} = 40.3$, $R^2 = 0.82$, P = <0.0001; Figure 1)

indicating that chimpanzee's consumption and subsequent dispersal of *S. guineense* increases as its fruit becomes more available. When we performed regressions on the mean number of seeds found in chimpanzee feces and the fruit availability index (FAI) for the top five large-seeded tree species, however, there was no significance ($F_{1,199} = 0.1$, $P = 0.75$; Figure 2). Additional regressions on a single species were also not significant (*E. capensis* $F_{1,39} = 0.57$, $P = 0.46$, *M. holstii* $F_{1,39} = 0.01$, $P = 0.92$, *O. rochetiana* $F_{1,39} = 0$, $P = 1$, *P. africana* $F_{1,39} = 1.5$, $P = 0.23$, and *S. guineense* $F_{1,39} = 0.07$, $P = 0.80$).

We found no relationship between fig fruit availability and forest-wide fruit availability ($F_{1,27} = 2.01$, $R^2 = 0.07$, $P = 0.17$) suggesting that fig fruits are no more or less available during times of forest-wide fruit scarcity. Furthermore there was no relationship between the proportion of chimpanzee feces containing figs seeds and the proportion of figs in fruit ($F_{1,33} = 0.16$, $R^2 = 0.01$, $P = 0.69$) or the proportion of all species in fruit forest-wide ($F_{1,24} = 0.03$, $R^2 = 0.001$, $P = 0.87$).

Discussion

Our study highlights that proportionately fewer seeds are dispersed by chimpanzees in montane forests than in other forests (Table 2). We found approximately 10% more fecal samples containing no seeds than in either of the other communities, suggesting that chimpanzees in the Nyungwe National Park disperse proportionately less seeds. Basabose [2002] described fruit presence (i.e. fruit skin, pulp, or seed) in chimpanzee feces that likely overestimates the proportion of chimpanzee feces with seeds. In contrast, our study's emphasis on seed dispersal and seed presence in chimpanzee fecal and wadge materials likely underestimates the fruiting species consumed by chimpanzees. In particular we directly observed

the Mayebe chimpanzee community's consumption of two large-seeded tree species' fruits, *Chrysophyllum gorungosanum* and *Parinari excelsa,* and ejection of seeds. The NNP had the lowest proportion of tree species consumed by chimpanzees compared to Kibale and Kahuzi and may be indicative of lower fruiting tree diversity in the Park (56.8, 59.5 and 67.8%, respectively). Plumptre *et al.* (2007) described a greater number of tree species in Kibale (Table 2) but the proportion of those tree species in fruit during the study of chimpanzee diet in Kibale is not presented.

Dispersal of the top five large-seeded tree species found in chimpanzee feces in NNP did not correlate with fruit availability in the forest suggesting that chimpanzees are choosing fruits not based on their availability. Our direct observation of the chimpanzees confirmed that they were only defecating the seeds of the top five tree species reducing the likelihood that we were missing seeds spit or wadged by chimpanzees for these tree species. Our findings are supported by Basabose [2002] who found no relationship between the monthly frequency of fruit materials in chimpanzee feces and fruit availability for the top ten fruit species in chimpanzee feces. In contrast, Wrangham *et al.* [1994] and J. Lambert [pers. com.] determined that the frequency of seeds in chimpanzee feces was a reflection of forest-wide fruit availability. We speculate that these findings may reflect differences in the fruiting communities of the respective forests (i.e. mid-elevation versus montane), with montane forests having lower fruiting tree diversity. The available fruiting species may be more limited in montane versus mid-elevation forests and less preferred by chimpanzees resulting in a shift in chimpanzees' food choice to a more preferred non-fruit item such as honey, meat, or terrestrial herbaceous vegetation.

Figs have been shown to be an important food resource in other tropical communities and are often referred to as a 'keystone' species (Terborgh 1986; Basabose 2002) based on the

prediction that their removal would result in a severe cascading effect on a wide range of species within an ecosystem (Paine 1966; Peres 2000). Furthermore figs are sometimes described as a chimpanzee fallback food (Wrangham et al. 1993; Tutin et al. 1997; Yamakoshi 1998; Furuichi et al. 2001; Lambert et al. 2004; Lambert 2007; Marshall & Wrangham 2007) in times of fruit scarcity. In the Nyungwe National Park, figs were found in proportionately less chimpanzee fecal samples than in the Kibale or Kahuzi communities, 67.1%, 89.9%, and 92%, respectively. Despite a relatively lower appearance rate in feces than in other chimpanzee communities, *Ficus* was the most common genus found in the NNP chimpanzee feces and had the highest mean number of seeds per defecation suggesting that chimpanzees are reliable dispersers of figs (Table 1). Our data do not, however, support the term fallback to describe chimpanzees' use of figs. In order to describe figs as a fallback food we would expect there to be a negative relationship between forest-wide fruit availability and fig fruit availability. In addition we would expect the proportion of chimpanzee feces containing fig seeds to increase in times of forest-wide fruit scarcity; neither of these relationships were demonstrated in our data.

The case of Syzygium guineense

Syzygium guineense was the only tree species whose fruits were predominantly processed by wadging, (occurring in 4.1% feces and 100% wadges). Wadging has been observed in other species (baboons, bats, bush pigs, and humans, N. Cordeiro and J. Lambert, pers. obs.) but is generally a poorly studied method of seed dispersal. Prior research conducted in the NNP demonstrated an increase in germination rate for chimpanzee-wadged *S. guineense* seeds suggesting the potential advantage of wadging to seed fate (Gross-Camp & Kaplin 2005). Our study corroborated chimpanzee dispersal of *S. guineense* seeds and revealed a highly significant

positive correlation between the dispersal of *S. guineense* seeds by chimpanzees with increasing

S. guineense fruit availability (Figure 1). Plumptre *et al.* (2002) described *S. guineense* as the

most common large (≥ 30 cm DBH) tree species in the NNP. The species has reliably fruited in

the past eight years (M. Masozera and B. Kaplin, unpublished data) and coincided with a shift in

the Mayebe chimpanzee community's diet and fruit-processing strategy, fruit swallowing to

wadging. So consistent is the Mayebe community's consumption of *S. guineense* that

chimpanzee trekkers often utilize *S. guineense* fruiting stands to locate the group on a day-to-day

basis. The consistent consumption of *S. guineense* fruits by chimpanzees and subsequent

influence of chimpanzee seed dispersal on seed fate suggests the importance of chimpanzee seed

dispersal to this species and begs the question of how the distribution and regeneration of *S.*

guineense might change if chimpanzee populations were to decline or be extirpated.

Acknowledgements

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Tables

Table 1. *Plant species found in chimpanzee defecations (and wadges*) over the study period. Life form indicates the plant's growth form including canopy tree (CT), herb (H), shrub (S), and understory tree (UT). Seed size was defined as small (S; < 0.1 cm) and large (L; $\geq$ 0.5 cm). The mean number of seeds per sample $\pm$ SE and maximum number of seeds per sample are also given. The top 10 species found in chimpanzee defecations are in bold.*

Family	Species	Life form	Seed size	% with seeds	Mean no of seeds/ sample	SE	Max seeds/ sample
Apocynaceae	*Tabernaemontana stapfiana*	UT	L	1.42	18.2	6.1	78
Araliaceae	*Schefflera goetzenii*	L	S	0.12	2.0		2
Celastraceae	*Salacia erecta*	S	L	0.59	6.8	5.3	28
Curcurbitaceae	*Coccinea mildbraedii*	L	S	0.24	1.0	0.0	1
Euphorbiaceae	***Cleistanthus polystachyus***	**UT**	**L**	**3.07**	**32.6**	**7.4**	**143**
	Croton megalocarpus	UT	L	0.35	3.7	1.5	6
Flacourtiaceae	*Casearia runssorica*	CT	S	0.47	16.0	8.4	41
Meliaceae	***Ekebergia capensis***	**CT**	**L**	**2.83**	**5.9**	**1.5**	**32**
Moraceae	***Ficus spp.***	**L**	**S**	**67.1**	**4009.2**	**388.0**	**70168**
	Myrianthus holstii	**UT**	**L**	**20.43**	**16.0**	**5.9**	**1024**
Myrsinaceae	*Embelia schimperi*	L	S	0.12	14.0	-	14
	Maesa lanceolata	**UT**	**S**	**4.84**	**145.6**	**31.8**	**1280**
Myrtaceae	***Syzygium guineense****	**CT**	**L**	**14.88**	**29.3**	**4.5**	**280**
Oleaceae	*Olea capensis*	CT	L	0.24	1.5	0.5	2
Oliniaceae	***Olinia rochetiana***	**CT**	**L**	**8.74**	**14.4**	**2.7**	**73**
Rhizophoraceae	*Cassipourea gummiflua*	UT	S	2.24	23.9	5.2	73
Rosaceae	***Prunus africana***	**CT**	**L**	**4.13**	**23.8**	**5.5**	**130**
Rubiaceae	*Ixora burunensis*	UT	L	0.47	2.3	0.8	4
	Rubus sp.	S	S	0.94	2.7	1.7	6
Rutaceae	*Oricia renieri*	S	L	1.53	21.2	7.5	96
	Vepris stolzii	**UT**	**S**	**6.73**	**69.6**	**14.7**	**608**
Sapotaceae	*Aningeria altissima*	CT	L	1.18	43.6	13.1	128
	Chrysophyllum gorungosanum	CT	L	0.12	4.0		4
	Chrysophyllum rwandense	CT	L	0.47	1.8	0.3	2
Theaceae	*Balthasarea schliebenii*	CT	S	0.12	-	-	-
Tiliaceae	***Grewia mildbraedii***	**UT**	**S**	**3.54**	**12.9**	**3.3**	**74**
Urticaceae	*Urera cameroonensis*	L	S	0.47	7680.0	3584.0	11264
	Urera hypselodendron	L	S	2.36	6812.6	932.9	16384

|							
	Urera sp.	L	S	2.01	3718.2	702.9	10240
Zingiberaceae	*Aframomum angustifolia*	H	S	0.47	10.0	6.1	28
Unknown	*Unknown 1*			0.12	1.0	-	1
	Unknown 2			0.24	18.0	13.0	31
	Unknown 3			0.35	11.0	7.0	25
	Unknown 4			0.12	2.0	-	2
	Unknown 5			0.24	2.0	1.0	3
	Unknown 6			0.71	7.5	1.5	12
	Unknown 7			0.83	34.1	12.3	76

Table 2. *Comparison of chimpanzee seed dispersal between two montane and a mid-elevation tropical forest. Comparison is between chimpanzee defecations only.*

Location	% of species that are trees forest-wide (n)*	Number of fruiting species[a] (in feces)	% of fruiting species that are trees (n)	% of feces with *Ficus spp.* seeds	% of feces with seeds	% of feces with fruit presence	N (defecations)	Source
Kibale National Park (mid-elevation)	62.0 (330)	59	67.8 (40)	89.9	98.5	-	1849	Wrangham *et al.* (1994)
Kahuzi-Biega NP (montane)	18.6 (218)	42	59.5 (25)	92.0	-	99	7212	Basabose (2002)
Nyungwe NP (montane)	23.5 (260)	37	56.8 (21)	67.1	85.8	-	882	This paper

* data from Plumptre et al. (2007)
[a] includes lianas, shrubs, and trees

Figure 1. Relationship between the fruit availability index for *S. guineense* and the mean number of seeds per chimpanzee wadge ($F_{1,10} = 40.3$, $R^2 = 0.82$, $P = <0.0001$). The pattern suggests an increase in chimpanzee dispersal with higher FAI.

Figure 2. Relationship between the fruit availability index for the top five large-seeded tree species found in chimpanzee defecations and the mean number of seeds per chimpanzee defecation ($F_{1,199} = 0.1$, $P = 0.75$). The pattern of clumping around zero suggests that chimpanzees choose fruits not based on fruit availability.
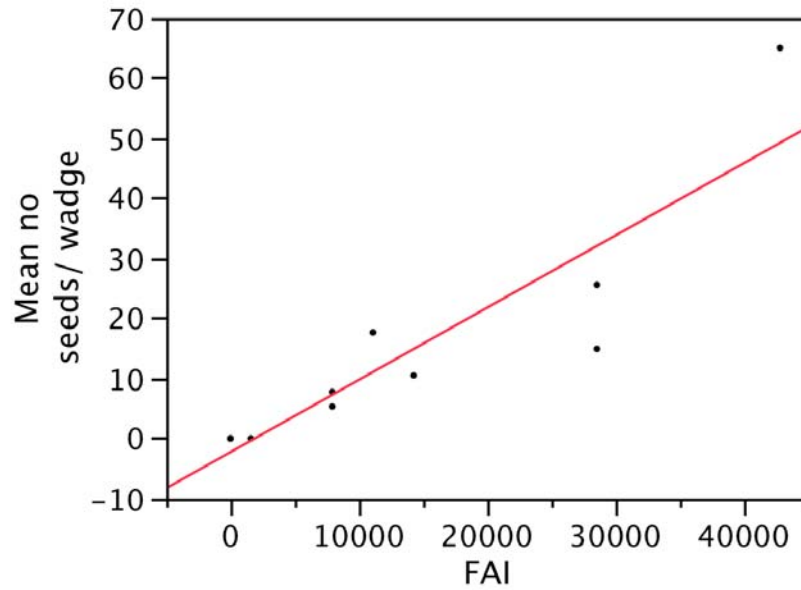
CHAPTER 4

LINKING RESEARCH WITH EDUCATION OUTREACH PROGRAMS TO

IMPROVE CONSERVATION EFFORTS IN PROTECTED AREAS

Introduction

Field researchers often work in protected areas surrounded by communities that have little or no understanding of what researchers are doing. These areas are frequently sites of conflict between local people's needs and desires, and conservation objectives. In developing nations, the gap separating researchers and laypeople may be exacerbated by a multitude of issues including the latter's poor access to education and communication, general lack of empowerment, and livelihood practices that may conflict with researchers' goals (Scoones et al. 1992; Vedeld et al. 2004). While many researchers acknowledge the importance of outreach, relatively few incorporate such activities into their projects due to poor incentives and/ or training. For example, many funding agencies mandate dissemination of research results to relevant professional bodies but only *encourage* outreach activities to non-specialists (i.e., the local community, among others). Furthermore, researchers may be intimidated by the creation of outreach programs due to little or no training as an educator. That said, researchers from a variety of institutions and disciplines have expressed interest in incorporating outreach activities into their projects, an interest borne out by the Ecological Society of America's 2008 meeting theme: *Enhancing Ecological Thought by Linking Research and Education.* In this paper we describe a simple outreach program involving communities living on the periphery of a protected area in Rwanda, east Africa.

Outreach programs are often mutually beneficial for protected areas, researchers and communities, serving to establish or strengthen the connection that local people have with their environment while helping to create a foundation on which longer term conservation plans can be built (Jacobson 1991; Mugisha & Jacobson 2004; Trewhella et

al. 2005; Kaimowitz & Sheil 2007). Outreach also can improve relations between local people and researchers and their affiliations by providing a forum for discussion on research and conservation issues, as well as access to management officials and information that may otherwise be difficult if not impossible for communities or researchers to obtain. In a diverse society (i.e. socioeconomic aspects, values, special interest groups, and governmental groups), the use of different strategies to communicate research and its findings may increase the likelihood that a project has a lasting impact, especially in research that has broad, far-reaching and/or long-term goals.

We shared findings from our ecological research on primate seed dispersal with local school leaders living in communities around our study site, a protected area. While we are not professional educators, collectively we have a strong foundation in conservation and ecology, non-government and government management of protected areas, and graduate-level teaching. Our paper is not intended to prescribe teaching methods so much as to emphasize ways in which field researchers might incorporate a broader audience – i.e. layman or non-specialist – into their realm of impact. We hope this article might catalyze other researchers interested in creating similar programs. To maximize the practical applications of this article, we have created a series of process-oriented questions to guide researchers through the formation of their own outreach program (Table A).

Primate seed dispersal ecology: an educational outreach workshop in Rwanda

We held a 1 ½ day workshop to highlight aspects of our research on primate seed dispersal ecology in the Nyungwe National Park (NNP), Rwanda. Basic research findings

were presented to educators and school administrators from ten sectors surrounding the park. We also shared ecological concepts and discussed potential research and management initiatives in which we might be able to work together.

The workshop was a collaborative effort by three organizations: Antioch University New England (ANE) in New Hampshire, USA, the Rwandan Office of Tourism & National Parks (ORTPN, a governmental organization), and the Wildlife Conservation Society of Rwanda (WCS). WCS has worked in NNP managing a number of long-term ecological research projects since 1988, as well as educational programs. WCS also works closely with ORTPN, the governmental management authority in NNP. ORTPN has been increasingly involved in outreach activities with communities living on NNP's boundaries, and this experience helped us to narrow the workshop's target audience and establish achievable objectives. Dr. Beth Kaplin, Associate Professor at ANE, began ecological research in NNP in 1990. The primate seed dispersal ecology research that this workshop was based on came from work being conducted by Kaplin and Gross-Camp.

Objectives of the Workshop

We had three objectives for the workshop: (1) to assess participants' understanding of basic ecological concepts and of primates specifically, and offer information where needed (2) to evaluate the role of educational programs as a complement to ecological research, and (3) to develop ideas for educational materials to accompany a display of fleshy-fruiting tree seeds dispersed by animals in NNP. We were especially interested in how our research findings could be used in the classroom setting,

as well as the establishment of future research priorities as perceived by local communities and management authorities. We used pre- and post-workshop questionnaires to evaluate whether we achieved our goals.

The Process

We invited three participants from ten sectors surrounding the park (for a total of 30) to the workshop based on our financial and logistical constraints. These participants were all Rwandan nationals who lived around the periphery of the protected area. We targeted primary and secondary school teachers and local government authorities, as previous experience by WCS and ORTPN in the communities surrounding Nyungwe demonstrated that these individuals are most likely to continue disseminating workshop materials within their respective sectors (both to students in the classroom and to potentially influential government officials). Of the total 50 sectors around the park, we chose ten based on proximity to the workshop venue location and reported incidents of crop-raiding by wildlife. Presence and degree of crop-raiding constituted a good criterion for sector selection since primates are often reported crop-raiders, and one of our secondary objectives was to better understand peoples' perceptions of and attitudes towards primates.

Though our objectives for the workshop were clearly defined, we wanted to maintain flexibility in how we communicated our message. That is, although we wanted participants to leave with an understanding of basic ecological principles and some of our research findings, we were equally interested in hearing participants' voices and knowledge of the forest. In order to fully engage all participants, we presented

information in a format that encouraged participant input, i.e. posing broad questions and pausing often. Each teaching segment was initiated by asking participants what they knew about a topic, followed by the lecturer's response addressing gaps in participant knowledge. For example, by asking participants what species of primates live in NNP we learned that most people only knew of baboons and vervet monkeys, both common crop-raiders, although there are 13 species of primates identified. In addition, many participants incorrectly thought that gorillas were present in the park. Participants were surprised to learn that NNP is exceptionally rich in primate species claiming 26% of Africa's primate diversity.

Conveying our research findings on primate seed dispersal ecology were facilitated through the creation of a visual display of seeds dispersed by vertebrates in NNP. We described how primate seed handling (i.e. swallowed and defecated versus orally-processed and discarded) may influence seed fate (i.e. increased rates of seed germination or secondary dispersal by a rodent or insect) highlighting primates' treatment of seeds from the primary forest tree, *Syzygium guineense* or *Umugote,* in the local dialect. The visual display helped generate additional questions from participants and greatly assisted the communication of research findings. For example, participants recognized a forest fruit, *Myrianthus holstii* or *Umwufe* that is consumed by both humans and primates. Recognition of this fruit stimulated a discussion on the overlap of fruits consumed by forest animals and humans, and how forest animals help to sustain wild plant populations through their seed dispersal behaviors. Similarly participants questioned how the characteristics of fruits (i.e. soft, fleshy versus hard) may influence the way in which a primate processes a seed.

We also broke into smaller groups to discuss potential methods to disseminate what participants had learned in the workshop. The majority of dissemination tools that participants came up with focused on students 12-15 years of age and used inexpensive materials. For example, one group suggested a matching game of frugivores and the fruits they consume, and an educational poster on the ecological services that the forest provides, i.e. water catchment and nutrient cycling. One group described an inexpensive teaching method to examine the potential benefit of vertebrate seed dispersal. Students would collect seeds dispersed by a primate or other frugivore as well as seeds harvested from intact fruits. These seeds would then be observed through time to see if there was a difference in germination; interestingly the group described a component of our research project which pleased participants greatly!

Of the 36 invited guests, the workshop had 22 participants, including 17 primary and secondary school teachers, 3 school principals, 2 local government authorities. An additional 5 ORTPN employees (Head of Community Conservation and 4 Community Conservation Officers) and the Community Outreach Officer for WCS employee attended the workshop. We received twenty-two pre-and post-workshop questionnaires, helping us to evaluate the achievement of our workshop objectives. The completed questionnaires provided us with a good understanding of the participants' knowledge of ecology and, more specifically, primates prior to the workshop (specifically of NNP), general attitudes towards park authorities (ORTPN and WCS), and areas where participants would likely benefit from additional information. We were particularly impressed by several unprompted comments from participants noting a connection between our research findings (i.e. the contribution of primate seed dispersers to forest

regeneration) and the need to find a peaceful resolution to primate crop-raiding in their communities. Participants' comments indicate a comprehension for the complexity of a conservation issue – primates are important to forest ecology and yet are problematic in their crop-raiding behaviors - and were impressive in that participants made this connection on their own without suggestion from the workshop organizers. Our projected goals were primarily met and we concluded that this kind of workshop complements ecological – and likely other – research projects. We came away from the workshop with an understanding, based on input from the participants, about how our research could be used by the communities living around the park. We had, in hand, a series of specific activities and ideas for curriculum development that incorporated findings from our primate ecology research project.

Conclusion

Our workshop represents a small but significant step towards incorporating ecological research findings into the lives of communities and local people in a collaborative way, and thus linking research to conservation efforts. Through our workshop, we also demonstrated how researchers can begin the process of incorporating citizens into their research projects by gaining an understanding of the needs and problems faced by people living around protected areas. We would argue that researchers have an ethical obligation to share their work with non-specialists, especially those whom the work most directly affects and whose own lives in turn directly impact the protected areas where researchers so often work.

Acknowledgements

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Table A. *Process-oriented questions to help guide researchers through the formation of their own outreach project.*

1	What does our outreach project hope to achieve? What is (are) the outcome(s) that we hope to attain?
2	Who is the target audience? How are they geographically distributed?
3	What are our limitations (i.e. financial and/ or logistical)?
4	What organizations might share (or be resistant to) the outcomes we are striving for? What assets (i.e. financial or credibility) do these organizations bring to an outreach project? Are they willing/ interested in collaborating?
5	Refine desired project outcomes with collaborators and brainstorm the appropriate method(s) for communication, e.g. workshop, audio-visual resource, or posters.
6	How will you illicit feedback and/ or ideas from the target audience to ensure that the outreach project is participatory? What kinds of benefits might be created by the outreach program for the community? For your research project?
7	Discuss project evaluation. How will you determine that the project's outcomes were met?

Conclusion

In the pursuit of my doctoral degree I have strived to develop a study grounded in conservation that would contribute to the larger field of seed dispersal ecology. Furthermore, I was interested in moving beyond traditional academic responsibilities and sought opportunities to engage people from a variety of backgrounds about my research and its significance. I viewed this less common but no less important aspect of my doctoral training as a vital component to my ability to succeed beyond the degree as a conservation professional. The preceding chapters describe the study design and methods that facilitated my achievement of these academic and professional goals. In this section I will summarize the major contributions of my dissertation research to seed dispersal theory highlighting areas that may be of interest for future research. I will also discuss the non-traditional aspects of my dissertation work (Chapter 4 - seed dispersal workshop) and the role that alternative learning and host-country relationships have played in my development as a professional.

Large-seeded trees need large-bodied frugivores

Recent research has explored how the loss of large-bodied frugivores may alter forest structure (Peres & Palacios 2007; Stoner et al. 2007; Wright et al. 2007) and dispersal recruitment of large-seeded plants (Cochrane 2003; Galetti et al. 2006). Nunez-Iturri & Howe (2007) demonstrated how a reduction in primate populations altered forest composition and the spatial distribution of large-seeded tree species in a Peruvian forest. My research (Chapter 1) showed that primates and large-bodied birds were the most effective dispersers of large-seeded tree species. Primates spent the most time in trees and

had the largest group size. Large-bodied birds and cercopithecines dispersed the most seeds per minute. Finally, large-bodied birds and cercopithecines potentially dispersed the most seeds for *Ekebergia capensis,* and chimpanzees potentially dispersed the most seeds for *Syzygium guineense.* My data strengthens the hypothesis that large-seeded trees are dependent on large-bodied frugivores for the dispersal of their seeds and that the loss of such frugivores will likely result in an alteration of the distribution and regeneration of these species.

Does seed handling matter?

Prior research on primate seed dispersal ecology has predominantly focused on seeds dispersed in defecations (Wrangham et al. 1994; Julliot 1996; Dew & Wright 1998; Stevenson 2000). Such emphasis was first challenged by the findings of Lambert (2002) in which seeds spit by *Cercopithecus* monkeys had significantly higher germination rates than seeds that had fallen unprocessed to the forest floor. My study (Chapter 2) and that of my master's work (Gross-Camp & Kaplin 2005) suggest similarly; seed dispersal via defecations is not representative of a frugivore's dispersal services. We must include the fate of orally-discarded seeds (i.e. spit or wadged) in order to determine a primate's effectiveness as a seed disperser as well as improve our understanding of their contribution to forest regeneration processes.

Future research

The results of my research highlight a couple potential avenues for future research. In chapter one, I discussed the absence of seed dispersal for the mature forest

tree species *Parinari excelsa,* describing possible reasons for my observations namely, the absence of elephants. Additional research on the frugivores dispersing the seeds of *P. excelsa* and its distribution may lend insight into how the loss of large-bodied frugivores impacts the regeneration and distribution of the species they dispersed.

In my first three chapters, I discuss the high quality dispersal of *Syzygium guineense* seeds by chimpanzees and chimpanzees' regular, and almost exclusive, consumption of *S. guineense* fruits for several months a year. The importance of *S. guineense* fruits to chimpanzees' diet is further supported by the positive relationship between *S. guineense* fruit availability and seed presence in chimpanzee feces (Chapter 3). Investigating the relationship between chimpanzees and their dispersal of *Syzygium guineense* seeds may help to describe the importance of *S. guineense* to the diet and continued survival of chimpanzees in the Nyungwe National Park.

Non-traditional aspects of the doctoral degree

In developing my dissertation proposal I wanted to incorporate activities that would enable me to engage a larger community of people beyond the realm of academia. I viewed the inclusion of these opportunities as personally desirable but equally important, an ethical obligation; my dissertation work was based in a developing country where very few individuals have access to education let alone at the graduate level. I firmly believe that the future of Rwandan's biodiversity lie not in the data generated from studies like my own but the perception and commitment of Rwandans to its protection.

With the encouragement of my committee members, I incorporated two additional aspects to my dissertation including mentoring two Rwandan University students and the

organization of a workshop (Chapter 4) using my research as a case study and involving

educators from communities living on the border of the Nyungwe National Park (NNP).

Both aspects required significant additional work on my part including securing the funds

to make it possible and developing relationships with individuals working in Rwandan

conservation. The opportunity to interact with the University students gave me a deeper

understanding of the difficulties associated with obtaining a higher degree in Rwanda and

brought me closer to the people whose country I was privileged to work in. I believe this

opportunity contributed to my ability to work as a conservation scientist and helped me to

develop greater empathy and insight into the complexities of conservation and

development that are so often discussed in isolation of one another. Furthermore the

opportunity to work with Rwandan conservation practitioners and educators in the

workshop connected me to the individuals whose lives would be most affected by

management protocols developed from my research findings. These interactions were

professionally significant as well creating a network of individuals and organizations that

I can now consider myself a part of and holds the potential to lead to additional

conservation work. Aspects like these are increasingly recognized in their ability to help

prepare graduate students like myself for the workforce (COSEPUP 1995; Noss 1997 ;

Duderstadt 1999; Golde & Gallagher 1999; Cannon et al. 2003; Zarin et al. 2003; Kainer

et al. 2006). I am grateful to my committee members for their support and encouragement

to include these aspects and believe that they have strengthened my competitiveness in

the conservation arena and ability to succeed in an increasingly interdisciplinary field.

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