

Chimpanzee (*Pan troglodytes*) Seed Dispersal in an Afromontane Forest: Microhabitat Influences on the Postdispersal Fate of Large Seeds¹

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ABSTRACT

We examined the postdispersal fate of large seeds (≥ 5 mm) dispersed by chimpanzees in an afromontane forest to evaluate aspects of the effectiveness of seed dispersal by chimpanzees, *Pan troglodytes*. We assessed the influence of six microhabitat characteristics on seed persistence and germination in seeds dispersed in chimpanzee feces and “wadges.” A total of 257 fecal samples and 56 wadges were located over a 4-mo period by tracking a semi-habituated chimpanzee community on day follows. Forty-nine (19.1%) of the fecal samples contained large seeds from five different tree species. The majority of fecal samples with seeds contained seeds from the mature forest tree *Olea capensis* (Oleaceae) (83.7%). Forty-two wadges (75%) contained seeds from the mature forest tree *Syzygium guineense* (Myrtaceae). Seeds were monitored at their deposition site for removal and germination up to 49 d following deposition. We collected data on the microhabitat surrounding each fecal and wadge sample. Multivariate analyses indicated that while fecal and wadge samples were not clustered into particular microhabitats, there was little overlap in the microhabitats in which wadges and fecal samples were deposited. Significantly more seeds persisted over 49 d in wadges (67.9%) than in feces (30.3%). Elevation was the only microhabitat variable determined to have a significant influence on seed persistence, whereas slope was determined to have a significant influence on germination.

RÉSUMÉ

Le destin des graines des grandes tailles (≥ 5 mm) qui sont dispersées par les chimpanzés, *Pan troglodytes*, dans une forêt ombrophiles de montagne fut étudié pour déterminer l'influence des six microhabitats sur l'habilité des graines de survivre et germer. Deux cent cinquante-sept échantillons des matières fécales et 56 “wadges” ont été trouvés en suivant journalièrement pendant quatre mois un groupe de chimpanzés semi habitués à la présence humaine. Quarante-neuf (19.1%) échantillons des matières fécales contenaient des larges graines provenant de 5 espèces d'arbres. La majorité des échantillons des matières fécales avec graines (83.7%) contenaient les graines d'une espèce d'arbre mature de la forêt *Olea capensis* (Oléacées). Quarante-deux wadges (75%) contenaient seulement des graines d'une espèce d'arbre mature de la forêt *Syzygium guineense* (Myrtacées). Les enlèvement et germination des graines ont été surveillées sur le site de déposition durant 49 jours suivant la déposition. En plus, nous avons récoltées des données sur les microhabitats environnant chaque échantillon des matières fécales et wadges. Les analyses multivariées ont indiquées que pendant que les échantillons des matières fécales et wadges n'étaient pas groupés dans des microhabitats particuliers, il y avait quelque empiètement entre les microhabitats qui recevaient les wadges et les habitats qui recevaient les échantillons des matières fécales. La proportion des graines persistant jusqu'au 49^{ème} jour était différente pour les échantillons des matières fécales et des wadges, 30.3% et 67.9% respectivement. L'élévation était la seule variable du microhabitat qui avait une importante influence sur la persistance des graines. La pente étaient le seule variable du microhabitat qui ont eu un effet important sur la germination des graines.

Key words: montane rain forest; *Pan troglodytes*; postdispersal fate of large seeds; Rwanda; seed dispersal; seed handling; wadging.

PRIMATES ARE IMPORTANT CONTRIBUTORS TO FOREST PROCESSES through their seed dispersal behavior (Lieberman *et al.* 1979, Julliot 1996, Chapman & Onderdonk 1998, McConkey 2000, Kaplin & Lambert 2002, Lambert 2002, Balcomb & Chapman 2003). In Africa, some of the largest forest frugivores are great apes (Pongidae), which play a significant role in the initial distribution of seeds (Lambert 1999; Voysey *et al.* 1999a,b). Common chimpanzees (*Pan troglodytes*) facilitate the wide distribution of seeds through the consumption of large quantities of fruit, tendency to swallow and not masticate large seeds (≥ 5 mm), long gut retention times, and large home ranges that promote long-distance dispersal away from underneath the parent crown (Chapman & Wrangham 1993; Wrangham *et al.* 1994; Lambert 1999, 2002). Gut passage in primates can speed germination time for some species (Lieberman *et al.* 1979, Estrada & Coates-Estrada 1986, Idani 1986, Wrangham *et al.* 1994). Distribution of seeds away from the parent crown may enhance seed survivorship by (1) reducing intraspecific

competition for spatially restricted resources and lowering the risk of mortality due to host-specific pathogens and seed predators (escape hypothesis); (2) promoting the colonization of open habitats (colonization hypothesis); and (3) directing dispersal to nonrandom locations where seeds will predictably survive better than in random sites (directed dispersal hypothesis) (Howe & Miriti 2000, Wenny 2001).

Relatively few studies have examined the role of chimpanzees in seed dispersal processes (but see Chapman & Wrangham 1993, Wrangham *et al.* 1994, Lambert 1999). In particular, determining the fate of chimpanzee-dispersed seeds is critical for assessing disperser effectiveness and thus, the overall contribution of dispersers to forest processes (Garber & Lambert 1998). Schupp (1993) describes the effectiveness of a disperser according to *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. Although some studies report that chimpanzees play an important role in forest processes by depositing large quantities of seeds into microsites suitable for both germination and establishment (Wrangham *et al.* 1994) and by using degraded or disturbed

¹ Received 24 May 2004; revision accepted 18 March 2005.

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forest (Fimbel 1994, Plumptre & Reynolds 1994, Hashimoto 1995, Chapman & Lambert 2000), these studies lack quantitative information on the effect of defecation site on germination and seedling establishment and therefore may miss important implications for seedling recruitment and forest regeneration.

Prior primate seed dispersal studies have focused on the content and fate of seeds dispersed through defecations and largely ignored seeds dispersed through spitting or in the case of the chimpanzee, wadging (Chapman 1989, Corlett & Lucas 1990, Wrangham *et al.* 1994, Julliot 1996). Recent studies on *Cercopithecine* monkeys, however, have demonstrated the significance of seed spitting on seed persistence and germination (Lambert & Garber 1998, Yumoto *et al.* 1998, Lambert 2001, Kaplin & Lambert 2002). The term “wadge” was developed by Goodall (1986) to describe the orally discarded fruit mass composed of pulp, skin, fiber, and seeds that chimpanzees create following consumption of some fruit species. By maneuvering the fruit in their lower lip, chimpanzees extract the juices and often discard the seeds intact (Lambert 1999). The emphasis on seed swallowing has been justified by the finding that swallowing seeds increases the likelihood of dispersion away from the parent tree where seeds are predicted to experience reduced mortality (Janzen 1970, Connell 1971). Furthermore, swallowing seeds improves germination rates for some seed species (Lieberman *et al.* 1979, Estrada & Coates-Estrada 1986, Idani 1986).

This study examines the postdispersal fate of large seeds deposited by chimpanzees in Nyungwe National Park, a tropical montane forest in Rwanda, by monitoring seed persistence and germination through time at the site of deposition. We chose to focus on chimpanzee seed dispersal given their seed-handling behaviors and status as the largest remaining frugivore in the park (Plumptre *et al.* 2002). We further limit the scope of our study to large-seeded tree species (≥ 5 mm) given the correlation of fruit and seed size with body size of vertebrate frugivores (Janson 1983, Gautier-Hion *et al.* 1985, Howe 1989), the likelihood that larger species play a significant role in the dispersal of large-seeded tropical trees (Terborgh 1988, Wrangham *et al.* 1994, Chapman & Chapman 1995), and the tendency for hunters to target large-bodied species (Redford 1992). We speculate that the loss of large-bodied frugivores such as the chimpanzee may change forest structure and diversity by reducing dispersal and recruitment patterns of certain tree species.

The specific research question of this study was: Are there differences in the persistence or germination of seeds between the microhabitats in which chimpanzees deposit seeds? Seeds dispersed in wadges and in defecations were monitored. Our selection of microhabitat characteristics was based on prior research that identified microhabitat influences on seed persistence and germination (for more details, see Howe *et al.* 1985, Wenny 2000 for canopy cover; Kiltie 1981, Kitchings & Levey 1981, Schupp *et al.* 1989, Hulme 1993, Levine & Murrell 2003 for vegetation density and distance to the nearest fallen log; and Janzen 1970, Howe & Smallwood 1982, Schupp 1988 for distance to an adult conspecific). This is the first study to examine in detail the ecological importance of chimpanzee seed dispersal in a montane environment by following

the persistence and germination of dispersed seeds at the site of deposition.

METHODS

STUDY SITE.—We conducted this research between August 2002 and January 2003 in the Nyungwe Forest National Park ($2^{\circ}15'–2^{\circ}55'S$, $29^{\circ}00'–29^{\circ}30'E$) located in southwestern Rwanda. This 1013 km² forest is adjacent to Kibira National Park, Burundi, and forms one of the largest contiguous blocks of lower montane forests in Africa (Vedder *et al.* 1992). The Nyungwe Forest is part of the Albertine Rift, an area recognized for its high proportion of endemic plants and animals. Although Nyungwe Forest is less species rich than other forests in the Albertine Rift (Omari *et al.* 1999), it sustains over 260 tree and shrub species (24 of which are endemic), 260 bird species, and 13 primate species. The chimpanzees of the Nyungwe Forest National Park represent a unique high elevation population in which individuals were observed to move as high as 2750 m above sea level (ASL) during the course of this study. Previously, chimpanzees had been observed to travel up to 2600 m (Basabose 2004), thereby making the Nyungwe community one of the highest elevation chimpanzee groups yet recorded.

The Nyungwe Forest has a challenging landscape (1600–2950 m ASL) containing a variety of habitats including secondary growth, closed canopy mature forest, natural open areas of herbaceous vegetation, and regenerating areas such as landslides, burned areas, and gold-mined valleys (Kaplin & Moermond 1998). There is relatively little daily temperature fluctuation with an average minimum of 10.9°C and an average maximum temperature of 19.6°C (Sun *et al.* 1996). The forest experiences one major and one minor rainy and dry season during the year with a mean annual rainfall of 1744 mm. Sun *et al.* (1996) describe a peak in fruiting during the major rainy season in March through May and during the major dry season of July through August, although fruits were also available in other months. Reduction in fruit production occurred in the beginning of each year during the minor dry season.

SEED DISPERSAL.—The partially habituated chimpanzee group was followed 5 d a week for a period of 4 mo from August through November 2002. Follows usually lasted from 7 to 9 h/d. Although direct observations of the animals were limited due to the rugged terrain, dense vegetation, and incomplete habituation of the chimpanzees to our presence, we were able to locate fecal and wadge samples as the group moved through the forest. In order to minimize our disturbance of their behavior and increase the probability of finding recently deposited fecal and wadge samples, we entered the forest early in the morning to locate the chimpanzees before they left their night nests. We remained at a distance, observing them through binoculars until the group moved off. In several instances, the chimpanzees climbed down to the forest floor, creating multiple trails. Once the animals left the area, we searched for feces and wadge samples. When the animals left their nests, we searched each trail they created for feces and wadge samples to ensure an accurate portrayal of the microsites where chimpanzees were dispersing seeds.

Once we exhausted our search of an area, we relocated the chimpanzee group by locating and following a single trail. Our study only included fecal samples deposited within 24 h, which we assessed following White and Edwards (2000), *i.e.*, no discoloration, warm, and absence of any malformation due to seed predator or secondary disperser activity.

When a chimpanzee feces or wadge containing seeds was encountered, it was marked with surveyor's tape, and the following data were recorded at the site of deposition: (1) identification of large seeds (≥ 5 mm) to family and species; (2) number of seeds per tree species; and (3) quality of seed handling. The latitude and longitude of each wadge or fecal unit was recorded using a Garmin II⁺ GPS unit (accuracy ± 100 m; Dominy & Duncan 2001) to facilitate relocation of the specimen on subsequent days. Fecal and wadge samples were temporarily transferred to a plastic plate, where they were easier to dissect but were reformed after the data were recorded, returned to the original site of deposition, and monitored for seed removal and germination on a weekly basis for the first 6 weeks, then every 2 weeks for 6 weeks, then monthly thereafter for the duration of the study (Rogers *et al.* 1998). The ultimate fate of the seeds removed from the fecal or wadge samples was not determined due to the time frame of this study; this information is important to consider given the findings of other studies in which secondary dispersal was found to enhance seed persistence and germination (Estrada & Coates-Estrada 1991, Andresen 1999, Feer 1999, Andresen & Levey 2004). In our study, however, we presumed that all seeds removed were dead (following Forget *et al.* 1998, Lambert 2002, Balcomb & Chapman 2003). We therefore likely underestimated the number of persisting or germinating seeds dispersed by chimpanzees, as we did not account for seeds that may have germinated as a result of secondary dispersal. Seeds damaged as a result of insect boring or pathogen activity were scored as "broken" and considered no longer viable. Seeds were scored as "germinated" after the emergence of one set of leaflets.

CHARACTERIZING THE MICROHABITAT.—To determine whether chimpanzees deposit seeds into distinct microhabitats where they may experience different rates of persistence and germination, we measured a series of variables to characterize the microhabitat in which chimpanzee deposited seeds were found. These variables included (1) percent of canopy closure with the use of a spherical densiometer (Lemmon 1957); (2) herbaceous vegetation coverage within a 1 m² area of the feces or wadge; (3) distance to nearest fallen log (≥ 10 cm in diameter) within a 30-m distance; (4) distance to nearest adult conspecific of each tree seed species found in a given pile within 50 m; (5) slope measured over a 4-m distance in the north-south and east-west directions using the fecal pile or wadge as a central point; and (6) elevation using a Sun[©] altimeter (accuracy ± 30 m). Herbaceous vegetation coverage was estimated by placing four stakes in a 1 m \times 1 m area around each fecal or wadge sample using the sample as the central point. The plot was further divided into four equal squares and an estimation of the percent area covered by herbaceous vegetation in each subsquare calculated. The sum of the subsquares divided by four determined the vegetation coverage for a given sample. The following microhabitat variables

were log transformed due to unequal distributions: slope, herbaceous vegetation coverage, and nearest fallen log. Log-transformed variables were used in all analyses unless otherwise noted.

Cluster analysis (CA) and principal components analysis (PCA) were performed using PC-ORD to determine if chimpanzees deposited seeds into distinct microhabitats (McCune & Mefford 1999). We report the principal component loadings 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. We report the results from CA using hierarchical, polythetic, agglomerative clustering using *minimum variance* or *Ward's* grouping method. This method was chosen based on its recommendation as a good general-purpose linkage method (Gauch 1982).

MANOVA using dispersal method and all the microhabitat variables was performed to determine whether there is a significant difference between these variables. Additional 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 feces and wadge material. A Bonferroni correction was applied to control for the occurrence of type I errors in multiple testing (Quinn & Keough 2002).

EXPERIMENTAL SEED FATE STUDIES.—*Microhabitat effect.*—To determine the influence of microhabitat on persistence and germination of seeds deposited by chimpanzees, we placed seeds of *Olea capensis* (Oleaceae) in two habitat types where seed deposition by chimpanzees commonly occurred. *Olea capensis*, a mature forest species, was chosen based on its regular appearance in the chimpanzees' feces (seed = 9–13 mm long by 4–10 mm in width; Troupin 1982). In fact, *O. capensis* was the only tree species reliably found in chimpanzee feces throughout the entire study period. *Olea capensis* seeds were never found in a wadge. Ripe fruits were collected from an adult *O. capensis* tree and cleaned of pulp. Although seeds were cleaned of pulp in an effort to simulate handling by a chimpanzee, piles lacked a fecal component and the effect of stomach acid which may scarify seeds. Sixteen seed piles ($N = 63$ seeds/pile) were randomly placed in two generalized habitat types: *herbaceous open* characterized by terrestrial ferns with no or minimal overstory canopy cover ($N = 8$ piles) and *mixed primary forest* characterized by a high canopy cover and less dense understory vegetation ($N = 8$ piles). To minimize the influence of other fruiting adult conspecifics, piles were placed ≥ 50 m away from an *O. capensis* in fruit. The number of seeds per pile was based on 1 mo of data collection in which the mean number of seeds per feces was calculated ($N = 37$, mean \pm SD = 63.1 ± 9.5). Piles were monitored and microsite data recorded as for the fecal and wadge samples described up to 107 d. ANOVAs of habitat type and proportion of seeds persisting or germinating were used to determine whether seed persistence and germination differed between habitats. Additional ANOVAs were performed between habitat type and a single microhabitat variable to tease apart the differences between the *mixed primary* and *open herbaceous* microhabitats.

Germination trial.—In mid-September of the study, the presence of seeds in chimpanzee feces dropped to almost nothing. Concurrently, chimpanzees began to discard large, purple wadges entirely comprised seeds of the tree species, *Syzygium guineense* (Myrtaceae). *Syzygium guineense* has a circular fruit containing a single seed (13 mm; Kaplin *et al.* 1998) and is used by local people to treat dysentery (Hines & Eckman 1993).

We compared the germination rates of *S. guineense* seeds dispersed in chimpanzee wadges to undispersed fruit fallen from an adult tree. We created a small nursery in which both seeds found in wadges and intact, undispersed whole ripe fruit were planted. Undispersed fruits were collected from underneath an adult tree and examined for pathogen and insect damage. Intact fruits with no visible damage were assumed to contain viable seeds. Seeds dispersed through chimpanzee wadges were collected from undisturbed wadges less than 12 h old. All intact seeds were assumed to be viable. A single seed was placed in a small cup filled with forest soil on the ground. Seeds in wadges ($N = 50$ seeds) and intact fruit ($N = 50$ seeds) were placed on top of forest soil and gently pressed to mimic natural conditions of deposition. Some fruit matter from the wadge was included with the wadge-dispersed seeds only. Seeds were monitored for persistence and germination on a daily basis to day 59 at which time the experiment was terminated due to seed predation by squirrels.

All statistical analyses with the exception of the PCA and CA were performed using SAS JMP IN 4.0 (SAS Institute 2000). Parametric tests were used unless the data violated the assumptions of normality and equal variance.

RESULTS

SEED DISPERSAL.—A total of 257 chimpanzee fecal samples and 56 wadges containing a total of 2613 and 701 large seeds, respectively, were located between August and November 2002. The largest number of seeds found in a single feces and wadge was 248 and 56, respectively. Only 49 (19.1%) of the 257 fecal samples found contained large seeds (≥ 5 mm), and all of these samples were found in the first 2 mo of the study (Fig. 1). No large seeds were found in chimpanzee feces after September. Five large-seeded tree species were found in the fecal samples of chimpanzees, but never in combinations of more than two seed species (Table 1). The most common and abundant tree seed species in chimpanzee feces was from the canopy tree *O. capensis*; seeds of this species were found in 83.7 percent of the fecal samples that contained seeds ($N = 41/49$). Forty-two wadges (75%) were found to contain large seeds from a single tree species, *S. guineense*. *Syzygium guineense* seeds occurred in only seven fecal samples and were consistently low in number ($x = 2.9 \pm 2.3$ seeds per fecal sample).

CHARACTERIZING THE MICROHABITAT.—In the PCA of the microhabitat characteristics associated with seeds deposited by chimpanzees in wadges and feces, the first two components explained 56.4 percent of the total variance. The first multivariate axis (PC1) was characterized by positive loadings for slope, distance to the near-

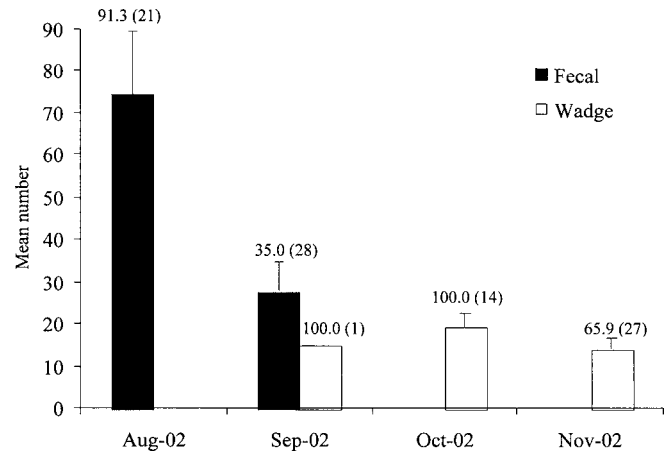


FIGURE 1. Mean number of fecal and wadge-dispersed large seeds by month with SE bars. Above each bar is the percentage of samples and number of samples containing seeds in parentheses.

est adult conspecific and vegetation cover, and negative loadings for elevation and canopy cover. The second principal component (PC2) was characterized by positive loadings for elevation, vegetation cover and distance to fallen log, and a negative loading for slope.

No distinct clumping patterns were apparent when mean loadings for PC1 and PC2 were plotted, suggesting that chimpanzees tend to distribute seeds to a variety of microhabitats with considerable overlap. When the two dispersion methods, fecal and wadge, are examined on a plot of the same principle components, however, a pattern emerged (Fig. 2). Mean loadings of defecated and wadge-dispersed samples differed significantly for PC1 (one-way ANOVA, $F_{1,59} = 63.9$, $P < 0.0001$), but not for PC2 ($F_{1,59} = 0.54$, $P = 0.47$). The mean MANOVA response between dispersal method, fecal or wadge, and all microhabitat variables was highly significant ($F_{5,55} = 0.86$, $P < 0.0001$). Additional analyses of dispersal method and a single microhabitat variable showed the difference was largely due to dispersal method and elevation, slope, and distance to a conspecific adult (Table 2). Relative to the defecations, wadge microhabitats were characterized by a lower slope, higher elevation, and a shorter distance to a conspecific adult.

Similar to the results of the PCA, fecal and wadge-dispersed seeds form two distinct groups in the cluster dendrogram indicating differences in the microhabitat variables associated with these two dispersal methods (data not shown).

POSTDISPERSAL SEED PERSISTENCE AND GERMINATION.—Seed persistence to day 49 was significantly higher in wadges than in feces (67.9%, range: 0–37 seeds, mean \pm SD: 11.9 ± 10.8 and 30.3%, range: 0–61 seeds, 2.5 ± 9.5 , respectively; one-way ANOVA, $F_{1,89} = 14.77$, $P = 0.0002$; Fig. 3a). Germination of seeds from fecal and wadge samples monitored where they had been deposited by the chimpanzees did not differ (one-way ANOVA, $F_{1,89} = 2.78$, $P = 0.1$; Fig. 3b).

TABLE 1. The five large-seeded species found in chimpanzee fecal and wadge samples.

Species name	Method of dispersal	% of samples containing seeds (N)	No. of samples found in combination of two species	Mean no. of seeds per sample ± SE (maximum)
<i>Allophylus</i> spp.	D	5.4 (5)	4	10.2 ± 4.5 (26)
<i>Olea capensis</i>	D	45.1 (41)	5	61.7 ± 9.7 (248)
<i>Sericanthe leonardii</i>	D	1.1 (1)	0	2.0 (2)
<i>Syzygium guineense</i>	D/W	7.7 (7)/46.2 (42)	1/0	2.9 ± 2.3/15.9 ± 2.1 (56)
Unknown species	D	1.1 (1)	0	1.0 (1)

D = defecated; W = wadged.

All samples, fecal and wadge, containing seeds were included in the calculation of this table (N = 91).

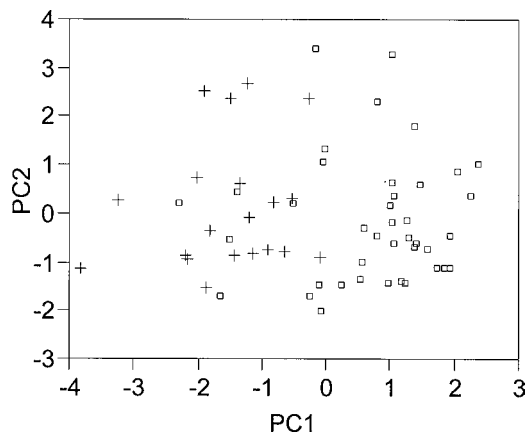


FIGURE 2. Plot of microhabitats on the first two axes determined by principal components analysis of the microhabitat variables (fecal = crosses and wadge = squares). Axis 1 is primarily a function of slope, distance to the nearest adult conspecific, vegetation cover, elevation and canopy cover, whereas axis 2 is primarily a function of elevation, vegetation cover, distance to fallen log, and slope.

TABLE 2. Summary of one-way analysis of variance tests for each microhabitat variable compared among samples dispersed via feces and wadge.

Variable	Feces	Wadge	F _{1,311}
Elevation (m)	2418.1 (98.2)	2488.0 (69.2)	25.62*
Slope	14.5 (9.0)	10.8 (8.2)	10.54*
Nearest adult conspecific (m)	15.9 (11.1)	9.7 (7.8)	7.52*
Herbaceous vegetation coverage (%)	20.3 (23.7)	20.5 (23.6)	0.17
Nearest fallen log (m)	5.1 (5.5)	6.4 (8.5)	0.01
Canopy cover (%)	79.7 (18.1)	84.2 (13.7)	3.01

Mean values are shown for each microhabitat variable before log transformation with the corresponding standard deviation in parentheses. Analysis was performed on log transformed data.

*Significance at *P* < 0.0001.

Due to collinearity between the microhabitat predictor variables as well as the complexity of interpreting a regression of the principal components and the probability that a seed will be removed and/or germinate, we performed regressions between a single microhabitat variable and the proportion of seeds persisting and

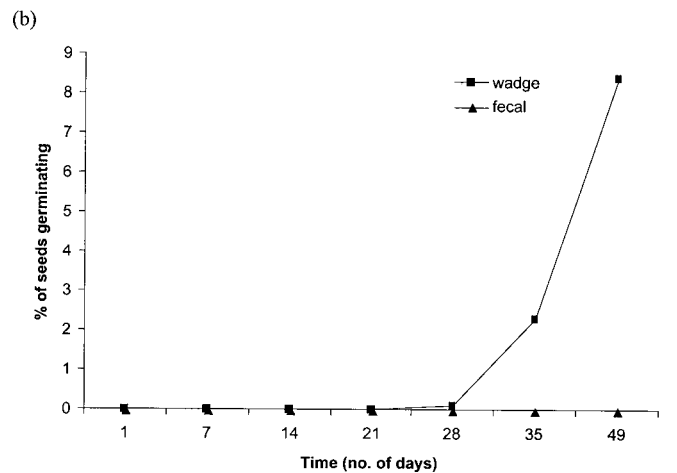
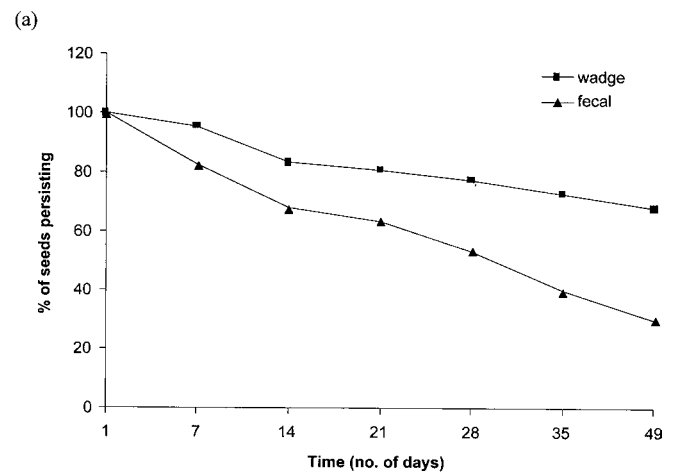


FIGURE 3. Proportion of seeds persisting (a) and germinating (b) through time in fecal versus wadges.

TABLE 3. Summary of one-way analysis of variance tests for each microhabitat variable compared among samples placed in mixed forest (MF) and open herbaceous (OH).

Variable	MF	OH	$F_{1,14}$
Elevation (m ASL)	2384 (5.2)	2365 (5.4)	50.8*
Slope	18.0 (4.0)	25.9 (5.8)	11.4*
Nearest adult conspecific (m)	14.3 (9.6)	23.0 (10.2)	3.1
Herbaceous vegetation coverage (%)	11.1 (10.0)	39.0 (23.6)	11.8*
Nearest fallen log (m)	2.3 (1.0)	NA	NA
Canopy cover (%)	85.7 (3.1)	43.7 (9.3)	145.7*

NA = not available.

Mean values are shown for each microhabitat variable before log transformation with the corresponding standard deviation below in parentheses. Analyses were performed on log transformed data.

*Significance at $P < 0.01$.

germinating at day 49. Regressions between a single microhabitat variable and the proportion of seeds persisting and germinating help to tease apart which variables are good predictors. We applied a Bonferroni correction to account for type I errors in multiple testing (Quinn & Keough 2002). Linear regressions between each microhabitat variable and the percentage of seeds persisting were significant for elevation only ($F_{1,86} = 18.72$, $R^2 = 0.18$, $P < 0.0001$). The proportion of seeds persisting in both feces and wadges increased with elevation. Slope was the only variable with a significant effect on the proportion of seeds germinating ($F_{1,85} = 11.42$, $R^2 = 0.12$, $P = 0.001$). The proportion of seeds germinated in deposition sites decreased with slope.

EXPERIMENTAL SEED FATE STUDIES.—Microhabitat effects.—The two habitat types in which seeds were placed, open herbaceous and mixed forest, differed significantly in all but two variables, distance to a conspecific adult and distance to a fallen log (Table 3). There were no fallen logs found in the open herbaceous area. The mixed forest habitat had shorter distances to a conspecific adult, higher canopy coverage, and lower herbaceous vegetation coverage and slope. The persistence of *O. capensis* seeds in the open herbaceous habitat was not significantly different from seed persistence in the mixed forest habitat at day 107 ($F_{1,14} = 0.99$, $P = 0.34$).

Germination trials.—Due to unanticipated seed removal by rodents, the germination trial of *S. guineense* had to be terminated at day 59. Twenty-six percent ($N = 50$ seeds) of the wedge-dispersed seeds had germinated by day 59, whereas no seeds in whole, intact fruits germinated. The majority of the dispersed seeds had split open and were showing signs of growth in contrast to the undispersed seeds in intact fruit whose skin had shriveled and began to discolor (Fig. 4).

DISCUSSION

The chimpanzees in this study dispersed seeds of mainly two large, mature forest tree species, although dispersal was not consistent

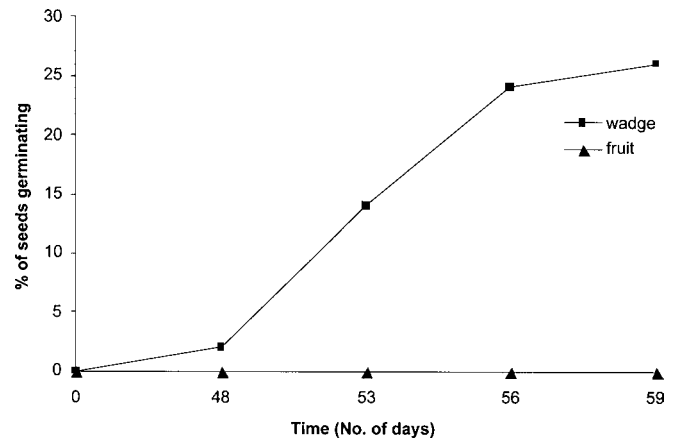


FIGURE 4. The proportion of *Syzygium guineense* seeds germinating in the germination trial. Seeds from chimpanzee wadges are indicated by squares ($N = 50$ seeds) and the undispersed seeds from ripe fruits are indicated by triangles ($N = 50$ seeds).

through time. During the first 2 mo of the study, *O. capensis* seeds were regularly found in chimpanzee feces. Feces were so full of *O. capensis* seeds that they would easily fragment when disturbed and were often difficult to reform due to the lack of fecal material. In September, large seeds in chimpanzee feces declined and were entirely absent through the months of October and November. The concurrent appearance of *S. guineense* wadges in September signified a change in chimpanzee seed dispersal behavior from swallowing to spitting seed. Such a shift in seed dispersal strategies may be attributed to fruit availability and seed and/or fruit characteristics such as fruit ripeness or seed shape (Chapman & Chapman 1996, Kaplin & Moermond 1998, Lambert & Garber 1998, Yumoto *et al.* 1998). For example, *O. capensis* fruits were hard and pulp adhered to the seed, which was ovate and elongate similar to a pill, whereas *S. guineense* fruits were soft and juicy and seeds were easily separated from the pulp. Chapman and Chapman (1996) speculate that pill-shaped seeds like *O. capensis* would encourage swallowing by frugivore dispersers but may be less likely than a round seed to be incorporated into a dung beetle's ball, thereby increasing the likelihood of germination and predator escape. In comparison, the rounded seeds of *S. guineense* were rarely found in feces and were predominantly dispersed in wadges. This dispersal method may be due to a combination of seed characteristics including the ease with which the seed is separated from the fruit and its relatively large size.

Wadged seeds showed a greater likelihood of persistence at the site of deposition than defecated seeds for some tree species. *Syzygium guineense* seeds deposited in chimpanzee wadges experienced significantly higher persistence rates than those of other species deposited in chimpanzee feces despite closer distances to an adult conspecific. In order to further examine this hypothesis, the seed persistence and germination of a tree seed species dispersed in both wadges and feces is necessary. However, observation of chimpanzee seed dispersal behaviors over the course of the year

(January 2003 through July 2004) did not reveal any other tree species regularly wadged, indicating that *S. guineense* may represent a species that is dispersed by a unique strategy (N. Gross-Camp, pers. obs.).

Independent of the material in which seeds are dispersed, seed removal may vary seasonally. In this study, seeds dispersed in feces were found and monitored during different months than those found in wadges. Therefore, differences in the proportion of seeds persisting may be attributable to seasonal fluctuations in predator and/or secondary dispersers as opposed to dispersal strategy or tree species characteristics. The complexity of multiple and synergistic interactions is a particular challenge for understanding postdispersal seed fate and is an area of increasing scientific inquiry (Andresen & Levey 2004).

The finding that seed persistence did not significantly differ between habitat types, mixed primary forest and open herbaceous, was contrary to prior research. In his review on postdispersal seed predation by small mammals, Hulme (1993) describes the tendency for rates of seed removal to decline with decreasing vegetation cover and small mammal abundance. In this study, the open herbaceous habitat differed from that of the mixed primary forest in that vegetation cover was significantly higher in the open herbaceous area (mean: 39.0 versus 11.1, respectively). The mixed primary forest habitat was characterized by an open understory with little vegetation (<1 m height) but was densely covered with leaf debris and tree boles that may serve as cover for small mammals and potential secondary dispersers and/or seed predators.

The results of the *S. guineense* seed germination trial further highlight the importance of wadging by chimpanzees for effective seed dispersal. In the germination trials, *S. guineense* seeds deposited in a chimpanzee wadge experienced higher germination rates than those seeds that had been planted as whole fruits. Seeds dispersed in chimpanzee wadges showed signs of germination, while the fruit skin surrounding the undispersed seeds in intact fruit had puckered and was showing evidence of pathogen attack. Lambert (2001) found seeds of *Strychnos mitis* (Loganiaceae) spit by *Cercopithecus ascanius* experienced higher germination and seedling establishment rates than those seeds that were dropped unprocessed from an adult conspecific. Her findings indicate the importance of *Cercopithecus* seed spitting in reducing seed mortality by mitigating the effects of fungal pathogens. Similarly, Yumoto *et al.* (1998) found *Myrica rubra* seeds processed in the cheek pouch of *Macaca fuscata yakui* experienced higher germination rates (94.3%) when compared to fruits deposited in feces (70.5%) and experimentally placed seeds harvested from intact fruits (68.3%) and seeds contained in whole intact fruits (51.7%). The results of these studies support the hypothesis that wadging may incur an advantage to seed persistence and germination at the site of deposition and thus appears to be a significant factor in our ability to assess the overall effectiveness of chimpanzees as seed dispersers (Schupp 1993, Basabose 2002, Lambert 2002). By focusing on seeds dispersed in chimpanzee feces, the importance of seed dispersal in wadges has been largely neglected and signifies an area of future research. This study highlights the importance of variation in disperser handling behavior with different fruit species.

This study also emphasizes the effects of elevation and slope on seed persistence and germination in montane forests. We found a higher proportion of seeds remaining at deposition sites with an increase in elevation, whereas a greater proportion of seeds germinated in deposition sites with lower slopes. Seeds deposited on a steep slope may be negatively affected by erosion or other disturbances. The increase in the proportion of seeds remaining at deposition sites with higher elevations may result from the loss of seed predators (Janzen *et al.* 1976) or secondary dispersers at higher altitudes. Harsher conditions at higher altitudes may exclude certain seed predators or secondary dispersers enabling seeds deposited into these areas to “escape” predation. There is a paucity of research on the role of secondary dispersers and seed predators in the Nyungwe Forest, representing an important research agenda to further our understanding of postdispersal seed fate in this ecosystem. The unique characteristics of montane communities, their relative scarcity, and historical importance as refuges for plant and animal communities, increase the need to understand the role of dispersers like the chimpanzee on forest dynamics (Vedder *et al.* 1992, Plumptre *et al.* 2002).

ACKNOWLEDGMENTS

We would like to thank the Rwandan Office for Tourism and National Parks (ORTPN) for their kind permission to conduct this research in the Nyungwe Forest National Park. The staff of the Nyungwe Forest Conservation Project (PCFN) provided generous support including Anastase Benimana, Jean-Baptiste Gakima, Ian Munanura, and Amida Umulisa. A special thanks is extended to Martin Nsengumuremyi whose help and friendship during our stay in Rwanda was priceless. We thank Simon Camp for his unwavering support and invaluable contributions to the success of this study. Additional thanks are extended to S. Gross and C. Gross, D. Feener, M. Masozera, and S. Torti who provided important guidance in the collection of data and preparation of the manuscript. Helpful comments on this manuscript were gratefully received from J.E. Lambert, D.E. Wenny, K. Vulinec, and two anonymous reviewers. We thank Dr. B. Hahn at the University of Alabama, Birmingham, for her helpful discussions. Funding for this study was obtained from grants from the American Society of Primatology, The Explorer's Club, Lincoln Park Zoo, and Primate Conservation, Inc. Additional support was received from the U.S. Environmental Protection Agency's Science to Achieve Results (STAR) program fellowship number 91618301. This paper is dedicated to the Rwandan field assistants who made the project a success: Fidèle Muhayeyezu, Augustin Mujyabwami, Abraham Ngiruwonsanga, and Innocent Semahoro.

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