Fragmentation and Alteration of Seed Dispersal Processes: An Initial Evaluation of Dung Beetles, Seed Fate, and Seedling Diversity[1]

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ABSTRACT

Given current accelerated trends of tropical land conversion, forest fragments are being incorporated into many conservation programs. For investing in fragments to be a viable conservation strategy, forest fragments must maintain their ecological integrity over the long term. Based on fieldwork in 22 forest fragments in the crater lakes region of western Uganda and in the continuous forest of Kibale National Park, we examined (1) seed predation on experimentally dispersed seeds, (2) abundance and composition of the dung beetle community that may play a major role in removing seeds from sites of high seed predation, and (3) compared the fragments' seedling community composition to adult tree community composition and the seedling community in continuous forest. First, the rate of seed removal at experimental stations was lower in forest fragments (85% remaining after 1 day) than at stations in the continuous forest (79% remaining) and the probability of stations being discovered by seed predators was lower in fragments (23%) than in the intact forest (41%). Second, there was a 62 percent decline in fragment dung beetle abundance. The magnitude of this decline varied among dung beetle guilds that process dung and seeds in different fashions. The abundance of large rollers that move large seeds away from sites of defecation did not differ, but medium and smaller rollers and burying beetles that process small and medium-sized seeds were less common in the fragments than in the intact forest. Finally, we compared the seedling community composition relative to adult tree community composition by identifying all adult trees in each fragment and by sampling the composition of the seedling community. We found some evidence to suggest that there was movement of seeds among forest fragments by large-bodied dispersers, particularly chimpanzees (*Pan troglodytes*) and hornbills (*Ceratogymna subcylindricus*).

Key words: Dung beetles; fragmentation; Kibale National Park; regeneration; rodents; seed dispersal; Uganda.

HUMAN MODIFICATION OF ECOSYSTEMS IS THREATENING BIODIVERSITY ON A GLOBAL SCALE (Laurance 1999, Nepstad *et al.* 1999, Chapman & Peres 2001). Modifications to tropical forests do not just result in forest being uniformly reduced in size; they also result in forest being fragmented. It is critical that we understand the conservation value of these fragments because less than 5 percent of tropical forests are legally protected (Oates 1996) and national parks and reserves, even if effectively protected, will fail to conserve species for which

ranges do not fall within a protected area. As a result, conservation of many tropical forest species will depend on the capacity of fragmented forests to support their populations.

For fragmented forest to have an important conservation value, they must maintain their ecological integrity sufficiently to maintain target species over the long term. This requires that (1) fragments are not further degraded by human activities and (2) ecological processes operating in fragments are maintained. With respect to the first requirement, unfortunately much of the previous work on fragmented habitats has involved the study of fragments in protected areas and has largely ignored

human use of fragments (Lovejoy *et al.* 1986, Tutin *et al.* 1997, Tutin 1999). In reality, most fragments are not protected; they are on land held by private citizens or local communities that depend on them for their livelihood. While these studies in protected reserves have provided us with many insights, they may have biased our perception regarding the value of forest fragments or they may not illustrate how ecological processes in fragments used by local landowners are altered by human use. Similarly, metapopulation theories proposed as a means by which fragmented populations may survive are based on the idea that random fluctuations in local populations cause local extinctions, and thus unoccupied fragments are available for recolonization (Hanski 1994, Hanski & Gilpin 1997). In forest fragments that are not protected, extinctions may be driven by increased levels of deforestation that degrade the habitat and make it unsuitable for wildlife. Once the fragments are deforested, they are used for agriculture and are not available for recolonization. Such limitations of metapopulation models have been previously recognized (Thomas 1994, Lawes *et al.* 2000).

The second requirement that must be met for fragmented forests to have an important conservation value is that important ecological processes in fragments need to be maintained (*e.g.*, seed dispersal, pollination; Didham *et al.* 1996). For example, stingless bees are important pollinators for species in as many as 30 plant families, and many species of orchids are obligately pollinated by one bee species. Powell and Powell (1987) demonstrated that fragmentation reduced visitation rates by male bees and that visitation rates declined with fragment size (see also Didham *et al.* 1996). Male bees of four deep forest species did not cross the 100 m clearing that separated the fragment from the continuous forest. Absence of these bees may be expected to decrease pollination rates in some plant species and may have cascading consequences for fruit set and forest regeneration.

We examined three aspects of forest regeneration in 22 forest fragments in the crater lakes region of western Uganda and compared them to the continuous forest of Kibale National Park. First, we examined the initial fate of dispersed seeds (after 24 hours) and compared the rate of seed disappearance in each fragment relative to that in the nearby continuous forest. While seed removal can vary tremendously over time, comparing removal after 24 hours provides a relative index of predation pressure.

Second, we quantified the abundance and composition of the forest fragment dung beetle community, since these animals can influence the fate of seeds dispersed in dung and thus the nature of forest regeneration (Klein 1989, Hanski 1991, Halffter *et al.* 1992, Shepherd & Chapman 1998, Vulinec 2002). Many post-dispersal events can have a profound influence on the survival of dispersed seeds. By incorporating seeds in the dung that dung beetles process for consumption and oviposition, dung beetles can enhance seed survival if they remove seeds from areas of high predation risk and place them in locations that avoid subsequent predation and are suitable for germination (Hanski 1991; Feer 1999; Andresen 2001, 2002). While it would be useful to know how fragmentation affects all seed dispersers, secondary dispersers, and predators, the dung beetle community can be relatively easy to describe. In contrast, many of the other animals involved in the seed dispersal/predation process (*e.g.*, primates, large birds) are known to move among fragments, making even describing their presence in a fragment difficult.

Finally, we compared the composition of the seedling communities relative to the adult tree communities. By identifying all adult trees in fragments, we evaluated the possibility that seeds are transported between fragments by long-distance dispersers. For those species of seedling that were found in the fragments, but for which there were no adults present, we evaluated whether or not the species were known to be dispersed by the two species of large frugivores that frequently move among fragments.

METHODS

STUDY SITE.—This study involved 22 forest fragments neighboring Kibale National Park, Uganda (766 km^2; 0°13′–0°41′N, 30°19–30°32′E; Chapman *et al.* 1997, Chapman & Lambert 2000) that were surveyed between May 2000 and May 2001. Kibale is a mid-elevational moist evergreen forest that receives *ca* 1749 mm of rainfall annually (1990–2001; C. A. Chapman & L. J. Chapman, pers. obs.). Prior to agricultural clearing, continuous forest existed throughout the study region, but the unprotected area has largely been deforested and is now dominated by smallholder agriculture.

The forests and wildlife of western Uganda have long been influenced by human activities, but these activities have dramatically intensified over the past 50 years (Howard 1991, Naughton-Treves 1999). Pollen records suggest that forest clearing began in Uganda at least 1000 years ago with the

introduction of agriculture and iron making (Hamilton 1974, 1984). By the end of the 20th century, nearly all forest outside of officially protected areas had been converted to farms, grazing areas, or tea plantations (Naughton-Treves 1997). Only small pockets of forest remain in areas unsuitable for agriculture. While the precise timing of when these forest remnants became isolated is not known, local elders describe them as "ancestral forests" (Naughton, pers. comm.). Aerial photographs from 1959 indicate that most remnant patches have been isolated from Kibale at least since that time, although many have decreased in size. Human population density surrounding Kibale has increased seven-fold since 1920, and surpasses 272 individuals/km² at Kibale's western edge (vs. 92/km² for the district; NEMA 1997). The fragments we studied provide multiple resources to local citizens, including medicinal plants, human foodstuffs, animal fodder, building material, and most importantly, fuelwood. The fragments are typically surrounded by small-scale agriculture, but in a few cases are surrounded by tea plantations.

FRAGMENT CHARACTERISTICS.—We examined if rates of seed removal and seed removal traits of the dung beetle community were related to characteristics of the fragments: size, degree of degradation, fragment type, and primate community supported. We measured the size of each fragment by taking GPS readings at different locations on fragment edges or by measuring fragment perimeters with a 50 m tape (Onderdonk & Chapman 2000). Degree of degradation was indexed as the density of stumps found in each fragment. Fragments were designated as one of three types: crater lakes, hillside, or valley bottom. Crater lake and hillside fragments were similar in that they were forests on steep hills or sides of explosion craters; for analyses they were considered together. Valley-bottom fragments had some swamp vegetation associated with their lowest levels. Since primates are some of the few remaining large mammals in the fragments and deposit considerable amounts of dung each day, we determined which primate species were present through observations made over 24 hours in each fragment. For each group of black-and-white (*Colobus guereza*) and red colobus (*Procolobus badius*), we determined their size and composition (following Oates 1974). From long-term research at one fragment (Lake Nkuruba; Chapman *et al.* 1998), we knew that redtail monkeys (*Cercopithecus ascanius*) and chimpanzees frequently moved among fragments (*i.e.*, they used multiple fragments during the week;

Naughton-Treves *et al.* 1998). In contrast, the colobines will show greater site fidelity and rarely move among fragments (*i.e.*, only to colonize a new fragment). As a result, it is very difficult to determine the amount of time chimpanzees or redtail monkeys spend in any particular fragments and these species were not considered.

SEED FATE.—To evaluate how fragmentation influences rates of seed removal, most likely by rodents, which are seed predators, we established 20 seed removal stations 5 m apart along a transect through a forested segment of the fragment on a single occasion at each of the 22 fragments. At each station, five *Diospyros abysinnica* (Ebenaceae) seeds, from which the pulp was removed to mimic seed processing by frugivores (Lambert & Garber 1998), were placed on top of the leaf litter in a slight depression. Seeds were placed in a depression to prevent/reduce the chance that they would be washed away by rain. *Diospyros abysinnica* seeds are hard (require 14.5 kg/mm² pressure to penetrate the seed coat), *ca* 0.75 cm long, 0.59 cm wide (Chapman *et al.* pers. obs.; Hamilton 1991), and have a seed mass averaging 0.115 g (Zanne 2003). The fruits are initially black in color, but upon ripening turn yellow and finally red (Hamilton 1991). The tree is abundant in both the natural forest (40 individuals/ha > 10 cm DBH [diameter at breast height]) and in the forest fragments and fruits regularly (Chapman *et al.* pers. obs.). This species was selected because it is a common species, seeds are intermediate in size (*i.e.*, dispersed by large birds and mammals), and seeds were readily available. We recorded the number of seeds remaining after 24 hours. This is one index of seed removal, and because seed removal can vary tremendously over time, examining removal at a different time frame may produce different patterns. This index, however, should be a relative index of predation risk that can be compared to the one in the continuous forest.

Seed removal is influenced by season (Chapman 1989); thus to control for this, removal rate for each fragment was evaluated relative to that in the intact forest of Kibale National Park. Each month, two similar transects were established in the national park, each with 20 stations in which five *D. abyssinica* seeds were placed. The location of the transects was varied each month, and we attempted to include the habitats found in the fragment being evaluated in proportion to their availability (*e.g.*, hillside, valley bottom). We reported differences between the average removal rate among the 40

forest stations and 20 fragment stations and the probability that stations were discovered in the two settings.

DUNG BEETLE COMMUNITY.—Beetles were surveyed using baited pitfall traps set at 5 m intervals along a route though a forested section of each fragment (following Vulinec 2002). Traps were baited with *ca* 25 cc of cattle dung. We set 20 traps each survey; these were collected after 24 hours. Contents of the traps at each fragment were pooled. As with seed removal, the dung beetle community likely experiences seasonal changes in abundance and composition; thus, dung beetle abundance and guild structure for each fragment was evaluated relative to that in continuous forest of Kibale National Park. Each month, a similar route was established in the national park with 20 stations. We reported differences between the average dung beetle abundance and guild structure among 20 forest stations and 20 fragment stations. It should be noted that not all dung beetles are attracted to fecal material (Davis & Sutton 1997, Estrada *et al.* 1998, Davis *et al.* 2001); thus we only compared that component of the community that could be captured with such traps. In addition, while some dung beetles have been recorded as traveling long distances in relatively short periods (*e.g.*, 1 km in 2 days; Peck & Forsyth 1982), many other species have movements restricted to their original habitat (Halffter *et al.* 1992). Thus, it seems likely that as long as the community of mammals providing dung remains stable, the community structure will remain stable.

Dung beetles were stored in alcohol and transported to Delaware State University, where they were identified to species or morphotyped. Morphotypes that could not be identified were sent to taxonomic experts for identification. Species were placed into one of five categories following Doube (1990) and Vulinec (2002), depending on how they handle dung and seeds. (1) These were very large (>400 mg) diurnal rollers (telecoprids) that removed dung quickly, usually within three hours (Doube 1990), and rolled it away to bury in relatively shallow burrows. Although these beetles may remove seeds from the dung and leave them at the surface of the soil, they typically move and bury seeds (Vulinec 2002). (2) This category included smaller (<400 mg) diurnal rollers that removed dung quickly, usually within two to three hours, and rolled it away (Doube 1990). These species were probably not as effective as category 1 species, especially for large seeds greater than 10 mm (Vu-

linec 2002). (3) These were fast-burying (within 6–24 hours) burrowers (paracoprids), which were medium- to large-sized crepuscular/nocturnal beetles (Doube 1990). These species frequently buried even large seeds. While they may bury some small seeds (<10 mm) too deeply for germination (Shepherd & Chapman 1998), they buried many seeds and were effective at getting a large amount of dung underground quickly away from potential seed predators (Vulinec 2002). (4) This category included slower-burying (up to six weeks) burrowers that were medium to large (>10 mg) and were active throughout the day and night (Doube 1990). These species were less effective at seed burial and would only bury small to medium seeds; they did not do so quickly and seeds may have been more vulnerable to rodent predation (Vulinec 2002). A few species in this group only shredded dung and did not bury it. (5) These were very small burrowers (<10 mg) that did not typically bury dung but only shredded it. They were active at all times of the day and night. When they did bury dung, they only buried it shallowly at the site of deposition; so if they did bury small seeds, rodents attracted to dung could easily find them.

ADULT TREE AND SEEDLING TREE COMMUNITY.—In each fragment, we identified and measured all trees greater than 10 cm DBH. When trees were on extremely steep sides of craters, their sizes were visually estimated (error in visual estimation = ±3.7%, $N = 46$). Two fragments were around crater lakes with sides that were too steep to navigate in several places; thus to determine tree and stump density, ten 60 × 10 m transects were systematically placed around the rim of the crater in locations where it was possible to traverse the sides. One fragment was too large to enumerate all trees and many sections were inaccessible, and tree density was not evaluated. The density of trees within unfragmented forest was estimated from 24 transects (200 × 10 m) established at four sites in Kibale National Park, which were separated by *ca* 12 km each along the north–south axis of the park (Sebatoli, Kanyawara K30, Dura River, Mainaro; Chapman *et al.* 1997). We also counted all tree stumps within the fragments that remained after trees had been removed. We were careful to search through vine tangles and dense herbaceous vegetation in search of hidden stumps.

To evaluate the composition of the tree community recruiting into each forest fragment, we identified and measured the height of all tree seedlings that were in twenty 1 × 1 m plots placed

along a third transect in a forested section of the fragment. Trees that were 1 m tall or less (including individuals with only cotyledons) were considered "early recruits," while trees between 1 and 5 m tall were regarded as "late recruits."

To make an initial evaluation of the possibility that seeds were transported among fragments by long-distance dispersers such as chimpanzees (*Pan troglodytes*) and hornbills (*Ceratogymna subcylindricus*), we determined how many tree species were represented only by young recruits (*i.e.,* but for which adult trees were not found) in the fragment and considered this in light of detailed studies on the seed dispersal abilities of these two species (Kalina 1988, Wrangham *et al.* 1994). For this analysis, the three fragments in which all trees had not been enumerated were not considered. Categorization of plants by disperser type followed Zanne (1998), while the categorization of habitat preference followed Katende *et al.* (1995), Hamilton (1991), Eggeling and Dale (1951), and Zanne (2003).

STATISTICAL ANALYSIS.—Seed removal rates and dung beetle community composition likely vary seasonally. To control for this, the values obtained for each fragment were evaluated relative to that in the continuous forest of Kibale National Park and we reported differences between the average values among the forest and fragment stations (*i.e.,* stations were not considered independent but fragments were) using a paired *t*-test in which samples were paired by date. To provide an initial evaluation of possible predictors of the parameters we estimated (*e.g.,* can differences in the number of dung beetles captured between fragments and continuous forest be predicted by the number of colobus monkeys providing dung?), we used correlations. If there were a number of possible predictors, we attempted to construct the best possible predictive model using forced entry multiple regression. When it was necessary to normalize the residuals, variables were log transformed.

RESULTS

SEED FATE.—The number of seeds remaining at seed stations after 24 hours was typically greater in forest fragments (85% remaining; $\bar{x} = 4.26$, SD = 0.58) than in intact forest (79% remaining; $\bar{x} = 3.94$, SD = 0.31, paired by date to control for seasonal effects $t = 2.58$, $P = 0.018$; Table 1). Similarly, the proportion of stations that had seeds removed was greater in the forest ($\bar{x} = 41\%$ of

stations had some seeds removed; SD = 16.9) than in the fragments ($\bar{x} = 23\%$, SD = 15.50, paired *t*-test, $t = -5.43$, $P < 0.0001$). Difference in number of seeds removed within 24 hours in fragments and those removed in intact forest at approximately the same time was not related to fragment size ($r = 0.283$, $P = 0.215$), tree density ($r = -0.11$, $P = 0.964$) or degree of degradation as indexed by stump density ($r = 0.216$, $P = 0.346$). An overall multiple regression model considering each of these variables (fragment size, tree density, stump density) did not predict a significant proportion of the variation in the difference in the number of seeds removed ($R^2 = 0.550$, $P = 0.115$). Similarly, seed removal rates did not differ among fragment types ($t = -0.446$, $P = 0.661$).

DUNG BEETLE COMMUNITY.—In total, 1921 beetles were collected, morphotyped, and assigned to a seed handling category. On average, traps attracted 25 dung beetles in fragments (SD = 39.2), while traps in the forest attracted 65 dung beetles (SD = 46.8; paired by date to control for seasonal effects $t = -3.00$, $P = 0.007$). Differences in beetle abundance among fragments and the intact forest varied depending on their seed handling category (Fig. 1). In general, there were no differences in the abundance of large rollers (category 1) that moved large seeds away from sites of defecation, but significant differences or marginal differences existed in the abundance of species that rolled medium-sized seeds away from defecation sites (category 2) or buried larger seeds at the site (categories 2 and 4; Fig. 1).

We collected 27 dung beetle morphotypes in total: 24 morphotypes in the continuous forest and 16 in the fragments. There were 11 morphotypes found only in the continuous forest. The richness of the dung beetle community was greater in the continuous forest (mean no. of morphotypes caught per sampling period = 6.5) than in the forest fragments ($\bar{x} = 3.6$; $t = 5.446$, $P < 0.001$).

The difference in number of dung beetles captured within 24 hours in fragments and those caught in intact forest at approximately the same time was correlated with colobus monkey number ($r = 0.435$, $P = 0.043$). This was driven primarily by declines in beetle numbers from seed handling category 2 (medium rollers: $r = 0.469$, $P = 0.028$; other seed handling categories were not significant). Differences between fragments and intact forest in the number of beetles (total and by category) were not related to the size of the fragment, the degree of fragment degradation (as indexed by

TABLE 1. *A description of fragments studied near Kibale National Park, Uganda, and characteristics of the tree communities found in those fragments. In addition, we present information on differences in the number of seeds removed from seed station in fragments versus in the peak (5 seeds per station). The column "Unique Seedlings" represents the number of seedlings found that did not have adults of that species in the fragment (this could not be done for the two Nkuruba fragments).*

Fragment	Size (ha)	Fragment type	Distance to Kibale (km)	Nearest fragment (m)	Trees/ha	Tree species/ ha	Stump density (no./ha)	Difference in seed removal	Early recruits (no./ha)	Late recruits (no./ha)
Bugembe	4.68	VB	2.5	500	52	8.76	71.18	0.90	5.30	0.90
CK Durama	8.70	VB/HS	0.2	150	41	4.94	45.75	1.15	1.45	1.00
Isunga 2	2.16	CL	1.1	60	77	15.28	73.04	0.65	0.75	0.45
Isunga 3	8.10	CL	1.2	60	50	6.05	82.59	0.50	0.70	0.55
Isunga 1 below Okots	5.25	CL	1.1	100	25.9	5.52	9.52	−0.20	6.10	0.75
Kaburara/Kanyosohera	49.60	VB	1.9	110	6	0.58		0.10	0.20	0.40
Kifuruka	7.24	CL	6.5	95	27	4.03	12.42	0.05	2.85	1.40
Kiko 2	5.00	VB	1.8	125	63	4.00	8.40	0.80	0.05	0.15
Kiko 3	1.70	VB	1.1	70	231	12.94	221.76	0.35	0.70	0.10
Kiko 4	1.20	VB	1.1	70	259	20.83	174.17	0.90	0.10	0.35
Kiko 1 (Nyabinamba)	6.20	VB	2.0	50	42	6.61	56.45	0.00	0.45	0.35
Kyamunaninga (Rusenyi)	0.82	VB	1.1	50	191	28.05	312.69	0.55	0.10	0.30
Lake Nyaherya	4.60	CL	6.1	300	27	4.78	15.00	−0.35	6.20	2.55
Lyantone	1.09	CL	7.8	200	203	33.94	175.63	0.55	4.10	1.20
Nkuruba (Fish Pond)	2.80	VB	3.7	70	354	32.00	0.71	0.50	4.95	2.75
Nkuruba (Lake)	6.40	CL	3.6	70	445	73.00	0.16	1.22	1.00	1.30
Ntungo	23.00	VB	2.5	85				0.85	0.15	0.45
Nyamirima	24.12	VB	1.1	90	9	1.00	10.61	0.65	4.75	1.95
Nyanswiga	2.20	CL	6.0	155	101	14.09	31.82	−0.75	16.15	2.05
Rutoma 1 (Nyamirima)	1.20	HS	2.4	80	167	30.83	337.50	−0.85	1.60	1.05
Rutoma 2	4.90	HS	3.0	150	34	7.76	32.24	0.15	0.90	0.60
Rwaihamba	2.40	VB	4.1	300	125	16.25	32.50	−0.58	0.85	1.15

TABLE 2.   *Tree species for which seedlings were found in fragments, but no adults, suggesting that for species that are animal-dispersed, seeds were brought to the fragment by animals moving among fragments. The number of fragments that this occurred in, disperser type, and whether or not they are known to be dispersed by chimpanzees (Wrangham et al. 1994), hornbills (Kalina 1988), both, or neither.*

Family	Unique seedling species	Habitat preference	Number of fragments	Dispersal type	Dispersed by
Annonaceae	*Uvariopsis congensis*	Forest	4	Large animal	Both
Apocynaceae	*Funtumia latifolia*	Forest	1	Wind	Neither
Apocynaceae	*Pleiocarpa pycnantha*	Gap	4	Large animal	Neither
Aquifoliaceae	*Ilex mitis*	Forest	1	Small animal	Neither
Bignoniaceae	*Kigelia africana*	Grassland	2	Large animal	Chimpanzee
Celtidaceae	*Celtis africana*	Edge	1	Small animal	Both
Celtidaceae	*C. durandii*	Gap	1	Small animal	Both
Ebenaceae	*Diospyros abyssinica*	Forest	2	Small animal	Both
Flacourtiaceae	*Casearia runssorica*	Forest	1	Small animal	Neither
Flacourtiaceae	*Dasylepis eggelingii*	Gap	5	Small animal	Chimpanzee
Flacourtiaceae	*Dovyalis macrocalyx*	Edge	4	Small animal	Chimpanzee
Flacourtiaceae	*Oncoba* sp.	Forest	2	Large animal	Chimpanzee
Guttiferae	*Symphonia globulifera*	Forest	1	Large animal	Chimpanzee
Leguminosae	*Newtonia buchananii*	Forest	1	Explosive	Neither
Malvaceae	*Pterygota mildbraedii*	Edge	1	Wind	Neither
Malvaceae	*Sterculia dawei*	Forest	1	Large animal	Both
Meliaceae	*Trichilia* sp.	Gap	2	Large animal	Both
Moraceae	*Trilepsium madagascariensis*	Forest	2	Large animal	Both
Moraceae	*Treculia africana*	Forest	1	Large animal	Chimpanzee
Oleaceae	*Olea capensis*	Edge	1	Small animal	Hornbill
Rhizophoraceae	*Cassipourea ruwensorensis*	Forest	1	Small animal	Chimpanzee
Rubiaceae	*Coffea canephora*	Gap	4	Small animal	Chimpanzee
Rubiaceae	*Rothmannia urcelliformis*	Forest	3	Small animal	Chimpanzee
Rutaceae	*Clausena anisata*	Edge	6	Small animal	Neither
Rutaceae	*Fagaropsis angolensis*	Edge	1	Small animal	Hornbill
Rutaceae	*Teclea nobilis*	Forest	1	Small animal	Both
Sapindaceae	*Aphania senegalensis*	Gap	1	Large animal	Chimpanzee
Sapindaceae	*Blighia* sp.	Gap	2	Large animal	Both
Sapotaceae	*Aningeria altissima*	Forest	1	Large animal	Chimpanzee
Sapotaceae	*Bequaertiodendron oblanceolatum*	Forest	1	Large animal	Both
Ulmaceae	*Chaetacme aristata*	Edge	1	Small animal	Neither

the density of stumps), the distance to the national park, the distance to the nearest fragment, or tree density. We were unable to build a significant predictive model of the difference in the number of beetles captured in the fragments and the continuous forest (total) considering the size of the fragment, the degree of fragment degradation, the distance to the national park, the distance to the nearest fragment, or tree density ($R^2 = 0.316$, $P = 0.911$). Similarly, declines between the intact forest and the fragments in beetle numbers from seed handling categories did not differ among fragment types ($P > 0.150$ for all seed handling categories), except for category 5 ($t = -2.101$, $P = 0.049$), in which the declines in the valley-bottom fragments were greater than the hillside/crater lake fragments.

ADULT TREE AND SEEDLING TREE COMMUNITY.—The average density of trees greater than 10 cm DBH

in intact forest was 359 individuals/ha, while in the fragments it was 120 individuals/ha (SD = 121, range = 6–445 individuals/ha; Table 1). We located 227 stumps ($\bar{x}$ per fragment = 85 stumps/ha, SD = 103, range = 0.2–338 stumps/ha).

We identified 1188 early recruits (<1 m tall; $\bar{x}$ density = $2.7/m^2$, SD = 3.69) and 435 late recruits (1–5 m tall, $\bar{x}$ density = $1.0/m^2$, SD = 0.76; Table 1). On average in each fragment, there were 10.3 species in the early recruit category (SD = 8.80, range = 1–21) and 6.4 species in the late recruit stage (SD = 4.81, range = 1–20). We have previously shown that a subset of the fragments had lower early recruit density (12.6 early recruits/m^2 in forest vs. 8.5 early recruits/m^2 in fragments) and fewer species of early recruits (5.1 spp. in forest vs. 4.2 in fragments) than the intact forest (Chapman & Onderdonk 1998). The lower density and fewer species obtained in the present study may
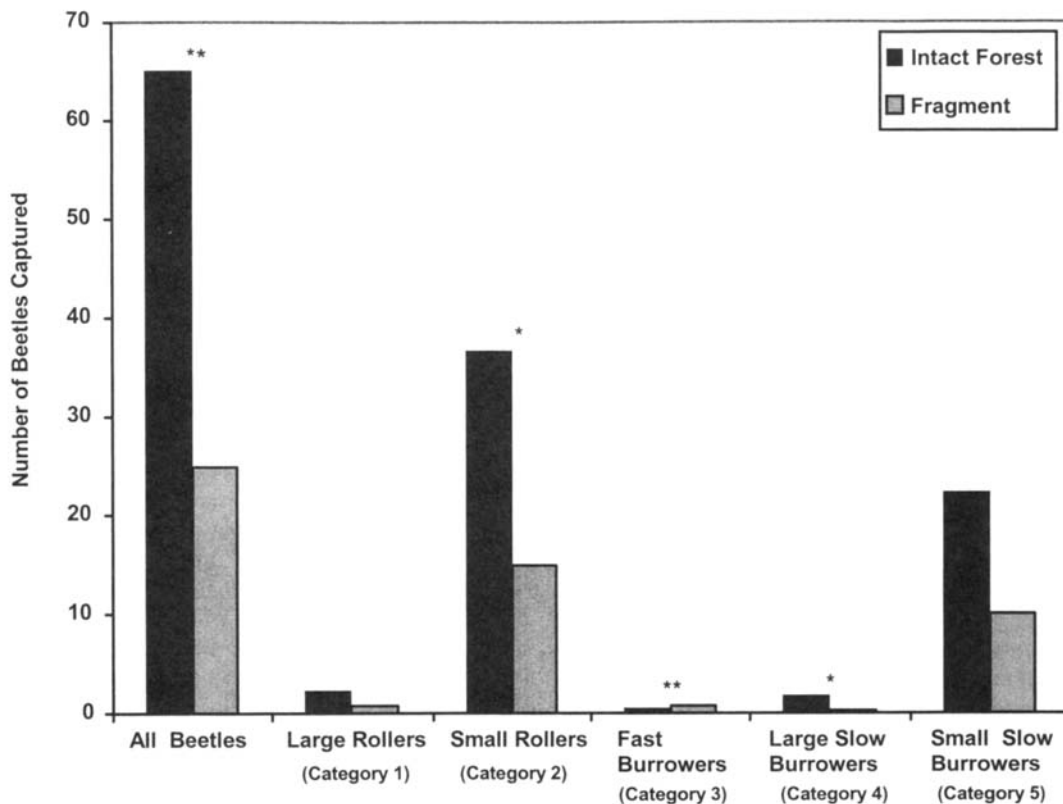
FIGURE 1.   Differences in the number of dung beetles captured among forest fragments and the intact forest (Kibale National Park, Uganda). See text for a description of the seed handling categories.

reflect the larger sample of fragments in this study and the fact that many were highly degraded. On average, there were 0.51 species of early recruits/m² in the fragments (SD = 6.44) vs 5.05/m² in the continuous forest.

In those fragments where we were able to conduct complete tree inventories ($N = 19$), we found no adult individuals for 31 species but did find early recruits (Table 3). Some species were found repeatedly in fragments as early recruits while no adults were present (e.g., *Clausena anisata*; there were a total of 60 incidences of early recruits being in a fragment when no adult of that species was found; *C. anisata* is not a species targeted for harvest by local people). The number of species of early recruits that were found in the fragments and for which there were no adults present, was not related to the distance to the nearest neighboring fragment ($r = 0.215$, $P = 0.363$) or the distance to Kibale ($r = 0.379$, $P = 0.099$; considering both variables in a multiple regression, $R^2 = 0.391$, $P = 0.266$). No difference existed between the dis-

tribution of seed dispersal types (e.g., wind, small animal, large animal) between fragments and intact forest ($\chi^2 = 2.43$, $P > 0.05$); however, 74 percent of the species for which there were no adults present are known to be dispersed by chimpanzees (68% by chimpanzees alone; Wrangham *et al.* 1994) or hornbills (39% by hornbills alone; Kalina 1988). Given the number of stumps in the fragments, it is likely that some incidences of seedlings for which no parent was present in the fragment represented cases in which adults were cut down and thus not present for us to inventory.

DISCUSSION

Fragmentation of this East African forested landscape can lead to predictable changes that alter the seed dispersal process. The rate that seeds were removed from the forest floor was slower in forest fragments than continuous forest. Given the importance of rodents as seed predators, this may have reflected changes in the rodent community.

Similarly, there was a decrease in dung beetle abundance and species richness. The decreases in the small rollers and in the large, slow burrowers are the differences that are most likely to affect secondary seed dispersal. The impact of these changes to the fate of dispersed seeds will vary depending on seed traits, particularly the size of a species' seeds. Effects of these changes, and ones that likely preceded them (*e.g.*, frugivore abundance), were evident in the lower density and species richness of seedlings in forest fragments when compared to the continuous forest.

We found some evidence to suggest that there may be movement of seeds among forest fragments by large dispersers. Chimpanzees are known to move readily among fragments, visiting a number of fragments in a single day, and are known to disperse seeds of many species (Wrangham *et al.* 1994). Similarly, hornbills were frequently seen flying among fragments and are important seed dispersers (Kalina 1988). Other potential dispersers, such as redtail monkeys (*C. ascanius*) and turacos (Great Blue Turaco, *Corythaeola cristata*; Ross's Turaco, *Musophaga rossae*; Black-billed Turaco, *Tauraco schuetti*) also travel among fragments. Some of the early recruits that did not have adults in the fragments were probably offspring of recently cut down trees. Seedlings can remain small for many years if conditions for growth are not favorable. For example, Connell and Green (2000) documented that the mean height of *Chrysophyllum* sp. seedlings that germinated in 1967 and survived until 1996 increased from 17.1 cm in 1967 to 34.9 cm in 1996; however, 74 percent of the species of early recruits that did not have adults in the fragment are known to be dispersed by chimpanzees or hornbills. Thus, some of these early recruits were likely the result of dispersal among fragments.

As studies of the effects of forest fragmentation accumulate (Laurance & Bierregaard 1997), there is increasing evidence that fragmentation causes some predictable changes which influence the conservation value of fragments and their long-term viability. For example, it is clear that there are predictable decreases in abundances of certain animal groups, such as primates (Estrada & Coates-Estrada 1996, Tutin *et al.* 1997, Onderdonk & Chapman 2000), birds (Newmark 1990, Stoufer & Bierregaard 1995), dung beetles (Klein 1989, Estrada *et al.* 1998, Halffter & Arellano 2002, this study), and euglossine bees (Powell & Powell 1987, Didham et al. 1996). It is also clear that these changes and others typically lower tropical tree recruitment (Benitez-Malvido 1998, Chapman &

Onderdonk 1998, Laurance *et al.* 1998, Cordeiro & Howe 2001). The next challenge for the application of this information will be to understand what causes variation in the responses of different communities to the general process of fragmentation. For example, contrasting our study to the literature illustrates variation in how both the dung beetle and seedling communities respond to fragmentation. In Klein's (1989) early study on the effects of forest fragmentation on an Amazonian dung beetle community (2–6 years after isolation), he documented a 48.1 percent decline in dung beetle abundance between continuous forest sites and 10 ha fragments. Subsequently, 13–18 years after isolation, Andresen (2003) documented that the same number of dung beetle species was captured in 10 ha fragments and the continuous forest and that these fragments had more than twice the number of individuals captured compared to the continuous forest. In contrast, we documented a 61.5 percent decline in dung beetle abundance and a 33% percent decline in species richness when contrasting our fragments ($\bar{x} = 7.9$ ha) to the continuous forest. While it is possible that the African beetle community we studied was inherently more susceptible to fragmentation than the Amazonian community studied by Klein (1989) and Andresen (2003), it seems more likely that these differences are due to characteristics of the particular fragments we studied and the nature of the surrounding matrix. Like the majority of fragments in the tropics, the fragments we studied are not protected; they are on land managed by private citizens or local communities that depend on them for fuelwood, grazing lands, medicines, or game. While the fragments outside of Kibale National Park are described by local elders as "ancestral forests," the trees in the fragments are occasionally harvested, resulting in canopy openings. Halffter and Arellano (2002) demonstrated that the extent of tree cover in the matrix surrounding fragments influenced dung beetle communities; the forest dung beetle community was rapidly reduced as the canopy was opened. Thus, the reduced dung beetle community we documented may, at least partially, have been due to the opening of the canopy associated with tree harvesting by the local landowner.

To understand determinants of dung beetle community structure in fragmented habitats, researchers have also stressed the importance of the matrix in which the fragments are embedded (Halffter *et al.* 1992, Estrada *et al.* 1998, Halffter & Arellano 2002). For example, Estrada *et al.* (1998) described the dung and carrion beetles in

forest fragments and agricultural habitats at Los Tuxtlas, Mexico. These researchers illustrated that a landscape in which the matrix contains arboreal crops and living fences is a more benign arrangement for the dung beetle fauna than pastureland alone. The landscape outside of Kibale supports small landholder agriculture with very few arboreal crops, no living fences, fallow land with tall grasses, and high human population densities. Such a landscape may not be as favorable to forest beetles as those studied elsewhere.

Comparing our results to those obtained in the Brazilian Amazon also suggests that differences exist in how tree communities respond to fragmentation. Benitez-Malvido (1998) reported an average density of seedlings (5–100 cm tall) in 10 ha fragments near Manaus, Brazil of 10.26 seedlings/m^2. The average size of our fragments was 7.9 ha, and yet the density of seedlings was only 2.7/m^2. This difference may represent the nature of the tree community found in this area of Africa. Data on growth and mortality of seedlings in forest understorey, treefall gaps, and large gaps suggest that this East African community lacks aggressive colonizing tree species (Chapman et al. 1999). This study also documented limited survival of seedlings in large gaps relative to the understory. Such large gaps are often found in privately owned fragments, as landowners often harvest several neighboring canopy trees because felling trees in close proximity is easier for pit sawing timber or making charcoal. The documented difference, however, may also have resulted from the fact that the understory of the fragments outside of Kibale is influenced by humans and occasionally, cattle trampling (it is rarely influenced by fire as the area receives two rainy seasons and the forest is generally not susceptible to burning).

Much of the previous work on the general effects of fragmentation has involved the study of fragments in protected areas or has largely ignored human use of fragments (Lovejoy et al. 1986, Klein 1989, Tutin et al. 1997, Benitez-Malvido 1998, Tutin 1999; cf. Halffter et al. 1992, Davis 1994, Estrada et al. 1998, Hingrat & Feer 2002). In reality, most fragments are not protected; they are on land managed by private citizens who depend on them for resources. While studies of fragments in protected reserves have provided us with many insights, they may have biased our perception of the value of forest fragments. Maintaining of the conservation value of unprotected fragmented landscapes that are not protected will require the cooperation of the local people and an evaluation of how the landscape can best be managed to maintain ecological processes. Thus, it will be important to understand many aspects of the ecology of fragments, including the role of the matrix surrounding the fragment and effects of extraction of forest products.

ACKNOWLEDGMENTS

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