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Dung Beetle Assemblages and Seasonality in Primary Forest and Forest Fragments on Agricultural Landscapes in Budongo, Uganda

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ABSTRACT

Very little is known about the diversity of arthropods in the fast-disappearing fragments of natural forests in sub-Saharan Africa. This study investigated: (1) the influence of forest fragment characteristics on dung beetle species richness, composition, abundance, and diversity; and (2) the relationship between dung beetle assemblages and rainfall pattern. Beetles were sampled through 12 mo using dung baited pitfall traps. A total of 18,073 dung beetles belonging to three subfamilies and 45 species were captured. The subfamily Scarabaeinae was the most abundant (99%) and species rich (89%). Fast-burying tunnellers (paracoprids) were the most dominant functional group. *Catharsius sesostris*, *Copris nepos*, and *Heliocopris punctiventris* were the three most abundant species, and had the highest contributions to dissimilarities between forests. With few exceptions, dung beetle abundance, species richness, and diversity were generally higher in larger forest fragments (100–150 ha) than in smaller ones (10–50 ha) and the nature reserve (1042 ha). Forest fragment size had a highly significant positive relationship with beetle abundance, but only when the nature reserve is excluded in the analysis. Dung beetle abundance and species richness showed direct weak relationships with litter depth (positive) and groundcover (negative) but not tree density, tree species richness, and fragment isolation distance. Dung beetle abundance and species richness were strongly correlated with monthly changes in rainfall. Results of this study indicate that forest fragments on agricultural lands in the Budongo landscape, especially medium-sized (100–150 ha) ones, represent important conservation areas for dung beetles.

Key words: Africa; beetle communities; biodiversity conservation; forest fragmentation; fragment characteristics; nature reserve.

Increasing expansion and intensification of agriculture in the tropics have created highly modified landscapes where remnant forest fragments are set in a matrix of agricultural landscapes and human settlements (Turner 1996). In Uganda, there is escalating clearance of native forest fragments on agricultural landscapes mainly for subsistence agriculture and growing commercial crops such as sugarcane, tea, coffee, and tobacco (Howard 1991, Kayanja & Byarugaba 2001). Such forest fragments may provide major opportunities for conservation of indigenous biodiversity in these agricultural landscapes. Unfortunately, very little is known about the indigenous species surviving in such forest fragments in the country. Adequate data are urgently required on key aspects such as species diversity and abundance, representation of species of high conservation values, and changes in these aspects over time to understand the contributions of individual fragments to the conservation of biodiversity. In this way, farmers, forest managers, and conservationists can make informed decisions and/or recommendations on the characteristics of forest fragments to be retained on agricultural landscapes, and on the restoration of degraded ones.

Dung beetles play vital ecosystem functional roles such as secondary seed dispersal, nutrient cycling, soil aeration, control of vertebrate parasites, and sometimes pollination (Estrada *et al.* 1998, Sakai & Inoue 1999, Vulinec 2002, Chapman *et al.* 2003), and may thus be important in agricultural productivity and forest regeneration. Dung beetles are also highly sensitive to habitat changes (Klein 1989, Nichols *et al.* 2007). Alteration in habit characteristics, including vegetation cover, edaphic conditions, and mammalian faunal composition influence the success of dung beetle groups differently (Davis 1996). Thus, practices that degrade or transform forest fragments may result in change in dung beetle community structure or local extinction of dung beetle species adapted to forest conditions. This may have significant negative consequences on processes such as dung degradation and secondary seed dispersal in the ecosystem (Davis 1996, Jankielsohn *et al.* 2001, Vulinec 2002).

The overall objective of this study was to gain an understanding of the diversity of dung beetle assemblages in native forest fragments on agricultural landscapes in Uganda to improve biodiversity conservation and land-use management. Specifically, I determined: (1) the influence of forest fragment characteristics on dung beetle species richness, composition, abundance, and diversity; and (2) the relationship between dung beetle assemblages and rainfall pattern.

METHODS

Study area.—This study was conducted from April 2006 to March 2007 in the Nature Reserve (primary forest) in Budongo Central Forest Reserve (BCFR; 1°35–55′ N, 31°18–42′ E, *ca* 1100 m asl; Howard 1991), western Uganda and six native forest fragments situated in surrounding agricultural landscapes (Table 1; Fig. 1). Records from Sonso weather station, located at the BCFR, indicate that the rainfall in Budongo is bimodal with annual precipitation of 1410 mm. The first rains are usually in April–May and the second rainy season is from August to October. The dry season is most pronounced from December to February. The mean monthly temperature range is 19–31°C. July and August are the coolest months while January and February are the hottest. Langdale *et al.* (1964)

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TABLE 1. Characteristics of forests selected for this study.

Name	Size (ha)[a]	Isolation (km)[a,b]	Type	Bordering vegetation	Ownership	Main threats
Nature Reserve	1042	0	Primary	Continuous secondary forest	Ugandan government	Illegal logging
Ongo	150	20	Secondary	Various agricultural crops and fallow land	Local community	Harvest of saplings for poles
Rwensama	127	10	Secondary	Sugarcane and various agricultural crops	Forestry college	Harvest of saplings for poles
Tengele	100	10	Secondary	Sugarcane, woodland, and various agricultural crops	Local community	Pitsawing and harvest of saplings for poles
Rwangara	50	10	Secondary	Sugarcane and various agricultural crops	An individual	Harvest of saplings for poles
Kanyege	15	2	Secondary	Sugarcane	Private sugarcane company	Sugarcane cultivation and human settlement
Simba	10	15	Secondary	Various agricultural crops and young (< 1 yr) pine	Local community	Pitsawing and harvest of saplings for poles

[a]Information obtained from the Uganda National Forestry Authority office at Budongo (for Nature Reserve and Rwensama) and owners of the forest fragments (Kanyege, Ongo, Rwangara, Simba, and Tengele).

[b]Approximate distance from forest fragment to the nearest edge of the nature reserve.

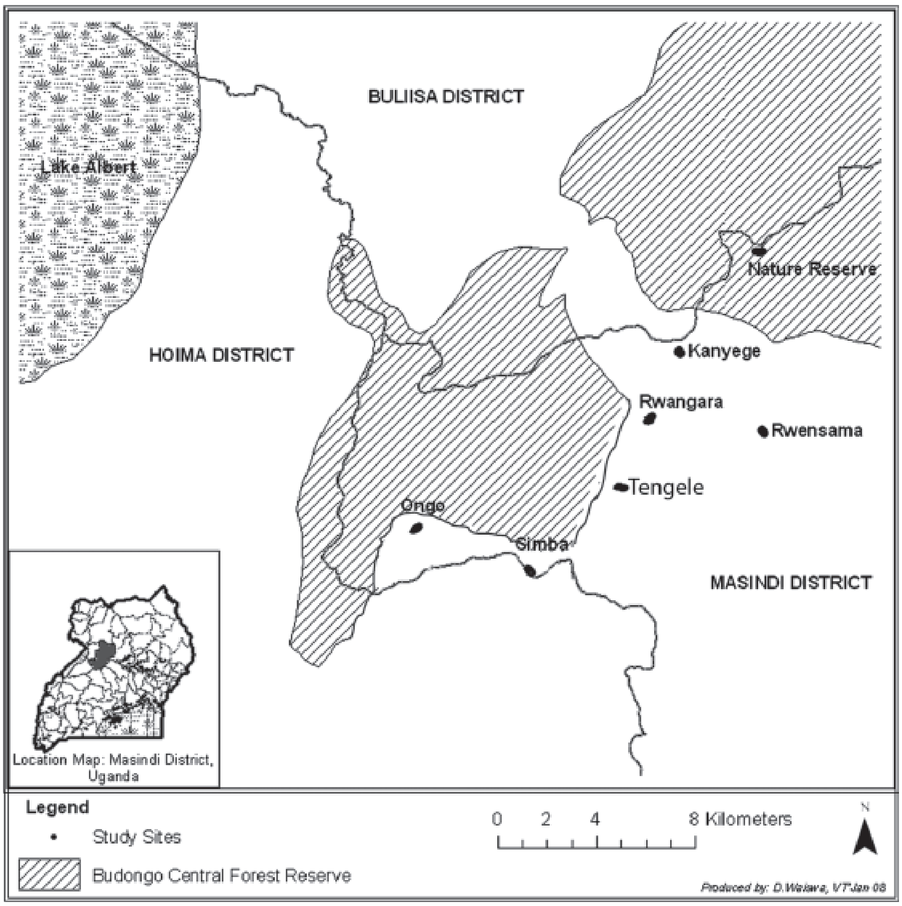

FIGURE 1. Location of study sites in and around Budongo central forest reserve in western Uganda.

classified Budongo forest as a medium altitude semideciduous forest. BCFR contains 37 percent of the 465 known tree and shrub species in Uganda, making it the most important forest for tree conservation in the country (Howard 1991).

Eggeling (1947) described the natural vegetation in the Budongo landscape as comprising of colonizing forest, mixed forest, climax forest dominated by *Cynometra alexandrii*, swamp forest, wooded grassland, and grassland. However, the vegetation in most of the landscape surrounding BCFR is rapidly changing due to increased conversion of forests for agriculture, including small-scale farming and commercial sugarcane and tobacco production (Kayanja & Byarugaba 2001; P. Nyeko, pers. obs.). According to Tweheyo (2003), the most abundant large mammalian fauna in BCFR are primates (*Colobus guerezal, Cercopithecus ascanius*, *Cercopithecus mitis*, *Papio anubis*, *and Perodicticus potto*). Others include mainly duikers (*Cephalophus rufilatus* and *C. monticola*), bush buck (*Tragelaphus scriptus*), bush pig (*Potamocherus porcus*), tree hyrax (*Dendrohyrax arbereus*) and porcupines (*Hystrix cristata*).

BEETLE TRAPPING.—In each forest I established one longitudinal transect at about the centre of the forest in order to avoid edge effects. Beetles were sampled using pitfall traps that provide a cost-effective, widely accepted, and efficient means of sampling ground-active arthropods (Niemelä *et al.* 1993, Driscoll 2005). Eight pitfall traps were established at 50-m intervals along the transect, resulting into a total of 56 pitfall traps for the seven forests. The location of transects and pitfall traps were determined using the global positioning system (GPS) and marked with red plastic tags to ease their identification during monitoring.

Individual pitfall traps consisted of two conical plastic jars (diam. 13 cm top and 10.5 cm bottom, length 12 cm). The jars were nested together and buried so that one was flush with the ground as a liner and the other placed into it. Traps were each filled with 100 ml of propylene glycol at every sampling occasion, as a preservative and killing agent. Each trap was covered with elevated circular plastic plate lid (diam. 21 cm), supported *ca* 5 cm above the rim by three metallic (binding wire) stands, to prevent flooding by rainwater and to protect the contents of the trap from birds. About 50 g of fresh goat dung bait was put in each trap at the beginning of the study and thereafter at every sampling occasion. Goat dung was used because it was readily available in sufficient quantities. Traps were monitored monthly for beetle abundance and diversity from April 2006 to March 2007. I did not observe any trap or beetle specimen damaged through predation possibly because the propylene glycol used was repellent to predators. For every sampling occasion, captured beetles were removed from pitfall traps and stored in vials containing 70 percent ethanol. The specimens were later separated into morphospecies by hand sorting, coded, counted, and recorded in the laboratory at the Faculty of Forestry and Nature Conservation (FFNC), Makerere University. The beetle specimens were identified using the expertise and reference collections at Makerere University and Kawanda Agricultural Research Institute, Uganda, and are deposited at FFNC for reference and teaching. Most vials containing beetle samples collected in October 2006 were damaged in an accident during transit from the field to Makerere University for laboratory work. Consequently, the beetle samples for this month were excluded from the study.

Some functional groups are more important than others, and are therefore of conservation priorities (Vulinec 2002). I used Doube's (1990) classification and examples from Davis (1996) and Jankielsohn *et al.* (2001) to categorize the dung beetle species into functional groups (FG) according to how they use dung. FG I includes large ball rollers (telecoprids); FG II small ball rollers (telecoprids); FG III fast-burying tunnellers (paracoprids); FG IV large slow-burying paracoprids; FG V small, slow, shallow-burying paracoprids; FG VI kleptocoprids, which use dung buried by other dung beetles; and FG VII endocoprids, which feed on dung within the pad.

VEGETATION SAMPLING.—At each sampling site (forest) vegetation characteristics, including tree species and their abundance, ground cover, and litter depth (accumulation of dead leaves and twigs) around each trap were determined to investigate their relationships with beetle assemblages. Data on tree abundance and species were collected at the beginning of the study. The Standard International Forestry Resources and Institutions method for vegetation sampling (Ostrom 1999) was used. Three concentric circles (1-m, 3-m, and 10-m radius) were established around each trap to record tree species and their abundance, ground cover, and litter. Tree seedlings (diam. $<$ 2.5 cm, height $\leq$ 1.5 m) were counted in the 1-m-radius circle, saplings (2.5–10 cm diameter) in the 3-m-radius circle, and mature trees ($>$ 10-cm diam.) in the 10-m-radius circle. Tree diameter at breast height (dbh) was taken at the standard 1.3 m height.

Ground cover and litter depth were determined in the 1-m-radius circles. Estimates of percentage ground cover were taken for herbs when individuals were impractical to count. This was done in each 1-m-radius circle in each forest during every trap visit for beetle sampling, except in a few cases where traps were found removed or damaged. For each trap, the ground cover was visually scored on five scales as follows: (1) $<$ 5 percent of the total area of the 1-m-radius circle; (2) 5–25 percent of the total area of the circle; (3) 25–50 percent of the total area of the circle; (4) 50–75 percent of the total area of the circle; and (5) $>$ 75 percent of the total area of the circle. Litter depth was measured during every beetle sampling occasion at five randomly selected points within the 1-m radius of every trap using a ruler. Monthly rainfall data were collected from the Sonso weather station at BCFR.

DATA ANALYSIS.—Dung beetle (Scarabaeidae) species richness within each of the seven forests and in all forests pooled together was determined using species accumulation curves and species richness estimates using the program EstimateS version 8.0 (Colwell 2006). The total number of individuals of each species captured in each trap for the entire sampling period was used in this analysis. Sample order was randomized 50 times to eliminate sampling error and heterogeneity among the forests sampled. Two nonparametric estimates (Chao 2 and Bootstrap) were used to determine the inventory completeness (Pineda *et al.* 2005). The number of dung beetle species shared between each pair of forest was determined using the Shared Species Analysis in EstimateS version 8.0, and the Bray–Cutis similarity index was used to show the level (in percentage) of similarity between the pairwise comparisons. For this, data were fourth root transformed to downweight the effect of common species, therefore taking account of rare species (Kotze & Samways 1999). Because Bray–Curtis index does not give significance values, I used analysis of similarity (ANOSIM) (Clarke 1993) in the Community Analysis Package (CAP) 3.1 (Seaby *et al.* 2004) to test for differences in dung beetle assemblages between paired forests. The similarity percentage (SIMPER) test (Clarke 1993) in CAP 3.1 was used to identify individual beetle species that were mainly responsible for forest distinctiveness.

The abundance and species richness of beetles and trees were compared between forests, and between seasons using ANOVA in SPSS Statistical Package, release 10.0. The main objective was to determine the variation in beetle and tree abundance and species richness among forests. Simpson's diversity index was determined for each forest using EstimateS version 8.0 and compared among forests using one-way ANOVA. Similarly, ANOVA was used to compare the litter depth and ground cover between the forests. Data were $\log_{10}$ (x + 1) transformed after checking for distribution using the Anderson–Darling test. For all variables analyzed using ANOVA, the least significant difference (LSD) in ANOVA post-hoc tests was used to determine differences between forests. I used simple linear regression in SPSS version 10 to determine the relationships of litter depth and ground cover with dung beetle abundance and species richness. Average litter depth and ground cover score per trap for each month was used in the regression. Multiple regression was used to determine the relationships between other forest characteristics (size, isolation, tree density, and tree species richness) and dung beetle abundance and species richness. Beetle data for April 2006 were used for regression of beetle assemblages with tree vegetation because the latter was sampled at the beginning of the study only. The relationship between monthly beetle abundance across all forests and total monthly rainfall was determined using Pearson correlation in SPSS. Rainfall data for October 2006 were excluded from this analysis because, for reasons mentioned earlier, beetle samples for this month were excluded from the analysis.

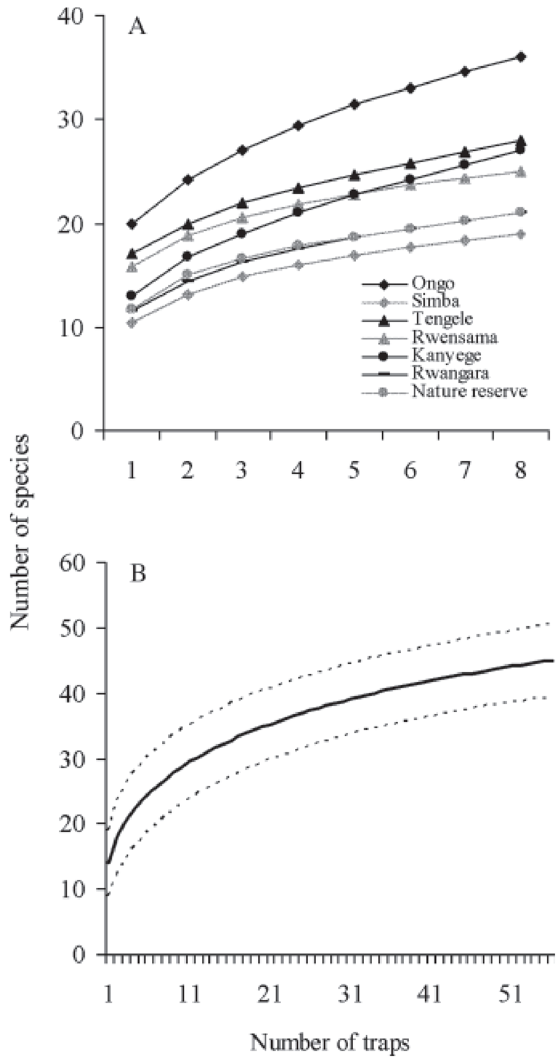

FIGURE 2. Dung beetle species accumulation curves for (A) the seven forests and (B) all forests pooled. Fitted doted lines in (B) indicate 95% CIs. Data for each trap are pooled for the entire sampling period.

RESULTS

VARIATION IN DUNG BEETLE ASSEMBLAGES BETWEEN FORESTS.—I captured a total of 18,073 dung beetles belonging to three subfamilies (Aphodinae, Geotrupinae, and Scarabaeinae) and 45 species (Table S1). Up to 99.8 percent of the dung beetles individuals and 88.8 percent of the species captured were Scarabaeinae. *Copris nepos* (23%), *Catharsius sesostris* (23%), *Heliocopris punctiventris* (21%), *Gymnopleurus crenulatus* (7%), and *Pedaria jacksoni* (7%) constituted most of the dung beetles captured. For 22 species, I captured < 10 individuals. The species accumulation curves did not reach an asymptote for any of the forests studied (Fig. 2). Species richness estimates (Chao 2 and Bootstrap) indicated that sampling was most complete in Rwensama (at least 92% of the species present were captured) followed by Simba (87%), Ongo (79%), Rwangara (76%), Tengele (76%), Kanyege (70%), and the Nature Reserve (62%). Chao 2 estimates that up to 52 species could be captured in the seven forests studied compared to the 45 observed.

Fast-burying tunnellers (FG III) were the most abundant in all the forests while endocoprids (FG VII) were the least (Table 2; Table S1). None of the dung beetles were large ball rollers (FG I) and small, slow, shallow-burying paracoprids (FG V). The abundance of dung beetles in specific functional groups differed significantly among forests (Table 2). Small ball rollers (FG II), fast-burying tunnellers (FG III), and kleptocoprids (FG VI) were significantly more abundant in Ongo than in any other forest. The abundance of slow-burying paracoprids (FG IV) was significantly higher in Tengele than in all the other forests, except Ongo. The Nature Reserve, Simba and Kanyege did not differ significantly in the abundance of any of the functional groups observed (Table 2).

TABLE 2. *Mean abundance, species richness and diversity of dung beetles in the forest fragments and nature reserve.*

Forest	Abundance						Species richness	Simpson's diversity index
	FG II	FG III	FG IV	FG VI	FG VII	Total		
Ongo	97.3[a]	455.0[a]	66.8[a]	122.9[a]	2.0[a]	743.9[a]	32.0[a]	7.2[a]
Tengele	64.9[c]	338.6[c]	80.5[a]	45.3[c]	1.1[ab]	530.4[c]	23.5[c]	6.7[b]
Rwensama	63.3[c]	310.5[c]	19.5[b]	32.8[bc]	0.4[b]	426.4[c]	23.3[c]	5.4[c]
Rwangara	5.8[b]	173.4[eb]	9.4[b]	10.4[bc]	0.5[ab]	199.4[b]	20.5[e]	4.2[d]
Nature Reserve	10.4[b]	122.4[b]	17.8[b]	16.5[bc]	0.1[b]	167.1[b]	20.1[e]	5.7[e]
Simba	17.5[b]	91.8[b]	8.4[b]	4.3[b]	0.0[b]	121.9[b]	19.0[b]	5.2[f]
Kanyege	10.3[b]	65.0[db]	20.1[b]	3.9[b]	0.3[b]	99.5[b]	25.3[d]	6.4[g]
P-value	<0.001	<0.001	<0.001	<0.001	0.140	<0.001	<0.001	<0 0.001

FG = functional group; means followed by the same letter within a column are not significantly different at 0.05 probability level.

Ongo forest had the highest mean total dung beetle abundance, species richness, and diversity, and the lowest values were observed in Kanyege, Simba, and Rwanagra, respectively (Table 2).

Overall Ongo, Tengele, and Rwensama forests differed significantly from each other in beetle assemblage structure, and from all the other forests (Table 3). At least 14 species (Simba-Nature Reserve) were shared in paired forest combinations (Table 3). The three most abundant species (*C. sesostris*, *C. nepos*, and *H. punctiventris*) consistently had the three highest contributions to the dissimilarities between all forest combinations (Table S2). Other species that were among the best five discriminators included *Pedaria jacksoni*, *G. crenulatus*, *Onthophagus multicornis, Sysiphus* sp. 1, *Onthophagus* sp.13, and *Pedaria* sp. 1.

TEMPORAL VARIATIONS IN DUNG BEETLE ASSEMBLAGES.—Beetle abundance varied markedly over the study period with the highest observed in August 2006 (32 individuals/trap) and the lowest in January 2007 (3 individuals/trap; Fig. 3). There was a very strong positive correlation between beetle abundance and total monthly rainfall ($r = 0.727$; $P = 0.011$). Beetle abundance and species richness were significantly higher in the wet season than in the dry season ($P < 0.001$).

TREE ABUNDANCE AND SPECIES RICHNESS.—In total, I recorded 1167 trees belonging to 131 species. The most abundant species was *C. alexandrii* with 21 percent of the total trees encountered followed by *Argomuellera macrophylla* (9%) and *Lasiodiscus mildbraedii* (6%). There were significant differences between forests in densities of saplings ($F = 2.94$, $P = 0.016$) and mature trees ($F = 8.50$, $P < 0.001$), but not seedlings ($F = 0.67$, $P = 0.678$). The Nature Reserve had the highest density of saplings (92.9/ha) and mature trees (328/ha). Tree species richness varied markedly between forests. Rwensama forest had the highest tree species richness (102 species encountered), followed by Kanyege (94), Nature Reserve (88), Simba (74), Ongo (73), Tengele (73), and Rwangara (68).

GROUND COVER AND LEAF LITTER.—Groundcover differed significantly among forests ($F = 19.7$, $P < 0.001$) and seasons ($F = 23.7$, $P < 0.001$). The highest mean average ground cover was observed in Kanyege (average class 4.2 ± 0.10) followed by the Nature Reserve (3.8 ± 0.08), Simba (3.6 ± 0.09), Tengele (3.5 ± 0.08), Ongo (3.3 ± 0.09), Rwangara (3.4 ± 0.09) and Rwensama (2.7 ± 0.09). The predominant groundcover species were *Leptaspis zylanica* (especially in the Nature Reserve), *Aframomun* species, and some unidentified herbaceous climbers. The ground cover species, particularly

TABLE 3. *Percentage Bray–Curtis similarity index (upper triangle) and ANOSIM pairwise comparisons (R statistic) (lower triangle) between forests.*

Forest (S)	Ongo (36)	Simba (19)	Tengele (28)	Rwensama (25)	Kanyege (27)	Rwangara (21)	NR (21)
Ongo	–	56.5 (17)	81.3 (25)	74.5 (23)	64.2 (23)	65.6 (20)	66.7 (21)
Simba	0.997**	–	66.7 (17)	73.7 (17)	81.0 (17)	76.5 (15)	75.6 (14)
Tengele	0.146*	0.890**	–	81.0 (20)	71.3 (21)	69.6 (16)	72.6 (19)
Rwensama	0.349**	0.866 **	0.180*	–	74.3 (20)	78.4 (18)	77.7 (17)
Kanyege	0.993**	0.115 ns	0.923**	0.916**	–	74.7 (17)	78.3 (18)
Rwangara	0.794**	0.184 ns	0.559**	0.512**	0.412*	–	76.4 (15)
NR	0.636**	0.062 ns	0.456**	0.395**	0.150*	0.021 ns	–

*$P < 0.05$; **$P < 0.005$. Values in parentheses are numbers of species shared in that comparison. S = total number of species captured in a forest; NR = Nature reserve.

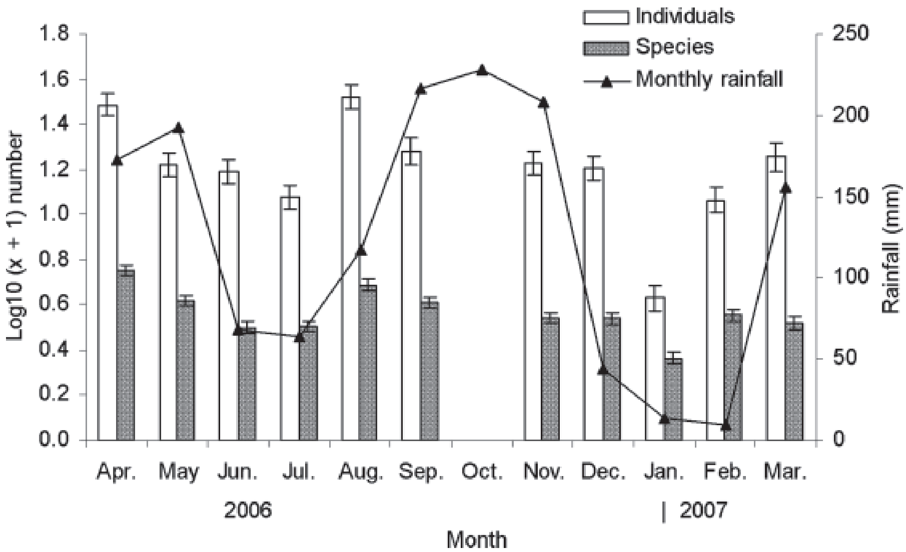

FIGURE 3. Monthly patterns of the number of dung beetle individuals and species, and total rainfall in Budongo during 2006 and 2007. Error bars are SDs.

Aframomun species and herbaceous climbers were generally more abundant in areas with open tree canopies. Among seasons, groundcover was significantly lower (average class 3.2 ± 0.06) in the long dry season (December–February) than in all the other periods: wet season 1 (average groundcover class 3.5 ± 0.07), dry season 1 (3.9 ± 0.07), and wet season 2 (3.8 ± 0.06). There was no significant difference in groundcover between the short dry season from June to July and the wet season from August to November.

Litter depth differed significantly among seasons (F = 18.7, P < 0.001) and forests (F = 16.4, P < 0.001). I observed the highest mean litter depth (2.21 ± 0.086 cm) in the second and longer dry season (December–February), followed by the first wet season in March–May (2.04 ± 0.01 cm), first dry season in June–July (1.96 ± 0.108 cm), and the second wet season from August–November (1.32 ± 0.091 cm). Ongo forest had the highest average litter depth (28 ± 0.13 cm) followed by Kanyege (2.2 ± 0.15 cm), Simba (2.1 ± 0.14 cm), Rwensama (2.1 ± 0.12 cm), Rwangara (2.0 ± 0.13 cm), Tengele (1.5 ± 0.12 cm), and the Nature Reserve (1.5 ± 0.13 cm).

RELATIONSHIP BETWEEN DUNG BEETLE ASSEMBLAGES AND FOREST CHARACTERISTICS.—Beetle abundance showed a very weak significant positive relationship with litter depth and a very weak negative relationship with groundcover (Fig. S1A, B). Similarly beetle species richness had weak significant relationships with litter depth and groundcover (Fig. S1C, D). Forest size had significant relationship with beetle abundance (R^2 = 0.87; P = 0.023) only when the Nature Reserve was excluded from the analysis. I did not find significant relationship between forest size and beetle species richness. Similarly, there were no direct relationships between beetle abundance or beetle species richness and density of trees of all age categories (seedlings, saplings, and mature), tree species richness, and fragment isolation.

DISCUSSION

VARIATION OF BEETLE ASSEMBLAGES BETWEEN FORESTS.—In general, dung beetle abundance was higher in larger fragments (100–150 ha) than in the smaller ones (10–50 ha) and the Nature Reserve. A similar trend was observed for dung beetle species richness and diversity, except in Kanyege (15 ha) versus Rwensama (127 ha). These results partially support the view that small fragments often have fewer biological individuals and species recorded for the same effort of observation than large fragments (Turner 1996, Nichols *et al.* 2007). *Catharsius sesostris*, *C. nepos*, and *H. punctiventris* contributed highly to the dissimilarities between forests. *Catharsius sesostris* is reportedly widespread in the Middle East and the Afrotropical region (Mathison *et al.* 2001). However, there are a number of varieties and close relatives of the species so it probably represents a species complex rather than a single species, but no revision has yet been published (A.L.V. Davis, pers. comm.). *Copris nepos* has a highland distribution (Davis & Dewhurst 1993) and is probably restricted to East Africa (A.L.V. Davis, pers. comm.). *Heliocopris punctiventris* has a widespread distribution from West to East Africa (A.L.V. Davis, pers. comm.).

There were also marked variations between forests in the distribution of rare dung beetle species (< 50 individuals captured). For example, *Copris orphanus*, *Onthophagus carbonaerius*, and *O. proteus* were either not captured or were less abundant in most forest fragments than in the Nature Reserve, suggesting that they are sensitive to forest fragmentation. However, variations in the abundance of species represented by a few individuals need to be viewed with caution as these could be a sampling artifacts, truly rare species, or the outcome of capturing transient species whose presence within a habitat is purely occasional (Pineda *et al.* 2005). Sampling a large number of forest fragments over a number of years may reveal a more complete picture of the range and occupancy of such species. Moreover, studies on the composition of dung beetles in the open, at the forest edge, and deeper into the forest are necessary to determine whether the species captured are habitat specialists or habitat generalists in the Budongo landscape.

In addition to fragment size, the variations in dung beetle assemblages observed in this study may be attributed to several factors. It is possible that there was invasion of the forest fragments by species from agricultural areas. This may explain the higher number of dung beetle individuals and species observed in some forest fragments (Ongo, Tengele, Rwensama, and Kanyege) than in the Nature Reserve. Driscoll and Weir (2005) reported increased beetle species richness in smaller fragments, and attributed it to influx of species from the surrounding landscape. Similarly, Niemelä *et al.* (1993) observed in Canada that the invasion of recently cut forest sites by ground beetle species of open habitat, together with the persistence of several mature forest generalists, initially increased carabid diversity in the regenerating stands in comparison to the mature stands. The fragments used in this study were either surrounded by private sugarcane estates or were islands in communally owned land under subsistence agriculture. There is insufficient published information on the habitat range of the species identified in this study to determine whether they are forest specialists or generalists. As mentioned earlier, sampling in the matrix habitats, forest-matrix ecotones, and the forest fragment interior is necessary to give a more complete picture of the habitat range of the species identified in this study.

Fragment characteristics such as vegetation structure, litter depth, age, and isolation distance may influence the communities of dung beetles and influence the roles that these insects play in ecosystem processes (Klein 1989, Andresen 2003, Chapman *et al.* 2003, Hill & Curran 2003, Quintero & Roslin 2005). In the present study, dung beetle abundance showed significant positive relationship with forest fragment size, but the Nature Reserve with a much more extensive area than the other fragments made the relationship not significant. Litter depth and ground cover were very weakly related to dung beetle abundance and species richness (explaining $< 4\%$ of the variation in the data). The very weak relationships are probably not biologically meaningful although litter has been reported to be important in modifying soil characteristics such as moisture, density, and nutrient load, which may increase the recruitment and/or reproduction of dung beetles (Sowig 1995, Larsen *et al.* 1996, Hall 2003). The lack of direct relationship between beetle assemblages (abundance and species richness) and fragment isolation distance, and tree density and species richness suggests that the surrounding agricultural land matrix facilitates dung beetle dispersal between fragments and BCFR thereby reducing the effects of fragmentation and tree harvesting in the fragments (Pineda *et al.* 2005, Quintero & Roslin 2005). Another possibility is that the narrow range of isolation distances and small sample size of fragments was not sufficient to show a pattern.

Studies conducted in Neotropical forests (*e.g.*, Gill 1991, Estrada *et al.* 1998, Andresen 2003) indicate that the composition and structure of dung beetle communities is highly correlated with the availability of fresh dung, and that some dung beetle communities are largely supported by howler monkey dung (Andresen 2003). The present study did not determine the demographic and behavioral characteristics of mammals inhabiting the study forests, but primates are known to be abundant in the Budongo landscape, especially in logged forest areas with abundant fruit trees (Tweheyo 2003, Tweheyo *et al.* 2003). The higher abundance and activity of primates in logged forests than in the Nature Reserve (Tweheyo *et al.* 2003) implies that disturbed forests in Budongo may have more food resources for dung beetles (primate dung) than primary forests. This may explain the lower dung beetle abundance and species richness observed in the Nature Reserve compared to the medium-sized forests. Hunting pressure in the forest fragments may also influence dung beetle assemblage structure due to its influence on dung abundance or variety, but no study has examined this in the Budongo landscape. The existence of human settlements near fragments, as was observed in Kanyege, may also influence beetle assemblage structure by increasing food resources for synanthropic dung beetles, for example, through grazing of livestock. This may partly explain the relatively high dung beetle species richness observed in Kanyege forest.

It is important to note that the use of single type of faecal bait, such as primate dung alone, in determining the influence of dung availability on dung beetle populations may be inappropriate as this underestimates the overall food availability in forest fragments, and responses of animal populations in fragments vary (Estrada *et al.* 1998, Nichols *et al.* 2007). The present study used only goat dung and this may explain why the results disagree with a number of previous studies that used other baits singly or in combination (*e.g.*, Klein 1989, Davis 1994, Estrada *et al.* 1998, Chapman *et al.* 2003, Gardner *et al.* 2008). It may also help explain the more impoverished dung beetle communities in forest fragments than in continuous or primary forests. The use of goat dung in combination with other baits such as human or pig dung to mimic excreta produced by herbivores and omnivores in the forests (Davis 1994, Estrada *et al.* 1998) would have probably resulted into more diverse communities of dung beetles captured in this study. The results of this study should be generalized in comparing communities of dung beetles captured only using goat dung bait.

Dung beetle response to seasonal changes.—Significantly higher numbers of beetle individuals and species were captured in the wet season than during the dry season. This concurs with Andresen (1999) who documented that beetles are much more abundant in the rainy season than in the dry season in forests that show pronounced seasonality. Such strong seasonality of beetle assemblages may have implications for the ecosystem roles of beetles, such as secondary seed dispersal and forest regeneration (Andresen 2002, Vulinec 2002). Hanzen (1983) argued that the possibility of dung beetle rescuing seeds is reduced in the dry season since the number of beetles that arrives at dung piles is substantially less than the number in the rainy season. The study by Hanzen (1983) also demonstrated that dung degradation is much slower during the dry season. Thus, it is likely that in forests having marked seasonality, secondary dispersal by dung beetles will be less important or even absent during dry months (Andresen 2002). Soil texture and hardness are important factors affecting the composition of local dung beetle communities and their dung-burying behavior (Hall 2003).

During the rainy season soils are softer, which may facilitate dung and seed burial by ground beetles.

CONSERVATION IMPLICATIONS.—As in most sub-Saharan Africa, forest conservation efforts in Uganda have often focused mainly on national parks and central forest reserves and vertebrates and plants of high tourism value. This study demonstrates that forest fragments on agricultural lands, especially medium-sized fragments (100–150 ha), have rich dung beetle assemblages and may represent important conservation areas for dung beetles should there be continued deforestation of the Budongo landscape (but see Gardner *et al.* 2008). The variations observed among the different forests in dung beetle assemblages may have consequences on the local ecosystem functions. When considering the role of dung beetles in their respective habitats the most important factor is the disposal of dung (Jankielsohn *et al.* 2001). In the present study paracoprids (functional groups III and IV) were by far the most abundant in terms of species and individuals. These species bury large amounts of dung in a short time, moving even large seeds away from potential seed predators in the process (Vulinec 2002). They process larger amounts of dung than roller dung beetles of equivalent size (Doube 1990), and are thus likely to be more important in secondary seed dispersal in the Budongo forests. The transfer of dung and associated seeds to the soil may result in an increase in aboveground primary production. Thus the higher abundance of dung beetles in the medium sized-forest fragments (*cf.* the smaller 10–50 ha fragments) may result in faster regeneration.

Given the high rates of loss of tropical forest remnants (Laurance 1999), it is likely that even the apparently species-rich beetle assemblages observed in some forest fragments in this study may increasingly be threatened. This is because beetle population decline, genetic drift, and even extinction may occur when minimal threshold levels are exceeded and movement of individuals between fragments becomes difficult after some threshold of interpatch distance has been surpassed (Niemelä *et al.* 1993, Vulinec 2002, Gardner *et al.* 2008). This emphasizes the need for developing and implementing sustainable conservation strategies for forest fragments on farmlands. A number of strategies for the conservation of fragments have been proposed, for example, increasing connectivity, conservation and expansion of existing fragments, buffering existing fragments, and improving matrix quality (Walker *et al.* 2004, Donald & Evans 2006, Bailey 2007). As pointed out by Chapman *et al.* (2003), most forest fragments in Uganda are on privately or communally owned land, implying that it is imperative to understand the ethnoecology and use of the fragments and the surrounding matrix if such efforts to maximize their conservation values are to succeed. Conservation strategies in such landscapes should therefore consider both research into the problems of the local inhabitants and the need to educate and empower them to conservation action. Research should be integrated with applied conservation strategies to help protect forest fragments through environmental education programs and local participation in the solutions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Species and abundance of dung beetles captured in six forest fragments and the Nature Reserve (NR) in Budongo.*

TABLE S2. *Percentage contributions of the top five beetle species to dissimilarity between paired combinations of the seven forests.*

FIGURE S1. Relationship between (A) litter depth and beetle abundance; (B) ground cover and beetle abundance; (C) litter depth and beetle species richness; and (D) ground cover and beetle species richness.

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