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Colonization of Forest Elephant Dung by Invertebrates in the Bossematié Forest Reserve, Ivory Coast

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Jörn Theuerkauf, Sophie Rouys, Arno L. van Berge Henegouwen, Frank-Thorsten Krell, Sławomir Mazur, and Michael Mühlenberg (2009) Colonization of forest elephant dung by invertebrates in the Bossematié Forest Reserve, Ivory Coast. *Zoological Studies* **48**(3): 343-350. We studied the temporal succession and species richness of invertebrates in 18 droppings of African forest elephants (*Loxodonta cyclotis*) in the Bossematié Forest Reserve, Ivory Coast. We identified 19 species of the Scarabaeidae and of Hydrophilidae each, and 9 species of Histeridae. The Hydrophilidae colonized fresh dung but quickly disappeared when droppings began to dry. The Scarabaeidae mainly occurred in 12-40-h-old droppings. Colonization by the predatory Histeridae peaked after 10 h, but this group persisted longer in dung than did either the Hydrophilidae or Scarabaeidae. The Staphylinidae and Diptera quickly colonized droppings, whereas Blattodea nymphs and predatory Acarina occurred relatively later. http://zoolstud.sinica.edu.tw/Journals/48.3/343.pdf

Key words: Coleoptera, Histeridae, Hydrophilidae, *Loxodonta cyclotis*, Scarabaeidae.

The importance of African forest elephants (*Loxodonta cyclotis* Matschie, 1900) as keystone species for plant biodiversity has long been discussed because forest elephants disperse the seeds of numerous plants (Alexandre 1978, Merz 1981, Gautier-Hion et al. 1985, Lieberman et al. 1987, Hawthorne and Parren 2000, Theuerkauf et al. 2000, Babweteera et al. 2007). Some invertebrates, such as the Scarabaeidae, are attracted to elephant dung and can act as secondary dispersers (Feer 1999, Andresen 2002) because they bury seeds providing an advantage for germination and security against seed predators such as rodents and invertebrates (Andresen and Levey 2004). Dung can also be an important resource to some species: savannah elephant (*L. africana* Blumenbach, 1797) dung contributes to the survival of a rare dung beetle (Kryger et al. 2006) and may be a keystone resource for wildlife communities that inhabit semiarid woodlands (Dudley 2000).

Although there is some knowledge of the ecology of the Scarabaeidae that colonize elephant dung in African rain forests (reviewed in Cambefort and Walter 1991), little is known about the Histeridae (Thérond 1967, Yélamos 1994) and nothing of the Hydrophilidae that feed in elephant droppings. We therefore studied the temporal succession of invertebrates in forest elephant dung in the Bossematié Forest Reserve

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(Ivory Coast). We attempted to determine the time during which invertebrates remained in the droppings and evaluated the species richness of the Scarabaeidae, Hydrophilidae, and Histeridae in the dung.

STUDY AREA AND METHODS

The Bossematié Forest Reserve (220 km^2) is a heavily exploited moist semi-deciduous rainforest in the southeastern lowlands of the Ivory Coast (3°24'-3°35'W, 6°22'-6°33'N). The annual distribution of rainfall (with an annual mean of 1330 mm) is bimodal with peaks in Apr.-July and Sept.-Oct. Aug. and Dec.-Feb. are dry, whereas Mar. and Nov. experience intermediate humidity. The northern part of the Bossematié is classified as "*Celtis* spp. forest with *Triplochiton scleroxylon*" whereas the southern part is a moister "variant with *Nesogordonia papaverifera* and *Khaya ivorensis*" (Guillaumet and Adjanohoun 1971). Forest elephants disperse seeds of at least 66 species of plants in the study area (Theuerkauf et al. 2000).

From Sept. 1993 to Feb. 1994, we followed the tracks of forest elephants as described in Theuerkauf et al. (2001). We collected 4300 invertebrates in 45 samples of 18 droppings of these elephants. A sample consisted of 1 bolus collected from the top of an elephant dung pile from which we extracted all invertebrates. The same person (JT) sampled each bolus with the same effort (about 30 min to extract all invertebrates from a bolus). Most invertebrates were inside the bolus, thus we did not assume that removing 1 bolus from the dung pile greatly affected further succession of invertebrates in the rest of the pile (usually containing a total of around 8-10 boli). We excluded 3 samples from the analyses of mean numbers per sample, because we did not take all individuals from those samples. We took samples only from droppings that we found when they were fresh. The age of droppings was estimated by an experienced elephant tracker (as described in Theuerkauf and Ellenberg 2000). In most cases, we sampled the same dung pile on 4 occasions: when we found it, the day after the first sample, 4 d after finding the dropping, and 1 wk after the first sampling. Because we took samples only from droppings that we found when they were fresh, we knew the age of all samples with a maximum error of a few hours. We took samples from droppings along elephant tracks in the rainforest (usually in the shade), on forest roads, and in clearings (in the sun). FTK identified the Scarabaeidae (specimens deposited in the Denver Museum of Nature and Science), SM the Histeridae, and ALvBH the Hydrophilidae. We sorted all other invertebrates into the following groups (we considered only groups of which we caught more than 10 individuals): predatory Acarina, Blattodea nymphs, Carabidae, Staphylinidae, coleopteran larvae, Diptera (imagines, larvae, and pupae), and Formicoidea. We then plotted the numbers of individuals or species against the age of each sample and tested several regression models (linear, logarithmic, inverse, S-curve, and growth) with SPSS 11.0 for Windows to determine the model that best described the increase (from beginning to maximum) and decrease (from maximum to the end) in insect numbers.

RESULTS

We identified 419 individuals of the Hydrophilidae, 219 Scarabaeidae, and 109 Histeridae, which respectively accounted for 19, 19, and 9 species (Table 1). The Hydrophilidae usually colonized dung in the first 10 h after an elephant had defecated, when the droppings were fresh (Fig. 1), but they disappeared as soon as the droppings began to dry (after about 1 d under sunny conditions and 2 d in the shade). The Hydrophilidae colonized droppings very fast, so we were only able to fit a regression for the decline in species and individuals (Table 2). The mean number of Hydrophilidae individuals per sample of dung fresher than 2 d was higher (*t*-test, $p = 0.036$) in the shade (61 individuals/sample, S.E. = 19) than in the sun (17 individuals/sample, S.E. = 4), but the numbers of species in the shade and in the sun were comparable ($p = 0.705$). The Scarabaeidae mainly occurred in elephant droppings that were 12-40 h old (Fig. 1). At that time, the mean number of individuals was higher (*U*-test, $p = 0.025$) under sunny conditions (25 individuals/sample, S.E. = 11) than in the shade (7 individuals/sample, S.E. = 1), but the mean number of species did not significantly differ ($p = 0.148$). Increases in numbers of species and individuals of the Scarabaeidae were best described by an S-curve model, whereas the decline was linear (Table 2). Colonization by the Histeridae, which are predators of Diptera, Scarabaeidae, and other insects, also peaked after 10 h, but the Histeridae persisted longer in the dung than did the Hydrophilidae or Scarabaeidae. The increase in numbers of the Histeridae was best described by either a linear or S-curve, while the decrease was best described by an inverse model.

The number of coleopteran larvae in droppings that were in the shade peaked at around 80 h, but at 30-40 h for droppings exposed to the sun. The Staphylinidae and Diptera quickly colonized droppings (Fig. 2). We found dipteran larvae in some fresh elephant droppings (about 1 h old) but the maximum number of larvae appeared at 30-40 h, when most adults had already disappeared. In the first 20 h after the dung was deposited, dipteran larvae were more abundant in piles in the sun than in the shade (Fig. 2). The situation was reversed for elephant droppings older than 30 h, as the abundance of dipteran larvae was higher in piles in the shade than in sunlight. Blattodea nymphs and predatory Acarina both colonized elephant droppings relatively late (Fig. 2). The regression models for the increase and decrease of these invertebrate groups were most often not significant because of the low numbers of individuals (Table 2). Other invertebrates occurred in lower numbers (fewer than 100 individuals sampled).

DISCUSSION

Most groups of invertebrates that colonized elephant dung within the first 2 d after it was deposited (such as the Scarabaeidae, Histeridae, Staphylinidae, and Diptera) increased in numbers of individuals or species following an S-curve model, with the exception of the Hydrophilidae, which colonized dung so quickly that we were not able to model the increase. This means that after a certain delay, most individuals and species of these groups arrive at about the same time. Insects that find the dropping might, intentionally or unintentionally, emit signals (e.g., pheromones: Tribe 1975, Burger et al. 1995), which attract other individuals. Mechanical actions (Thomé and Desière 1979) by first arrivers might also facilitate the colonization by other insects. Dung beetles can form aggregations (Palestrini et al. 1998, Hutton and Giller 2004), but the underlying physiological mechanisms of these phenomena are unknown. After 2 d, the first colonizers had mainly left the droppings (generally modeled as logarithmic decreases). In contrast, those groups that appeared at later stages (such as the Acarina, Blattodea nymphs, and coleopteran larvae) increased in numbers following growth or linear models. Thus, they colonized droppings over a longer time span but with a smaller number of individuals than the first colonizers (Figs. 1, 2).

In our study, species richness and abundance of the Scarabaeidae were especially high under sunny conditions. This coincides with a higher germination success of plants in elephant droppings under sunny conditions than in the shade (Theuerkauf et al. 2000). A positive effect of the Scarabaeidae on seed germination success in our study area is therefore possible, although we cannot rule out other factors influencing germination success. Species richness of the Scarabaeidae in our study area was highest when droppings were 1-2 d old, whereas this variable was highest when Indian elephant (*Elephas maximus* Linnaeus, 1758) dung was about 3 d old (Sabu et al. 2006). We assume that colonization

Table 1. Numbers of individuals of the Scarabaeidae, Histeridae, and Hydrophilidae found in 45 boli of forest elephant droppings in the Bossematié Forest Reserve (Ivory Coast) from Nov. 1993 to Feb. 1994 (except for 6 individuals of *Anachalcos cupreus* indicated by [1], which were sampled in Sept. 1993). [D], diurnal; [N], nocturnal; [F], forest species; [S], savannah species; [a] preference for elephant dung (following Cambefort 1984 and Cambefort and Walter 1991); [b] presumed elephant dung specific (so far found in elephant dung only); [c] previously reported from elephant dung (Yélamos 1994)

Exposure	Shade					Sun				
Age of droppings (h)	1-9	12-16	29-39	72-84	160-178	4-8	12-20	32-40	75-84	172-178
Number of samples	5	5	7	6	8	2	2	4	3	3
Scarabaeidae rollers (telecoprids)										
Anachalcos cupreus (Fabricius, 1775) [N, S]	6[1]	1								
Neosisyphus tai Cambefort, 1984 [D, F]			3				1			
Sisyphus eburneus Cambefort, 1984 [D, F]		2	1							

Table 1. (Cont.)

Exposure	Shade					Sun				
Age of droppings (h)	1-9	12-16	29-39	72-84	160-178	4-8	12-20	32-40	75-84	172-178
Number of samples	5	5	7	6	8	2	2	4	3	3
Sisyphus gazanus Arrow, 1909 [D, S]		1								
Scarabaeidae tunnelers (paracoprids)										
Allonitis nasutus (Felsche, 1907) [N, F, a]		1						1		
Onitis subcrenatus Kolbe, 1897 [N, F]					1			1		
Copris phylax Gillet, 1908 [N, F, b]							2			
Caccobius cribrarius Boucomont, 1928 [D, F, a]		1	3				1	3		
Caccobius elephantinus Balthasar, 1967 [D, F, b]	4	9	4			2	2			
Onthophagus deplanatus van Lansberge, 1883 [N, F]		2								
Proagoderus ritsemai van Lansberge, 1883 [D, F]							3			
Drepanocerus caelatus (Gerstaecker, 1871) [D, F]			1							
Euoniticellus fumigatus (Boucomont, 1923) [D, F/S, a]								5	1	
Euoniticellus tai Cambefort, 1983 [D, F, b]		13	17	4		2	2	4		
Tiniocellus cf. *spinipes* (Roth, 1851) [D, F/S]			2					37		
Scarabaeidae dwellers (endocoprids)										
Oniticellus pseudoplanatus Balthasar, 1964 [D, F]				1			3		1	
Aphodius (*Pharaphodius*) sp. nov. A [b]					1			1		
Aphodius (*Pseudopharaphodius*) sp. nov. A [b]		14	12	1	1		12	28		
Aphodius (*Pseudopharaphodius*) sp. nov. B [b]							1			
Histeridae										
Chaetabraeus (s. str.) *brasavolai* (Müller, 1944)	4	5	24				1	12	3	
Chaetabraeus (s. str.) *mulleri* Thérond, 1967			3							
Chaetabraeus (s. str.) *setosellus* (Blickhardt, 1921)			1							
Chaetabraeus (s. str.) *setulosus* (Fåhraeus, 1851)	2	1	4	2			2	5		
Chaetabraeus (*Mazureus*) *cyclonotus* (Marseul, 1856)			6	1			1	1	11	1
Pachylister adjectus (Marseul, 1861) [c]		2	1							
Atholus cycloides (Burgeon, 1939) [c]			4		1		3			
Atholus erichsoni Lundgren, 1991 [c]			3		1					
Atholus rubricatus (Lewis, 1897) [c]			4							
Hydrophilidae										
Sphaeridium simplicipes Marcuzzi, 1943	43	34	17			6	8	4		
Sphaeridium abditum d'Orchymont, 1943	10	10				13	1	5		
Sphaeridium bottegoi Marcuzzi, 1943	10	9	1			10				
Sphaeridium jongemai van Berge Henegouwen, 1987	1									
Sphaeridium sp. nov. A	5	1								
Sphaeridium sp. nov. B	7	14	2			1	1	1		
Cyrtonion ghanense Hansen, 1989		4	8							
cf. *Cercillum* sp.		2								
Pachysternum-Cryptopleurum-Cycrillum-complex		4								
Pachysternum capense (Mulsant, 1844)								1		
Pachysternum cf. *capillatum* Orchymont, 1942	18	6	5			6	2	3		
Gen. nov. sp. nov. near *Pachysternum*	20	3	12		1	5		2	1	
Gen. nov. sp. nov. near *Cryptopleurum*		1								
Gen. near *Cycrillum*	6		9	2	1	3	1	4	3	
Tectosternum exstriatum Balfour-Browne, 1958	2	4	2	2	5		1	3	9	1
Tectosternum sp. non.	1		2	2				3	1	
Cercyon (s. str.) sp. A	8	11	8			2	1			
Cercyon (s. str.) sp. B	1	1	1							
Cercyon (s. str.) sp. C	1									
unidentified Hydrophilidae	324	294	57	6		7	5	4		2

of the dung by the Scarabaeidae in our study area occurred earlier because many droppings were exposed to the sun. However, even dung in the shade may dry out after a few days due to the activity of scarabaeid tunnelers (Anderson and Coe 1974). This drying-out phenomenon due to the activity of the Scarabaeidae might therefore contribute to a higher germination success of

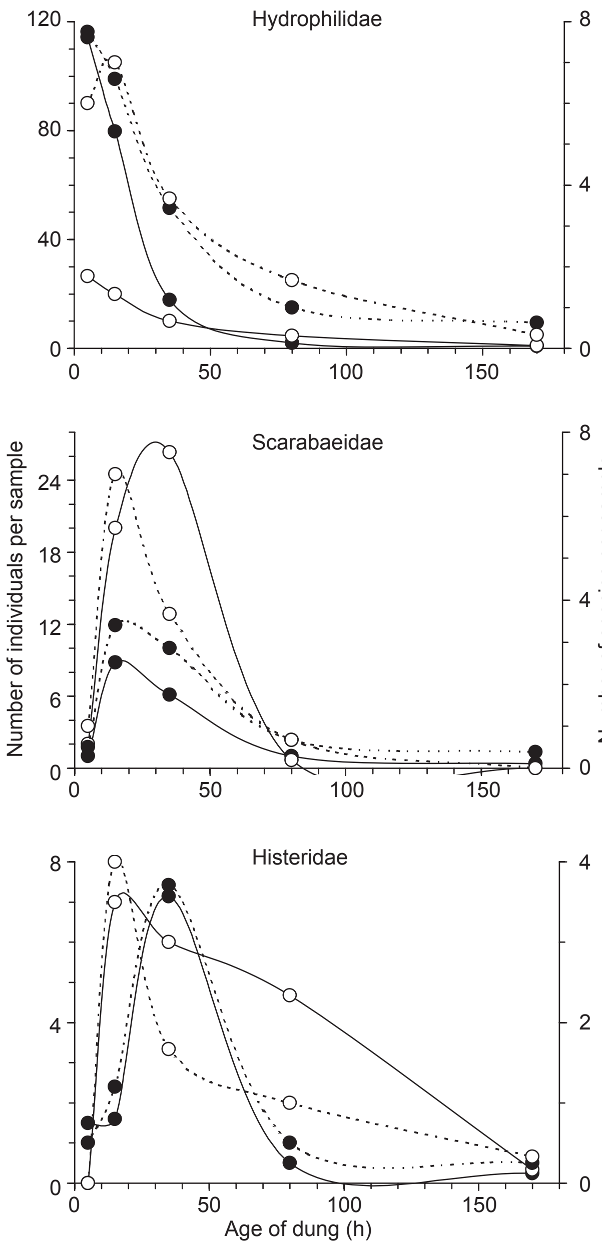

Fig. 1. Mean numbers of individuals (continuous lines) and mean number of species (dashed lines) of the Hydrophilidae, Scarabaeidae, and Histeridae per bolus of a forest elephant dropping in relation to the age of the dropping and its exposure to the sun (open circles, exposed; closed circles, shaded) from Nov. 1993 to Feb. 1994 in the Bossematié Forest Reserve, Ivory Coast (n = 12 droppings in the sun, n = 30 in the shade).

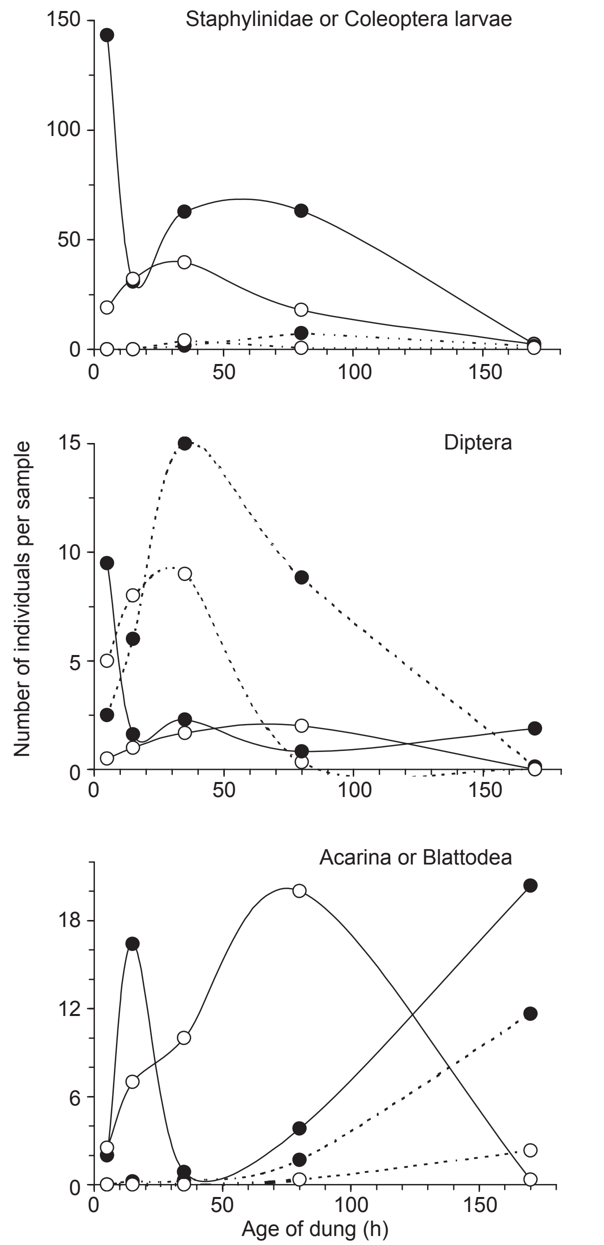

Fig. 2. Mean numbers of adult Staphylinidae (continuous lines), coleopteran larvae (dashed lines), dipteran larvae (dashed lines) and adults (continuous lines), Blattodea nymphs (dashed lines), and Acarina (continuous lines) per bolus of forest elephant droppings in relation to the age of the dropping and its exposure to the sun (open circles, exposed and closed circles, shaded) from Nov. 1993 to Feb. 1994 in the Bossematié Forest Reserve, Ivory Coast (n = 12 droppings in the sun, n = 30 in the shade).

plants by shortening the period during which other invertebrates can feed in dung, since many species of invertebrates and fungi prefer humid droppings (Masunga et al. 2006).

Despite a short sampling period that mainly took place in the dry months, which coincides with a low flight activity for many invertebrates, and despite coprophilous beetles in Africa being much less abundant in forests than in savannas (Krell et al. 2003), we identified 747 beetles of 47 species from 18 elephant droppings. The association of elephants with a high species richness of Scarabaeidae was already known (Cambefort and Walter 1991, Botes et al. 2006). The reason for this high invertebrate diversity may be that elephant droppings provide a reliable and comparably abundant food source (with about 3 new droppings per km^2 per day, Theuerkauf et al. 2000), while droppings of buffalo (*Syncerus caffer* Sparrman, 1779) and chimpanzee (*Pan troglodytes* (Blumenbach, 1775)) are rare in our study area (J. Theuerkauf pers. observ.). The mean distance between droppings found on elephant trails in the Bossematié Forest Reserve was about 100 m (calculated from 629 elephant droppings on 57.9 km of elephant tracks; Theuerkauf and Ellenberg 2000). Many insect species are probably able to follow elephants over this short distance. This might also explain why most invertebrates could colonize fresh elephant droppings so quickly and leave them within a few days. However, the next generation that develops in elephant dung needs to find fresh elephant droppings, which is more difficult than following elephant tracks. The highly developed olfactory sense of dung beetles (Shibuya and Inouchi 1982, Dormont et al. 2007) probably helps detect fresh droppings, as these insects must find droppings that might be several kilometers away. A high forest elephant density could therefore be an important factor for the biodiversity of invertebrates that depend on dung. Davis et al. (2005) assumed that the reintroduction of savannah elephants might increase dung beetle diversity. Although our study was not designed to determine whether some species depend on elephants, we think that the relatively high number of species found during the limited study period and in the small number of elephant droppings is

Table 2. Best fit models ([1], logarithmic; [2], growth; [3], S-curve; [4], linear; [5], inverse) for the increase (in) and decline (de) in numbers (y) of individuals or species in relation to the age of dung in hours (x). Hours of the age classes of maximum insect numbers are included in the regressions of both the increase and the decline

		In the shade				In the sun			
Invertebrate group		Age (h)	*n*	Best fit model	*p*	Age (h)	*n*	Best fit model	*p*
Hydrophilidae (adults)	de	1-178	30	$^{2}y = e^{25.4 - 0.75x}$	< 0.001	4-178	12	$^{1}y = 37 - 7.2\ln(x)$	< 0.001
Hydrophilidae (species)	de	1-178	30	$^{1}y = 9.7 - 1.7\ln(x)$	< 0.001	4-178	12	$^{1}y = 9.5 - 1.7\ln(x)$	0.001
Scarabaeidae (adults)	in	1-16	9	$^{3}y = e^{22.8 - 252.6/x}$	< 0.001	4-40	6	$^{3}y = e^{51.8 - 971.8/x}$	0.016
	de	12-178	26	$^{1}y = 17.9 - 3.5\ln(x)$	< 0.001	32-178	9	$^{2}y = e^{55.8 - 1.6x}$	0.007
Scarabaeidae (species)	in	1-16	9	$^{3}y = e^{21.9 - 251.7/x}$	< 0.001	4-12	3	$^{3}y = e^{153 - 1498/x}$	0.151
	de	12-178	26	$^{1}y = 7.2 - 1.4\ln(x)$	< 0.001	12-178	10	$^{1}y = 12.7 - 2.6\ln(x)$	< 0.001
Histeridae (adults)	in	1-39	16	$^{3}y = e^{-20.7 - 204.9/x}$	0.008	4-12	3	$^{4}y = -4.7 + 0.9x$	0.333
	de	29-178	21	$^{5}y = -2.2 + 299.7/x$	< 0.001	12-178	10	$^{4}y = 7.8 - 0.04x$	0.035
Histeridae (species)	in	1-39	16	$^{3}y = e^{-21.2 - 204.4/x}$	0.008	4-12	3	$^{4}y = -2.7 + 0.5x$	0.333
	de	29-178	21	$^{5}y = -0.9 + 151.5/x$	< 0.001	12-178	10	$^{5}y = 0.3 + 46.3/x$	0.004
Coleoptera (larvae)	in	1-84	22	$^{2}y = e^{-250.3 + 3.16x}$	< 0.001	4-40	6	$^{4}y = -0.8 + 0.13x$	0.414
	de	72-178	14	$^{3}y = e^{-206.4 + 16019/x}$	0.052	32-178	9	$^{5}y = -0.7 - 157.5/x$	0.273
Staphylinidae (adults)	in					4-40	6	$^{5}y = 44 - 136.1/x$	0.328
	de	1-178	30	$^{4}y = 88 - 0.5x$	0.008	32-178	9	$^{5}y = -7 + 1711.1/x$	0.028
Diptera (adults)	in					4-84	9	$^{5}y = 2 - 8/x$	0.259
	de	1-178	30	$^{2}y = e^{-87.4 - 0.48x}$	0.153	75-178	6	$^{4}y = 3.5 - 0.02x$	0.145
Diptera (larvae)	in	1-39	16	$^{3}y = e^{-103.7 + 104.9/x}$	0.271	4-40	6	$^{4}y = 5.6 + 0.09x$	0.707
	de	29-178	21	$^{2}y = e^{14.7 - 1.14x}$	0.005	32-178	9	$^{3}y = e^{-279.1 + 9776.4/x}$	0.008
Blattodea (nymphs)	in	1-178	30	$^{2}y = e^{-222 + 0.96x}$	0.001	4-178	12	$^{2}y = e^{-264.1 + 1.49x}$	< 0.001
Acarina	in	1-178	30	$^{4}y = 3.2 + 0.09x$	0.331	4-84	9	$^{4}y = 0.2 + 0.27x$	0.251
	de					75-178	6	$^{4}y = 33.9 - 0.19x$	0.433

an indicator of the important role in invertebrate biodiversity that elephants may play in forested areas.

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REFERENCES

Alexandre DY. 1978. Le rôle disséminateur des éléphants en forêt de Taï, Côte d'Ivoire. Rev. Ecol. Terre Vie **32:** 47-72.

Anderson JM, MJ Coe. 1974. Decomposition of elephant dung in an arid, tropical environment. Oecologia **14:** 111-125.

Andresen E. 2002. Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. Ecol. Entomol. **27:** 257-270.

Andresen E, DJ Levey. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia **139:** 145-154.

Babweteera F, P Savill, N Brown. 2007. *Balanites wilsoniana*: regeneration with and without elephants. Biol. Conserv. **134:** 40-47.

Botes A, MA McGeoch, BJ van Rensburg. 2006. Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland centre of endemism. Biol. Conserv. **130:** 573-583.

Burger BV, WJG Petersen, GD Tribe. 1995. Pheromones of the Scarabaeinae. IV. Identification of an attractant for the dung beetle *Pachylomerus femoralis* in the abdominal secretion of the dung beetle *Kheper lamarcki*. Z. Naturforsch. C **50:** 675-680.

Cambefort Y. 1984. Etude écologique des Coléoptères Scarabaeidae de Côte d'Ivoire. Travaux Chercheurs Station Lamto **3:** 294 + 12 pp.

Cambefort Y, P Walter. 1991. Dung beetles in tropical forests in Africa. *In* I Hanski, Y Cambefort, eds. Dung beetle ecology. Princeton, NJ: Princeton Univ. Press, pp. 198-210.

Davis ALV, CH Scholtz, C Deschodt. 2005. A dung beetle survey of selected Gauteng nature reserves: implications for conservation of the provincial scarabaeine fauna. Afr. Entomol. **13:** 1-16.

Dormont L, S Rapior, DB McKey, JP Lumaret. 2007. Influence of dung volatiles on the process of resource selection by coprophagous beetles. Chemoecology **17:** 23-30.

Dudley JP. 2000. Seed dispersal by elephants in semiarid woodland habitats of Hwange National Park, Zimbabwe. Biotropica **32:** 556-561.

Feer F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. J. Trop. Ecol. **15:** 129-142.

Gautier-Hion A, JM Duplantier, R Quris, F Feer, C Sourd, JP Decoux, G Dubost, L Emmons, C Erard, P Hecketsweiler, A Moungazi, C Roussilhon, JM Thiollay. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia **65:** 324-337.

Guillaumet JL, E Adjanohoun. 1971. La végétation de la Côte d'Ivoire. Mém. O.R.S.T.O.M. **50:** 157-263.

Hawthorne WD, MPE Parren. 2000. How important are forest elephants to the survival of woody plant species in Upper Guinean forests? J. Trop. Ecol. **16:** 133-150.

Hutton SA, PS Giller. 2004. Intra- and interspecific aggregation of north temperate dung beetles on standardised and natural dung pads: the influence of spatial scale. Ecol. Entomol. **29:** 594-605.

Krell FT, S Krell-Westerwalbesloh, I Weiβ, P Eggleton, KE Linsenmair. 2003. Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae). Ecography **26:** 210-222.

Kryger U, KS Cole, R Tukker, CH Scholtz. 2006. Biology and ecology of *Circellium bacchus* (Fabricius 1781) (Coleoptera Scarabaeidae), a South African dung beetle of conservation concern. Trop. Zool. **19:** 185-207.

Lieberman D, M Lieberman, C Martin. 1987. Notes on seeds in elephant dung from Bia National Park, Ghana. Biotropica **19:** 365-369.

Masunga GS, Ø Andresen, JE Taylor, SS Dhillion. 2006. Elephant dung decomposition and coprophilous fungi in two habitats of semi-arid Botswana. Mycol. Res. **110:** 1214-1226.

Merz G. 1981. Recherches sur la biologie de nutrition et les habitats préférés de l'éléphant de forêt, *Loxodonta africana cyclotis* Matschie, 1900. Mammalia **45:** 299-312.

Palestrini C, E Barbero, A Rolando. 1998. Intra- and interspecific aggregation among dung beetles (Coleoptera: Scarabaeoidea) in an Alpine pasture. J. Zool. **245:** 101-109.

Sabu TK, KV Vinod, PJ Vineesh. 2006. Guild structure, diversity and succession of dung beetles associated with Indian elephant dung in South Western Ghats forests. J. Insect Sci. **6:** 1-12.

Shibuya T, J Inouchi. 1982. Fine structure and odor responses of olfactory sensilla of the Japanese dung beetle, *Copris pecuarius* (Coleoptera: Scarabaeidae). Jpn. J. Appl. Entomol. Zool. **26:** 194-195. (in Japanese)

Thérond J. 1967. The scientific results of the Hungarian Soil Zoological Expedition to the Brazzaville-Congo. 26. Espèces de la famille Histeridae (Coleoptera). Opuscula Zool. (Budapest) **7:** 271-291.

Theuerkauf J, H Ellenberg. 2000. Movements and defaecation of forest elephants in the moist semi-deciduous Bossematié Forest Reserve, Ivory Coast. Afr. J. Ecol. **38:** 258-261.

Theuerkauf J, H Ellenberg, WE Waitkuwait, M Mühlenberg. 2001. Forest elephant distribution and habitat use in the Bossematié Forest Reserve, Ivory Coast. Pachyderm **30:**

37-43.
Theuerkauf J, WE Waitkuwait, Y Guiro, H Ellenberg, S Porembski. 2000. Diet of forest elephants and their role in seed dispersal in the Bossematié Forest Reserve, Ivory Coast. Mammalia **64:** 447-459.
Thomé JP, M Desière. 1979. Observations préliminaires sur les mécanismes d'attraction de quelques espèces de coléoptères Hydrophilidae coprophiles. Bull. Ecol. **10:** 211-221.
Tribe GD. 1975. Pheromone release by dung beetles (Coleoptera: Scarabaeidae). S. Afr. J. Sci. **71:** 277-278.
Yélamos T. 1994. Data on Afrotropical Histeridae (Coleoptera), with description of *Hister sindarae* n. sp. Misc. Zool. **16:** 37-43.