



Dung Beetles of the Kwamalasamutu Region, Suriname (Coleoptera: Scarabaeidae: Scarabaeinae)

Author: Larsen, Trond H.

Source: A Rapid Biological Assessment of the Kwamalasamutu region,
Southwestern Suriname: 91

Published By: Conservation International

URL: <https://doi.org/10.1896/054.063.0108>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Chapter 5

Dung beetles of the Kwamalasamutu region, Suriname (Coleoptera: Scarabaeidae: Scarabaeinae)

Trond H. Larsen

SUMMARY

Dung beetles are among the most cost-effective of all animal taxa for assessing biodiversity patterns, but relatively little is known about the dung beetle fauna of Suriname. I sampled dung beetles using baited pitfall traps and flight intercept traps in the Kwamalasamutu Region of southern Suriname. I collected 4,554 individuals represented by 94 species. Species composition and abundance varied quite strongly among sites. Dung beetle diversity correlated positively with large mammal species richness, and was highest at the most isolated site (Kutari), suggesting a possible cascading influence of hunting on dung beetles. Small-scale habitat disturbance also caused local dung beetle extinctions.

The dung beetle fauna of the Kwamala region is very rich relative to other lowland forests of Suriname and the Guianas, and contains a mix of range restricted endemics, Guiana Shield endemics, and Amazonian species. I estimate that about 10–15% of the dung beetle species collected here are undescribed. While most species were coprophagous, 26 species were never attracted to dung; 4 of these were attracted exclusively to carrion or dead invertebrates and the other 22 were only captured in flight intercept traps. The abundance of several large-bodied dung beetle species in the region is indicative of the intact wilderness that remains. These species support healthy ecosystems through seed dispersal, parasite regulation and other processes. Maintaining continuous primary forest and regulating hunting (such as through hunting-restricted reserves) in the region will be essential for conserving dung beetle communities and the ecological processes they sustain.

INTRODUCTION

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are an ecologically important group of insects. By burying dung as a food and nesting resource, dung beetles contribute to several ecological processes and ecosystem services that include: reduction of parasite infections of mammals, including people; secondary dispersal of seeds and increased plant recruitment; recycling of nutrients into the soil; and decomposition of dung as well as carrion, fruit and fungus (Nichols et al. 2008). Dung beetles are among the most cost-effective of all animal taxa for assessing and monitoring biodiversity (Gardner et al. 2008a), and consequently are frequently used as a model group for understanding general biodiversity trends (Spector 2006). Dung beetles show high habitat specificity and respond rapidly to environmental change. Since dung beetles primarily depend on dung from large mammals, they are excellent indicators of mammal biomass and hunting intensity. Dung beetle community structure and abundance can be rapidly measured using standardized transects of baited traps, facilitating quantitative comparisons among sites and studies (Larsen and Forsyth 2005).

METHODS

I sampled dung beetles at all three sites (Kutari, Sipaliwini, and Werehpai) using standardized pitfall trap transects. Ten traps baited with human dung were placed 150 m apart along a linear transect at each site (see Larsen and Forsyth 2005 for more details). Traps consisted of 16 oz plastic cups buried in the ground and filled with water with a small amount of liquid detergent. A bait wrapped in nylon tulle was suspended above the cup from a stick and covered with a large leaf. At each site, traps were collected every 24 hours for four days, and were re-baited after two days. I set three flight intercept traps at each site to passively collect dung beetle species that are not attracted to dung. I also placed additional pitfall traps whenever possible with other types of baits that included rotting fungus, carrion, dead millipedes, and injured millipedes. All traps were collected daily. I opportunistically collected dung beetles that I encountered in the forest, usually perching on leaves during both day and night.

From August 19–24, 2010, I collected dung beetles at the Kutari site (N 02° 10' 31", W 056° 47' 14") in primary forest characterized by small hills and several swampy areas. From August 27 – September 4, 2010, I collected dung beetles at the Sipaliwini site (N 02° 17' 24", W 056° 36' 26") in primary forest with small hills and relatively dry, hard soils with high bedrock. From September 2–7, 2010, I collected dung beetles at the Werehpai site (N 02° 21' 47", W 056° 41' 52") in primary forest as well as in bamboo (1 dung trap) and secondary forest (1 dung trap). Beetles were identified and counted as they were collected in the field and voucher specimens were stored in ethanol for further study and museum collections. Beetle specimens are deposited at the National Museum of Natural History at the Smithsonian Institution in Washington, DC, USA and at the National Zoological Collection of Suriname in Paramaribo.

To estimate total species richness at each site and assess sampling completeness, I compared the observed number of species with the expected number of species on the basis of randomized species accumulation curves computed in EstimateS (version 7, R. K. Colwell, <http://purl.oclc.org/estimates>) (Colwell and Coddington 1994). I used an abundance-based coverage estimator (ACE) because it accounts for species abundance as well as incidence, providing more detailed estimates. I also used EstimateS to calculate similarity among sites, using the Morisita-Horn similarity index which incorporates species abundance as well as incidence.

RESULTS AND DISCUSSION

I sampled a total of 94 species and 4,554 individuals of dung beetles during the RAP (Table 1, Appendix A). Species richness was similar at all sites. Among dung traps, for which sampling effort was identical at all sites, species richness was highest at Sipaliwini (49 species), followed by Werehpai

(47 species) and Kutari (44 species) (Table 1, Fig. 1). Species accumulation curves for dung-baited pitfall traps (based on abundance-based coverage estimator) indicated that I sampled an estimated 88% of all coprophagous species occurring in the area. However, sampling completeness was lowest at Werehpai where I sampled only 72% of the dung-feeding species likely to occur at the site (Table 1, Fig. 1). Consequently, species richness estimators predict that Werehpai supports the highest number of coprophagous species (65 species), followed by Kutari (60 species) and Sipaliwini (57 species) (Table 1).

These differences between observed and predicted species richness are probably explained by strong differences in abundance among sites. As with observed species richness, abundance was highest at Sipaliwini and lowest at Kutari; Sipaliwini supported almost three times as many individuals as Kutari (Table 1, Fig. 1). Low abundance at Kutari may have been influenced by the large areas of swamp and

Table 1. Diversity and abundance of dung beetles in Kwamala region.

	All sites	Kutari	Sipaliwini	Werehpai
Species richness (all samples)	94	70	62	67
Species richness (dung traps)	68	45	49	47
Estimated richness (ACE) (dung traps)	77	60	57	65
% Sampling completeness (dung traps)	88	75	86	72
Shannon diversity (H) (dung traps)	2.84	2.85	2.57	2.78
Abundance/trap (all samples)	23.6	13.8	34.3	23.5
Abundance/trap (dung traps)	33.9	16.7	49.3	35.7

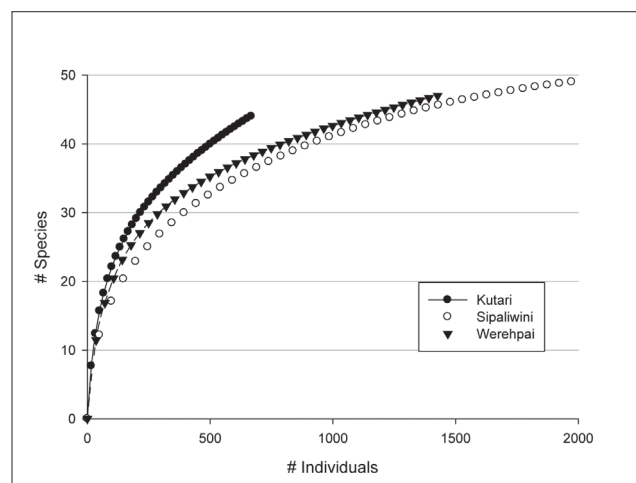


Figure 1. Species accumulation curves for each site based on dung-baited pitfall traps (40 trap samples for each site).

flooded forest at the site, conditions which negatively affect many dung beetle species whose larvae develop in the soil. However, diversity, measured by the Shannon index, showed the opposite pattern to observed species richness. Diversity was highest at Kutari and lowest at Sipaliwini, due to greater evenness of species' abundance distributions at Kutari (Table 1).

Out of 94 species sampled during this RAP survey, only 68 were attracted to dung. Considering all trap types and capture methods, Kutari supported the greatest number of dung beetle species (70 species) (Appendix A, B). Four species were attracted only to carrion or to dead invertebrates (Appendix B). 22 species were sampled only in flight intercept traps (Appendix B), and many of these species are poorly represented in collections because they are difficult to sample and in some cases, their diet is unknown. Some of these species show unusual specializations, such as millipede predation or colonization of leaf-cutter ant nests (see interesting species discussion below).

Species composition and community structure varied strongly among sites (Table 2). Sipaliwini and Werehpai were relatively similar in terms of community structure, showing a high Morisita-Horn index. Kutari was very distinct from both Sipaliwini and Werehpai, and contained many species not present at the other sites. Some of the most abundant species at a particular site were rare or completely absent from other sites (Appendix A). For example, I caught 211 individuals of *Ateuchus simplex* at Sipaliwini, and none at Kutari, despite the relative close proximity of both sites.

Dung beetle species richness was strongly reduced by habitat disturbance. Second growth forest supported only 70% of the total species richness found in primary forest, while bamboo supported only 40% of primary forest species richness (Fig. 2). Only one species, *Uroxys gorgon*, occurred in bamboo or secondary forest but did not occur in primary forest. *Uroxys gorgon* is known to be phoretic in sloth fur, and sloths are often hyper-abundant in secondary forest. The absence of other disturbance-adapted species in the Kwamala region was somewhat surprising, given the high number of 'weedy' species found in other parts of South America. Their absence might be explained by the extraordinarily low proportion of disturbed habitats occurring in southern Suriname.

Dung beetle diversity (measured by the Shannon index) was strongly positively correlated with species richness of

large mammals (Fig. 3), with the highest beetle diversity and mammal richness occurring at Kutari. Kutari also appeared to support the most primate species of all sites (see Large Mammals Chapter), and primates provide one of the most important food sources for dung beetles. High dung beetle diversity at Kutari may have been influenced by higher mammal richness and by lower hunting intensity, although further data are needed. On the other hand, dung beetle species richness and abundance were not correlated with the large mammal community, although no robust analysis was possible due to the short sampling period for mammals and the small number of sites for both groups (N=3). Furthermore, dung beetle abundance and species richness may have been influenced by differences in habitat and soil conditions, as discussed above.

At least 23 dung beetle species sampled during this RAP survey are known to be distributed across the Amazon basin. Many of the Amazonian species were locally rare and sampled at Kutari (Appendix A), which was the southernmost site sampled during the RAP. Out of these 23 Amazonian species, 20 occurred at Kutari, and only 16 at Werehpai and 15 at Sipaliwini. The Kwamala area may straddle the northern range limit for these species.

For the few genera that have been revised and for which good distributional data exist, many of the remaining species are restricted to the northern Amazon region, the Guiana Shield, or show an even more restricted range, while several are data deficient (see also interesting species discussion below). For example, *Coprophanæus parvulus*, *Oxysternon festivum*, and *Eurysternus balachowskyi* are endemic to the Guiana Shield and northern Amazon, while *Oxysternon durantoni* and *Eurysternus cambeforti* occur only in the extreme northeastern Guianas (Edmonds and Zidek 2004, Genier 2009, Edmonds and Zidek 2010).

Dung beetle species richness is high in the Kwamala region relative to other areas in northeastern South America and the Guianas (Table 3). Similar RAP surveys at Lely and Nassau in Suriname yielded only 35–48% of the species

Table 2. Dung beetle community similarity among sites.

1st	2nd	S 1st	S 2nd	Shared Species	Morisita-Horn
Kutari	Sipaliwini	44	49	35	0.57
Kutari	Werehpai	44	47	30	0.61
Sipaliwini	Werehpai	49	47	37	0.90

N = 40 dung traps at each site, S = species richness

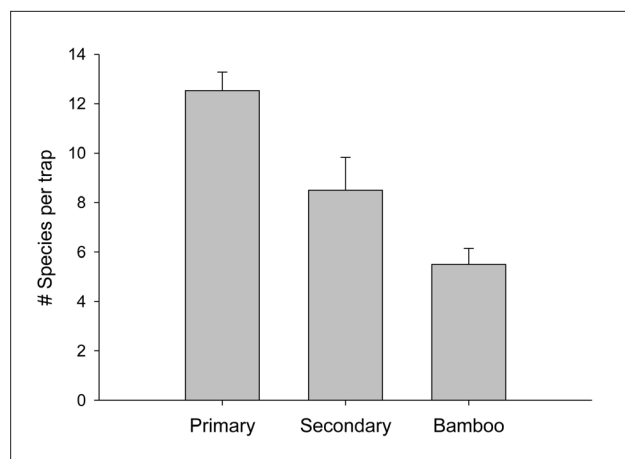


Figure 2. Impacts of habitat disturbance on species richness: primary forest, secondary forest and bamboo (mean \pm 1 SE).

richness found around Kwamala. Other studies from Venezuela, French Guiana, and Brazil also showed lower species richness in lowland primary forest with comparable sampling effort. Further sampling around Kwamala may yield as many or more species than were found in French Guiana and at Jari, Brazil, where greater sampling effort was employed (Table 3).

Table 3. Comparison of dung beetle species richness in primary lowland forests in northeastern South America.

	Kwamala region	Nassau, Suriname ¹	Lely, Suriname ¹	Guri, Venezuela ²	Nouragues, F. Guiana ^{3,4}	Kaw Mtn, F. Guiana ⁴	Jari, Amapa, Brazil ⁵	Marajoara, Para, Brazil ⁶
S (all samples)	94	27	38	41				
S (dung traps)	68	24	33	24 (32)	42 (78)	33 (47)	41–51 (72)	47

First number indicates species richness observed with comparable sampling effort to this RAP survey. Number in parentheses indicates species richness observed with more extensive long-term sampling effort, or across a broader landscape. ¹Larsen 2007; ²Larsen et al. 2008, Larsen unpub. data; ³Feer 2000; ⁴Price & Feer in prep.; ⁵Gardner et al. 2008b; ⁶Scheffler 2005

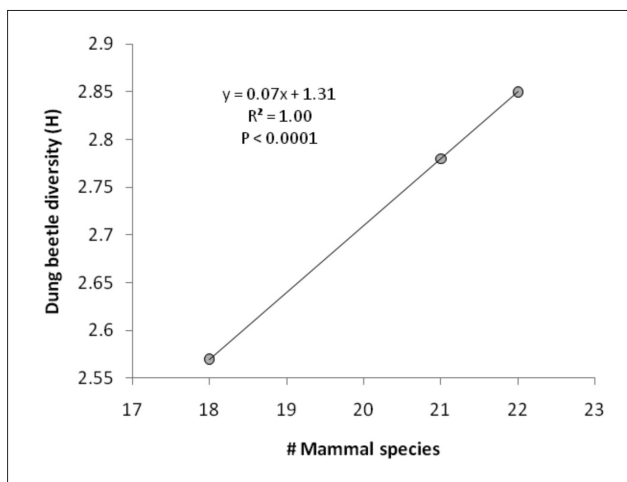


Figure 3. Linear regression of dung beetle diversity (Shannon diversity index) against large mammal species richness across all three sites.

INTERESTING SPECIES

I estimate that about 10–15% of the dung beetle species collected during this RAP (10 to 14 species) are undescribed. However, most of the genera collected here have never been revised, and determination of these undescribed species will require further comparisons with other museum collections. I sampled 26 species of *Canthidium* in the Kwamala area. *Canthidium* is a hyper-diverse yet very poorly known genus, and many of these species are almost certainly new to science. *Ateuchus* is also a poorly known yet diverse genus, and several *Ateuchus* species from the RAP are likely to be new. *Canthon* sp. 2 represents an undescribed species that is currently under study (see Appendix A).

Several large-bodied dung beetle species, such as *Coprophanæus lancifer* (the largest Neotropical dung beetle species), *Oxysternon festivum*, and *Dichotomius boreus*, were sampled at all three sites. These species move long distances and require large, continuous areas of forest to persist. Their presence at the sites is indicative of the intact, contiguous landscape around Kwamala. These large dung beetle species are also the most ecologically important for burying seeds and controlling parasites.

Six species (*Dendropaemon* sp. 1, *Deltorhinum guyanensis*, and four *Anomiopus* species) were only sampled in flight intercept traps and their distinctive morphology, with strongly reduced tarsi and stout, compact bodies, suggest that they are myrmecophilous (associated with ant nests), as are several other dung beetle species. Based on a recent revision of the genus *Anomiopus*, this is the first record for all four of these species in Suriname (Canhedo 2006), although I collected *A. parallelus* and *A. lacordairei* on another RAP survey in Suriname (Larsen 2007; Appendix A). Both species were previously known only from French Guiana and northern Brazil. *Deltorhinum guyanensis*, endemic to the Guianas, was only described after this RAP survey was conducted (Genier 2010), and this is the first record of this species in Suriname.

Deltocolium valgum is a highly specialized predator of millipedes, and adults decapitate and feed on millipedes that are much larger than themselves. This unusual behavior was only discovered and described last year (Larsen et al. 2009). *Canthidium* cf. *chrysis* is a member of the escalerei species group which commonly feed on dead invertebrates. It was captured mostly with dead millipedes, but occasionally with carrion, and may be specialized to feed on millipedes. *Canthidium* sp. 20 (aff. *chrysis*), *Canthon* sp. 1 and *Canthon* sp. 2 were also most abundant at dead millipedes, but whether they specialize on millipedes or on dead invertebrates in general is not yet clear. *Canthidium* cf. *gigas*, which was represented by only one individual in a flight intercept trap, is a member of an unusual species group which may feed on fungus. This group includes by far the largest of all *Canthidium* species. *Canthidium* cf. *minimum* is an unusual species that may need to be transferred to a different genus (see Appendix A for this and other taxonomic notes).

CONSERVATION RECOMMENDATIONS

The Kwamala area supports vast tracts of intact primary forest, which is important for many dung beetle species. Consequently, I found extremely high species richness of dung beetles in the area (94 species). To put this diversity into perspective, during a RAP survey at the Nassau and Lely plateaus in Suriname, I sampled only 24 species and 33 species at each site respectively (Table 3). I sampled extensively in lowland forest around Lago Guri in Bolivar, Venezuela, and found only 41 species (Larsen et al. 2008). On the other hand, small-scale habitat loss and disturbance around Kwamala led to local dung beetle extinctions, which would likely be exacerbated by more widespread habitat loss. Preventing mining operations and other drivers of deforestation from entering the area will be important for maintaining the high biodiversity of the Kwamala region.

In addition to high overall species richness, I found high Beta diversity at the sites across very small spatial scales, and Kutari supports a very distinct dung beetle community than the other sites. Consequently, it is important to protect the diversity of soils and habitats that occur in the Kwamala region even at small spatial scales. Plans for protected areas or reserves should incorporate this small-scale spatial heterogeneity.

Tropical ectotherms, such as dung beetles, are among the most sensitive organisms on Earth to climate change (Larsen et al. 2011). Climate warming is forcing many species to shift their distribution poleward or upslope, and these effects are strongest at the edge of species' ranges. Since the Kwamala area contains many Amazonian species near the edge of their range limit, it may present an excellent opportunity to monitor the response of populations and species' distributions to climate change.

High dung beetle diversity at Kutari, the most isolated site, was correlated with high mammal, including primate, species richness, and this may be explained by lower hunting pressures. The abundance and biomass of dung beetles in the Kwamala area overall was relatively high, and was higher than I observed at Nassau and Lely in other parts of Suriname. This suggests that in addition to the pristine state of the forest, populations of large birds and mammals are relatively stable. However, dung beetle abundance was lower than I expected based on surveys in other Neotropical primary forests where no hunting occurs. This is likely to reflect the relatively low abundance of spider monkeys, howler monkeys, and white-lipped peccaries, which are among the most important species for dung beetles but are also preferred for bushmeat. Reduced hunting on these key species would help to stabilize ecosystem dynamics not just for dung beetles, but for seed dispersal and other ecological processes as well. The establishment of hunting-restricted reserves such as the one at Iwana Samu is an excellent way to maintain sustainable populations of large mammals.

ACKNOWLEDGEMENTS

I would like to thank the Trio People of Kwamalasamutu, the game wardens, and the park guards, as well as Leeanne Alonso and Brian O'Shea for coordinating the RAP survey. Dana Price and Francois Feer provided valuable comparative data from French Guiana.

LITERATURE CITED

- Canhedo, V. L. 2006. Revisao taxonomica do genero *Anomiopus* Westwood, 1842 (Coleoptera, Scarabaeidae, Scarabaeinae). [Taxonomic revision of the genus *Anomiopus* Westwood, 1842 (Coleoptera, Scarabaeidae, Scarabaeinae)]. *Arquivos de Zoologia Sao Paulo* 37:349–502.
- Colwell, R. K. and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 345:101–118.
- Edmonds, W. D. and J. Zidek. 2004. Revision of the Neotropical dung beetle genus *Oxysternon* (Scarabaeidae: Scarabaeinae: Phanaeini). *Folia Heyrovskyana Supplementum* 11:1–58.
- Edmonds, W. D. and J. Zidek. 2010. A taxonomic review of the neotropical genus *Coprophanæus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). *Insecta Mundi* 0129:1–111.
- Feer, F. 2000. Dung and carrion beetles of the rain forest of French Guiana: composition and structure of the guild. *Annales De La Societe Entomologique De France* 36:29–43.
- Gardner, T. A., J. Barlow, I. S. Araujo, T. C. Avila-Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. I. M. Hernandez, M. S. Hoogmoed, R. N. Leite, N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. A. M. Mestre, R. Miranda-Santos, W. L. Overall, L. Parry, S. L. Peters, M. A. Ribeiro, M. N. F. da Silva, C. D. S. Motta, and C. A. Peres. 2008a. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters* 11:139–150.
- Gardner, T. A., M. I. M. Hernandez, J. Barlow, and C. A. Peres. 2008b. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology* 45:883–893.
- Genier, F. 2009. Le Genre *Eurysternus* Dalman, 1824 (Scarabaeidae: Scarabaeinae: Oniticellini) Pensoft, Bulgaria.
- Genier, F. 2010. A review of the Neotropical dung beetle genera *Deltorhinum* Harold, 1869, and *Lobidion* gen. nov. (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 2693:35–48.
- Larsen, T. H. 2007. Dung beetles of the Lely and Nassau plateaus, Eastern Suriname. Pages 99–101 *in* L. E. Alonso and J. H. Mol, editors. *A rapid biological*

- assessment of the Lely and Nassau plateaus, Suriname (with additional information on the Brownsberg Plateau). Conservation International, Arlington, VA, USA.
- Larsen, T. H., F. Escobar, and I. Armbrrecht. 2011. Insects of the Tropical Andes: diversity patterns, processes and global change. Pages 228–244 *in* S. K. Herzog, R. Martinez, P. M. Jorgensen, and H. Tiessen, editors. Climate Change and Biodiversity in the Tropical Andes. Inter-American Institute of Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), São José dos Campos and Paris.
- Larsen, T. H. and A. Forsyth. 2005. Trap Spacing and Transect Design for Dung Beetle Biodiversity Studies. *Biotropica* 37:322–325.
- Larsen, T. H., A. Lopera, and A. Forsyth. 2008. Understanding Trait-Dependent Community Disassembly: Dung Beetles, Density Functions, and Forest Fragmentation. *Conservation Biology* 22:1288–1298.
- Larsen, T. H., A. Lopera, A. Forsyth, and F. Genier. 2009. From coprophagy to predation: a dung beetle that kills millipedes. *Biology Letters* 5:152–155.
- Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amequita, and M. E. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141:1461–1474.
- Scheffler, P. Y. 2005. Dung beetle (Coleoptera : Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology* 21:9–19.
- Spector, S. 2006. Scarabaeine dung beetles (Coleoptera : Scarabaeidae : Scarabaeinae): An invertebrate focal taxon for biodiversity research and conservation. *Coleopterists Bulletin* 60:71–83.

Appendix A. Dung beetle species abundance (number individuals collected), including taxonomic notes and amended species list from RAP #43.

	Kutari	Sipaliwini	Werehpai	Nassau	Lely	Old species name (from RAP #43 Lely and Nassau)
# Species	70	62	67	27	38	
Total abundance	910	2093	1551	204	906	
# Trap samples	66	61	66	51	53	
<i>Agamopus castaneus</i> Balthasar	0	8	23			
<i>Anomiopus andrei</i> Canhedo	1	0	0			
<i>Anomiopus globosus</i> Canhedo	2	0	0			
<i>Anomiopus lacordairei</i> Waterhouse	3	0	0	1	0	<i>Anomiopus</i> sp. 2
<i>Anomiopus parallelus</i> Harold ¹	3	0	1	0	1	<i>Anomiopus</i> sp. 1
<i>Ateuchus cereus</i> Harold ²	2	0	0			
<i>Ateuchus</i> cf. <i>obscurus</i> Harold ³	4	15	9			
<i>Ateuchus</i> cf. <i>sulcicollis</i> Harold ⁴	1	0	4			
<i>Ateuchus murrayi</i> Harold	27	42	7	1	1	<i>Ateuchus</i> sp. 1
<i>Ateuchus pygidialis</i> Harold ⁵	1	0	3			
<i>Ateuchus simplex</i> LePeletier & Serville ⁶	0	211	74	1	13	<i>Ateuchus</i> sp. 2
<i>Ateuchus substriatus</i> Harold	1	12	44			
<i>Ateuchus</i> sp. 3 ⁷	1	3	1			
<i>Ateuchus</i> sp. 4	0	1	0			
<i>Ateuchus</i> sp. 5 ⁸	10	7	9			
<i>Ateuchus</i> sp. 6 (aff. <i>murrayi</i>) ⁹	3	0	0			
<i>Ateuchus</i> sp. 7 (aff. <i>aeneomicans</i>) ¹⁰	0	2	2			
<i>Canthidium</i> cf. <i>chrysis</i> Fabricius ¹¹	1	19	2			
<i>Canthidium</i> cf. <i>gigas</i> Balthasar ¹²	0	0	1			
<i>Canthidium</i> cf. <i>kirschi</i> Harold ¹³	17	1	1	0	1	<i>Canthidium</i> cf. <i>bicolor</i>
<i>Canthidium</i> cf. <i>minimum</i> Harold ¹⁴	0	2	0			
<i>Canthidium</i> cf. <i>onitoides</i> Perty ¹⁵	1	0	0			
<i>Canthidium deyrollei</i> Harold	13	71	32			
<i>Canthidium dobrni</i> Harold ¹⁶	3	4	0			
<i>Canthidium gerstaeckeri</i> Harold	19	12	7	0	6	<i>Canthidium</i> sp. 1
<i>Canthidium gracilipes</i> Harold	12	1	3			
<i>Canthidium splendidum</i> Preudhomme de Borre	0	0	11			
<i>Canthidium</i> sp. 5 (aff. <i>funebre</i>) ¹⁵	1	4	1			
<i>Canthidium</i> sp. 6 ¹⁷	30	3	2	0	4	<i>Canthidium</i> sp. 2
<i>Canthidium</i> sp. 7 (aff. <i>histrion</i>)	0	2	0			
<i>Canthidium</i> sp. 8 (aff. <i>quadridens</i>)	5	4	1			
<i>Canthidium</i> sp. 9	3	2	1			
<i>Canthidium</i> sp. 10	2	0	0			
<i>Canthidium</i> sp. 11 (aff. <i>guyanense</i>) ¹⁸	7	0	0			
<i>Canthidium</i> sp. 12 (aff. <i>latum</i>)	8	0	5			

table continued on next page

	Kutari	Sipaliwini	Werehpai	Nassau	Lely	Old species name (from RAP #43 Lely and Nassau)
<i>Canthidium</i> sp. 13	3	0	0			
<i>Canthidium</i> sp. 14 (centrale grp) ¹⁹	0	0	2			
<i>Canthidium</i> sp. 15	1	0	1			
<i>Canthidium</i> sp. 16	0	2	0			
<i>Canthidium</i> sp. 17	0	0	1			
<i>Canthidium</i> sp. 18 (aff. <i>bicolor</i>) ¹³	20	2	3			
<i>Canthidium</i> sp. 19 (aff. <i>kirschi</i>) ¹³	1	0	0			
<i>Canthidium</i> sp. 20 (aff. <i>chrysis</i>) ¹¹	3	8	7			
<i>Canthon bicolor</i> Castelnau	9	32	31	2	46	<i>Canthon bicolor</i>
<i>Canthon quadriguttatus</i> Olivier	1	0	0	1	7	<i>Canthon quadriguttatus</i>
<i>Canthon semiopacus</i> Harold	0	1	0			
<i>Canthon sordidus</i> Harold	21	0	12	9	19	<i>Anisocanthon</i> cf. <i>sericinus</i>
<i>Canthon triangularis</i> Drury	150	155	184	13	14	<i>Canthon triangularis</i>
<i>Canthon</i> sp. 1 ²⁰	0	5	1			
<i>Canthon</i> sp. 2 ²¹	2	4	3			
<i>Canthonella silphoides</i> Harold	0	0	1			
<i>Coprophanaeus jasius</i> Olivier	2	1	2			
<i>Coprophanaeus lancifer</i> Linnaeus	2	1	1	0	1	<i>Coprophanaeus lancifer</i>
<i>Coprophanaeus parvulus</i> Olsoufieff	0	1	1	0	1	<i>Coprophanaeus</i> cf. <i>parvulus</i>
<i>Deltochilum carinatum</i> Westwood	4	0	0	2	2	<i>Deltochilum carinatum</i>
<i>Deltochilum guyanense</i> Boucomont	2	3	1	8	0	<i>Deltochilum</i> sp. 1
<i>Deltochilum icarus</i> Olivier	3	1	7	1	3	<i>Deltochilum icarus</i>
<i>Deltochilum septemstriatum</i> Paulian	4	4	6	4	0	<i>Deltochilum</i> sp. 2
<i>Deltochilum valgum</i> Burmeister	3	0	1			
<i>Deltorbinum guyanensis</i> Genier	2	0	0			
<i>Dendropaemon</i> sp. 1	3	0	0			
<i>Dichotomius boreus</i> Olivier	52	123	44	4	7	<i>Dichotomius</i> sp. aff. <i>podalirius</i>
<i>Dichotomius</i> cf. <i>lucasi</i> Harold	38	168	154			
<i>Dichotomius mamillatus</i> Felsche	2	1	1	0	1	<i>Dichotomius mamillatus</i>
<i>Dichotomius robustus</i> Luederwaldt	1	1	1			
<i>Dichotomius subaeneus</i> Castelnau	0	1	0			
<i>Dichotomius</i> sp. 2	2	0	1			
<i>Dichotomius</i> sp. 3 (batesi-inachus grp) ²²	0	0	2			
<i>Dichotomius</i> sp. 4	1	2	2			
<i>Dichotomius</i> sp. 5 (calcaratus grp)	1	0	0			
<i>Eurysternus atrosericus</i> Genier	9	35	42			
<i>Eurysternus balachowskyi</i> Halffter & Halffter	0	2	1	1	0	<i>Eurysternus</i> sp. 2
<i>Eurysternus cambeforti</i> Genier	0	6	2	0	1	<i>Eurysternus</i> cf. <i>hirtellus</i>
<i>Eurysternus caribaeus</i> Herbst	21	125	150	5	16	<i>Eurysternus caribaeus</i>
<i>Eurysternus cyclops</i> Genier	1	0	0	4	17	<i>Eurysternus</i> sp. aff. <i>caribaeus</i>

table continued on next page

	Kutari	Sipaliwini	Werehpai	Nassau	Lely	Old species name (from RAP #43 Lely and Nassau)
<i>Eurysternus foedus</i> Guerin-Meneville	4	9	4			
<i>Eurysternus hamaticollis</i> Balthasar	0	2	0			
<i>Eurysternus ventricosus</i> Gill	1	2	0	0	1	<i>Eurysternus</i> sp. 1
<i>Hansreia affinis</i> Fabricius	25	53	19	88	569	<i>Hansreia affinis</i>
<i>Onthophagus</i> cf. <i>xanthomerus</i> Bates ²³	14	6	2			
<i>Onthophagus haematopus</i> Harold	46	589	294	34	52	<i>Onthophagus</i> sp. 1
<i>Onthophagus rubescens</i> Blanchard	134	128	26	1	11	<i>Onthophagus</i> cf. <i>haematopus</i>
<i>Oxysternon durantoni</i> Arnaud	29	19	8	0	24	<i>Oxysternon</i> cf. <i>durantoni</i>
<i>Oxysternon festivum</i> Linnaeus	4	9	26			
<i>Oxysternon spiniferum</i> Castelnau	1	1	1			
<i>Phanaeus bispinus</i> Bates	0	1	0			
<i>Phanaeus cambeforti</i> Arnaud	5	5	31			
<i>Phanaeus chalcomelas</i> Perty	40	131	165	2	7	<i>Phanaeus chalcomelas</i>
<i>Sulcophanaeus faunus</i> Fabricius	1	0	0			
<i>Sylvicanthon</i> cf. <i>securus</i> Schmidt ²⁴	0	4	1	0	4	<i>Sylvicanthon</i> sp. nov.
<i>Trichillum pauliani</i> Balthasar	0	2	21			
<i>Uroxys gorgon</i> Arrow	0	0	1			
<i>Uroxys pygmaeus</i> Harold	23	7	15	4	1	<i>Uroxys</i> sp. 2
<i>Uroxys</i> sp. 3	38	15	28	6	29	<i>Uroxys</i> sp. 3
Additional species sampled during RAP #43						
<i>Canthidium guyanense</i> Boucomont				2	20	<i>Canthidium</i> sp. 4
<i>Canthidium</i> sp. 3				0	3	<i>Canthidium</i> sp. 3
<i>Canthon mutabilis</i> Lucas				0	3	<i>Canthon mutabilis</i>
<i>Coprophanaeus dardanus</i> MacLeay				0	3	<i>Coprophanaeus</i> cf. <i>dardanus</i>
<i>Deltochilum orbiculare</i> Lansberge				3	1	<i>Deltochilum</i> sp. 3
<i>Dichotomius</i> sp. 1				1	0	<i>Dichotomius</i> sp. 1
<i>Eurysternus hypocrita</i> Balthasar				1	1	<i>Eurysternus velutinus</i>
<i>Eurysternus vastiorum</i> Martinez				0	2	<i>Eurysternus</i> sp. 1
<i>Oxysternon silenus</i> Castelnau				0	2	<i>Oxysternon aeneum</i>
<i>Scybalocanthon pygidialis</i> Schmidt				1	10	<i>Scybalocanthon cyanocephalus</i>
<i>Uroxys</i> sp. 1				4	2	<i>Uroxys</i> sp. 1

¹Individuals here are larger than *A. parallelus* revised by (Canhedo 2006), and are also larger and differ in pronotal patterning from the individual from the Lely RAP survey

²Species needs to be transferred from genus *Canthidium*. *Ateuchus scatimoides* (Balthasar, 1939) is a junior synonym of *Ateuchus cereus*

³May match *Canthidium obscurum*, although I have not yet seen this species; if so, species needs to be transferred from genus *Canthidium*

⁴Species needs to be transferred from genus *Canthidium*

⁵Probably represents a species complex; need to study types

⁶The species I collected here matches the type specimen of *Ateuchus setulosus* (Balthasar, 1939); based on museum specimens and the original description, *A. setulosus* appears to be a junior synonym of *A. simplex*, but I have not seen *A. simplex* types.

⁷Similar to *A. pygidialis*, but body more elongate and narrow

⁸Similar to *A. murrayi*, but smaller pygidium with dorsal punctures, among other differences

⁹Similar to *A. murrayi*, but larger, more heavily punctate pygidium, etc. Matches a probably undescribed species I have collected in southeastern Peru at dung and fruit

¹⁰Smaller than *A. aeneomicans* and with prominent swelling on pygidium which is not present in *A. aeneomicans*

¹¹The only obvious difference I can find between *Canthidium* cf. *chrysis* and *Canthidium* sp. 20 (aff. *chrysis*), both of which were collected sympatrically, is color (*C.* sp. 20 is orange and black, while *C.* cf. *chrysis* is green). The aedeagus appears identical. Further study is needed, and these identifications are also based on uncertain museum labels

¹²Part of a species group that needs revision

¹³*Canthidium kirschi* and *Canthidium bicolor* are members of a taxonomically difficult species group which includes several undescribed species. All are very small species with a yellow/orange pronotum, dark brown/black elytra and head, and unarmed head lacking tubercles. Both species, and others, are frequently mixed and misidentified in collections. Key differences include punctures on the pronotum and shape of the male foretibial teeth and claw

¹⁴This is a curious species. It closely resembles *Canthidium minimum*, although the hind tibia is slightly less curved in the specimens from this survey. *Canthidium minimum* shares characters with two genera, *Canthidium* and *Sinapisoma*, and might need to be transferred to *Sinapisoma*. *Sinapisoma* is currently a monospecific genus, and the only known species possesses a more elongate and curved inner margin of the hind tibia (which until recently caused it to be erroneously considered a canthonine roller) than in *C. minimum*. However, the hind tibia of *C. minimum* is more elongate and curved than other *Canthidium* species. Both share other characters, including a narrow mesosternum.

¹⁵*Canthidium onitoides* and *Canthidium funebre* are members of a species complex whose species are frequently misidentified in collections and needs further revision. I have seen the *C. funebre* type, which is from Suriname, and it has microsculptured, matte elytra and yellow femora, in contrast to other species with shining, glabrous elytra and/or unicolor legs. *Canthidium* cf. *onitoides* collected during this RAP has glabrous elytra, and needs to be compared with *C. onitoides* type.

¹⁶A similar species from southeastern Peru has two long fovea along the posterior elytral striae, rather than three as in the species collected here. It's unclear which of these two species is actually *Canthidium dohrni*; the type is from Para, Brazil

¹⁷Matches a possibly undescribed species collected in Colombia

¹⁸Very similar to *Canthidium guyanense*, which was collected during Nassau and Lely RAP surveys, but can be separated based on the second and third elytral striae which are not deeply impressed posteriorly

¹⁹Matches a possibly undescribed species I have collected in SE Peru. Perhaps the smallest member of the lentum-centrale species group

²⁰Very similar to *Canthon* sp. 2 (possibly same species), but pronotum appears more glabrous and shining, with less microsculpturing

²¹Matches a species currently being described, *Canthon doesburgi* (Huijbregts, in litt.), but no name is yet available and the species remains formally undescribed

²²Matches a possibly undescribed species from SE Peru. Possesses an unusual fovea on the posterior portion of the head

²³*O. xanthomerus* is part of a difficult species group (clypeatus species group), that needs revision. *O. xanthomerus* usually has dark legs with yellow femora, although the species collected here has dark, unicolor legs. *O. clypeatus* has dark legs, but the male pronotal carinae are much sharper and more pronounced, while they are relatively smooth and rounded in *O. xanthomerus*.

²⁴I have not seen any specimens of *Sylvicanthon securus*, but the species collected here appears to match the original description, and the type locality is Suriname. I have often seen this species misidentified as *Sylvicanthon candezei*, but *S. candezei* has 2 foretibial teeth rather than 3 as in the species here

Appendix B. Diet preference/capture method for dung beetles. Data are number of individuals collected.

	Dung	Carrion	Dead millipedes	Injured millipedes	Fungus	FIT
# Species	67	21	4	2	2	58
Total abundance	4123	105	26	2	7	290
# Trap samples	124	17	4	2	8	38
<i>Agamopus castaneus</i> Balthasar	31					
<i>Anomiopus andrei</i> Canhedo						1
<i>Anomiopus globosus</i> Canhedo						2
<i>Anomiopus lacordairei</i> Waterhouse						3
<i>Anomiopus parallelus</i> Harold						4
<i>Ateuchus cereus</i> Harold	1	1				
<i>Ateuchus</i> cf. <i>obscurus</i> Harold	28					
<i>Ateuchus</i> cf. <i>sulcicollis</i> Harold	2					3
<i>Ateuchus murrayi</i> Harold	69					7
<i>Ateuchus pygidialis</i> Harold	3					1
<i>Ateuchus simplex</i> LePeletier & Serville	282	1				2
<i>Ateuchus substriatus</i> Harold	52	2				3
<i>Ateuchus</i> sp. 3	5					
<i>Ateuchus</i> sp. 4						1
<i>Ateuchus</i> sp. 5	7	3			4	12
<i>Ateuchus</i> sp. 6 (aff. <i>murrayi</i>)						3
<i>Ateuchus</i> sp. 7 (aff. <i>aeneomicans</i>)						4
<i>Canthidium</i> cf. <i>chrysis</i> Fabricius		3	15			4
<i>Canthidium</i> cf. <i>gigas</i> Balthasar						1
<i>Canthidium</i> cf. <i>kirschi</i> Harold	1					18
<i>Canthidium</i> cf. <i>minimum</i> Harold						2
<i>Canthidium</i> cf. <i>onitoides</i> Perty						1
<i>Canthidium deyrollei</i> Harold	114	2				
<i>Canthidium dobrni</i> Harold	5					2
<i>Canthidium gerstaeckeri</i> Harold	37					1
<i>Canthidium gracilipes</i> Harold	1					15
<i>Canthidium splendidum</i> Preudhomme de Borre	11					
<i>Canthidium</i> sp. 5 (aff. <i>funebre</i>)	5					1
<i>Canthidium</i> sp. 6	34					1
<i>Canthidium</i> sp. 7 (aff. <i>histrion</i>)						2
<i>Canthidium</i> sp. 8 (aff. <i>quadridens</i>)						10
<i>Canthidium</i> sp. 9	5					1
<i>Canthidium</i> sp. 10	2					
<i>Canthidium</i> sp. 11 (aff. <i>guyanense</i>)	5					2
<i>Canthidium</i> sp. 12 (aff. <i>latum</i>)						13
<i>Canthidium</i> sp. 13						3
<i>Canthidium</i> sp. 14 (centrale grp)	1					1
<i>Canthidium</i> sp. 15						2

table continued on next page

	Dung	Carrion	Dead millipedes	Injured millipedes	Fungus	FIT
<i>Canthidium</i> sp. 16	2					
<i>Canthidium</i> sp. 17	1					
<i>Canthidium</i> sp. 18 (aff. <i>bicolor</i>)	5					20
<i>Canthidium</i> sp. 19 (aff. <i>kirschi</i>)						1
<i>Canthidium</i> sp. 20 (aff. <i>chrysis</i>)		7	4	1		6
<i>Canthon bicolor</i> Castelnau	68					4
<i>Canthon quadriguttatus</i> Olivier	1					
<i>Canthon semiopacus</i> Harold	1					
<i>Canthon sordidus</i> Harold	20	13				
<i>Canthon triangularis</i> Drury	469	18				2
<i>Canthon</i> sp. 1		1	3			2
<i>Canthon</i> sp. 2		2	4			3
<i>Canthonella silphoides</i> Harold						1
<i>Coprophanaeus jasius</i> Olivier	2	3				
<i>Coprophanaeus lancifer</i> Linnaeus	4					
<i>Coprophanaeus parvulus</i> Olsoufieff						2
<i>Deltochilum carinatum</i> Westwood	4					
<i>Deltochilum guyanense</i> Boucomont	3	3				
<i>Deltochilum icarus</i> Olivier	9	2				
<i>Deltochilum septemstriatum</i> Paulian	1	13				
<i>Deltochilum valgum</i> Burmeister						4
<i>Deltorhinum guyanensis</i> Genier						2
<i>Dendropaemon</i> sp. 1						3
<i>Dichotomius boreus</i> Olivier	219					
<i>Dichotomius</i> cf. <i>lucasi</i> Harold	305	12		1	3	39
<i>Dichotomius mamillatus</i> Felsche	4					
<i>Dichotomius robustus</i> Luederwaldt	3					
<i>Dichotomius subaeneus</i> Castelnau	1					
<i>Dichotomius</i> sp. 2	1					2
<i>Dichotomius</i> sp. 3 (batesi-inachus grp)	2					
<i>Dichotomius</i> sp. 4	4					1
<i>Dichotomius</i> sp. 5 (calcaratus grp)	1					
<i>Eurysternus atrosericus</i> Genier	77	8				1
<i>Eurysternus balachowskyi</i> Halffter & Halffter	3					
<i>Eurysternus cambeforti</i> Genier	7	1				
<i>Eurysternus caribaeus</i> Herbst	293	3				
<i>Eurysternus cyclops</i> Genier	1					
<i>Eurysternus foedus</i> Guerin-Meneville	17					
<i>Eurysternus hamaticollis</i> Balthasar	2					
<i>Eurysternus ventricosus</i> Gill	3					
<i>Hansreia affinis</i> Fabricius	97					
<i>Onthophagus</i> cf. <i>xanthomerus</i> Bates	15	5				2

table continued on next page

	Dung	Carrion	Dead millipedes	Injured millipedes	Fungus	FIT
<i>Onthophagus haematopus</i> Harold	920					9
<i>Onthophagus rubescens</i> Blanchard	285					3
<i>Oxysternon durantoni</i> Arnaud	56					
<i>Oxysternon festivum</i> Linnaeus	36					3
<i>Oxysternon spiniferum</i> Castelnau						3
<i>Phanaeus bispinus</i> Bates	1					
<i>Phanaeus cambeforti</i> Arnaud	36					5
<i>Phanaeus chalcomelas</i> Perty	332					4
<i>Sulcophanaeus faunus</i> Fabricius	1					
<i>Sylvicanthon</i> cf. <i>securus</i> Schmidt	4					1
<i>Trichillum pauliani</i> Balthasar	22					1
<i>Uroxys gorgon</i> Arrow	1					
<i>Uroxys pygmaeus</i> Harold	37					8
<i>Uroxys</i> sp. 3	47	2				32