Dung Beetles of the Upper Palumeu River Watershed (Grensgebergte and Kasikasima) of Southeastern Suriname (Coleoptera: Scarabaeidae: Scarabaeinae)

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Chapter 5

Dung beetles of the Upper Palumeu River Watershed (Grensgebergte and Kasikasima) of Southeastern Suriname (Coleoptera: Scarabaeidae: Scarabaeinae)

Trond H. Larsen

SUMMARY

Dung beetles are among the most cost-effective of all animal taxa for assessing biodiversity patterns, yet RAP's recent surveys are among the few that are expanding our knowledge of Suriname's little known dung beetle fauna. In addition to cost-effective sampling using standardized pitfall traps, dung beetles depend upon large mammals for food and consequently can be used to rapidly assess the health of the overall mammal community and hunting impacts in a fraction of the time it would take to survey the mammals themselves. I sampled dung beetles using baited pitfall traps and flight intercept traps in the Grensgebergte and Kasikasima regions of Southeastern Suriname. I collected 4,483 individuals represented by 107 species. This ranks among the most diverse places on the planet for dung beetles, and exceeds the extraordinarily high species richness observed in nearby southwestern Suriname (94 species, Larsen 2011). Ten species are most likely new to science, while an additional 10–20 species may be undescribed pending further taxonomic revisions.

Dung beetle species richness, abundance and biomass were higher around Upper Palumeu than at Kasikasima, probably due to the extensive intact forest and lack of hunting pressure in this remote headwater region where no one currently lives. Dung beetle diversity and abundance at Kasikasima were still relatively high, indicating only mild to moderate hunting of large mammals and birds in the region. All sites, including the Grensgebergte Mountains, supported high endemism, including several rare species, demonstrating the exceptional biodiversity value of the region. Surprisingly, dung beetle species composition varied strongly among sites within this survey, as well as among sites sampled on previous surveys, including nearby southwestern Suriname. This high Beta diversity shows that the forests of Suriname and the Guiana Shield are not nearly as homogenous as is often assumed, and consequently protecting this varied biodiversity requires conserving many different forest areas.

The high 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. These results indicate that the intact headwater region of the Upper Palumeu watershed merits the highest conservation priority.

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 both primary camp sites (Upper Palumeu (Juuru camp) and Kasikasima), as well as on top of the Grensgebergte mountains, using standardized pitfall trap transects (see Executive Summary for site details). 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), except the mountaintop where only six traps could be placed due to space constraints. 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, except the mountaintop (two days), 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. Beetle specimens are deposited at the National Museum of Natural History at the Smithsonian Institution in Washington, DC, USA and will also be deposited 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 collected 107 species and 4,483 individuals at the study sites (Table 5.1, Appendix 5.1). I encountered ten species that appear to be new to science (including *Canthidium*, *Dichotomius* and *Uroxys*), and I estimate an additional 10–20 species are undescribed pending further taxonomic revisions. Species richness and abundance was highest around Juuru camp, intermediate at Kasikasima, and lowest on the Grensgebergte mountaintop. Species accumulation curves for dung-baited pitfall traps (based on abundance-based coverage estimator) indicated that I sampled an estimated 91% of all coprophagous species occurring in the area (Table 5.1). However, sampling completeness was lowest on the Grensgebergte Mountain where sample size was limited by logistical constraints, and I sampled only 68% of the dung-feeding species likely to occur at the site (Table 5.1, Fig. 5.1).

In addition to coprophagous species, I captured 31 dung beetle species that appear not to feed on dung at all, including those attracted only to carrion or to dead invertebrates, fruit, or fungus (Appendix 5.2). Additional species were sampled only in flight intercept traps, and many of these species are poorly represented in collections because they are difficult to sample and in some cases, their diet is unknown (Appendix 5.2). Some of these species show unusual specializations, such as millipede predation or colonization of leaf-cutter ant nests (see interesting species discussion below).

Upper Palumeu, the site with the highest dung beetle abundance and biomass, was also the most isolated from human communities and hunting pressures, suggesting that hunting has had a mild to moderate impact on dung beetle populations around Kasikasima and elsewhere.

The study sites contained a mixture of widely distributed Amazonian species, species restricted to the northern Amazon, Guiana Shield endemics, and some species with even

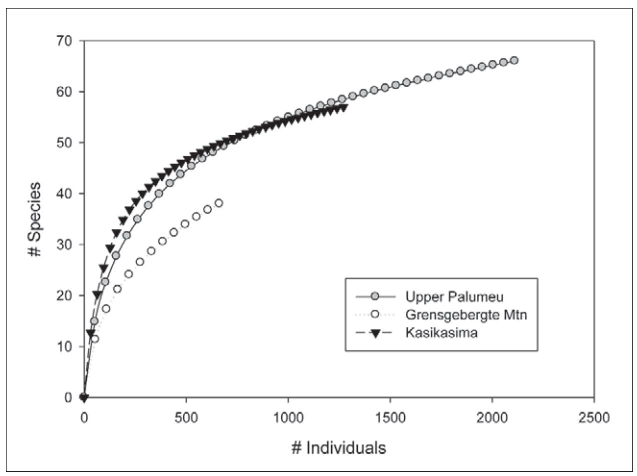

Figure 5.1. Species accumulation curves for each site based on dung-baited pitfall traps

Table 5.1. Diversity and abundance of dung beetles in Grensgebergte and Kasikasima regions

	All sites	Upper Palumeu	Grensgebergte	Kasikasima
Species richness (all samples)	107	93	40	74
Species richness (dung traps)	76	66	38	57
Estimated richness (ACE) (dung traps)	83	83	56	66
% Sampling completeness (dung traps)	0.91	0.80	0.68	0.87
Shannon diversity (H) (dung traps)	3.14	3.05	1.89	3.08
Abundance/trap (all samples)	33.5	37.3	48.6	24.9
Abundance/trap (dung traps)	44.0	52.8	55.3	31.8

more restricted range size. Several species represented new records for Suriname. Species composition varied strongly among sites within this survey, and also among sites sampled on previous RAP surveys in Suriname (Table 5.2). Despite its low overall species richness, the Grensgebergte Mountains appear to support a dung beetle community that is very distinct from the surrounding lowlands. Interestingly, species composition of Grensgebergte was quite similar to the Nassau and Lely Plateaus, and each of these three high elevation habitats are characterized by species that appear to be specialized to these habitats (Table 5.2; Appendix 5.1; Larsen 2007). Surprisingly, species composition of the lowland forests of Upper Palumeu differed fairly strongly from structurally similar lowland forests in nearby Southwestern Suriname around Kwamalasamutu(Table 5.2).

Dung beetle species richness is very high in the Grensgebergte region relative to other areas in northeastern South America and the Guianas, and even higher than the previous record for dung beetle richness in the Guianas in the pristine forests surrounding Kwamalasamutu (Table 5.3; Larsen 2011). Similar RAP surveys at Lely and Nassau in Suriname yielded less than a third of the species richness found around Grensgebergte. Other studies from Venezuela, French Guiana, and Brazil also showed lower species richness in lowland primary forest with comparable sampling effort.

INTERESTING SPECIES

Several species appear to be new to science, including *Canthidium* cf. *minimum* (see page 22), *Canthidium* sp. 25 (miscellum grp.), *Canthon* sp. 2, *Dichotomius* sp. fissus grp. 1 (and probably the other fissus grp. species as well), and *Uroxys* sp. 1. *Canthidium* cf. *minimum* and *Canthidium* sp. 25 (miscellum grp.) also appear to represent new genera to science.

Table 5.2. Dung beetle community similarity among sites within this survey and compared with other RAP surveys throughout Suriname

1st	2nd	S 1st	S 2nd	Shared Species	Morisita-Horn
Upper Palumeu	Grensgebergte	93	40	37	0.28
Upper Palumeu	Kasikasima	93	74	62	0.81
Grensgebergte	Kasikasima	40	74	33	0.46
Upper Palumeu	Kwamala region	93	94	71	0.67
Upper Palumeu	Nassau	93	27	24	0.39
Upper Palumeu	Lely	93	38	28	0.27
Grensgebergte	Kwamala region	40	94	29	0.08
Grensgebergte	Nassau	40	27	16	0.87
Grensgebergte	Lely	40	38	20	0.95
Kasikasima	Kwamala region	74	94	57	0.40
Kasikasima	Nassau	74	27	25	0.48
Kasikasima	Lely	74	38	28	0.42
Kwamala region	Nassau	94	27	21	0.36
Kwamala region	Lely	94	38	28	0.13
Nassau	Lely	27	38	22	0.91

S: Species Richness; Morisita-Horn represents community similarity

Table 5.3. Comparison of dung beetle species richness in primary lowland forests in northeastern South America

	Grensgebergte region	Kwamala region[1]	Nassau, Suriname[2]	Lely, Suriname[2]	Guri, Venezuela[3]	Nouragues, F. Guiana[4, 5]	Kaw Mtn, F. Guiana[5]	Jari, Amapa, Brazil[6]	Marajoara, Para, Brazil[7]
S (all samples)	107	94	27	38	41				
S (dung traps)	76	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. [1]Larsen 2011; [2]Larsen 2007; [3]Larsen et al. 2008, Larsen unpub. data; [4]Feer 2000; [5]Price & Feer 2012; [6]Gardner et al. 2008b; [7]Scheffler 2005

Several large-bodied dung beetle species, such as *Coprophanaeus lancifer* (the largest Neotropical dung beetle species) and *Dichotomius boreus*, were commonly sampled at both lowland 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 in the region. These large dung beetle species are also the most ecologically important for burying seeds and controlling parasites.

Deltochilum 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 recently (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. *Anomiopus globosus* and *Anomiopus parallelus* are two unusual species with unknown natural history, although their morphology suggests an association with ant nests.

Several species represent new records for Suriname, including *Ateuchus oblongus*, *Eurysternus howdeni*, and *Feeridium woodruffi*. The presence of *E. howdeni* is very surprising, and represents a massive extension of its known range. *F. woodruffi* was only described in 2008, and is an unusual and extremely rare species known only from a few specimens (Vaz-de-Mello 2008). It is the only species in its genus.

CONSERVATION RECOMMENDATIONS

The Grensgebergte 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, and the highest known record for dung beetle diversity in the Guiana Shield (107 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, and in the Kwamala region, I sampled a total of 94 species across three distinct sites (Table 5.3). As dung beetles are highly sensitive to forest loss and degradation, preventing mining operations and other drivers of deforestation from entering the area will be important for maintaining the high biodiversity of the region.

In addition to high overall species richness, I found high Beta diversity at the sites across very small spatial scales. Consequently, it is important to protect the diversity of soils and habitats that occur in Southeastern Suriname even at small spatial scales. Plans for protected areas or reserves should incorporate this small-scale spatial heterogeneity, as well as taking into consideration that Southeastern Suriname is quite distinct from southwestern and other parts of Suriname.

High dung beetle diversity and biomass at Upper Palumeu, the most isolated site, may be explained by lower hunting pressures. The abundance and biomass of dung beetles in the Grensgebergte area overall was relatively high, and was higher than observed at Nassau, Lely, Kwamala, and 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, it is important to regulate hunting intensity, and maintain healthy populations of large mammals such as spider monkeys, howler monkeys and peccaries, as these are among the most important species for dung beetles. Reduced hunting on large, 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 areas such as the tourist area at Kasikasima is an excellent way to maintain sustainable populations of large mammals.

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Appendix 5.1. Dung beetle species abundance (number individuals collected), including taxonomic notes and amended species list from RAP #43 & 63

Site	Upper Palumeu (Juuru)	Grensgebergte rock	Kasikasima	Kwamala region (3 sites)	Nassau	Lely	Old species name (from RAP #63 Kwamala)
# Species	**93**	**40**	**74**	**94**	**27**	**38**	
Total abundance	**2460**	**681**	**1342**	**4554**	**204**	**906**	
# Trap samples	**66**	**14**	**54**	**193**	**51**	**53**	
Agamopus castaneus Balthasar	1		12	31			
Anomiopus globosus Canhedo	1			2			
Anomiopus parallelus Harold[1]	1			4		1	
Ateuchus cereus Harold	1		1	2			
Ateuchus cf. *sulcicollis* Harold	2		15	5			
Ateuchus murrayi Harold	132	7	142	76	1	1	
Ateuchus oblongus Harold	25						
Ateuchus pygidialis Harold	1			4			
Ateuchus simplex LePeletier & Serville	291		94	285	1	13	
Ateuchus substriatus Harold	12	1	17	57			
Ateuchus sp. 3	1			5			
Ateuchus sp. 4	1			1			
Ateuchus sp. 5	7	2	1	26			
Ateuchus sp. 6 (aff. *murrayi*)			1	3			
Ateuchus sp. 7 (aff. *aeneomicans*)			1	4			
Ateuchus sp. 8 (carbonarius grp.)[2]	2	1	14	28			*Ateuchus* cf. *obscurus* Harold
Canthidium cf. *chrysis* Fabricius			1	22			
Canthidium cf. *kirschi* Harold	13		3	19		1	
Canthidium cf. *minimum* Harold[3]	9			2			
Canthidium cf. *onitoides* Perty	1			1			
Canthidium depressum Boucomont[4]		6			2	20	*Canthidium guyanense* Boucomont
Canthidium deyrollei Harold	14		9	116			
Canthidium dohrni Harold	4		6	7			
Canthidium funebre Balthasar	1						
Canthidium gerstaeckeri Harold	7		3	38		6	
Canthidium gracilipes Harold	6		2	16			
Canthidium latipleurum Preudhomme de Borre	2		3				
Canthidium sp. 5 (aff. *funebre*)	2			6			
Canthidium sp. 6	1	6	15	35		4	
Canthidium sp. 8 (aff. *quadridens*)	3			10			
Canthidium sp. 9	15	6	1	6			
Canthidium sp. 10	47	2	15	2			
Canthidium sp. 12 (aff. *latum*)	3		3	13			
Canthidium sp. 13	1			3			
Canthidium sp. 15	2			2			

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Appendix 5.1. continued

Site	Upper Palumeu (Juuru)	Grensgebergte rock	Kasikasima	Kwamala region (3 sites)	Nassau	Lely	Old species name (from RAP #63 Kwamala)
Canthidium sp. 18 (aff. *bicolor*)	1			25			
Canthidium sp. 19 (aff. *kirschi*)	1			1			
Canthidium sp. 20 (aff. *chrysis*)	7		3	18			
Canthidium sp. 21 (aff. *persplendens*)	3		1				
Canthidium sp. 22 (aff. *chrysis*)			1				
Canthidium sp. 23	1						
Canthidium sp. 24			2				
Canthidium sp. 25 (miscellum grp.)			4				
Canthidium sp. 26 (aff sp. 10)	11	1	2				
Canthidium sp. 27		1					
Canthon bicolor Castelnau	141	1	27	72	2	46	
Canthon quadriguttatus Olivier	9	18	6	1	1	7	
Canthon sordidus Harold	5		3	33	9	19	
Canthon subhyalinus Harold	1						
Canthon triangularis Drury			5	489	13	14	
Canthon vulcanoae Pereira & Martinez[5]	25		5	1			*Canthon semiopacus* Harold
Canthon sp. 2	1			9			
Canthonella silphoides Harold			1	1			
Coprophanaeus jasius Olivier	6	3	3	5			
Coprophanaeus lancifer Linnaeus	16	2	23	4		1	
Deltochilum carinatum Westwood	12		1	4	2	2	
Deltochilum guyanense Boucomont	24	4	5	6	8		
Deltochilum icarus Olivier	3		3	11	1	3	
Deltochilum orbiculare Lansberge	4	1	1		3	1	
Deltochilum septemstriatum Paulian	14		3	14	4		
Deltochilum valgum Burmeister	1			4			
Deltochilum sp. 1	4	2					
Deltochilum sp. 2	2		3				
Deltorhinum guyanensis Genier	1			2			
Dichotomius apicalis Luederwaldt	11	40	12		1		*Dichotomius* sp. 1
Dichotomius boreus Olivier	191	16	118	219	4	7	
Dichotomius cf. *lucasi* Harold	98	11	28	360			
Dichotomius cf. *horridus* Felsche			1	1			*Dichotomius* sp. 5 (calcaratus grp)
Dichotomius melzeri Luederwaldt	1		1				
Dichotomius robustus Luederwaldt	6	1	1	3			
Dichotomius subaeneus Castelnau	78	7		1			
Dichotomius worontzowi Pereira[6]	3	1	1	5			*Dichotomius* sp. 4
Dichotomius sp. 3 (batesi-inachus grp)	5		4	2			
Dichotomius sp. fissus grp. 1	2		3				

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Appendix 5.1. continued

Site	Upper Palumeu (Juuru)	Grensgebergte rock	Kasikasima	Kwamala region (3 sites)	Nassau	Lely	Old species name (from RAP #63 Kwamala)
Dichotomius sp. fissus grp. 2	1						
Dichotomius sp. fissus grp. 3	2						
Dichotomius sp. fissus grp. 4			1				
Dichotomius sp. fissus grp. 5	1						
Eurysternus atrosericus Genier			7	86			
Eurysternus balachowskyi Halffter & Halffter	3		7	3	1		
Eurysternus cambeforti Genier		1	11	8		1	
Eurysternus caribaeus Herbst	78	1	48	296	5	16	
Eurysternus cf. *cayennensis* Castelnau[7]	4	47	2				
Eurysternus cyclops Genier	13		17	1	4	17	
Eurysternus foedus Guerin-Meneville	7	2	20	17			
Eurysternus hamaticollis Balthasar	20			2			
Eurysternus howdeni Genier	1	1					
Eurysternus hypocrita Balthasar	108	70	25		1	1	
Eurysternus ventricosus Gill	21	1	21	3		1	
Feeridium woodruffi Vaz-de-Mello	1		2				
Hansreia affinis Fabricius	189	368	199	97	88	569	
Onthophagus cf. *xanthomerus* Bates	20		23	22			
Onthophagus haematopus Harold	233		6	929	34	52	
Onthophagus rubrescens Blanchard	259	5	177	288	1	11	
Oxysternon durantoni Arnaud	16	2	4	56		24	
Oxysternon festivum Linnaeus	1		16	39			
Oxysternon spiniferum Castelnau	1			3			
Phanaeus bispinus Bates	1			1			
Phanaeus cambeforti Arnaud	3	1		41			
Phanaeus chalcomelas Perty	45	2	20	336	2	7	
Scybalocanthon pygidialis Schmidt	44	8	42		1	10	
Sulcophanaeus faunus Fabricius	10	2	3	1			
Sylvicanthon cf. *securus* Schmidt	7	27		5		4	
Trichillum pauliani Balthasar	10		1	23			
Uroxys pygmaeus Harold	16		29	45	4	1	
Uroxys sp. 1	8	2	2		4	2	
Uroxys sp. 3	40	1	29	81	6	29	
Additional species sampled on other RAP surveys in Suriname							
Anomiopus andrei Canhedo				1			
Anomiopus lacordairei Waterhouse				3	1		
Canthidium cf. *gigas* Balthasar				1			

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Appendix 5.1. continued

Site	Upper Palumeu (Juuru)	Grensgebergte rock	Kasikasima	Kwamala region (3 sites)	Nassau	Lely	Old species name (from RAP #63 Kwamala)
Canthidium guyanense Boucomont[4]				7			*Canthidium* sp. 11 (aff. *guyanense*)
Canthidium splendidum Preudhomme de Borre				11			
Canthidium sp. 3						3	
Canthidium sp. 7 (aff. *histrio*)				2			
Canthidium sp. 14 (centrale grp)				2			
Canthidium sp. 16				2			
Canthidium sp. 17				1			
Canthon mutabilis Lucas						3	
Canthon sp. 1				6			
Coprophanaeus dardanus MacLeay						3	
Coprophanaeus parvulus Olsoufieff				2		1	
Dendropaemon sp. 1				3			
Dichotomius mamillatus Felsche				4		1	
Dichotomius sp. 2				3			
Eurysternus vastiorum Martinez						2	
Oxysternon silenus Castelnau						2	
Uroxys gorgon Arrow				1			

[1]As with individuals collected on the RAP survey around Kwamalasamutu, the individual of *A. parallelus* collected here is much larger than those revised by Canhedo (2006), and are also larger and differ in pronotal patterning from the individual from the Lely RAP survey. These specimens may represent an undescribed species.

[2]The name used in the previous RAP survey, *Ateuchus* cf. *obscurus* is apparently incorrect, as *Canthidium obscurum* is a valid species within *Canthidium*. This species belongs to the carbonarius group and may be undescribed.

[3]As described in RAP 63 from Kwamala, *Canthidium* cf. *minimum* is a curious species. It closely resembles *Canthidium minimum*, although the hind tibia is slightly less curved in the specimens from this survey, and all specimens from this survey are much smaller in size. *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. I believe the species collected here is likely to be undescribed.

[4]Based on comparison of specimens with original type descriptions, it appears that two species from previous RAP surveys were switched (Vaz-de-Mello, pers. comm.). *Canthidium depressum* (misidentified as *C. guyanense* in previous RAP reports) appears to be completely specialized to granite outcrops and plateaus, while *Canthidium guyanense* (identified previously as *Canthidium* sp. 11) is found in lowland forests of southwestern Suriname. The two species are very closely related, but can be separated based on the second and third elytral striae which are deeply impressed posteriorly in *C. depressum*, while the first three elytral striae are all weakly but equally impressed posteriorly in *C. guyanense*.

[5]All specimens identified as *Canthon semiopacus* on previous RAP surveys and also in various museum collections that are from the Guiana shield are probably misidentified, and represent *Canthon vulcanoae* (Vaz-de-Mello, pers. comm.). *C. semiopacus* is a closely related Amazonian species, and can be distinguished by its larger size, red elytra, genitalia, and other characters

[6]The species collected here represents the true *Dichotomius worontzowi*, and is distinct from a common and widespread Amazonian species often misidentified as *D. worontzowi* (Vaz-de-Mello, pers. comm.). *D. worontzowi* has four head tubercles rather than two

[7]The population of *Eurysternus cayennensis* from this survey, which was primarily specialized to the Grensgebergte mountaintop, differs quite strongly from the widespread *E. cayennensis* found farther south and west throughout the Amazon. In addition to a distinct ventral color pattern, the basal tooth and setae of the male hind femur are very distinct. Further comparisons are needed to determine whether this represents an undescribed species.

Appendix 5.2. Diet preference/capture method for dung beetles. Data are number of individuals collected. FIT: flight intercept trap (unbaited).

	Dung	FIT	Dead insects	Dead millipede	Fungus	Fruit
# Species	76	71	15	3	2	4
Total abundance	4045	312	108	3	5	10
# Trap samples	92	29	7	3	1	1
Agamopus castaneus	13					
Anomiopus globosus		1				
Anomiopus parallelus		1				
Ateuchus cereus	1	1				
Ateuchus cf. *sulcicollis*	14	3				
Ateuchus murrayi	266	15				
Ateuchus oblongus		24				1
Ateuchus pygidialis		1				
Ateuchus simplex	338	17	25			5
Ateuchus substriatus	29	1				
Ateuchus sp. 3	1					
Ateuchus sp. 4		1				
Ateuchus sp. 5	4	6				
Ateuchus sp. 6 (aff. *murrayi*)		1				
Ateuchus sp. 7 (aff. *aeneomicans*)	1					
Ateuchus sp. 8 (carbonarius grp.)	17					
Canthidium cf. *chrysis*		1				
Canthidium cf. *kirschi*	2	14				
Canthidium cf. *minimum*		9				
Canthidium cf. *onitoides*	1					
Canthidium depressum	6					
Canthidium deyrollei	22	1				
Canthidium dohrni	9	1				
Canthidium funebre	1					
Canthidium gerstaeckeri	8	2				
Canthidium gracilipes		8				
Canthidium latipleurum		5				
Canthidium sp. 5 (aff. *funebre*)	2					
Canthidium sp. 6	21	1				
Canthidium sp. 8 (aff. *quadridens*)		3				
Canthidium sp. 9	17	5				
Canthidium sp. 10	57	7				
Canthidium sp. 12 (aff. *latum*)	1	5				
Canthidium sp. 13	1					
Canthidium sp. 15		2				
Canthidium sp. 18 (aff. *bicolor*)		1				
Canthidium sp. 19 (aff. *kirschi*)		1				
Canthidium sp. 20 (aff. *chrysis*)		6	3	1		
Canthidium sp. 21 (aff. *persplendens*)		4				

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Appendix 5.2. continued

	Dung	FIT	Dead insects	Dead millipede	Fungus	Fruit
Canthidium sp. 22 (aff. *chrysis*)		1				
Canthidium sp. 23		1				
Canthidium sp. 24		2				
Canthidium sp. 25 (miscellum grp.)	4					
Canthidium sp. 26 (aff sp. 10)	14					
Canthidium sp. 27	1					
Canthon bicolor	169					
Canthon quadriguttatus	32	1				
Canthon sordidus	7	1				
Canthon subhyalinus	1					
Canthon triangularis	5					
Canthon vulcanoae	28	2				
Canthon sp. 2		1				
Canthonella silphoides		1				
Coprophanaeus jasius		6	6			
Coprophanaeus lancifer	27		14			
Deltochilum carinatum	3	3	7			
Deltochilum guyanense	20	1	11	1		
Deltochilum icarus	4		2			
Deltochilum orbiculare	6					
Deltochilum septemstriatum	5	1	11			
Deltochilum valgum		1				
Deltochilum sp. 1	5	1				
Deltochilum sp. 2		4	1			
Deltorhinum guyanensis		1				
Dichotomius apicalis	63					
Dichotomius boreus	325					
Dichotomius cf. *lucasi*	78	52	1	1	4	1
Dichotomius cf. *horridus*	1					
Dichotomius melzeri	2					
Dichotomius robustus	7	1				
Dichotomius subaeneus	70	12				3
Dichotomius worontzowi	5					
Dichotomius sp. 3	7	2				
Dichotomius sp. fissus grp. 1		5				
Dichotomius sp. fissus grp. 2		1				
Dichotomius sp. fissus grp. 3		2				
Dichotomius sp. fissus grp. 4		1				
Dichotomius sp. fissus grp. 5		1				
Eurysternus atrosericus	7					
Eurysternus balachowskyi	10					

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Appendix 5.2. continued

	Dung	FIT	Dead insects	Dead millipede	Fungus	Fruit
Eurysternus cambeforti	12					
Eurysternus caribaeus	124	2	1			
Eurysternus cf. *cayennensis*	43	1	9			
Eurysternus cyclops	30					
Eurysternus foedus	28	1				
Eurysternus hamaticollis	20					
Eurysternus howdeni	2					
Eurysternus hypocrita	201	2				
Eurysternus ventricosus	41	2				
Feeridium woodruffi	3					
Hansreia affinis	755		1			
Onthophagus cf. *xanthomerus*	27	9	7			
Onthophagus haematopus	238	1				
Onthophagus rubrescens	434	7				
Oxysternon durantoni	15	7				
Oxysternon festivum	13	4				
Oxysternon spiniferum		1				
Phanaeus bispinus	1					
Phanaeus cambeforti	4					
Phanaeus chalcomelas	65	2				
Scybalocanthon pygidialis	69	15	9		1	
Sulcophanaeus faunus	15					
Sylvicanthon cf. *securus*	33	1				
Trichillum pauliani	11					
Uroxys pygmaeus	45					
Uroxys sp. 1	9	3				
Uroxys sp. 3	69	1				