

Assemblages of Dung Beetles Using Cattle Dung in Madagascar

Authors: Rahagalala, P., Viljanen, H., Hottola, J., and Hanski, I.

Source: African Entomology, 17(1) : 71-89

Published By: Entomological Society of Southern Africa

URL: <https://doi.org/10.4001/003.017.0109>

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.

Assemblages of dung beetles using cattle dung in Madagascar

P. Rahagalala^{1*}, H. Viljanen^{2†}, J. Hottola² & I. Hanski²

¹Département d'Entomologie, Faculté des Sciences, B.P. 906, Université d'Antananarivo, Madagascar

²Department of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, Viikinkaari 1, FI-00014 Finland

Malagasy dung beetles have evolved with a diverse group of primates (lemurs), the largest extant native herbivores on the island. The two main radiations include the endemic subtribe Helictopleurina (65 species) and the tribe Canthonini with several endemic genera (c. 170 species), both of which occur primarily in forests and feed on lemur faeces and carrion. Cattle were introduced to Madagascar about 1000 years ago, thereby establishing a completely new type of resource (cattle dung) for indigenous dung beetles. We report three striking patterns in the occurrence of dung beetles in cattle dung based on semi-quantitative sampling at nearly 80 localities across Madagascar. First, no dung beetles have shifted to use primarily cattle dung in wet forests, in contrast to other tropical regions, where ungulate dung is a key resource for dung beetles. Second, the community in open habitats includes 21 species (three Canthonini, six Helictopleurina, one Scarabaeini, four Onthophagini, six Aphodiini, and one Didactyliini), which is only a small fraction of the species number in comparable communities in mainland Africa. Third, nearly all species using cattle dung have maximally large geographic ranges across Madagascar, in marked contrast to relatively small ranges among forest-inhabiting species. This latter point applies also to four endemic Helictopleurina species, which have shifted to cattle dung in open areas and have subsequently expanded their ranges in comparison with their relatives inhabiting forests. The most numerous species in the community is the introduced *Digitonthophagus gazella*. We show that the abundance of *D. gazella* in local communities has no noticeable effect on the species composition in the remaining community.

Key words: cattle dung, community structure, dung beetles, Helictopleurina, introduced species, Madagascar.

INTRODUCTION

The true dung beetles (Scarabaeoidea Laparoticti) consist of some 7000 described species of Scarabaeidae (Scarabaeinae and Aphodiinae) and Geotrupinae (Geotrupidae). Although dung beetles may date back to the late Mesozoic and were well differentiated during the Cenozoic, dung beetle biogeography and the occurrence of dung beetles in different ecosystems mostly reflect evolution since the Miocene to Pleistocene (Cambefort 1991) and the great influence of humans in the past hundreds and even thousands of years. Human impact in the form of deforestation, extermination of large native mammals, introduction of domesticated mammals, and changing practices of animal husbandry have all played a role in structuring dung beetle communities in many parts of the world (Halffter & Arellano 2002; Vulinec 2002; Scheffler 2005).

Madagascar has a unique and distinctive mam-

malian fauna and an unusual dung beetle fauna (Orsini *et al.* 2007). Before the arrival of humans about 2300 years ago, there were at least 17 species of large-bodied lemurs, including *Archaeoindris* (160 kg) and *Babakotia* (20 kg), three species of hippopotami, the elephant bird (500 kg) and other related species, and giant tortoises, which all became exterminated in the next 1000 to 1500 years (the last hippopotamus was seen in the 1900s; Burney *et al.* 2004 and references therein). On the other hand, other than Hippopotamidae, there have never been native ungulates (Artiodactyla, Perissodactyla and Proboscidea) in Madagascar. From the perspective of dung beetles, this is a major limitation, as many groups of dung beetles have radiated on large herbivore dung, and especially on ungulate dung, in mainland Africa (Cambefort 1991). At present, cattle dung is the primary resource for thousands of dung beetle species worldwide, and species richness in beetle communities using cattle dung is very high in many parts of the world.

*To whom correspondence should be addressed.

E-mail: prahagalala@yahoo.fr

†P.R. and H.V. contributed equally to this work.

In Madagascar, dung beetles are primarily represented by two large tribes, the endemic subtribe Helictopleurina (Oniticellini) with 65 species and Canthonini with around 170 described species in several endemic genera (*O. Montreuil, pers. comm.; Paulian & Lebis 1960; Orsini et al. 2007*). Helictopleurina and Canthonini occur mostly in forests, using lemur dung and carrion (Koivulehto 2004; Viljanen 2004; Viljanen *et al.*, in prep). In addition, there are records of three species of Scarabaeini, six species of Onthophagini (Paulian & Lebis 1960), and 30 species of Aphodiini and Didactyliini (Aphodiinae, Bordat *et al.* 1990) representing both endemic and introduced species with mostly unknown ecologies.

Cattle were introduced to Madagascar about 1000 years ago (Burney *et al.* 2003). At present, cattle are abundant and widespread, occurring mostly in open areas but there are also feral cattle called 'Baria' in low densities in many forest areas. In this paper, we analyse the communities of Malagasy dung beetles using the introduced new resource of cattle dung based on extensive sampling across Madagascar. The questions we ask include whether any native endemic species have been able to switch to cattle dung, and if so which kinds of species and in which habitats? How common are the introduced species, and is there any indication that they might have an impact upon the native species? What are the patterns in the community of cattle dung-using beetles in different ecosystems and in different parts of Madagascar?

INTRODUCTION TO AND PRESENT ABUNDANCE OF CATTLE IN MADAGASCAR

The introduction of cattle to Madagascar has been inferred from an increase in the spores of the coprophilous fungus *Sporormiella*, a proxy of the presence of large herbivorous mammals (Burney *et al.* 2004). The dates 1130 ± 50 and 9600 ± 90 yr BP have been reported for the island Nosy Be and Lake Kavitaha in the highlands (Burney *et al.* 2003). Assuming that the presence of the cattle in the highlands indicates widespread occurrence across much of Madagascar, we may conclude that cattle dung has been an important resource in Madagascar for at least 1000 years and probably for somewhat longer. Currently, there are about 7 million bovines, which are important socio-culturally as well as economically. In terms of the geographical distribution, the density of cattle is

highest around the capital Antananarivo in central Madagascar, in the south and in northwestern Madagascar (Fig. 1). Cattle densities range from zero to a few animals per ha, where the density is highest.

Concerning other domestic mammals, sheep, goats, pigs, horses and donkeys have been introduced to Madagascar. Horses and donkeys were introduced in 1817 under the reign of King Radama I, but their numbers are currently very low. There are about 1.5 million goats and sheep. Converting all domestic animals apart from cattle into bovine equivalents adds roughly 0.5 million more 'cattle'.

MATERIAL AND METHODS

Museum and literature records of Malagasy dung beetles

The existing knowledge on the systematics, phylogeny, distribution and ecology of endemic Malagasy dung beetles in the subtribe Helictopleurina and the tribe Canthonini have been summarized in a series of recent papers, mostly based on studies conducted since 2002 (Hanski *et al.* 2007; Orsini *et al.* 2007; Viljanen *et al.*, in prep.; Wirta *et al.* 2008). The vast majority of both Helictopleurina and Canthonini species occur in wet forests, using lemur dung and carrion (Koivulehto 2004; Viljanen 2004; Viljanen *et al.*, in prep.).

Concerning species in the other tribes with clearly fewer species, previous limited information on habitat selection and diet of the introduced and endemic Aphodiini, Didactyliini, Onthophagini and Scarabaeini in Madagascar and mainland Africa is summarized in Table 1. Bordat *et al.* (1990) has summarized the distributional data for Aphodiini and Didactyliini.

Sampling

During the course of our extensive sampling of dung beetles in forest localities across Madagascar since 2002, small-scale manual searching of cattle dung pats in open habitats and wet forests has been conducted in Ranomafana National Park (NP) and in Andringitra NP in December 2003, in open areas in Manombo on the east coast in November 2004, in Ambila in November 2005, and in Sambava in December 2007 (Appendix 1, Fig. 1). In addition, Viljanen (2004) conducted a small-scale pitfall trapping (30 trap-nights) in wet forest in Ranomafana NP.

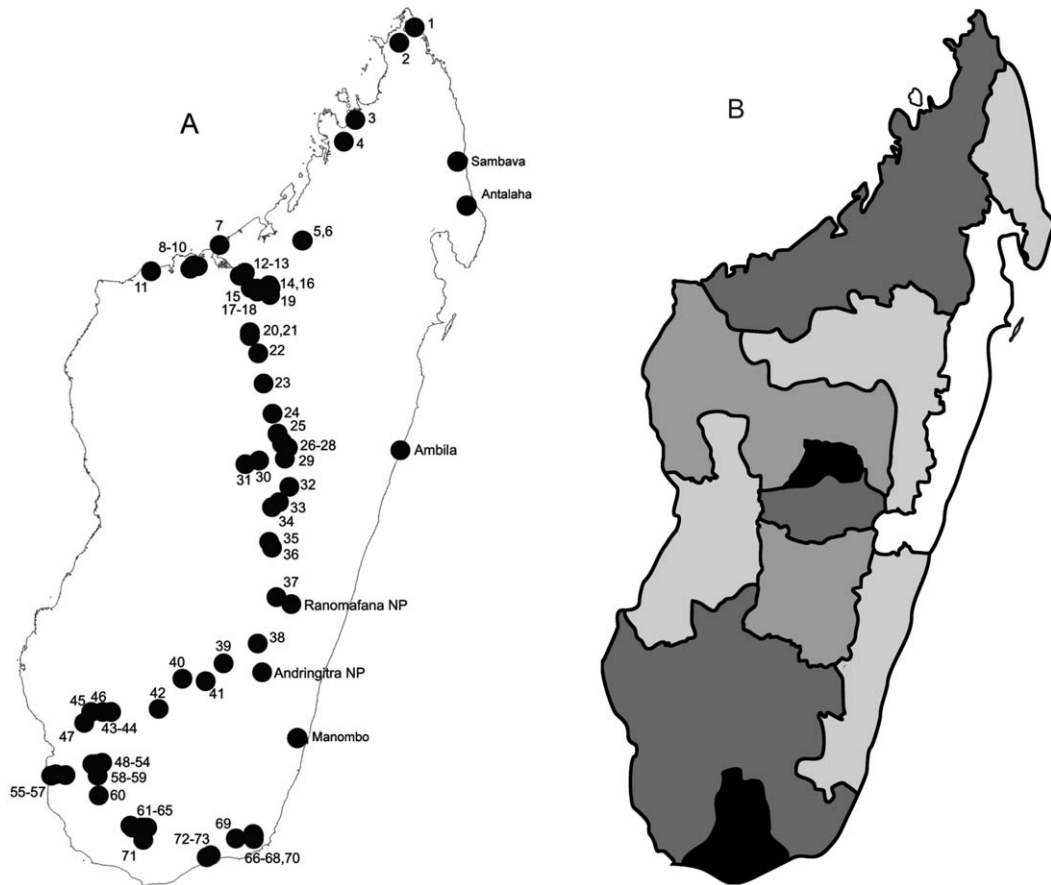


Fig. 1. A, Sampling localities in open areas. B, Cattle density in Madagascar: black 230–410, dark grey 175–230, grey 122–175, light grey 60–122, and white 44–60 heads/km².

A large-scale inventory of dung beetles in cattle dung pats in open areas was conducted in 2006 and 2007 (Appendix 1, Fig. 1). First, a transect of 47 localities was sampled by four people from the capital Antananarivo to southern Madagascar during six weeks from March to May in 2006. The second transect included 22 localities from Antananarivo towards north, sampled in November and December 2006. This transect was sampled by five people in three weeks. The third transect in northern Madagascar included six localities sampled by three people in two weeks in May 2007.

Samples were collected at roughly 50 to 150 km intervals while driving along the main roads (Fig. 1). The time spent at each locality was roughly proportional to the numbers of dung pats present and varied from approximately 10 minutes to 2 hours. At each site, we checked all dung pats that

appeared to be of suitable age (not too dry). All individuals encountered were collected for subsequent identification and counting, with the exception of the often very abundant *Digitonthophagus gazella*, which was mostly counted in the field. Due to differences in search effort and sample size, the observed species numbers in different localities are not directly comparable. To account for variation in sample size in regression analyses of the number of species in local communities, we used the logarithm of sample size as a covariate. An alternative analysis was conducted by rarefaction, modelling the number of species in a random subsample of 30 individuals per locality.

Ordination of dung beetle communities

We used Kruskal's non-metric multidimensional scaling (NMDS) to characterize the species composition in the 73 local communities in open

Table 1. Dung beetle species collected in cattle dung or which potentially occur in cattle dung in Madagascar (the latter for Aphodiinae only). Habitat: O = open habitats, DR = dry forest, WF = wet forest. Other resource types apart from cattle dung (CD): H = human faeces, LF = lemur faeces, PD = *Propithecus diadema* faeces, BD = buffalo dung, Ba = baboon faeces, D = dog faeces, BP = bush pig dung, T = tortoise dung, C = carrion, L = light trap, UV = UV light, *P. Bordat (pers. comm.), **Paulian (1992), () = data from Africa (P. Bordat, unpubl.). For details of our own trapping results see Appendix 2.

Scrabaeidae	This study	Endemic	Distribution	Habitat	Other resources
Canthonini					
<i>Arachnodes cuparius</i> (Fairmaire, 1889)	Yes	Yes	All Madagascar	O	
<i>A. morio</i> (Harold, 1897)	Yes	Yes	All Madagascar	O DF	C
<i>A. sp.</i>	Yes	Yes	East	O	
<i>A. new sp.</i>	Yes	Yes	South	O	
Helictopleurini					
<i>Helictopleurus giganteus</i> (Harold, 1869)	Yes	Yes	East	DF WF	C
<i>H. littoralis</i> Monteruil, 2005	Yes	Yes	All Madagascar	O	
<i>H. marsyas</i> (Olivier, 1789)	Yes	Yes	All Madagascar	O DF	C
<i>H. neoamplicollis</i> Krell, 2000	Yes	Yes	All Madagascar	O DF	C
<i>H. nicollei</i> Lebis, 1960	Yes	Yes	East	WFO	CH
<i>H. perrieri</i> (Fairmaire, 1889)	Yes	Yes	All Madagascar	DF O	CT
<i>H. quadripunctatus</i> (Olivier, 1789)	Yes	Yes	All Madagascar	O DF WF(HA)	C D PP
<i>H. rudicollis</i> (Fairmaire, 1889)	Yes	Yes	East	WF	C
<i>H. sinuaticornis</i> (Fairmaire, 1889)	Yes	Yes	East	O WF	
Onthophagini					
<i>Digitonthophagus gazella</i> Fabricius, 1787	Yes		Afro-Eurasian	O	CH
<i>Onthophagus delphinensis</i> d'Orbigny, 1914		Yes	Southwest	O	
<i>O. depressus</i> Harold, 1914			Southwest, Northeast	O	
<i>O. elegans</i> Klug, 1832	Yes	Yes	All Madagascar	O	D
<i>O. hinnulus</i> Klug, 1832	Yes	Yes	All Madagascar	O	C
<i>O. pipitzi</i> Ancey, 1882	Yes	Yes	All Madagascar	O	
Scarabaeini					
<i>Scarabaeus radama</i> (Fairmaire, 1895)	Yes	Yes	Southwest	O	CH
<i>S. sevoistra</i> (Allaud, 1902)		Yes	South	DF O	
<i>S. viettei</i> (Paulian, 1953)		Yes	West	DF O	C
<i>Aphodiidae (Aphodiini and Didactyliini)</i>					

Continued on p. 75

Table 1 (continued)

Scrabaeidae	This study	Endemic	Distribution	Habitat	Other resources
Open area / dry forest species					
<i>Aganocrossus amoenus</i> Boheman, 1857		Yes	Afrotropics		(CD BD UV)
<i>Blackburneus radamus</i> Petrovitz, 1958		Yes	South		
<i>Koshantschikovius lateinctus</i> Fairmaire, 1903			West		
<i>Labarrus madagassius</i> Petrovitz, 1961	Yes		All Madagascar	O	C
<i>L. sublividus</i> Balthasar, 1941	Yes		Afrotropics	O	
<i>Mesontoplatys dorsalis</i> Klug, 1855	Yes		Afrotropics	O DF	C
<i>M. parvulus</i> Harold, 1871			Afrotropics		(Ba CD H L)
<i>Neocalaphodius moestus</i> Fabricius, 1801	Yes		Oriental, Afrotropics	O DF	C
<i>Nialaphodius nigrita</i> Fabricius, 1801	Yes		Mesoamerica, Afrotropics	O DF	C
<i>Paradidactylia dionysii</i> (Clément, 1958)		Yes	All Madagascar		L**
<i>Pharaphodius pseudoignotus</i> Bordat, 1986		Yes	West		
<i>Pleuraphodius leo</i> (Paulian, 1942)			Afro-oriental		(CD UV)
<i>Pseudopharaphodius apicesetosus</i> (Clément, 1969)	Yes		Afrotropics	O	
<i>Didactylia pictipennis</i> (Fairmaire, 1897)	Yes	Yes	East		
<i>D. pittinoti</i> Bordat, 1986		Yes	West	O	
<i>D. rosickyi</i> (Balthasar, 1963)		Yes	Southwest		
Wet forest species					
<i>Blackburneus vadoni</i> Bordat, 1986		Yes	East		CLH**
<i>Koshantschikovius schmitzi</i> Bordat, 1990		Yes	West and East		
<i>Madagaphodius didactyloides</i> Bordat, 1990		Yes	East		
<i>Neoemadellius humerosaqueineum</i> Mate, 2007	Yes	Yes	Southeast		CLF
<i>N. peyrierasi</i> Bordat, 1990		Yes	East		
<i>N. perinetensis</i> Bordat, 1990		Yes	East		
<i>N. ranomadyrensis</i> Bordat, 1990	Yes	Yes	Southeast		LF
<i>N. uxoris</i> Clément, 1987		Yes	East		PD*
<i>N. unctus</i> Bordat, 1990		Yes	East		PD*
<i>N. new sp.</i>	Yes	Yes	Southeast		CLF
<i>Pharaphodius impurissimus</i> Roth, 1851			North		(CD UV L)
<i>P. mangaroensis</i> Bordat, 1990		Yes	East		L**
<i>Pleuraphodius clementi</i> Bordat, 1986		Yes	East		
<i>Didactylia exsecta</i> Schmidt, 1911		Yes	East		

habitats sampled across Madagascar (Fig. 1). We examined whether cattle density, altitude, latitude and longitude explained the structure of the local communities in a three-dimensional ordination. We used the same method to study possible effects of the introduced and numerically dominant species, *Digitonthophagus gazella*, on the species composition of the remaining species in local communities.

NMDS is an unconstrained ordination method used for exploratory analyses of the relationships between species occurrences and environmental variables (Legendre & Legendre 1998; Venables & Ripley 2002). NMDS does not assume any particular functional forms for the responses of species to environmental variables, and it is not severely affected by the zero observations that are typical for community data. By fitting a monotonic regression to the data, NMDS places sample plots into the ordination space in such a manner that the ordination distances correspond to differences in species composition and abundances. The locations of the species in the ordination space are calculated as locality (sample) averages weighted by species abundances (Legendre & Legendre 1998; Venables & Ripley 2002; Oksanen *et al.* 2008). The distances between the localities were calculated using the Bray-Curtis dissimilarity index. We applied square-root transformation and Wisconsin double-standardization to use relative abundances and to reduce the weight of the most abundant species in the analysis (Faith *et al.* 1987, Oksanen *et al.* 2008).

For each continuous explanatory variable (cattle density, altitude, latitude and longitude), a vector was fitted onto the ordination space to yield maximal correlation between the variable and the locality (sample) values. Thus each vector points to the direction in the ordination space where its value increases most rapidly. The relative length of the vector is proportional to the strength of the variable's effect on the ordination. To compare the communities in northern, central and southern Madagascar, and communities with small (relative abundance <10 %), medium (10–50 %), and high (>50 %) numerical dominance by *D. gazella* in the sample, we calculated averages of the ordination scores for the factor levels (Legendre & Legendre 1998; Venables & Ripley 2002; Oksanen *et al.* 2008). The significance of the explanatory variables was tested with a permutation test. Ordination analyses were carried out with version 1.11-0 of the community ecology package *vegan* (Oksanen *et al.*

2008) as implemented in version 2.6.2 of R (R Development Core Team 2008).

RESULTS

Species composition

Table 1 summarizes the data on the dung beetle species that occur in cattle dung in Madagascar. For completeness, we have included in this table all species of Aphodiini, Didactyliini, Scarabaeini and Onthophagini known from Madagascar, though especially the poorly known wet forest species of Aphodiini may use mostly resources other than cattle dung.

In the systematic sampling conducted at 73 localities in open habitats across Madagascar in 2006–07 (Fig. 1), we sampled altogether 21 species, including 3 Canthonini, 6 Helicopleurina, one Scarabaeini, 4 Onthophagini, 6 Aphodiini, and 1 Didactyliini (Table 1). Our trappings in eastern Madagascar in Manombo, Andringitra NP, Ranomafana NP, Andasibe NP, Antalaha and Sambava added five more species, of which *Helicopleurus rudicollis* has been sampled in wet forests only (Table 1).

Habitat selection and diets

There are only three species that use cattle dung regularly in wet forests in Madagascar, and none of them is a cattle dung specialist. The most frequent species is *Helicopleurus rudicollis*, which is a generalist feeding on both dung and carrion across the entire eastern wet forest belt. In the well-studied Ranomafana NP, cattle dung-baited pitfall traps yielded regularly two species of *Neoemadiellus*, *N. humerosanquineum* and *Neoemadiellus* sp. 2 (Appendix 2; Viljanen 2004). Six other species, all common on some other resources, were caught in very small numbers and most likely accidentally rather than being attracted by the bait.

In contrast to the lack of cattle dung-using species in wet forests, in open habitats there are several species that are true cattle dung specialists, including both native species and all four introduced Onthophagini species and all ten introduced Aphodiini. In Helicopleurina, there are four species that can be classified as cattle dung specialists in open habitats and in semi-open dry forests (see also Wirta *et al.* 2008, Hanski *et al.* 2008), and further four species that use cattle dung to some extent in dry forests (Table 1). Canthonini includes four cattle dung-using species in open

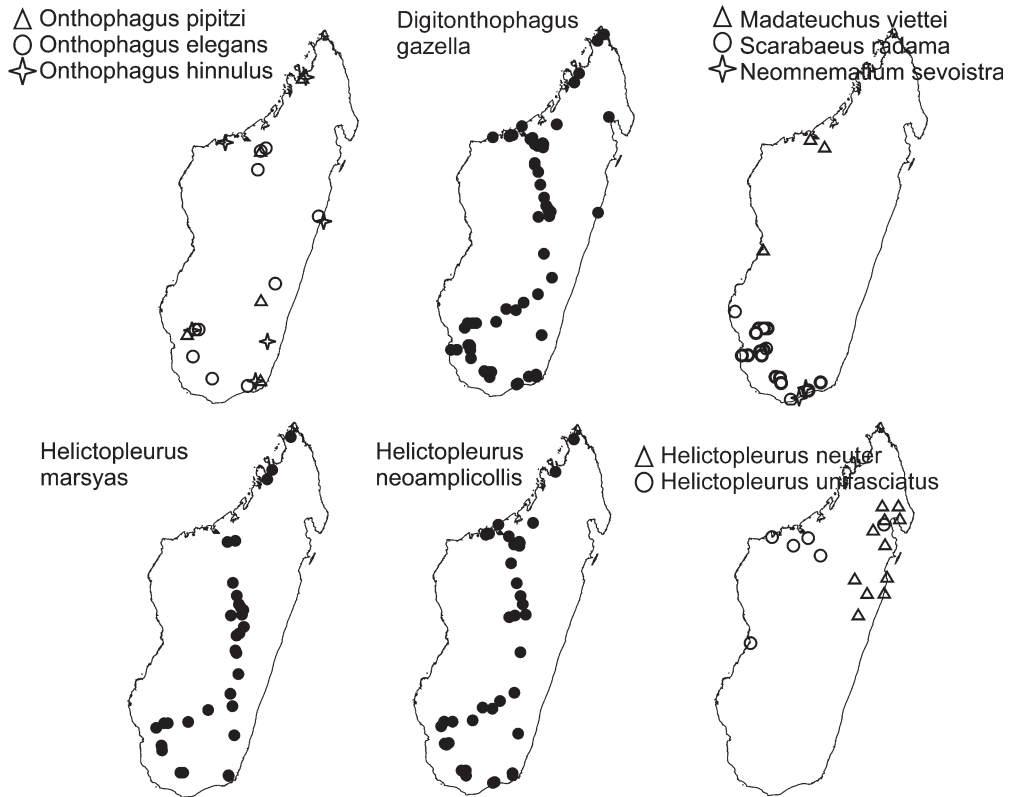


Fig. 2. Geographical ranges of selected dung beetle species that use cattle dung. Upper row: Four species of Onthophagini and three species of Scarabaeini. The lower row shows the distributions of two *Helictopleurus* species using cattle dung in open areas and, for comparison, the much more restricted ranges of two common forest-inhabiting *Helictopleurus* species.

habitats, while all the three Scarabaeini species occur in open habitats and semi-open dry forests, with some ecological differences among the species that are discussed in the Discussion.

Practically all species using cattle dung in open areas occur across Madagascar (Fig. 2, Appendix 2), including *Labarrus madagassius*, *Mesontoplatys dorsalis* and *Pseudopharaphodius apicesetosus* (Aphodiini) (Bordat *et al.* 1990), though they were not included in our northern samples. The exceptions are the three species of Scarabaeini and two *Onthophagus* species, which have more restricted distributions in western and southern Madagascar (Fig. 2, Table 1). The three most numerous dung beetle taxa in cattle dung, Helictopleurina, Onthophagini, and Aphodiinae, are rather equally represented across Madagascar and each taxon is numerically the most abundant in many individual local communities. Thus of the 73 local communities sampled, 16 were numerically domi-

nated by Helictopleurina, 24 by Onthophagini, and 25 by Aphodiinae.

Local communities in cattle dung

Sample size (number of beetles collected) decreased with increasing longitude and altitude (linear regressions, $t = -2.32$, $P = 0.02$ and $t = -2.00$, $P = 0.05$, respectively), though the amount of variation explained by the models was small, less than 6%. Latitude had no significant effect. These results must be interpreted with caution because of great differences in the numbers of cattle in different sampling localities and consequent differences in the sampling effort.

As expected, sample size had a major effect on the number of species. Log-transformed sample size explained 53% of variation in log-transformed species number (Fig. 3a). Species number ranged from one to 12 per local community.

We tried to explain variation in species number

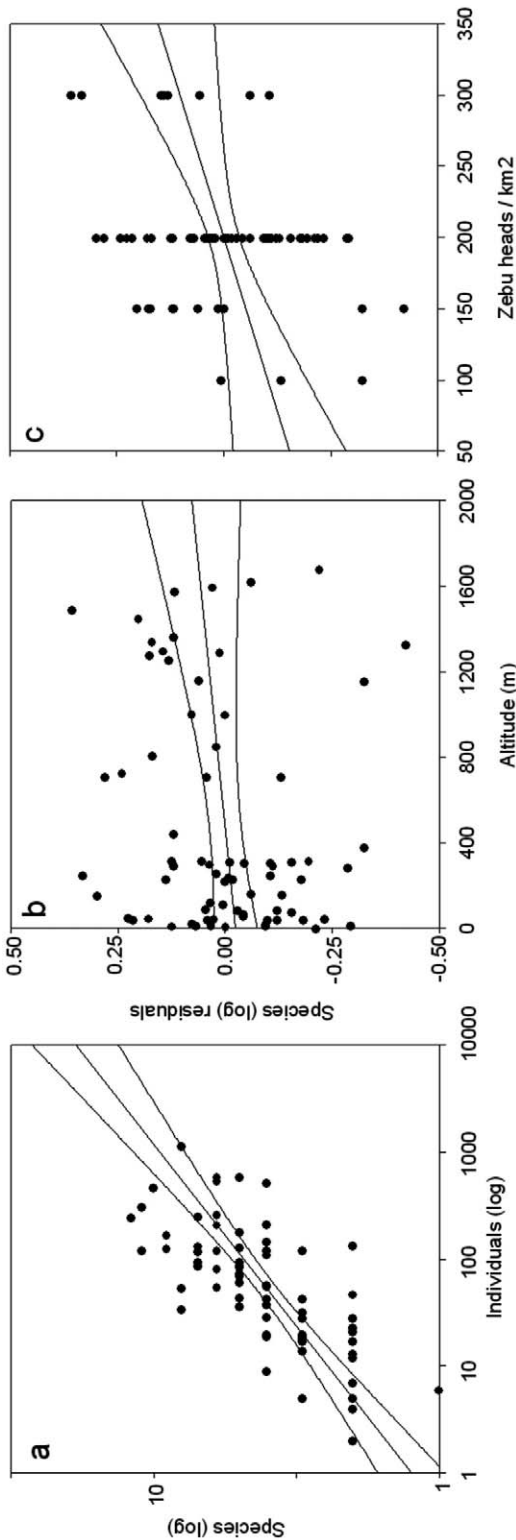


Fig. 3. a, Number of species plotted against the logarithm of pooled sample size (number of individuals). In panels (b) and (c), the residual from panel (a) is plotted against altitude and cattle density, respectively. For statistics see Table 2.

by cattle density, altitude, longitude, latitude, and annual precipitation. The effect of sample size on species number was corrected in two different ways. First, we modelled variation in the number of species in a random subsample of 30 individuals, in which case the rarefied species number increased with cattle density and altitude (Table 2). Second, we included sample size as a covariate in a multiple regression model. In this analysis, cattle density had a significant effect, altitude a nearly significant effect (Figs 3b and 3c, Table 2), and longitude, latitude and precipitation had no significant effects and were excluded from the model. Recall that sample size (number of beetles sampled) decreased with altitude (above), and hence high-altitude communities had many species with low density.

In the NMDS ordination, latitude, longitude and altitude had significant effects on species composition, suggesting that the structure of local communities in the high central plateau of Madagascar differs from those at low coastal areas (Fig. 4a, Table 3a). This is supported by significant variation in community structure between northern, central and southern Madagascar. The significant effect of altitude is apparently largely due to the dominance of Aphodiinae in the central plateau, where the subfamily accounted for 75 % of the pooled sample of 1465 individuals, compared with 37 % (pooled sample 3624 individuals) in northern and 25 % in southern Madagascar (3843 individuals).

There was less variation among local communities in the ordination in northern than in central and southern Madagascar, which is at least partly due to the systematically high prevalence of the numerically dominant introduced species *Digitonthophagus gazella* in northern Madagascar. Local communities with dissimilar relative abundance of *D. gazella* did not differ from each other in terms of the species

Table 2. Least squares linear regression of species (log-transformed number of species collected) number and rarefied species number (species in a subsample of 30 individuals) explained by cattle density, altitude, and sample size (log-transformed number of beetles collected). Statistics for the full model: species (log) number, $F_{3,69} = 32.70$, $P < 0.0001$, $R^2 = 0.57$; and rarefied species number, $F_{2,45} = 4.38$, $P < 0.05$, $R^2 = 0.13$.

Predictor variables	Species (log)				Rarefied species number			
	Coeff.	S.E.	<i>t</i>	<i>P</i>	Coeff.	S.E.	<i>t</i>	<i>P</i>
Constant	-0.160	0.104	-1.54	0.127	1.872	0.914	2.05	0.046
Cattle density	0.001	<0.001	2.58	0.012	0.009	0.004	2.14	0.025
Altitude	<0.001	<0.001	1.74	0.087	<0.001	<0.001	2.32	0.038
Log sample size	0.300	0.0323	9.20	<0.0001				

composition of the rest of the species (Fig. 4b, Table 3b). Cattle density had no systematic effect on the species composition in the local communities.

DISCUSSION

Nearly 300 species of true dung beetles in the subfamilies Scarabaeinae and Aphodiinae are known from Madagascar. The vast majority of them are endemic, including all the species not mentioned in Table 1. Cattle dung is used by a diverse set of about 30 endemic Helictopleurina,

Canthonini, Scarabaeini, Onthophagini, Aphodiini, and Didactyliini, two introduced Onthophagini and several introduced Aphodiini (Table 1).

There are two striking patterns in the occurrence of cattle dung-using beetles in Madagascar. First, there is not a single wet forest-inhabiting species that would use cattle dung in preference to other resource types. Second, the species that use cattle dung in open habitats mostly occur all over Madagascar, in contrast to the forest-dwelling species that have more restricted geographical ranges (discussed below). These observations suggest that the endemic dung beetle species that colonized

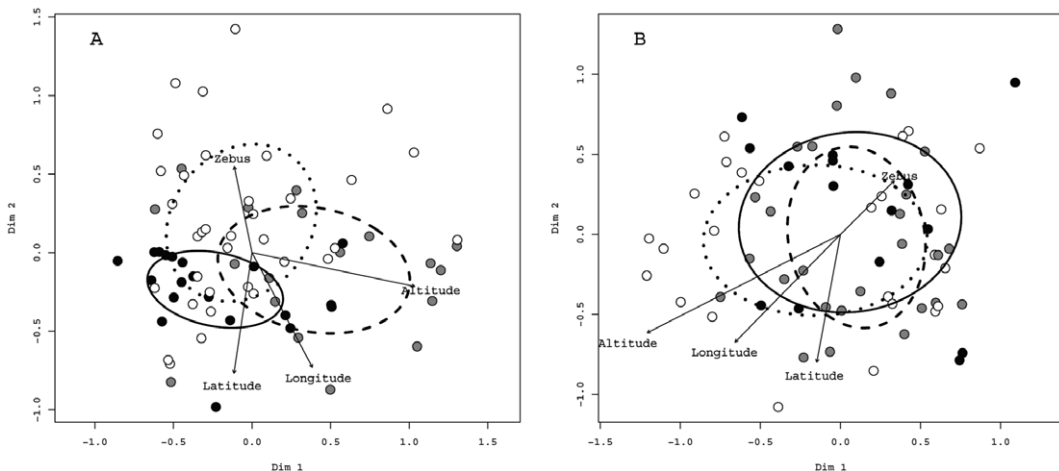


Fig. 4. Plot of the first two dimensions of NMDS ordinations. **A**, The configuration of northern (between latitudes -12 and -17°N ; black dots), central (-17 and -22°N ; grey) and southern (-22 and -26°N ; white) localities based on the composition of their dung beetle communities. The ellipses indicate one standard deviation of the weighted average of site scores in northern (solid line), central (dashed) and southern (dotted) Madagascar. **B**, As **A**, but here local communities without *Digitonthophagus gazella* were ordinated and the localities are grouped based on the relative abundance of *D. gazella*: high ($>50\%$; black, solid line), intermediate (10 to 50%; grey, dashed line) or low ($<10\%$; white, dotted line). In both ordinations latitude, longitude and altitude had statistically significant effects (Table 3). Cattle density (in **A** and **B**) or the relative abundance of *D. gazella* (in **B**) had no significant effects on the community structure.

Table 3. Permutation tests (1000 permutations) for the significance of environmental vectors (latitude, longitude, altitude, and cattle density) and factors (northern, central, or southern Madagascar, and the relative abundance of *Digitonthophagus gazella* in the community) in the NMDS ordinations (Fig. 4). (A) All species included and (B) *D. gazella* omitted. The location (northern, central or southern Madagascar) of a local community had a significant effect on the species composition. Goodness of fit in panel A: $r^2 = 0.1627$, $P < 0.001$, in panel B: $r^2 = 0.1781$, $P < 0.001$. Cattle density or the relative abundance of *D. gazella* did not affect the species composition in the community. Goodness of fit in panel B for the proportion of *D. gazella*: $r^2 = 0.0305$, $P = 0.363$

(A)					
Vectors	Dim1	Dim2	Dim3	r^2	P
Altitude	0.81316	-0.16860	0.55708	0.4053	<0.001
Latitude	-0.14481	-0.96528	0.21741	0.1580	0.005
Longitude	0.43503	-0.82775	0.35438	0.1945	0.001
Zebu head/km ²	-0.19416	0.94123	-0.27637	0.0847	0.111
(B)					
Vectors	Dim1	Dim2	Dim3	r^2	P
Altitude	-0.889289	-0.452869	0.063835	0.3200	<0.001
Latitude	-0.131289	-0.706769	-0.695155	0.2218	<0.001
Longitude	-0.543710	0.556056	-0.628635	0.25463	<0.001
Zebu head/km ²	0.54427	0.543771	0.638811	0.0660	0.196

cattle dung after its introduction to Madagascar 1000 years ago have shifted both their resource use and habitat selection and have subsequently greatly extended their geographic ranges.

Use of cattle dung in forests and open habitats

Buffalo and cattle dung are widely used resources by dung beetles, particularly in tropical savannas in Africa and the western Orient, apparently because these resource types and other similar resources have been very abundant for a long time in grasslands with high density of large herbivorous mammals. Though the dung of ungulates (Artiodactyla, Perissodactyla and Proboscidea) is generally less abundant in forests than in grasslands, ungulate dung is used by a diverse community of dung beetles in tropical forests worldwide. For instance, in the Tai forest in the Ivory Coast, elephant dung and human excrement attracted about equal numbers of dung beetle species (Cambefort & Walter 1991). In striking contrast, in Madagascar there are only three species of dung beetles that have been caught in some numbers in cattle dung in wet forests, *Helictopleurus rudicollis* and two species of Aphodiini, and they all have a wide diet.

The likely explanation for the lack of cattle dung-using dung beetles in wet forests is the

historical lack of Bovini in Madagascar. Even today, the vast majority of the seven-million-strong cattle population occurs in open areas, though there is a significant feral cattle population in forests in many parts of Madagascar. In spite of no extant species using cattle dung, it is likely that the ancestors of Helictopleurina used the dung of comparable mammalian herbivores in mainland Africa some tens of millions of years ago (Wirta *et al.* 2008), as most of the other Oniticellini and many related Onthophagini do today (Cambefort 1991). Apparently, the evolution of Helictopleurina over the past 20–30 million years (Wirta *et al.* 2008) has modified them sufficiently to make the shift to cattle dung difficult. This shift has occurred, as we discuss below, but only in species that occur in open habitats at present.

In contrast to the cattle dung pats in wet forests that are devoid of dung beetles, in open areas cattle dung is used by a characteristic community of dung beetles. In our samples, there were typically two to six species per locality (average 4.6, standard deviation 2.5, range 1 to 12), which is an underestimate of the true number, as our samples were collected within a short period of time and were typically rather small. The total number of about 30 species for the whole of Madagascar (Table 1) is however reliable, as most species are

widely distributed and were sampled repeatedly in multiple localities (discussed below).

Compared to dung beetle communities using cattle dung in mainland Africa, the Malagasy communities are species-poor. In the Ivory Coast, more than 100 species use ungulate dung in humid and dry savannas (Cambefort 1991). In a single locality, Abokouamekro in the humid savanna biome, 64 dung beetle species were sampled from cattle dung. In South Africa, local communities have typically 40 to 60 species in bush and grassveld areas and grasslands (Doube 1991; Davis *et al.* 1999, 2004; Krüger & Scholtz 1998). The lowest numbers have been sampled from cattle dung in improved pastures, but even then the number of species in a local community is typically over 30 (Davis *et al.* 2004). Thus the Malagasy communities have roughly an order of magnitude fewer species than local communities in mainland Africa. Incidentally, the total number of dung beetle species known from African savannas is around 1500 species (Cambefort 1991).

Apart from being species-poor, the dung beetle communities in open areas in Madagascar are strikingly homogeneous, as most of the species occur across the entire island. The only exceptions are the three endemic scarabaeines and one endemic onthophagine. *Scarabaeus sevoistra* (Scarabaeini) has been collected in only one area in southernmost Madagascar (Fig. 2), and *S. radama* and *S. viettei*, though locally abundant, have restricted ranges in southern and northwestern Madagascar, respectively. The endemic *Onthophagus delphinensis* has been collected from only Forth Dauphin in the south, and it may have already gone extinct, as there are no records since 1901. In the high plateau of central Madagascar, the relative abundance of Aphodiinae is higher than at lower altitudes. This pattern fits the global distribution of dung beetle subfamilies, as Aphodiinae are most numerous in temperate and Scarabaeinae in tropical regions (Hanski & Cambefort 1991).

Lack of radiation in Scarabaeini and Onthophagini

Scarabaeini and Onthophagini have colonized Madagascar over a prolonged period of time, including recent colonizations by the two introduced species of *Onthophagus* (they are considered to be introduced based on their occurrence in mainland Africa and elsewhere). Scarabaeini are

represented by three species in Madagascar. The species are considered endemic because they are not known from elsewhere, but the monotypic Malagasy genera *Neomnematum* and *Madateuchus* have been synonymized with *Scarabaeus* by Mostert & Scholtz (1986) and confirmed by Forgie *et al.* (2005). Given that Scarabaeini and probably also Onthophagini with four endemic species are likely to have colonized Madagascar multiple times (H. Wirta, pers. comm.) and have been there for a long time, we may ask why they have not radiated like the Helictopleurina and Canthonini (Orsini *et al.* 2007; Wirta *et al.* 2008)

First of all, no species of Scarabaeini or Onthophagini occurs in wet forests in Madagascar. In the case of Scarabaeini this is not entirely surprising, because in mainland Africa Scarabaeini typically occur in arid regions, and especially the most speciose genus *Scarabaeus* is proportionally most prominent in the dry southwestern parts of southern Africa (Davis 1997). In the case of Onthophagini, lack of forest species in Madagascar is unexpected because hundreds of *Onthophagus* species worldwide occur in forests (see many chapters in Hanski & Cambefort 1991). For instance, in the Taï forest in the Ivory Coast (Cambefort & Walter 1991) and in the Gunung Mulu NP in Borneo (Hanski 1983) there are 27 and 37 *Onthophagus* species, respectively. Lack of forest species in Madagascar cannot be easily explained by diet either, because *Onthophagus* have adapted to use practically any kind of decomposing animal and even plant material that any dung beetles use (Cambefort 1991; Hanski 1989). The most probable reason for lack of forest-dwelling *Onthophagus* in Madagascar is competition with the diverse communities of Canthonini and Helictopleurina. Helictopleurina resemble greatly Onthophagini in appearance and ecology. The ancestors of Helictopleurina have been inferred to have arrived at Madagascar 37 to 23 million years ago and radiated rapidly soon afterwards (Wirta *et al.* 2008). It is probable that by the time Onthophagini arrived at Madagascar, the Onthophagini-type dung beetle niche in forests was already taken up, and hence *Onthophagus* have been unable to colonize forests. It would be helpful and informative to have a time-calibrated phylogeny of African *Onthophagus* including the endemic Malagasy species to infer the likely time of their arrival in relation to the colonization and radiation by Helictopleurina.

The three Malagasy Scarabaeini show some differences in their ecologies, apparently reflecting their long history in Madagascar. Thus only *Scarabaeus radama* is common in open areas in most of southwestern Madagascar using cattle dung, human excrement, and carrion. *Scarabaeus viettei* occurs in dry forests and may mostly use carrion. *Scarabaeus sevoistra* is very rare, only ever collected from two localities in southern Madagascar: Analavondrove in Antanimora (1901) and Marovato (1939). These localities used to have the characteristic spiny forest vegetation, which has, however, been greatly reduced in area and quality by cutting and invasion by *Opuntia*. *Scarabaeus sevoistra* has not been collected for 70 years and may be extinct or effectively extinct.

We do not know which resources Scarabaeini and endemic Onthophagini used following their arrival at Madagascar, but possible candidates include faeces of the now-extinct megafauna, especially the large-bodied lemurs. Following the arrival of cattle in Madagascar, Onthophagini and at least *S. radama* were able to switch back to cattle dung, or perhaps they had never lost their ability to use ungulate dung.

Endemic and introduced species of Aphodiinae

We have compiled (Table 1) all of the information available for Aphodiinae regardless of whether the species use cattle dung, which is not known for most species. Of the 30 species, 10 are considered to be introduced and 20 endemic to Madagascar. As a rule, the endemic species occur in wet forests, while the introduced species occur in open areas and many if not all of them use cattle dung. The same pattern is found in Scarabaeinae (above), though in Scarabaeinae there are only two introduced species.

One striking exception is *Didactylia pictipennis*, one of the four endemic Didactyliini, which occurs in cattle dung in open areas and is strikingly abundant in many local communities (Appendix 2). Apparently *D. pictipennis* has made a shift of resource use and habitat selection similar to the shift made by the few species of *Helictopleurus* discussed below. Two genera, *Pharaphodius* and *Pleuraphodius*, include both introduced and endemic species (Table 1).

Of the 20 Aphodiinae not sampled in our study (Table 1), 11 species (10 endemic) have been found

only in the eastern wet forest region and may be generalists like the three endemic *Neomadiellus* species in Ranomafana NP (Viljanen *et al.*, in prep.). They may also have restricted geographical ranges, as so many wet forest dung beetles (Wirta *et al.* 2008) and many other taxa do (Wilme *et al.* 2006, and references therein). Four endemic species have been found only in the westernmost or southernmost Madagascar, where we did not conduct sampling in 2006–07. The remaining five species include species with a wide range and species with unknown distributions in Madagascar (Bordat *et al.* 1990). Three of these species have been sampled from cattle dung in the African mainland (*Aganocrossus amoenus*, *Mesontoplatys parvulus*, and *Pleuraphodius leo*), and the two other species have been sampled with carrion (*Didactylia rosickyi*) or with light (*Paradidactylia dionysii*) in Madagascar.

In contrast to Onthophagini and Scarabaeini, Aphodiini have entered and speciated in wet forests, where many endemic species now occur. A probable reason for the success of Aphodiini in entering forests is their much smaller size and hence different biology compared with the forest-dwelling Helictopleurina and Canthonini. Aphodiinae are generally most active around dawn and dusk, while Helictopleurina are diurnal and Canthonini are mostly nocturnal (Viljanen *et al.*, in prep.). In contrast to forests, Aphodiini have not radiated in open areas, perhaps because of shortage of appropriate resources until the arrival of cattle in the past 1000 years. This agrees with lack of radiation in Scarabaeini and Onthophagini.

Shift to cattle dung in Helictopleurina

Helictopleurina arrived at Madagascar 37 to 23 million years ago and went through an adaptive radiation concurrently with the adaptive radiation of lemurs (Wirta *et al.* 2008). Most species have evolved a broad diet and they feed on both carrion and dung, especially on lemur faeces, the dominant herbivorous mammals in Madagascar. Following the arrival of cattle to Madagascar about 1000 years ago (Burney *et al.* 2003), four species have been able to switch to cattle dung in open habitats: *H. quadripunctatus*, *H. marsyas*, *H. neoamplicollis* and *H. sinuatocornis*. The first three species are very abundant and occur, exceptionally for Helictopleurina, across all of Madagascar, while *H. sinuatocornis* is less common.

Most *Helictopleurina* (63 %) occur in wet forests in Madagascar, but none of these species has shifted to use cattle dung in open areas (Wirta *et al.* 2008). Species inhabiting wet forests are poorly adapted to change their habitat selection, which would involve moving to a very different environment in terms of temperature and humidity, particularly in the case of diurnal species such as *Helictopleurina* (Cambefort 1991; Viljanen *et al.*, in prep.), which experience the maximal contrast in temperature and humidity between forests and open habitats. Koivulehto (2004) has shown that the wet forest-dwelling *Helictopleurina* simply do not cross the forest edge.

If not coming from wet forests, the species of *Helictopleurus* now using cattle dung in open areas are likely to have originally occurred in different types of dry forests, where they probably used the dung of lemurs and the dung of the extinct Malagasy megafauna: giant tortoises, elephant bird, and hippopotami, which appear to have occurred especially in dry forests in southeastern Madagascar (Goodman *et al.* 2003; Hawkins & Goodman 2003). There is a gradient in environmental conditions from entirely open habitats to closed dry forests, via various kinds of intermediate savanna-type habitats, in which the open habitat *Helictopleurus* can be found even today. This concerns particularly *H. neoamplicollis*, *H. marsyas*, and *H. quadripunctatus* (Wirta *et al.* 2008). The situation may be somewhat different in the case of *H. sinuatocornis*, which occurs as an uncommon species at high elevations along the western range boundary of *H. giganteus*, its closest relative. These two species occur in sympatry, but *H. giganteus* occurs in forests while *H. sinuatocornis* occurs primarily in open habitats.

Apart from the difficulty of changing habitat selection from forest to open habitats, the shift to cattle dung from lemur dung involves a shift to a very different type of resource in terms of texture, fibre content, and size of droppings. Most dung beetles exhibit selectivity for the dung of particular animals based on the size of the dropping and qualities such as moisture, nitrogen and fibre content. Most of the strictly coprophagous dung beetles are specialized to use either herbivore or omnivore dung, although there may be seasonal changes in preference or differences in resource use for adult feeding versus provisioning the nest for oviposition (Hanski & Cambefort 1991).

Regardless of exactly how the shift to cattle

dung took place in *H. neoamplicollis*, *H. marsyas* and *H. quadripunctatus*, resource shift has apparently allowed the species to greatly expand their geographical ranges. At present, the species that occur in wet forests have significantly smaller geographical ranges than these three common cattle dung-using species (Wirta *et al.* 2008). The most likely explanation is that reduced competition in open areas allowed the latter species to expand their ranges, while any expansion of the forest species is hindered by competition with other species outside the ranges of focal species. Rapid range expansion is supported by exceptionally low genetic diversity across the ranges of the three cattle dung-using species (Hanski *et al.* 2008).

Impact of the introduced *Digitonthophagus gazella*

Digitonthophagus gazella, an Afro-Eurasian species, is one of the most frequently introduced dung beetle species worldwide, and a species that has become successfully established in Australia, North America, and Madagascar (Hanski & Cambefort 1991). Howden & Scholtz (1986) reported changes in the abundances of native species ten years after the introduction of *D. gazella* to Texas in 1972. The previously dominant *O. pennsylvanicus*, and probably a few other species, appeared to have declined due to competition with *D. gazella*. In Australia, the previously introduced *Euoniticellus intermedius* declined following the establishment of *D. gazella* (Doube *et al.* 1991). In contrast, the more than 300 native Australian species have not been greatly affected by the many introduced dung beetle species, largely because the native and introduced species exhibit clear habitat segregation, the former living in forests and the latter in open habitats.

The situation in Madagascar is similar to that in Australia: the vast majority of the endemic species occurs in forests and is hence not affected by the abundant and widespread *D. gazella*, which occurs only in open habitats. Concerning the species in open habitats, our results indicate that the relative abundance of *D. gazella* in the community did not have a systematic effect on the species composition among the rest of the species, suggesting that *D. gazella* has no major influence on community structure. Nonetheless, occasionally *D. gazella* is so abundant that the population uses a substantial fraction of the cattle dung available and there is likely to be competition with the endemic

Helictopleurus species living in cattle dung in open habitats. More detailed quantitative studies are required to elucidate these interactions.

ACKNOWLEDGEMENTS

The authors would like to thank P. Bordat and O. Montreuil for help in species identification, and T. Avomaa, S. Gripenberg, R. Kaartinen, J. Lehtomäki, J. Lehtonen, T. Randriamanaitra, J. R. Rasoloariniaina, and A. H. Rakotosalama for assis-

tance in the field, and three anonymous referees for detailed and helpful comments. We thank ANGAP (Association Nationale pour la Gestion des Aires Protegees) and MICET (Madagascar Institute pour la Conservation des Environnements Tropicaux) for help in research arrangements in Madagascar. This work has been supported by the Academy of Finland (grant numbers 64350, 20286 and 213457, Finnish Centre of Excellence Programme, 2000-08).

REFERENCES

- BORDAT, P., PAULIAN, R. & PITTINO, R. 1990. *Faune de Madagascar, 74: Insectes, Coléoptères Aphodiidae*. Muséum National d'Histoire Naturelle, Paris, France.
- BURNEY, D.A., ROBINSON, G.S. & PIGOTT BURNEY L. 2003. *Sporormiella* and the late Holocene extinctions in Madagascar. *PNAS* **100**: 10800–10805.
- BURNEY, D.A., PIGOT BURNEY, L., GODFREY, L.R., JUNGERS, W.L., GOODMAN, S.M., WRIGHT, H.T. & JULL, A.J.T. 2004. A chronology for late prehistoric Madagascar. *Journal of Human Evolution* **47**: 25–63.
- CAMBEFORT, Y. 1991. Biogeography and evolution. In: Hanski, I. & Cambefort, Y. (Eds) *Dung Beetle Ecology*. 51–67. Princeton University Press, Princeton.
- CAMBEFORT, Y. & WALTER, P. 1991. Dung beetles in tropical forest in Africa. In: Hanski, I. & Cambefort, Y. (Eds) *Dung Beetle Ecology*. 198–210. Princeton University Press, Princeton.
- DAVIS, A.L.V. 1997. Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae s. str.). *African Journal of Ecology* **35**: 10–38.
- DAVIS, A.L.V., SCHOLTZ, C.H. & CHOWN, S.L. 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography* **26**: 1039–1055.
- DAVIS, A.L.V., SCHOLTZ, C.H., DOOLEY, P.W., BHAM, N. & KRYGER, U. 2004. Scarabaeine dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *South African Journal of Science* **100**: 415–424.
- DOUBE, B.M. 1991. Dung beetles of Southern Africa. In: Hanski, I. & Cambefort, Y. (Eds) *Dung Beetle Ecology*. 133–155. Princeton University Press, Princeton.
- DOUBE, B.M., MACQUEEN, A., RIDSHILL-SMITH, T.J. & WEIR, T.A. 1991. Native and introduced dung beetles in Australia. In: Hanski, I. & Cambefort, Y. (Eds) *Dung Beetle Ecology*. 255–278. Princeton University Press, Princeton.
- FAITH, D.P., MINCHIN, P.R. & BELBIN, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**: 57–68.
- FORGIE, S.A., PHILIPS, T.K. & SCHOLTZ, C.H. 2005. Evolution of the Scarabaeini (Scarabaeidae: Scarabaeinae). *Systematic Entomology* **30**: 60–96.
- GOODMAN, S.M., GANZHORN, J.U. & RAKOTONDRAVONY, D. 2003. Mammals. In: Ganzhorn, J.U. & Benstead, J.P. (Eds) *The Natural History of Madagascar*. 1159–1186. University of Chicago Press, Chicago.
- HALFFTER, G. & ARELLANO, L. 2002. Response of dung beetle diversity to human-induced changes in a tropical landscape. *Biotropica* **34**: 144–154.
- HANSKI, I. 1983. Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forest in Sarawak, Borneo. *Acta Zoologica Fennica* **167**: 1–45.
- HANSKI, I. 1989. Dung beetles. In: Lieth, H. & Werger, M.J.A. (Eds) *Tropical Rain Forest Ecosystems*. 489–511. Elsevier Science Publishers, Amsterdam.
- HANSKI, I. & CAMBEFORT, Y. 1991. *Dung Beetle Ecology*. Princeton University Press, Princeton.
- HANSKI, I., KOIVULEHTO, H., CAMERON, A. & RAHAGALALA, P. 2007. Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biology Letters* **3**: 344–347.
- HANSKI, I., WIRTA, H., NYMAN, T. & RAHAGALALA, P. 2008. Resource shifts in Malagasy dung beetles: contrasting processes revealed by dissimilar spatial genetic patterns. *Ecology Letters* **11**: 1208–1215.
- HAWKINS, A. & GOODMAN, S.M. 2003. Introduction to the birds. In: Ganzhorn, J.U. & Benstead, J.P. (Eds) *The Natural History of Madagascar*. 1019–1044. University of Chicago Press, Chicago.
- HOWDEN, H.F. & SCHOLTZ, C.H. 1986. Changes in Texas dung beetle community between 1975 and 1985 (Coleoptera: Scarabaeidae, Scarabaeinae). *Coleopterists Bulletin* **40**: 313–316.
- KOIVULEHTO, H. 2004. Madagascar's dung beetles—rain forest species avoid open areas. M.Sc. thesis, University of Helsinki, Helsinki.
- KRÜKER, K. & SCHOLTZ, C.H. 1998. Changes in the structure of dung insect communities after ivermectin usage in a grassland ecosystem. I. Impact of ivermectin under drought conditions. *Acta Oecologica* **19**: 425–438.
- LEGENDRE L. & LEGENDRE P. 1998. *Numerical Ecology*. 2nd English Edition. Elsevier, Amsterdam
- MOSTERT, L.E. & SCHOLTZ, C.H. 1986. Systematics of the subtribe Scarabaeina (Coleoptera: Scarabaeidae). *Entomology Memoir, Department of Agriculture and Water Supply, Republic of South Africa* **65**: 1–25.
- OKSANEN, J., KINDT, R., LEGENDRE, P., O'HARA, B., SIMPSON, G.L. & STEVENS, M.H.H. 2008. vegan: Community Ecology Package. R package, version

- 1.11-0. Online at: <http://cran.r-project.org/>, <http://vegan.r-forge.r-project.org/>
- ORSINI, L., KOIVULEHTO, H. & HANSKI, I. 2007. Molecular evolution and radiation of dung beetles in Madagascar. *Cladistics* **23**: 145–168.
- PAULIAN, R. & LEBIS, E. 1960. *Faune de Madagascar 11: Insectes, Coléoptères, Scarabaeidae, Scarabaeina et Onthophagini par R. Paulian, Helictopleurini par E. Lebis*. Publications de l'Institut de Recherche Scientifique, Tsimbazaza, Tananarive, Madagascar.
- PAULIAN, R. 1992. Les Scaraboidea (Coléoptères) obtenus d'excréments de *Propithecus diadema* à Madagascar. *Bulletin de la Société Entomologique de France* **96**: 355–359.
- R DEVELOPMENT CORE TEAM 2008. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Online at: <http://www.R-project.org>
- 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.
- VENABLES W.N. & RIPLEY B.D. 2002. *Modern Applied Statistics with S*. 4th Edition. Springer, New York.
- VILJANEN, H. 2004. Diet specialization among endemic forest dung beetles in Madagascar. M.Sc. thesis, University of Helsinki, Helsinki.
- VULINEC, K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. *Biotropica* **34**: 297–309.
- WILMÉ, L., GOODMAN, S.M. & GANZHORN, J.U. 2006. Biogeographic evolution of Madagascar's microendemic biota. *Science* **312**: 1063–1065.
- WIRTA, H., ORSINI, L. & HANSKI, I. 2008. An old adaptive radiation of forest dung beetles in Madagascar. *Molecular Phylogenetics and Evolution* **47**: 1076–1089.

Accepted 20 November 2008

Appendix 1. Sampling localities, numbers of individuals and species, rarefied species number (Rar, sample size in brackets).

ID	Locality	Date	Latitude	Longitude	Altitude (m)	Zebus/km ²	Individuals	Species	Rar (30)	Rar (50)	Rar (100)
	Ranomafana NP	Nov 03	-21.23	47.45	600–1000	100	310	6			
	Andringitra NP	Nov 03	-22.29	47.00	1000	100	26	3			
	Manombo	Nov 04	-23.35	47.07	50	100	181	9			
	Ambila	Nov 05	-18.83	49.15	0	50	23	7			
	Sambava	Dec 07	-14.50	50.17		100	7	3			
	Antalaha	Dec 07	-14.75	50.20		100	35	4			
1	Orangea-Antsiranana	27.4.2007	-12.25	49.37	65	200	7	2			
2	Mahamasina-Ankarana	24.4.2007	-12.49	49.13	120	200	86	5	4.09	4.658	
3	Androhibe CNIA-Ambanja	21.4.2007	-13.69	48.45	14	200	122	6	4.343	5.251	5.962
4	Beraty-Manongarivo	16.4.2007	-14.03	48.27	55	200	7	2			
5	Ambohimalaza-Boriziny	30.4.2007	-15.57	47.62	41	200	38	4	3.802		
6	Andohaomby-Boriziny	30.4.2007	-15.57	47.63	40	200	21	2			
7	Grand Pavois Majunga	7.12.2006	-15.64	46.34	10	200	20	4			
8	Antongomena Bevary	6.12.2006	-15.96	45.93	12	200	87	5	4.061	4.491	
9	Tsiombikibo Mitsinjo	2.12.2006	-15.97	46.00	13	200	519	4	1.898	2.293	2.947
10	Mitsinjo	5.12.2006	-16.01	45.88	11	200	1154	8	3.193	4.39	5.35
11	Belambo Baly	29.11.2006	-16.05	45.27	0	200	588	5	3.178	3.56	4.03
12	Mandrosoa 12 km Marovoay	27.11.2006	-16.07	46.73	23	200	29	4			
13	Marovoay	8.12.2006	-16.12	46.65	8	200	20	3			
14	Andranomiditra	26.11.2006	-16.27	47.11	151	200	54	8	6.887	7.857	
15	Ampijoroa	25.11.2006	-16.31	46.82	74	200	17	2			
16	Betara Mahamay	24.11.2006	-16.31	47.13	89	200	14	3			
17	Ampondrabe Ankarafantsika	23.11.2006	-16.32	46.92	256	200	17	3			
18	Mandritsarhely & Maevarano	25.11.2006	-16.37	46.92	84	200	262	6	4.002	4.749	5.677
19	Amborondolo PK414	8.12.2006	-16.42	47.12	40	200	543	6	2.739	3.425	4.401
20	Mahazoma	9.12.2006	-17.00	46.81	110	100	19	3			
21	Beanana	9.12.2006	-17.06	46.81	157	100	591	6	3.29	3.808	4.396
22	Ambodiriana Begisa Antsiafabisitra	22.11.2006	-17.33	46.94	376	100	6	1			
23	Andalamahitsy Mahatsinjo	22.11.2006	-17.80	47.02	1158	150	70	5	4.121	4.664	
24	Andoharano Ankazobe	9.12.2006	-18.27	47.16	1342	150	55	6	5.291	5.903	

Continued on p. 86

Appendix 1 (continued)

ID	Locality	Date	Latitude	Longitude	Altitude (m)	Zebus/km ²	Individuals	Species	Rar (30)	Rar (50)	Rar (100)
25	Ambohimarina / Fihaonana	9.12.2006	-18.58	47.24	1362	150	44	5	4.677		
26	Andrianampela	11.5.2006	-18.70	47.31	1289	150	18	3			
27	Ampantokana	11.5.2006	-18.73	47.31	1328	150	135	2	1.417	1.624	1.934
28	Sakamarina	11.5.2006	-18.79	47.40	1277	150	5	3			
29	Beronono RN1	10.12.2006	-18.96	47.35	1297	300	36	5	4.785		
30	Faliarivo RN1	10.12.2006	-18.99	46.95	1491	300	34	8	7.769		
31	Sahapetraka Ampely	10.12.2006	-19.05	46.74	1255	300	19	4			
32	Ambatolampy Malamamaina	31.3.2006	-19.40	47.42	1622	200	32	3	2.998		
33	Manetivohitra PK117	31.3.2006	-19.64	47.26	1595	200	4	2			
34	Ambohimarina PK 144	31.3.2006	-19.72	47.15	1677	200	28	2			
35	Ambohimanjaka PK215	1.4.2006	-20.26	47.11	1576	150	2	2			
36	Soavina Bepombo PK229	1.4.2006	-20.35	47.15	1448	150	170	9	5.569	6.24	7.577
37	Ambohimahasoa	1.4.2006	-21.12	47.22	1154	150	6	1			
38	Ambalavao Zebu market	2.4.2006	-21.84	46.93	999	150	210	6	4.164	4.951	5.646
39	Ambasazo	9.5.2006	-22.15	46.40	850	200	95	5	4.064	4.571	
40	Ihorombe	8.5.2006	-22.39	45.76	1000	200	61	5	4.731	4.966	
41	Ihosity Zebu market	8.5.2006	-22.43	46.12	726	200	126	9	5.802	7.176	8.691
42	Sakarivohazo Ranohira	8.5.2006	-22.86	45.39	807	200	94	7	5.307	6.027	
43	Andranomaitso Sakaraha	6.4.2006	-22.91	44.65	709	200	252	7	5.39	5.987	6.692
44	Andranomaitso Sakaraha	7.4.2006	-22.91	44.65	709	200	146	4	3.511	3.837	3.998
45	Mahaboboka	7.5.2006	-22.91	44.34	314	200	133	7	4.28	5.152	6.44
46	SF Sakaraha	6.4.2006	-22.91	44.52	707	200	247	12	4.986	5.659	6.318
47	Tranokaky	7.5.2006	-23.08	44.23	442	200	466	10	4.27	5.131	6.519
48	Besely Betioky	12.4.2006	-23.70	44.51	285	200	47	2	1.622		
49	Betioky area	6.5.2006	-23.72	44.36	230	200	130	5	4.745	4.973	5
50	Antoby Betioky	6.5.2006	-23.72	44.42	292	200	82	6	5.045	5.579	
51	Betioky	11.4.2006	-23.72	44.42	292	200	12	2			
52	Vohipea Betioky	5.5.2006	-23.75	44.39	299	200	85	5	4.096	4.566	
53	Antsakoandahy Betioky	11.4.2006	-23.76	44.43	312	200	57	4	3.512	3.869	
54	Betioky	11.4.2006	-23.76	44.42	309	200	17	2			
55	Ambelailalike	3.5.2006	-23.88	43.79	40	200	43	3	2		
56	Ankazoabo	5.5.2006	-23.89	43.94	83	200	13	2			
57	Anevoevo	3.5.2006	-23.90	43.72	18	200	110	4	2.945	3.366	3.9
58	Besely Betioky	12.4.2006	-23.90	44.44	305	200	120	4	2.618	3.129	3.836
59	Besely Betioky	11.4.2006	-23.90	44.44	305	200	28	3			
60	Behoka Beahitse	1.5.2006	-24.21	44.46	316	200	23	2			
61	Amborompotsy Ampanihy	14.4.2006	-24.68	44.95	230	200	212	4	2.511	2.899	3.401
62	Imaola WP187		-24.71	44.98	219	200	5	2			
63	Tsotso Tranoroa	30.4.2006	-24.71	45.14	249	300	122	11	6.552	8.336	10.565
64	Tranoroa +6km East	30.4.2006	-24.71	45.11	228	300	119	7	4.422	5.28	6.669
65	Mangolovoka Bereha	30.4.2006	-24.71	45.21	316	300	73	5	4.033	4.628	
66	Ankilitelo Isaka Ivondro	25.4.2006	-24.81	46.86	39	200	306	11	6.337	7.432	8.826
67	Ihazoambo	23.4.2006	-24.83	46.87	42	200	122	3	2.674	2.891	3
68	Ihazoambo	24.4.2006	-24.83	46.87	42	200	43	4	3.605		
69	Mangatsiaka AHL P3	25.4.2006	-24.88	46.59	49	200	9	4			
70	Evonje Ifarantsa	27.4.2006	-24.89	46.87	46	200	87	7	4.99	5.723	
71	Andamilany Maromaso	14.4.2006	-24.90	45.15	246	200	121	4	3.93	3.996	4
72	Ambovombe	14.4.2006	-25.14	46.20	237	200	56	4	3.08	3.785	
73	Ambolo Ambovombe	29.4.2006	-25.17	46.14	161	300	181	5	3.777	4.182	4.555

Appendix 2. Species composition and abundances of dung beetles in different local communities across Madagascar. Upper panel: limited sampling in various local communities and cattle dung-baited pitfall trapping in Ranomafana NP, Ranomafana NP and Andringitra NP include both open habitat and wet forest-inhabiting species. *13 individuals from cattle dung-baited pitfall traps, two individuals from dung pats in forest. **one individual from cattle dung-baited pitfall trap and another one from a cattle dung pat in forest. ***from open area in Ranomafana village. Lower panel: systematic sampling of cattle dung pats across Madagascar in 2006 and 2007. Localities sorted by latitude from north to south. Sample sizes are not comparable due to differences in search effort.

ID	Locality	<i>Helicophorus giganteus</i>	<i>Helicophorus littoralis</i>	<i>Helicophorus marsyas</i>	<i>Helicophorus neoaemphicolis</i>	<i>Helicophorus nicolei</i>	<i>Helicophorus perrieri</i>	<i>Helicophorus quadripunctatus</i>	<i>Helicophorus ruficollis</i>	<i>Helicophorus sinuaticornis</i>	<i>Arachnoides</i> sp.	<i>Arachnoides</i> new sp.	<i>Arachnoides cuprarius</i>	<i>Arachnoides morio</i>	<i>Digitonthophagus gazella</i>	<i>Onthophagus elegans</i>	<i>Onthophagus hinulius</i>	<i>Onthophagus pizizi</i>	<i>Scarabaeus radama</i>	<i>Neomadiellus humerosanguineum</i>	<i>Neomadiellus ranomadryensis</i>	<i>Neomadiellus</i> new sp.	<i>Labarrus sublividus</i>	<i>Labarrus madagassicus</i>	<i>Mesonotoplatys dorsalis</i>	<i>Neoclatrophodius moestus</i>	<i>Niataphodius nigrita</i>	<i>Pseudopharaphodius apicesetosus</i>	<i>Didactylia pictipennis</i>
	Ranomafana NP								15*	11					6***	2***			247	2**	38								
1	Andringitra NP							11							40	8	1	2						1	32	9	5		
2	Manombo	4	4	75	7			1			1			8	1	1							4						
3	Ambila	4	4	4				2						6															
4	Sambava	20	4					5																					
5	Antalaha																												
6	Orangea-Antsiaranana													2															
7	Mahamanina-Ankarana	2	2					5						52															
8	Andronibe CNI/A-Ambanja	4	5					3						101			7	2											
9	Berety-Manongarivo	2		2				1						5															
10	Ambohimalaza-Boriziny			3										26															
11	Andohaomby-Boriziny			1										20															
12	Grand Pavois Majunga			13										6															
13	Antongomena Bevaray			1										22															
14	Tsiombikibo Mitsinjo			n				9						12															
15	Mitsinjo			9				2						n															
16	Belambo Baly			n										n															
17	Mandrosoa 12 km Marovoay			4										14															
18	Marovoay			2				5						12															
19	Andranomiditra			2				5						6															
20	Ampijoroa			5										12															
21	Betara Mahanay			1				2						4															
22	Ampondrabe Ankarafantsika			8				6						7															
23	Mandritsarahely & Maevarano			153				4						86															
24	Amoronidolo PK414			14										19															
25	Mahazoma			2				13						2															
26	Beanana			2				6						22															
27	Amboodriana Begisa Antsiabobositra			1				7						6															
28	Andalamahitsy Mahatsinjo			1				25						25															
29	Andoharano Ankazobe			1				3						23															
30	Ambohimananirina /Fhaonana			6				7						5															
31	Andrianampela			1										5															
32	Ampanotokana													2															
33														16															
34														2															
35														133															

Continued on p. 88

Appendix 2 (continued)

ID	Locality	<i>Helictophorus giganteus</i>	<i>Helictophorus littoralis</i>	<i>Helictophorus marsyas</i>	<i>Helictophorus neocamplicollis</i>	<i>Helictophorus nicollei</i>	<i>Helictophorus perrieri</i>	<i>Helictophorus quadripunctatus</i>	<i>Helictophorus rudicollis</i>	<i>Helictophorus sinuaticornis</i>	<i>Arachnoides</i> sp.	<i>Arachnoides</i> new sp.	<i>Arachnoides cupratus</i>	<i>Arachnoides morio</i>	<i>Digitonthophagus gazella</i>	<i>Onthophagus elegans</i>	<i>Onthophagus hinnullus</i>	<i>Onthophagus pfitzi</i>	<i>Scarabaeus radama</i>	<i>Neomadiellus humerosanguineum</i>	<i>Neomadiellus ranomadryensis</i>	<i>Neomadiellus</i> new sp.	<i>Labarrus sublividus</i>	<i>Labarrus madagascicus</i>	<i>Mesontoplatys dorsalis</i>	<i>Neocalahodius moestus</i>	<i>Nialaphodius nigrita</i>	<i>Pseudopharaphodius apicesetosus</i>	<i>Didactylia pictipennis</i>
28	Sakamarina	1																											
29	Beronono RN1	3	2												1														
30	Faliarivo RN1	3	7											3	8														
31	Sahapetraka Ampely	11	5											2	2														
32	Ambatolampy Malamaina	6																											
33	Manetivohitra PK117	3																											
34	Ambohimarina PK 144	23																											
35	Ambohimanjaka PK215	1																											
36	Soavina Bepombo PK229	7	1											78															
37	Ambohimaosoa	6	9																										
38	Ambalavao Zebu market	2	2																										
39	Ambasazo		13																										
40	Ihorombe		2																										
41	Ilosy Zebu market	2	3																										
42	Sakarivohazo_Ranohira	1	30	26																									
43	Andranomaitso Sakaraha	7	65																										
44	Andranomaitso Sakaraha	28																											
45	Manaboboka	13	9																										
46	SF Sakaraha	3	251																										
47	Tranokaky	1	1																										
48	Besely Betioky	1	24																										
49	Betioky area		26																										
50	Antoby Betioky	1	11																										
51	Betioky		5																										
52	Vohipea Betioky		1																										
53	Antsakoandahy Betioky	1	5																										
54	Betioky		1																										
55	Ambelaililike																												
56	Ankazoabo																												
57	Anevoevo																												
58	Besely Betioky	3																											
59	Besely Betioky																												
60	Behoka Beahitse																												
61	Amborompotsy Ampanihy																												
62	Imaola WP187		1																										
63	Tsoiso Tranoroa	2	3																										
64	Tranoroa + 6 km east	1	9																										
65	Mangolovoka Bereha		2																										

Continued on p. 89

Appendix 2 (continued)

ID	Locality	<i>Helictophleus giganteus</i>	<i>Helictophleus littoralis</i>	<i>Helictophleus maryas</i>	<i>Helictophleus neoamplicollis</i>	<i>Helictophleus nicollei</i>	<i>Helictophleus perrieri</i>	<i>Helictophleus quadripunctatus</i>	<i>Helictophleus ruficollis</i>	<i>Helictophleus sinuaticornis</i>	<i>Arachnodes sp.</i>	<i>Arachnodes new sp.</i>	<i>Arachnodes cuprarius</i>	<i>Arachnodes morio</i>	<i>Digitonthophagus gazella</i>	<i>Onthophagus elegans</i>	<i>Onthophagus himulus</i>	<i>Onthophagus picipiti</i>	<i>Scarabeus radama</i>	<i>Neomadiellus humerosanguineum</i>	<i>Neomadiellus ranomadriensis</i>	<i>Neomadiellus new sp.</i>	<i>Labarrus sublividus</i>	<i>Labarrus madagassicus</i>	<i>Mesonptelatus dorsalis</i>	<i>Neocataphodius moestus</i>	<i>Nialaphodius nigrita</i>	<i>Pseudopharaphodius apicesetosus</i>	<i>Didactylia pictipennis</i>	
66	Ankililelo Isaka Ivondro			31	166			10							44	2	?	4					10	1	32			5		
67	Ihazoambo			4	53											65							2	25	15			1		
68	Ihazoambo							2							2															
69	Mangatsiaka AHL P3							1				2			15	12			3					1						
70	Evonje Ifarantisa				27										28															
71	Andamiany Maromaso				9										23															
72	Ambovombe				31			1							12															
73	Ambolo Ambovombe				132																									