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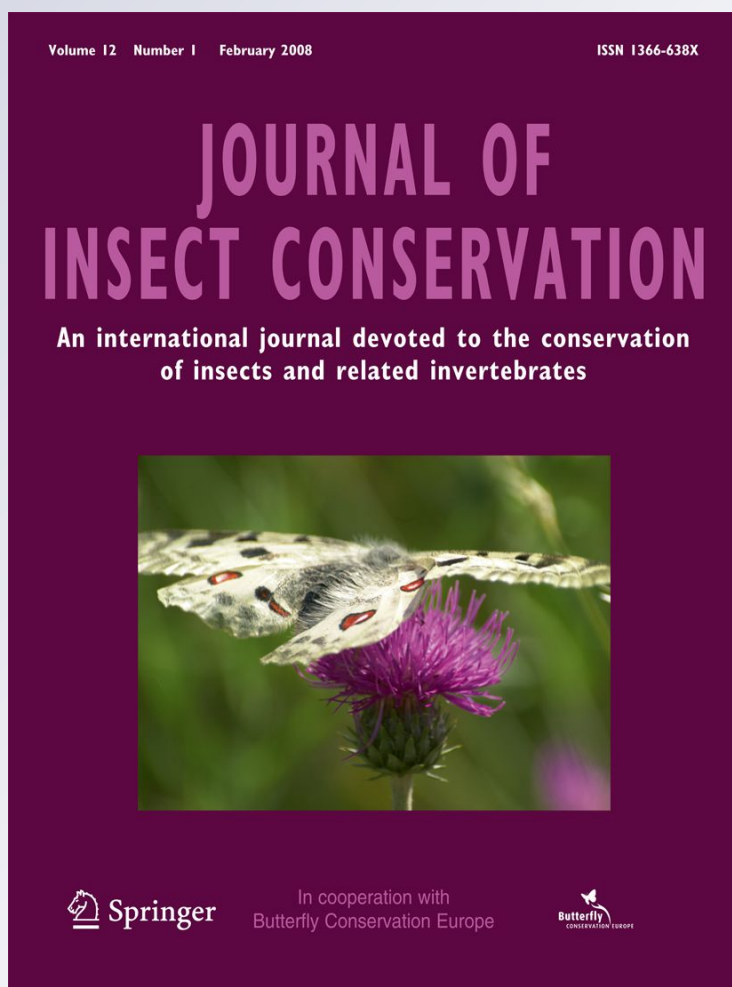of insects and related invertebrates

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Effects of land usage on dung beetle assemblage structure: Kruger National Park versus adjacent farmland in South Africa

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Abstract Little quantitative evidence exists regarding how effective protected areas are for preserving species. We compared dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) inside and outside of the Kruger National Park, which protects indigenous flora and fauna over a large area of savanna in the northeast lowlands of South Africa. Although it is contiguous with other reserves in South Africa, Zimbabwe and Mozambique, parts of its border abut onto farmland. Some effects of differing land usage either side of this border were studied at the South African Wildlife College (24.541° S 31.335° E) and the nearby farming village of Welverdiend using dung beetle assemblage structure (Coleoptera: Scarabaeidae: Scarabaeinae) as indicators. Samples were taken from gabbro-derived and granite-derived soils in open woody vegetation, both within the reserve and on adjoining farmland, using composite pig, elephant and cattle dung baits in the early rainy season (November 2009) and separate pig and elephant dung baits in the late rainy season (March 2010). Despite much higher large mammal density around Welverdiend, significantly greater species richness, abundance, and biomass of dung beetles were recorded in the reserve where mammal species diversity is greater and elephants produce much larger droppings than any mammal in the farmland. Assemblage structure also differed strongly between dung types, weather conditions on sample days, and season, but weakly between sampled soil types. These differences in assemblage structure were recorded over short distances as the sites in the reserve were only 3–4 km from those in farmland at Welverdiend.

Keywords Conservation · Dung · Elephant · Farmland · Kruger National Park · Land usage · South Africa

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Introduction

Creation of protected areas is considered to be the cornerstone strategy for preventing biodiversity loss, yet little is known about how effective they are for protecting species and ecosystems (Gaston et al. 2008). South Africa contains an extensive network of national parks and private game reserves, many of which were established to protect the various charismatic large mammal species indigenous to the region. While protected areas have succeeded in conserving these species, very little is known regarding their effectiveness for conservation of overall biodiversity or that of specific groups, including dung beetles that are primarily dependent on the excrement of these mammals.

The Kruger National Park (KNP) is one of the oldest and largest conserved areas in the world as well as the largest protected area ($\sim$20,000 km^2) in South Africa. For over 100 years, it has successfully conserved all of the large mammals that historically occurred in the low-lying savannas of north-eastern South Africa. In total, it currently protects a diverse assemblage of 147 mammal species, including elephant (SANparks 2010). By contrast, in much of the remainder of the Savanna Biome, vegetation has been modified and large indigenous mammals have been extirpated to be replaced by a handful of species of

domestic livestock, both on commercial farms and in rural, communally-owned rangelands (Fairbanks et al. 2000). It has been suggested that such depletions in mammal assemblages may result in a co-decline in associated dung beetle assemblages (Nichols et al. 2009).

It is well known that dung beetle assemblages are strongly influenced by major habitat modification (Estrada et al. 1998; Jankielsohn et al. 2001; Nichols et al. 2007; Viera et al. 2008). In South Africa, the replacement of natural vegetation by flora of differing physiognomy is responsible for extreme differences between dung beetle assemblages of indigenous dune forest compared to unshaded post-mining vegetation (Davis et al. 2002, 2003). It is also responsible for marked differences between assemblages of indigenous shrubland and cultivated farm pastures (Davis 1993; Davis et al. 2004) as well as between those of natural grassland and invasive dense shrubland (Steenkamp and Chown 1996). Changes from natural to cultivated grassland are also paralleled by appreciable changes in dung beetle assemblage structure (Davis et al. 1999). However, there is limited information on the effect of less drastic changes in habitat structure where land-use differs but natural vegetation is only modified rather than completely replaced. This occurs, for example, across the boundary between protected areas and communal, rural areas that are both major land-use types in South Africa.

Furthermore, there is poor understanding of how dung beetle assemblages might be affected by changes in dung type diversity even though habitats retain similar vegetation structure. Somewhat contrasting results were obtained in two studies made in reserves and adjoining farmland at the southern edge of the Kalahari deep sands in South Africa. One study showed that abundance and biomass of dung beetles were greater in a nature reserve than in similar disturbed vegetation types (grassland or bushveld) on two nearby farms (Jankielsohn et al. 2001). The other study showed that, although not statistically significant, abundance of dung beetles in a traditional cattle grazing system was greater than in woodland of a national park (Simelane 2009) where protection is provided for black rhinoceros and various pellet-dropping antelope. Similarly, an unpublished comparison between three wildlife areas and adjacent rangeland with domestic livestock in Zimbabwe also gave conflicting results with two wildlife areas showing greater species richness, abundance, and biomass than rangeland and one showing an opposite trend for species richness and abundance (Gardiner 1995).

Few quantitative studies have examined dung beetle assemblages in the KNP or surrounding areas (Paetel 2002). Here, we report on differences in dung-beetle assemblage structure between the KNP and adjoining rural rangeland. Such differences were expected considering the extreme transformation in both the composition of the large mammal assemblages and the diversity of available dung types outside of the KNP boundary. Differences might also emanate from modifications to both the tree and grass layer that are evident in the rural areas bordering the KNP.

Methods

Study area and study sites

The study area was centred in a soil type mosaic at the edge of two vegetation units that result from differences in the underlying geology. These comprise Granite Lowveld (19,839 km^2) and Gabbro Grassy Bushveld (760 km^2) (Mucina and Rutherford 2006). Soils derived from granite bedrock are generally sandier than finer-grained soils derived from gabbro bedrock. Compared to Gabbro Grassy Bushveld, the Granite Lowveld supports a taller, more open tree layer but a lower cover of herbaceous vegetation.

The study sites were situated adjacent to the South African Wildlife College (SAWC) in the Kruger National Park (KNP) (24.541° S 31.335° E) and in rangeland outside of the village of Welverdiend (24.571° S 31.345° E). These sites lay 1–2 km either side of the KNP boundary fence and were less than 4 km apart. Welverdiend is a typical village in the rural area bordering the KNP with approximately 1,500 centrally located households surrounded by approximately 2,200 ha of communal grazing land (R. Matskika unpubl data). For over 50 years, this land has been used for natural resource extraction comprising the cutting of trees for firewood and building material as well as for widespread grazing by domestic livestock (Table 1) and the cultivation of arable crops in plots cleared of natural vegetation. Large and medium-sized indigenous mammal species have all been extirpated through hunting and trapping. By contrast, the area around the SAWC, inside the KNP, has been formally protected since the 1950s. Although hunting caused the local extirpation of elephants by the end of the nineteenth century, they have since recovered to a density of approximately 0.63 individuals/km^2 (Carruthers 2008). Various other relatively large, indigenous, dung-producing mammals are, also, regularly observed at the KNP sites. Table 1 lists those species occurring at a density >0.1/km^2.

Although study sites were standardized as far as possible, there were substantial differences in vegetative physiognomy between sites due to the long history of differing land use and management. In the KNP, the savanna is more open due to regular fires and the loss of trees that are pushed over by browsing elephants. Therefore, woody plant density stands at 2700 per ha on the granite and 1,300 per ha on the gabbro (A.M. Swemmer unpubl data). Despite the collection of wood, woody plant density around Welverdiend is substantially higher with a mean density of

Table 1 Mean mass ±SD (Silva and Downing 1995), spatial density (*SANParks, unpubl; **Carruthers 2008; ***South African Department of Agriculture, Forestry and Fisheries, unpubl; [a, b]estimates), and dung type of large-bodied mammals commonly observed at study sites in the Kruger National Park (KNP) or the nearby farming village of Welverdiend

Species		Mass (kg)	Density/km^2	Dung type classification
Indigenous mammals (KNP)				
Impala	*Aepyceros melampus*	48.6 ± 9.0	7.10*	Pellets
Blue wildebeest	*Connochaetes taurinus*	184.5 ± 26.5	1.00*	Pellets or small fine-fibred pads
Greater kudu	*Tragelaphus strepsiceros*	194.0 ± 46.0	0.41*	Pellets
Giraffe	*Giraffa camelopardalis*	903.8 ± 213.8	0.40*	Pellets
African buffalo	*Syncerus caffer*	486.9 ± 112.1	1.20*	Large fine-fibred pads
Warthog	*Phacochoerus aethiopicus*	61.5 ± 18.2	0.29*	Small coarse-fibred
Burchell's zebra	*Equus quagga*	251.0 ± 48.9	1.20*	Large coarse-fibred
White rhinoceros	*Ceratotherium simum*	1,850.0 ± 255.9	0.64[a]	Very large coarse-fibred
African elephant	*Loxodonta africana*	2,493.4 ± 702.1	0.63**	Very large coarse-fibred
Domestic livestock (Welverdiend)				
Goat	*Capra aegagrus hircus*	52.4 ± 23.5	8.50[b]	Pellets
Cattle	*Bos primagenius indicus*	290.0 ±10.0	45.30***	Large fine-fibred pads
	Bos primagenius taurus			
Donkey	*Equus africanus asinus*	165.0	0.90[2]	Large coarse-fibred

*Unpublished annual census averages from 1978 to 1993 in Kingfisherspruit Ranger Section, KNP (adjoins SAWC)

***Cattle counted at Welverdiend dipping stations, 16 June 2011, divided by area of communal grazing (=22 km^2)

[a] White Rhinoceros observed within a 2 km radius of the SAWC in early 2011, divided by area

[b] Goats and donkeys observed around Welverdiend, June 2011 (AM Swemmer), divided by communal land area

3,900 per ha on the granite, and 3,600 per ha on the gabbro. Similarly, total woody plant cover is less in the KNP (57% on the granite, 14% on the gabbro) than at Welverdiend (71% on the granite, 49% on the gabbro).

Soil texture also differed between study sites based on measurements comprising the percentage of sand, silt and clay (Table 2). Principal differences were between gabbro-derived and granite-derived soils with each soil type essentially similar between the KNP and Welverdiend. These measurements were based on two or three cores taken from within each study area at a depth of 5 cm.

Table 2 Soil texture at study sites in the Kruger National Park and adjoining farmland at Welverdiend

Mean % grain composition ±SD

Study site and base rock	Sand	Silt	Clay	n samples
Kruger N.P. Gabbro	76.3 ± 0.7	7.1 ± 4.6	16.6 ± 5.4	2
Kruger N.P. Granite	87.9 ± 3.0	9.3 ± 3.6	2.8 ± 1.2	3
Welverdiend Gabbro	75.4 ± 1.0	11.6 ± 6.8	13.0 ± 7.7	3
Welverdiend Granite	86.7 ± 5.9	8.6 ± 1.5	4.7 ± 4.4	2

A total of four sampling sites was selected, two in the KNP (24.5375° S 31.3336° E; 24.5405° S 31.3395° E), and two at Welverdiend (24.5625° S 31.3620° E; 24.5665° S 31.3360° E). For each pair of sampling sites, one was on gabbro-derived soils and the other on granite-derived soils. A 2 × 3 grid of pitfall traps was embedded at each sampling site. Each trap was separated by a distance of 50 m and comprised a 5 l bucket (dimensions: top diameter = 22 cm, depth = 16 cm) dug into the soil up to its rim. On trapping occasions, dung baits were supported over the centre of each trap using two strong wires.

Dung beetles were sampled over two consecutive 24 h occasions in both November 2009 (early rainy season) and March 2010 (late rainy season). In November, traps were baited with ca 1 l composite baits comprising equal proportions of pig, elephant and cattle dung wrapped in cloth to exclude dung beetles. Baiting commenced early morning on November 23rd 2009 with baits replaced with fresh dung every 12 h until late afternoon on November 24th. Samples were removed and stored in 70% alcohol in the early morning of November 24th and 25th. In March, three traps at each site were baited with ca 1 l of pig dung and three with an equal measure of elephant dung. Baiting commenced late afternoon on March 8th 2010 with baits replaced with fresh dung every 12 h until late afternoon on March 9th. Samples were removed and stored in 70% alcohol in the late afternoon of March 9th and 10th.

Weather conditions varied on each trapping occasion. This is supported by rainfall data from Kingfisherspruit (24.463° S 31.442° E), which lies some 14 km from the KNP sites, and temperature data from Talamati (24.447° S 31.555° E), which lies some 22.5 km from the KNP sites. In November 2009, there was widespread heavy rainfall just before sampling commenced, which led to cooler weather followed by increased temperatures over the following few days (Fig. 1). In March 2010, light rainfall prior to sampling was again followed by increased temperatures over the following few days. On both sampling occasions, day 2 was warmer than day 1.
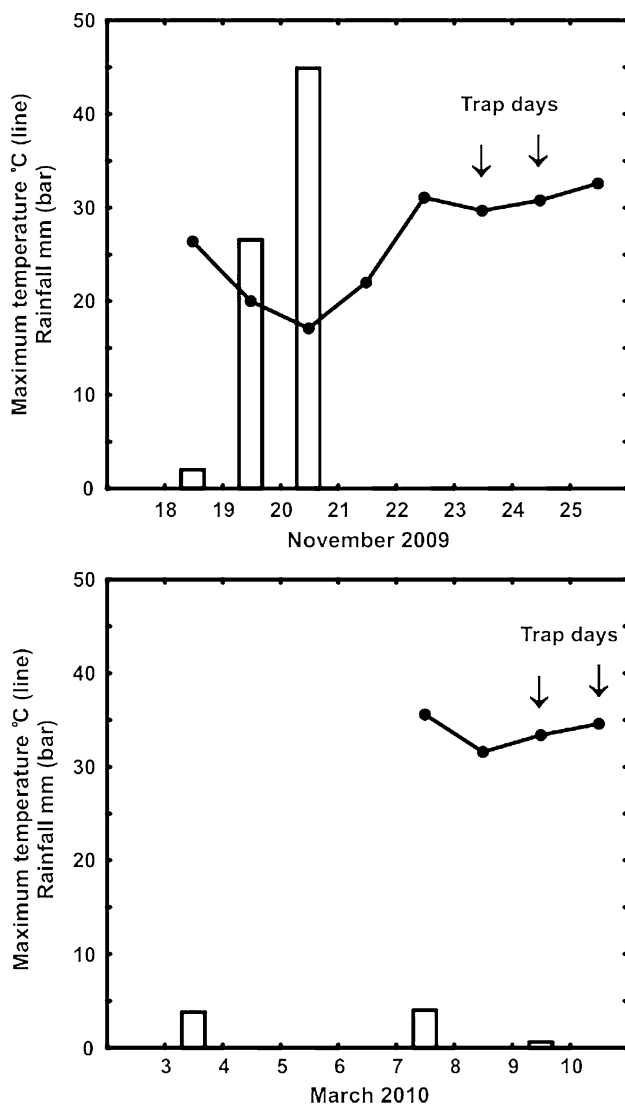

Fig. 1 Temperature (Talamati, 24.447° S 31.555° E) and rainfall data (Kingfisherspruit, 24.463° S 31.442° E) for the study region prior to and during dung beetle sampling (no temperature data available for early March 2010)

Data analysis

The Steinhaus Similarity Index (S) was used to construct a similarity matrix of paired comparisons between the pooled species abundance compositions of assemblages in each habitat ("Appendix"). The index is expressed as: $S = 2 W/(A + B)$, in which W is the sum of the smaller numbers in pairs of species abundance data converted to decimal proportions for each assemblage and in which A (=1) and B (=1) are the total proportional abundances of the two assemblages (=2), that is, if $A = B = 1$, $S = W$ (Legendre and Legendre 1983). The results are expressed as percentage similarity (S × 100).

The data recorded in November 2009 were analyzed to determine spatial differences in species abundance structure between 24 traps at the four study sites. For each day, the data matrix of 101 species by 24 traps was 4th root transformed, converted to a correlation matrix, and analyzed using non-metric multidimensional scaling (NMDS) (Statistica v9, Statsoft 2009). A minimum spanning tree was fitted to each ordination plot using the Kruskal algorithm (Arlequin v3, Excoffier et al. 2006). Factorial ANOVA was used to test for significant differences in species richness, abundance and biomass between sampling days, soil types, and land under different usage.

The data recorded in March 2010 were analyzed to determine spatial and trophic differences in species abundance structure between 24 traps at the four study sites. Data for each day were pooled and the data matrix of 78 species by 24 traps was 4th root transformed and converted to a similarity matrix using the 1-Pearson r similarity coefficient. This matrix was subjected to cluster analysis using Ward's method. Factorial and main effects ANOVA were used to test for significant differences in species richness, abundance and biomass between sampling days, soil types, dung types, and land under different usage.

Results

We recorded a total of 76 176 individuals and 113 species of dung beetles, 100 in the KNP and 94 at Welverdiend. A total of 101 species was recorded after heavy rainfall in the early rainy season (November 2009) and 78 after light rainfall in the late rainy season (March 2010) with 35 species recorded only in November and 12 only in March ("Appendix").

On both sampling occasions there were clear differences in species abundance structure between the KNP and Welverdiend assemblages (Figs. 2, 3) with greater similarity between the KNP assemblages than between those at Welverdiend (Table 3). Consistent differences in structure were found for the November assemblages recorded on the

Fig. 2 NMDS ordination plots with minimum spanning trees showing the relative distance between species abundance structure of dung beetle assemblages at study sites on two soil types in both the Kruger National Park and the farming village of Welverdiend (November 2009)
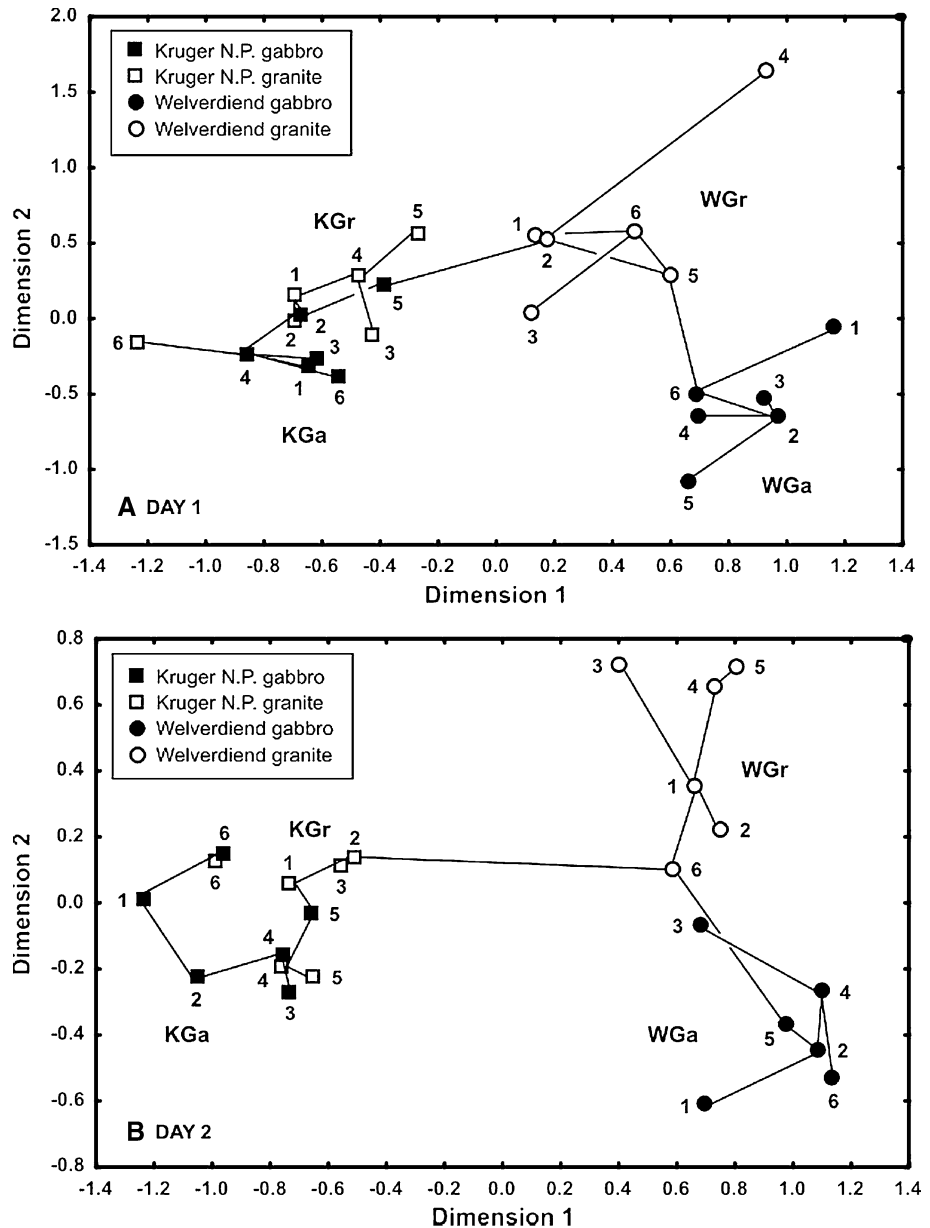
gabbro and granite soils at Welverdiend (Fig. 2), while there was some overlap between assemblage structure on the same two soil types in the KNP (Day 1: Ga2, Ga5, Day 2: Ga5 clustered with assemblages on granite-derived soils; Day 1: Gr6, Day 2: Gr4, Gr6, clustered with assemblages on gabbro-derived soils). March assemblage structure was consistently different between pig and elephant dung (Fig. 3). However, in the KNP, there was greater similarity between assemblages on different soil types than between those on different dung types, whereas the opposite was true at Welverdiend. Nevertheless, there was a little overlap between assemblages on different soil types in both the KNP (Gr4e clustered with elephant dung assemblages on gabbro-derived soils) and Welverdiend (Ga5e clustered with elephant dung assemblages on granite-derived soils).

When treating species richness, overall abundance, and overall biomass in November 2009 as joint dependent variables, both soil type (Wilks test $F_{(3,38)} = 3.403*$) and sample day ($F_{(3,38)} = 14.240***$) showed significant influences. Although land usage had by far the strongest effect ($F_{(3,38)} = 36.523***$), both sample day ($F_{(3,38)} = 6.099**$) and soil type ($F_{(3,38)} = 7.881***$) showed significant interactions with land usage. Treated separately, soil type had a significant influence only on abundance whereas conditions on sample days significantly influenced both abundance and biomass. However, all three variables were very strongly influenced by land usage with many numbers significantly greater in the KNP than the adjoining farmland (Table 4). Such trends in abundance were followed by many, though not all individual species
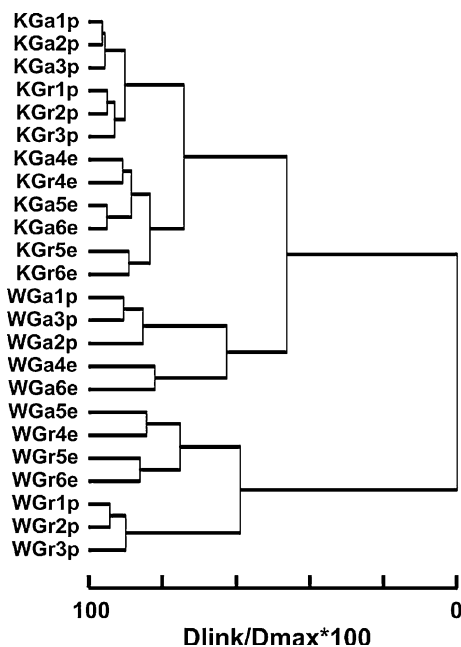
Fig. 3 Dendrogram showing the percentage similarities between species abundance structure of dung beetle assemblages attracted to two dung types at study sites on two soil types (*Ga* gabbro-derived, *Gr* granite-derived) in both the Kruger National Park (K) and the farming village of Welverdiend (W) (March 2010)

Table 3 Similarity matrices comparing species abundance composition of dung beetle assemblages in November 2009 and March 2010 (see "Appendix")

November 2009				
KGa	–			
KGr	79.7	–		
WGa	39.0	50.2	–	
WGr	55.6	67.9	62.4	–
	KGa	KGr	WGa	WGr
% Steinhaus similarity (S × 100)				

March 2010				
Kp	–			
Ke	81.0	–		
Wp	54.8	45.1	–	
We	55.8	47.7	62.6	–
	Kp	Ke	Wp	We
% Steinhaus similarity (S × 100)				

K = Kruger National Park, W = Welverdiend, Ga = gabbro-derived soils, Gr = granite derived soils, p = pig dung bait, e = elephant dung bait

("Appendix"). In addition to trends related to land usage, there was lower abundance and higher biomass on day 2 (Table 4), which was somewhat hotter than day 1 (Fig. 1). This was a result of fewer small beetles and greater

numbers of large individuals on day 2. Significant interactions in Table 4 identified marked inconsistencies in some trends, such as higher abundance on gabbro compared to granite in the KNP and the reverse at Welverdiend, whereas results for post hoc tests showed the relative strength of differences between values. The greater dominance of small beetles in the KNP was reflected by lower indices of diversity and mostly lower average body size of beetles than at Welverdiend (Table 4).

In the late rainy season in March 2010, much lower species richness, abundance, and biomass were recorded than in the early rainy season in November 2009 (Tables 4, 5). When treating species richness, overall abundance, and overall biomass as joint dependent variables, all independent variables showed a significant influence although soil type was again a weaker influence (Wilks test $F_{(3,30)} = 4.379*$) than land usage ($F_{(3,30)} = 12.980***$), sample day ($F_{(3,30)} = 14.920***$) and dung type ($F_{(3,30)} = 17.014***$). Of nine possible interactions, only three with land usage were significant, comprising soil type ($F_{(3,30)} = 3.489*$), sample day ($F_{(3,30)} = 5.056**$), and dung type ($F_{(3,30)} = 3.138*$). Light rainfall prior to day 1 of sampling was followed by a highly significant decline in numbers on the warmer day 2 (Fig. 1; Table 5). Although all the dependent variables again had higher values for the KNP, compared to Welverdiend, the difference in species richness was not statistically significant. Soil type again had insignificant influence on abundance and biomass although there was significantly greater species richness on granite-derived soil. Dung type was a consistently significant influence on all dependent variables although species richness was higher on elephant dung whereas abundance and biomass were higher on pig dung. In the case of species richness, differences in results between November and March were probably due to high richness on elephant dung at Welverdiend granite in March, hence the lack of significant differences for land usage and the presence of significant differences between soil types.

Discussion

Greater species richness, abundance and biomass of dung beetles were recorded for assemblages from the KNP compared to those in the adjoining rural rangeland. Clear differences in species abundance structure were also evident. This is consistent with changes observed across the boundaries of some other protected areas in Southern African savannas (Gardiner 1995; Jankielsohn et al. 2001) but contrasts with the results of Simelane (2009) at Vaalbos National Park and Gardiner (1995) at one Zimbabwe locality. The differences observed here probably result from the combined effects of multiple ecological differences

Table 4 Comparison of species richness, Shannon Wiener diversity, abundance, biomass, and average body size in dung beetle assemblages of the Kruger National Park and adjoining farmland over 2 days in November 2009 with results for factorial ANOVA

Study sites	Total spp.	Diversity (H′) in 6 traps	Mean spp/ trap ± SD[1]	Mean abundance/ trap ± SD[1]	Mean dry biomass trap ± SD (g)[1]	Average body size (g)
Day 1 samples						
Kruger N.P. Gabbro	72	2.06	45.7 ± 4.1[a]	2,881 ± 956[a]	97.2 ± 27.9[ab]	0.034
Kruger N.P. Granite	72	2.59	47.3 ± 7.7[a]	2,343 ± 1032[a]	83.0 ± 34.5[bc]	0.035
Welverdiend Gabbro	53	2.69	35.7 ± 5.1[b]	429 ± 150[b]	65.6 ± 12.5[bc]	0.152
Welverdiend Granite	57	2.81	36.2 ± 4.1[b]	466 ± 200[b]	38.0 ± 8.0[c]	0.082
Day 2 samples						
Kruger N.P. Gabbro	71	2.16	44.2 ± 2.8[ab]	2,092 ± 424[ac]	103.4 ± 21.3[ab]	0.049
Kruger N.P. Granite	68	2.45	42.8 ± 3.9[ab]	1,144 ± 259[bc]	141.6 ± 40.8[a]	0.123
Welverdiend Gabbro	58	3.01	35.7 ± 5.2[b]	385 ± 170[b]	82.4 ± 44.6[bc]	0.213
Welverdiend Granite	66	3.18	40.7 ± 4.9[ab]	502 ± 105[b]	64.2 ± 17.2[bc]	0.127

ANOVA results	Species $F_{(1,44)}$	Abundance $F_{(1,44)}$	Biomass $F_{(1,44)}$
Sampling day	0.070	10.271**	10.566**
Land usage	31.433***	114.942***	27.895***
Soil type	1.055	4.572*	0.433
Day × land usage[2]	3.420	10.113**	0.435
Land usage × soil[2]	0.828	6.925*	4.441*

[1] In each column, values followed by a different letter differed significantly (Tukey's HSD)

[2] Only independent variables showing some significant interactions have been reported

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

inside and outside of the KNP, particularly dung type availability and vegetative physiognomy. Various studies have demonstrated the importance of these variables and soil type in structuring dung beetle assemblages (Nealis 1977; Cambefort 1982; Davis 1994, 1996a). Although it is apparent that weather conditions on different sampling days also strongly influenced some of the results, it is probable that their effects were largely independent of those exercised by the other variables.

Several studies have demonstrated that species abundance composition of dung beetles differs between sand and clay soils (Nealis 1977; Davis 1996a) that represent extremes in grain size structure and which result in differing physical properties including relative hardness (Davis 1996b). Grain size profiles of the soils sampled in the present study would fall between these extremes. Although gabbro-derived and granite-derived soils showed differences in texture, they did not differ greatly between the KNP and Welverdiend (Table 2). However, there was an appreciable overlap between the dung beetle faunas of the two soil types in the KNP whereas those at Welverdiend showed limited overlap. This may be related to the greater geographical proximity of the study sites in the KNP where the woodland is more open than at Welverdiend. However, compared to the KNP, there was also

greater distance between assemblages from individual traps at Welverdiend, which suggests greater overall habitat heterogeneity even on the same soil type. This may be reflected by the slightly greater standard deviations in grain size profiles at Welverdiend.

Although soil associations in some species appear to be obligate, Davis (1996a) has shown that those of others may vary across regions suggesting that soil type is not, necessarily, responsible for their observed distribution patterns. The species recorded in the present study include 22 sand specialists, 16 finer-grained soil specialists and 18 soil generalists according to data from savanna sites (25.567°S 28.483° E; 25.600° S 28.350° E) near Pretoria, Gauteng, South Africa (Davis 1996a). However, 13 of these species showed different soil biases in another protected savanna area in KwaZulu-Natal, South Africa (Mkuze Game Reserve—27.633° S 32.250° E), including the most abundant species recorded in the present study, *Onthophagus stellio* (strong sand bias in Gauteng—80.6%; soil generalist in Mkuze—46.9% on sand) (Davis 1996a). Such adaptability might account for the weak influence of soil type in the present study.

Dung beetle assemblage structure is also strongly influenced by differences in vegetative physiognomy, particularly structural classes comprising unshaded grassland,

Table 5 Effects of sample day (differing weather conditions), land usage (national park vs. farmland), soil type, and dung type on species richness, abundance, and biomass of dung beetle assemblages recorded in March 2010 at the periphery of the Kruger National Park with results for main effects ANOVA

Variables	Mean spp/trap ± SD[a]	Mean abundance/trap ± SD[a]	Mean dry biomass/trap ± SD (g)[a]
Day 1 samples	22.9 ± 7.5[a]	465 ± 368[a] 1	2.0 ± 8.6[a]
Day 2 samples	14.9 ± 6.1[b]	148 ± 136[b]	3.3 ± 3.8[b]
ANOVA $F_{(1,43)}$	22.272***	25.811***	26.427***
Kruger N.P.	20.1 ± 6.7 [ns]	456 ± 368[a]	10.0 ± 9.4[a]
Welverdiend farms	17.7 ± 8.9 [ns]	157 ± 157[b]	5.3 ± 5.3[b]
ANOVA $F_{(1,43)}$	1.942	22.866***	7.870**
Gabbro-derived soil	16.2 ± 6.2[b]	255 ± 289 [ns]	6.4 ± 8.4 [ns]
Granite-derived soil	21.6 ± 8.6[a]	359 ± 342 [ns]	8.9 ± 7.4 [ns]
ANOVA $F_{(1,43)}$	10.261**	2.778	2.152
Pig dung	16.8 ± 5.9[b]	389 ± 372[a]	9.8 ± 9.4[a]
Elephant dung	21.0 ± 9.1[a]	225 ± 232[b]	5.5 ± 5.5[b]
ANOVA $F_{(1,43)}$	6.343*	6.922*	6.512*

[a] In each column for each variable, values followed by a different letter differed significantly (Tukey's HSD)

ns = no significant differences between results for that variable

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

partially shaded open woodland, and strongly shaded thickets, dense woodland or forest (Howden and Nealis 1975; Cambefort 1982; Davis 1996a). The differences in the structure of the woody layer could therefore account for some differences between the KNP and Welverdiend assemblages in addition to differences in dung availability. Various studies suggest that dung beetle assemblage structure would be modified by increased insolation due to opening out of woody vegetation (Davis 1996a; Steenkamp and Chown 1996). It was noted that abundances of several species, known to be more closely associated with open woodland (*Garreta nitens*, *Phalops smaragdinus*) or dense shaded vegetation (*Sarophorus costatus*) (Davis 1996a), were greater in the slightly more dense vegetation at Welverdiend.

There are a large number of variables to consider when assessing dung type association and its implications. Mammal droppings vary in spatial frequency, size, physical structure, and chemical characteristics that are related to spatial density of mammals, their body size, diet, and type of digestive system. Dung beetles vary from generalists to specialists in their associations with different dung types (Davis 1994; Dormont et al. 2004, 2007; Tshikae et al. 2008). Selectivity is permitted through their variable

responses (Shibuya and Inouchi 1982) to the many different volatile chemicals (Dormont et al. 2010) that are released by the dung of ruminant herbivores, monogastric herbivores, or omnivores due to their different diets and digestive systems. This selectivity has been demonstrated to be innate rather than an acquired response although it may be modified by interactions with other dung beetle species (Dormont et al. 2010). Other than responses to soil or vegetation type, the significant structural differences that were demonstrated between assemblages are likely related to a complex of factors involving dung type selectivity, physical attributes of dung, as well as diversity and spatial density of droppings.

In the present study, the possibility of some results driven by selective response to specific chemical cues is implied by the distribution in southern Africa of a group of species primarily centred on game reserves (Davis 1997) that showed a strong bias to records made from the dung of monogastric herbivores such as elephant that are now largely centred around or restricted to reserves in this region (Blanc et al. 2007). However, species included in this group (e.g. *Proagoderus* spp., *Onitis inversidens*, *Milichus apicalis*) were recorded with similar frequency in both the KNP and at Welverdiend where elephants no longer occur, although a few donkeys are present.

Another influence on selectivity might be related to the duration that a dung type remains attractive. Small amounts of coarse fibred elephant dung tend to dry rapidly and may become unattractive more quickly than a similar amount of pig or cattle dung. This might account for the greater abundance on pig dung compared to elephant dung in the present study despite the greater species richness on elephant dung. On deep sand in Chobe National Park in Botswana (17.915° S 25.019° E), where density of elephants is also high, results were similar although both numbers of species and dung beetle abundance were greater on pig and cattle dung compared to elephant dung (Tshikae et al. 2008). However, most of the limited published data do not permit useful comparison with the present study. For instance, Paetel (2002) did not use omnivore dung as bait but found that mean abundance of dung beetles, both per elephant dropping or elephant dung-baited pitfall trap, consistently far exceeded those recorded on other dung types sampled near Skukuza, KNP (24.983° S 31.600° E), including rhinoceros, zebra, and buffalo dung.

In both November and March, significantly greater numbers of dung beetles were recorded in the KNP compared to Welverdiend. Such trends were also shown by most of the more abundant individual species. These patterns could reflect differences in dung type diversity and dung beetle selectivity, spatial frequency and size variation of droppings, as well as the overall amounts of

dung available. For instance, Lobo et al. (2006) found a strong correlation between spatial concentrations of sheep dung and both species richness and abundance of dung beetles. Furthermore, replacement of sheep by cattle resulted in a 300% increase in both the amounts of dung and abundance of dung beetles as well as a change in the relative frequencies of the species (Lumaret et al. 1992). Differences in the size of the same dung type are also known to influence species composition, species frequency, abundance, and biomass of dung beetles (Peck and Howden 1984). Thus, the results of the present study have probably been influenced by interactions between several dung variables. Greater mammal dung type diversity may result in greater species abundance of dung beetles in the KNP, particularly the occurrence of elephants whose droppings are much larger than any dropped by domestic livestock at Welverdiend. Furthermore, observations suggest that many small beetles are characteristically present in elephant dung, which could account for the lower alpha diversity and mostly lower average body size in the KNP dung beetle assemblages compared to the farmland. Although comparable dung beetle densities at Welverdiend were about 2–6 times lower than those recorded in the KNP, overall large mammal density in the communal grazing area was around four times greater than that in the KNP study area. Possible reasons for lower dung beetle abundance in the farmland are less abundant representation in pellets and bovine pads compared to elephant droppings (see Paetel 2002) and/or deleterious effects of pesticide residues following cattle dipping for pest control (see Davis et al. 2004 and included references).

High numbers of dung beetles were recorded in the early rainy season (November 2009) and lower numbers in the late rainy season (March 2010). These patterns are consistent with seasonal declines shown elsewhere in the summer rainfall region of South Africa (Gauteng) where both species richness (Davis 1996c) and biomass (Davis 1996d) are much greater in the early than the late rainy season under non-drought conditions. In the present study, there was a net loss of 23 species in the late rainy season with some genera that were abundant in November absent in March, i.e., *Phalops*, *Garreta*.

Incidence of substantial summer rainfall is known to significantly influence dung beetle activity (Davis 1995) with immediate post-rainfall increases in species richness, abundance, and biomass probably related to reduced temperature maxima and longer daily duration of equitable conditions for dung colonization. There is also the added advantage of softer soil, which facilitates tunnel construction. Decline in numbers that soon follow these increases

are significantly correlated to increasing soil hardness (Davis 1995) that results from hot, dry weather. Similar significant declines in numbers on day 2 of each sampling occasion in the present study may also be related to reduced duration of suitable conditions and greater maximum temperatures that were recorded on day 2 of each sampling occasion, particularly in March when pre-sampling rainfall was much lower and day 2 maximum temperatures were at least 2°C warmer than in November.

In conclusion, this preliminary study showed differing assemblage structure and greater species richness, abundance, and biomass of dung beetles in the Kruger National Park compared to neighbouring rural rangeland. While slight differences in soil type and vegetative physiognomy between study sites did influence assemblages, it is likely that dung type variables were principally responsible for the differing patterns. However, a simple interpretation is ruled out owing to the complexity of the processes involved. These derive from interactions between several co-variables and may include, (1) selective responses to different sizes of droppings and the different volatiles released by different dung types; (2) variation in duration of dung attractiveness driven by differences in rates of drying related to dropping size, fibre content, and original moisture content; (3) variable population responses to differences in dung type diversity and the spatial frequency of each; and (4) presence or absence of pesticide residues. Further work should consider these interactions more thoroughly, particularly since differences between the results of the present study, and others that compare diversity inside and outside of protected areas, e.g. Vaalbos National Park (Simelane 2009), are likely related to geographical variation in the different suites of local edaphic, vegetative, and dung type factors that are important in shaping dung beetle assemblages.

Appendix

See Table 6.

Table 6 Dung beetle species inventory (113 spp.)** and abundance on two soil types (November 2009) and two dung types (March 2010) at the South African Wildlife College (Kruger National Park = KNP) and in nearby farmland (Welverdiend)

Species**	Dry weight (mg)*	Average/trap November 2009 (soil type)				Average/trap March 2010 (dung type)			
		Kruger N.P.		Welverdiend		Kruger N.P.		Welverdiend	
		Gabbro	Granite	Gabbro	Granite	Gabbro	Granite	Gabbro	Granite
Rollers									
Anachalcos convexus Boheman	669.2	10.6	12.8	5.4	5.2	8.9	3.4	1.8	0.8
Odontoloma sp.	1.4[e]	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Pachylomera femoralis (Kirby)	1,776.5[rb]	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0
Scarabaeus (*Kheper*) *cupreus* (Castelnau)	950.0[e]	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scarabaeus (*Kheper*) *lamarcki* Macleay	1,403.8	0.3	0.4	0.2	0.3	0.1	0.0	0.1	0.2
Scarabaeus (*Kheper*) *nigroaeneus* (Boheman)	850.6	81.7	97.8	58.1	36.5	4.3	1.3	1.0	0.9
Scarabaeus (*Kheper*) *prodigiosus* (Erichson)	1,403.8[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1
Scarabaeus (*Kheper*) *subaeneus* Harold	1,057.9	1.4	1.6	10.6	7.2	0.0	0.1	0.1	0.1
Scarabaeus (*Scarabeolus*) *bohemani* Harold	52.0	0.0	0.0	0.7	0.2	0.0	0.0	0.0	0.0
Scarabaeus (*Scarabeolus*) *clanceyi* Ferreira	30.0[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Scarabaeus (*Scarabaeus*) *galenus* Westwood	431.2[nc]	0.0	0.2	0.0	0.0	0.0	0.1	0.0	0.0
Scarabaeus (*Scarabaeus*) *goryi* (Castelnau)	1,198.6	0.2	0.0	0.4	0.2	0.0	0.0	2.0	0.7
Scarabaeus (*Scarabaeus*) *interstitialis* Boheman	80.0[e]	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Allogymnopleurus thalassinus (Klug)	76.4	1.0	1.8	2.3	4.2	0.0	0.0	0.1	0.3
Garreta lugens (Fairmaire)	180.0[e]	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Garreta nitens (Olivier)	207.8	3.3	4.4	11.3	9.7	0.0	0.0	0.0	0.0
Gymnopleurus humeralis Klug	60.0[e]	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0
Gymnopleurus virens Erichson	49.6	7.6	11.7	5.8	5.0	0.1	0.1	0.0	0.0
Neosisyphus calcaratus (Klug)	9.9	0.5	1.6	0.0	0.2	0.3	0.3	0.1	0.4
Neosisyphus fortuitus (Péringuey)	22.0[g]	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Neosisyphus infuscatus (Klug)	12.4	0.8	0.9	0.0	0.2	0.2	0.6	0.0	0.3
Neosisyphus rubrus Paschalidis	11.8	0.0	0.8	0.0	0.3	0.1	0.3	0.0	0.3
Sisyphus goryi Harold	9.8	32.4	48.3	42.9	22.3	35.0	10.8	2.2	6.1
Sisyphus sordidus Boheman	19.0[rb]	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tunnellers, Kleptocoprids, Endocoprids									
Heliocopris andersoni Bates	1,606.1	0.3	0.8	0.0	0.2	0.1	0.0	0.0	0.0
Heliocopris neptunus Boheman	1,046.3	0.5	0.3	0.3	0.0	0.3	0.0	0.1	0.0
Pedaria sp. 1	9.3	5.1	2.8	0.0	0.3	1.5	0.6	0.6	2.3
Pedaria sp. 3	12.3[nc]	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Pedaria sp. 5	12.0[e]	0.0	0.0	0.0	0.0	0.1	0.3	0.0	0.2
Pedaria sp. 6	15.0[e]	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sarophorus costatus Fahraeus	21.5	0.1	0.2	1.0	3.8	0.0	0.0	0.0	0.1
Catharsius philus Kolbe	187.6	1.5	0.0	0.1	1.1	0.0	0.0	0.1	0.9
Catharsius pandion Harold	404.6	0.2	0.0	0.1	0.0	0.3	0.2	0.2	0.3
Catharsius sp.	600.0[e]	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copris amyntor Klug	102.5	33.0	16.2	1.7	1.3	1.1	2.8	0.0	0.1
Copris elphenor Klug	352.5	0.3	0.2	0.0	0.1	0.0	0.8	0.0	0.4
Copris evanidus Klug	52.6[g]	0.2	0.0	0.0	0.0	0.0	0.4	0.0	0.3
Copris macer Péringuey	33.3	0.2	0.1	0.0	0.1	0.0	1.3	0.0	0.3
Copris mesacanthus Harold	107.0[g]	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Metacatharsius opacus (Waterhouse)	72.8	0.4	0.2	0.5	1.0	0.0	0.0	1.3	0.3
Metacatharsius troglodytes (Boheman)	43.5	0.0	0.0	0.2	0.3	0.0	0.0	0.1	2.5
Onitis alexis Klug	102.6	0.3	0.2	0.6	1.0	0.0	1.1	0.0	0.8

Table 6 continued

Species**	Dry weight (mg)*	Average/trap November 2009 (soil type)				Average/trap March 2010 (dung type)			
		Kruger N.P.		Welverdiend		Kruger N.P.		Welverdiend	
		Gabbro	Granite	Gabbro	Granite	Gabbro	Granite	Gabbro	Granite
Onitis fulgidus Klug	121.9	0.6	0.9	0.0	0.2	0.2	0.2	0.1	0.3
Onitis inversidens van Lansberge	168.6	0.3	0.1	0.1	0.7	0.0	0.0	0.0	0.0
Onitis picticollis Boheman	102.6[e]	0.1	0.1	0.0	0.1	0.0	0.2	0.0	0.8
Onitis uncinatus Klug	141.8	1.8	1.8	4.5	2.4	0.0	0.1	0.0	0.4
Onitis viridulus Boheman	110.0[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Onitis westermanni van Lansberge	90.0[e]	0.0	0.0	0.0	0.0	0.8	0.8	0.0	0.0
Caccobius ferrugineus Fahraeus	5.3	81.5	57.3	5.1	31.8	0.8	0.4	4.8	8.5
Caccobius nigritulus Klug	3.3	44.3	46.0	15.8	17.0	0.3	0.7	0.3	2.4
Caccobius sp. 2	1.5	23.8	35.2	3.4	7.5	21.0	15.8	0.3	0.9
Caccobius sp.	7.0[e]	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Caccobius sp. 4	6.0[e]	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cleptocaccobius convexifrons (Raffray)	2.6[g]	0.0	0.1	0.0	0.2	0.0	0.0	0.1	0.1
Cleptocaccobius viridicollis Fahraeus	0.9	26.0	37.0	6.2	15.4	0.0	0.0	0.1	0.1
Euonthophagus carbonarius (Klug)	18.0	260.8	236.3	52.8	28.2	40.2	29.0	5.2	7.7
Euonthophagus sp.	13.6	1.6	1.2	2.3	0.3	0.1	0.0	0.0	0.0
Hyalonthophagus alcyonides (d'Orbigny)	22.2	7.3	9.3	7.5	14.7	0.0	0.0	0.0	0.1
Milichus apicalis (Fahraeus)	12.8	53.0	30.7	51.9	29.8	0.2	2.5	0.4	4.1
Digitonthophagus gazella (Fabricius)	35.4	17.2	25.5	11.4	19.7	5.1	6.1	3.9	8.9
Onthophagus aeruginosus Roth	9.2	0.6	0.6	0.3	0.0	1.3	1.8	0.5	0.4
Onthophagus albipodex d'Orbigny	15.4	0.2	0.3	1.2	0.8	0.0	0.0	0.0	0.1
Onthophagus apiciosus d'Orbigny	12.5	0.9	0.5	0.1	0.0	4.0	0.1	2.3	0.0
Onthophagus beiranus Péringuey	10.2	14.8	14.8	0.5	0.2	1.4	1.0	0.1	0.1
Onthophagus corniculiger d'Orbigny	9.0[e]	0.4	0.1	0.1	0.1	0.0	0.0	0.0	0.0
Onthophagus cribripennis d'Orbigny	14.0[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Onthophagus ebenus Péringuey	34.9	0.0	0.1	0.0	0.3	1.4	0.7	0.7	0.0
Onthophagus flavolimbatus Klug	2.9	11.0	25.3	2.9	5.5	6.3	3.3	2.6	6.9
Onthophagus fimetarius Roth	9.5	19.3	10.7	1.1	5.0	11.0	5.0	1.8	2.6
Onthophagus interstitialis Fahraeus	15.8	5.8	2.7	1.2	0.2	5.0	10.1	5.8	1.7
Onthophagus jeaneli d'Orbigny	13.3	3.8	2.6	0.8	0.3	0.0	0.1	0.0	0.0
Onthophagus lamelliger Gerstaecker	4.2	383.9	168.7	2.6	11.3	229.3	105.3	8.8	3.3
Onthophagus obtusicornis Fahraeus	15.2	0.8	1.3	0.4	0.6	0.0	0.0	0.0	0.0
Onthophagus pallidipennis Fahraeus	6.0	4.8	9.9	0.5	2.4	0.5	0.1	0.3	1.0
Onthophagus quadrinodosus Fahraeus	23.5[g]	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1
Onthophagus sp. nr *probus*	1.0[nc]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Onthophagus sp. nr *pullus*	1.2[g]	0.0	0.0	0.0	0.0	4.9	16.2	0.3	2.8
Onthophagus sp. *pullus* gp	1.2[g]	0.3	0.0	0.0	0.1	0.0	0.0	0.0	0.1
Onthophagus sp. nr *pullus* (sp. a)	1.0[nc]	0.0	0.0	0.0	0.0	0.0	0.0	5.3	2.8
Onthophagus rasipennis d'Orbigny	3.4	87.0	97.8	12.3	35.8	19.0	9.3	7.2	3.8
Onthophagus ?rugulipennis Fairmaire	2.0[e]	0.3	0.1	0.0	0.3	0.0	0.0	0.0	0.0
Onthophagus signatus Fahraeus	6.4	3.0	3.7	0.2	0.0	0.0	0.0	0.0	0.0
Onthophagus stellio Erichson	2.8	1,094.5	536.1	17.3	103.6	197.4	55.1	97.8	53.6
Onthophagus suffusus Klug	4.3	92.1	101.4	11.4	12.3	0.0	0.0	0.0	0.0
Onthophagus sp. nr *sugillatus* (sp. 3)	3.2[g]	0.1	0.5	0.6	0.3	0.1	0.0	0.3	0.0
Onthophagus verticalis Fahraeus	7.8	2.3	3.3	0.3	0.2	0.0	0.0	0.0	0.1
Onthophagus vinctus Erichson	7.6	14.0	12.8	0.8	0.6	11.8	6.3	3.8	3.8

Table 6 continued

Species**	Dry weight (mg)*	Average/trap November 2009 (soil type)				Average/trap March 2010 (dung type)			
		Kruger N.P.		Welverdiend		Kruger N.P.		Welverdiend	
		Gabbro	Granite	Gabbro	Granite	Gabbro	Granite	Gabbro	Granite
Onthophagus virescens Harold	6.0[e]	0.3	0.2	0.4	0.1	0.0	0.0	0.0	0.0
Onthophagus sp. A	6.0[e]	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Onthophagus sp. B	12.5	0.5	1.3	0.3	0.4	0.2	0.0	0.0	0.1
Onthophagus sp. C	6.0[e]	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Onthophagus sp. D	6.0[e]	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Onthophagus sp. E	5.0[e]	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phalops ardea (Klug)	42.5	18.7	29.0	10.8	6.1	0.0	0.0	0.0	0.0
Phalops boschas Klug	26.1	9.1	6.9	5.4	8.3	0.0	0.0	0.0	0.0
Phalops dregei Harold	27.8	2.3	4.2	7.3	4.7	0.0	0.0	0.0	0.0
Phalops flavocinctus Klug	33.1	8.8	12.1	9.3	4.0	0.0	0.0	0.0	0.0
Phalops smaragdinus Harold	49.8	1.8	2.3	11.9	6.7	0.0	0.0	0.0	0.0
Proagoderus bicallosus (Klug)	70.0[e]	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Proagoderus loricatus (Klug)	53.5	0.5	0.1	0.8	0.8	0.0	0.0	0.0	0.1
Proagoderus rangifer (Klug)	38.7	0.3	0.8	0.7	0.2	0.0	0.0	0.0	0.0
Proagoderus tersidorsis d'Orbigny	55.5	0.9	2.2	0.1	0.1	0.0	0.0	0.0	0.0
Stiptopodius sp.	4.0[e]	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Drepanocerus kirbyi Kirby	1.7	0.1	0.8	0.1	0.1	0.2	0.8	0.0	2.1
Eodrepanus fastiditus (Péringuey)	2.8[g]	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Ixodina freyi (Janssens)	1.0[e]	0.1	0.0	0.0	0.1	0.0	0.2	0.0	0.0
Latodrepanus laticollis (Fahraeus)	2.8[g]	0.0	0.5	0.0	0.1	0.0	0.3	0.1	7.3
Euoniticellus intermedius (Reiche)	8.6	0.3	1.1	0.3	1.0	0.0	0.1	0.2	2.4
Euoniticellus sp.	3.0[e]	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Liatongus militaris (Castelnau)	27.1[g]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Oniticellus egregius Klug	40.0[e]	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Oniticellus formosus Chevrolat	23.2[g]	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Tiniocellus spinipes Roth	10.5	1.5	3.8	2.6	3.0	0.4	1.2	0.2	3.8

*Average dry weight per individual after 5 days at 55°C measured from up to 100 specimens of each species from the KNP and/or Welverdiendunless otherwise indicated: superscripted letters, *e* estimated, *rb* material recorded from Richards Bay, *nc* Northern Cape, *g* Gauteng

**156 spp. known from entire KNP (Paetel 2002, National Collection of Insects, Pretoria), 96 spp. in KNP collection, Skukuza, KNP

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