A dung beetle survey of selected Gauteng nature reserves: implications for conservation of the provincial scarabaeine fauna

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A quantitative dung beetle survey (Coleoptera: Scarabaeidae: Scarabaeinae) was conducted in six Gauteng nature reserves (Tswaing, Leeuwfontein, Roodeplaat, Ezemvelo, Abe Bailey, Suikerbosrand) representative of the provincial range in environmental conditions. The study provided a provincial species inventory that has been tested for completeness by comparison with museum reference material. It also permitted an analysis of major influences on regional (altitude, annual rainfall) and local (soil and vegetation type) patterns of species abundance. The survey recorded a total of 152 species. Although a further 29 species were represented in reference collections, their absence from the present work was probably due to habitat, food, or temporal specializations. Multivariate analyses (clustering, MDS) of species abundance data formed six clusters, each comprising exclusively the sites in single reserves. This indicates that regional between-reserve faunal differences are greater than local within reserve differences, thus demonstrating the value of each reserve. In a hierarchical analysis of oblique factors, five out of seven statistically defined clusters comprised exclusively the sites in single reserves with Suikerbosrand split in two. These clusters were variously correlated with nine extended factors. Along seven factors, correlations were unique or essentially unique to single reserves and were fairly high, particularly at intermediate altitude. Along the remaining two shared factors, there were opposing trends in that correlations either decreased with higher altitude or decreased with lower altitude. Thus, each cluster shows three coefficients of determination, one representing the proportion of variance due to shared highland faunal influence, one representing that due to shared lowland faunal influence and the third representing that due to unique local faunal composition. The analyses identify the transition from lowland to highland-dominated faunas, the relative faunal distinctiveness of each reserve, and omissions from the provincial reserve system.

Key words: conservation, dung, Gauteng, nature reserve, Scarabaeinae, South Africa, survey.

INTRODUCTION

Gauteng is the smallest and most densely populated province of South Africa. Many localities are under threat of development or exploitation due to population pressures. Therefore, the Gauteng Nature Conservation section of the Gauteng Department of Agriculture, Conservation, Environment and Land Affairs (GDACEL) is pursuing a programme that aims to define and protect as much as possible of the provincial floral and faunal diversity. This will be marketed for ecotourism and local economic development. As part of this programme, a quantitative dung beetle survey was conducted in order to inventory the fauna, characterize regional to local variation, and determine how the species survey of the provincial dung beetle fauna protected in reserves compares to museum reference collections for the province as a whole.

A number of variables strongly influence dung beetle distribution. These include regional gradients in altitude and annual rainfall regime (Davis & Dewhurst 1993; Jay-Robert *et al.* 1997; Davis *et al.* 1999) as well as local variation in soil, vegetation and dung type (Fincher *et al.* 1970; Nealis 1977; Cambefort 1982; Doube 1991a; Davis 1994, 1996; Davis *et al.* 2002). Therefore, the survey was conducted across the range of conditions present in Gauteng nature reserves. Six large reserves were selected across the north–south gradient in altitude and rainfall that represents a transition zone from the warmer and dryer, woodland-dominated plant communities of the lower-lying

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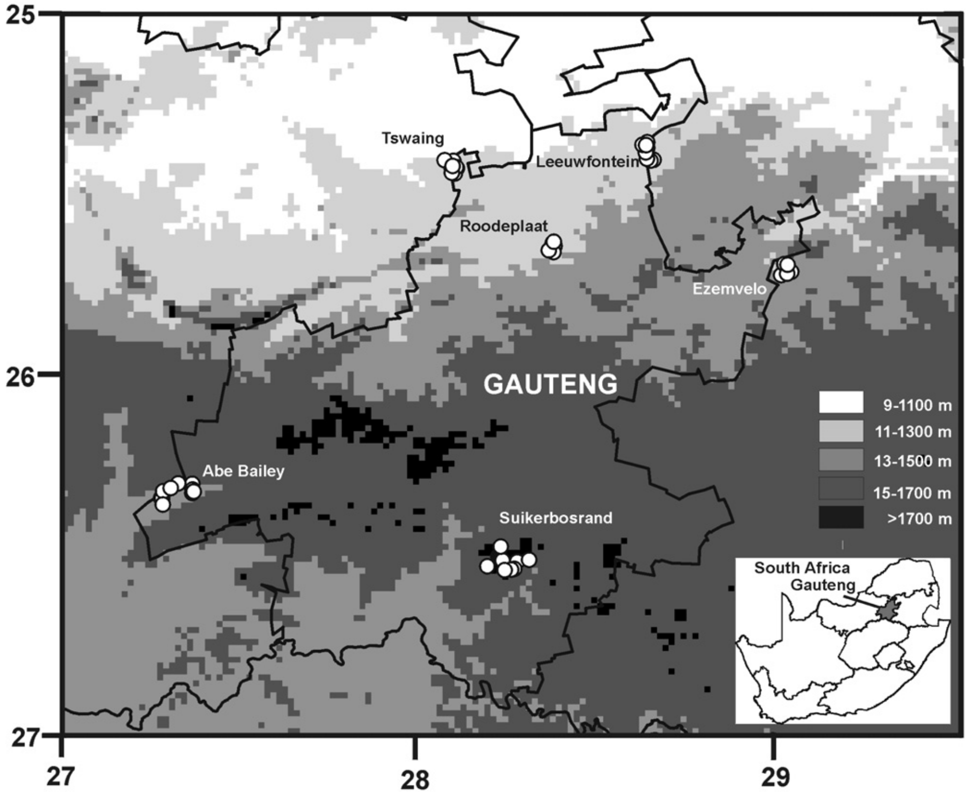

Fig. 1. Map showing the location of study sites in six Gauteng nature reserves.

bushveld to the cooler and moister, higher-lying, grassland-dominated plant communities of the highveld (Low & Rebelo 1998). In these reserves, soil types ranged from predominantly sandy to finer-grained with a larger clay fraction. Vegetation types ranged from grassland to open woodland to shaded thicket that variously represented natural or modified physiognomy. Dung types of larger mammals ranged from large pads of ruminant cattle to a mixture of coarse-fibred droppings of indigenous non-ruminant equines and small pads or pellets of antelope, also with small omnivore and/or predator droppings in some reserves.

The survey was designed to provide as complete an inventory as possible. All dominant soil and vegetation types were surveyed in each reserve. Composite baits of different dung types were used as attractants. Although quantitative data on environmental and habitat variables were desirable in order to assist interpretation of results, it was only possible to obtain measurements of altitude and annual rainfall. Qualitative assessments were all that were available for habitat and trophic variables.

METHODS

Study sites and trapping procedure

All six of the major nature reserves that were selected for the survey (Fig. 1) comprised reclaimed farms. Three reserves were selected in the lower-lying northern region of Gauteng. These were all dominated by dense to open woodland but varied in altitude or soil type. Finer-grained soils dominated at Roodeplaat whereas sandy loam to sandier soils occurred at Leeuwfontein and the lower-lying Tswaing. Further south, at intermediate altitude, both Abe Bailey and Ezemvelo were dominated by grassland with patches of woodland, but observations suggest that open woodland was once locally more prominent. Ezemvelo in the central east showed predominantly sandy soils whereas Abe Bailey in the central west showed sandy loam. On the higher-lying and higher rainfall, southeastern highveld, Suikerbosrand was dominated by natural grassland on finer-grained soils with patches of woodland. In each reserve, an assessment was first made of the range of conditions in order to define major habitats, usually two to three per reserve. The survey was then designed to examine dung beetle distribution across these major habitat variants. Three sites were selected in each habitat type and five pitfall traps were placed 10 m apart at each. The traps comprised 2 l plastic buckets containing a little water and detergent to immobilize the catches that were attracted by chiffon-wrapped dung baits supported at ground level by two wires. In the case of Tswaing Nature Reserve, there was a good deal of disturbance that resulted in small patches of unique vegetation so that no replication of disturbed habitats was possible. Trapping was conducted over a single 24 h occasion using 250 ml composite baits of pig and cattle dung that acted as surrogates for most of the dung types present in the reserves. This was sufficient to determine spatial distribution patterns of dung beetles. Traps were baited in the early morning and rebaited with fresh dung in the late afternoon or vice versa. Trapping was conducted between late November and early February. This period coincides with the seasonal peak in dung beetle activity in Gauteng, which lies within the mid-summer rainfall region of South Africa (Davis 2002).

Lower-lying reserves

Tswaing Nature Reserve (area: 2000 ha, alt.: 1113–1167 m, mean annual rainfall: 622–632 mm, surveyed 14–15 November 2001). This bushveld reserve is divided into northern and southern sections by a main gravel road. Whereas comparatively unmodified open woodland lies to the south (sites: Open Wood 1, 2, 3, the latter just to the north of the road), the northern vegetation shows various degrees of modification. The modification is centred on a meteorite crater, which was once used for the industrial exploitation of phosphates. At distance from the crater, the woodland was slightly to moderately thinned and in a few spots reduced to shrubland (Fig. 2 – site 4) as in the area beyond the western margins of the reserve. Close to the western edge of the crater, there was a cover of blue buffalo grass (*Cenchrus ciliaris*) with the woodland severely thinned (site 5) or removed (site 7). There were also some regenerating patches of *Acacia* woodland, either young and impenetrable or older and open (site 6), bordered by a grassland site maintained as cattle pasture (site 8). The crater rim bore a possibly secondary cover of fairly dense woodland offering moderate shade (site 9). The soil types at each site comprised primarily sandy loam with sand development in the pasture and the regenerating *Acacia* woodland. The reserve was stocked with an indigenous breed Nguni cattle primarily restricted to the southern open woodland. Otherwise, only very small antelope, black-backed jackal and vervet monkeys were present.

Leeuwfontein Nature Reserve (area: 2281 ha, alt.: 1225–1302 m, average annual rainfall: 617–619 mm, surveyed 21–22 January 2003). This bushveld reserve comprises primarily open boekenhout-dominated woodland (*Faurea* sp.) with a little *Acacia* woodland in places and some grassland along the watercourse, around pans and across a sizeable cleared patch in the north of the reserve. There is a gradient in soil type from stony sandy loam in the north to sandy loam in the centre to loamy sand in the south. Except for one site in the cleared grassland patch at the edge of the woodland in the north (Stony sandy loam 1), all trapping sites were situated in open woodland, three in each soil type. Dung type diversity is high as the reserve is stocked with different large mammalian herbivores (Burchell's zebra, Cape buffalo, blue wildebeest, eland, kudu, giraffe, red hartebeest, impala) and omnivores (chacma baboons). The reserve is administered as a collaborative effort between provincial government and local landowners.

Roodeplaat Nature Reserve (area: 795 ha, alt.: 1254–1288 m, average annual rainfall: 655–660 mm, surveyed 13–14 November 2001). This bushveld reserve comprises open woodland with many isolated, strongly shaded thickets and a few patches modified to grassland on deep, finer-grained soils that are stony and shallow on the rocky outcrops closest to the edge of Roodeplaat Dam (sites: Open Wood 2, Thicket 2). Three trapping sites were selected in each of the three physiognomic vegetation types, grassland, open woodland and thickets. Burchell's zebra, blue wildebeest, kudu, waterbuck, black-backed jackal and vervet monkeys are present.

Intermediate altitude reserves

Ezemvelo Nature Reserve (area: 11000 ha, partly in Gauteng, partly in Mpumalanga, alt.: 1338–1452 m, mean annual rainfall: 624–631 mm, surveyed 4–5 February 2003). This upland reserve comprises primarily sandy soils supporting grass-

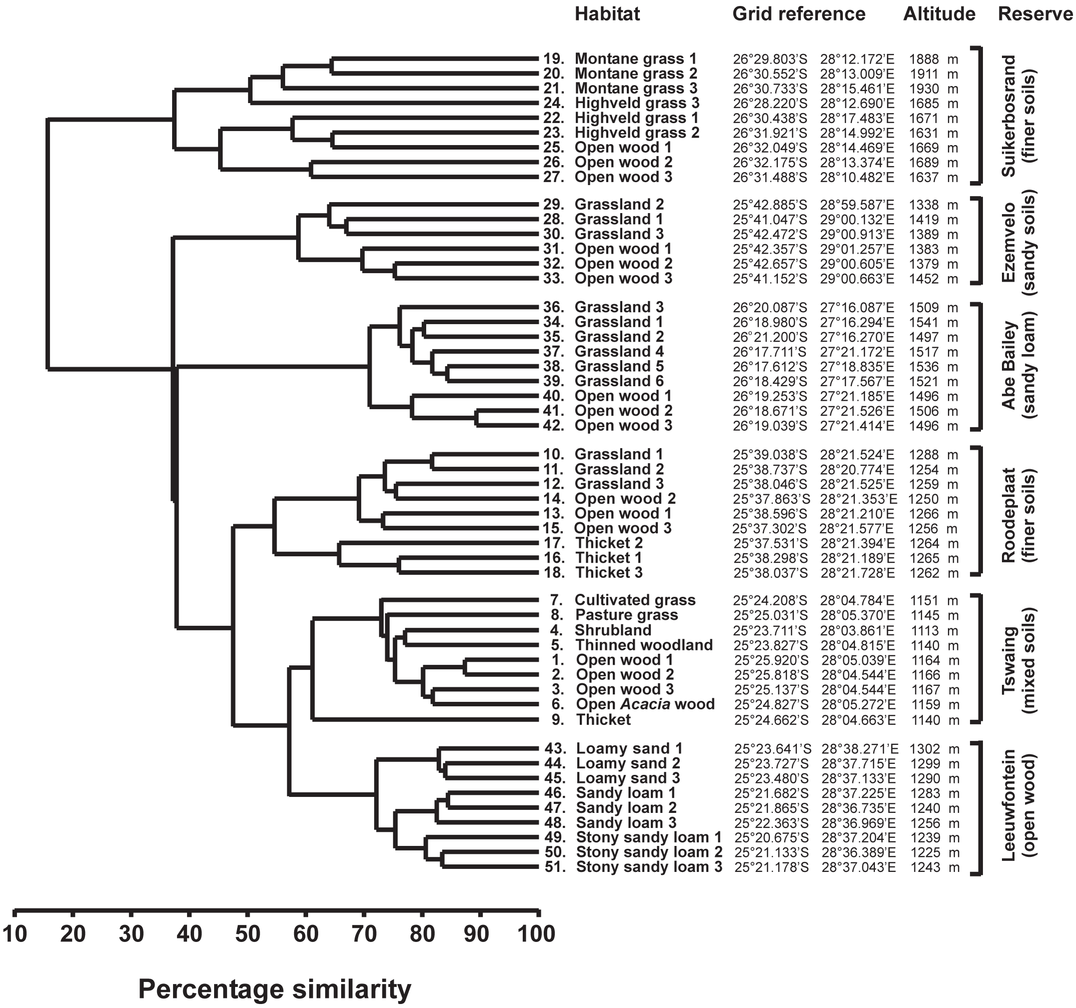

Fig. 2. Dendrogram showing percentage similarities between the species abundance composition of dung beetle assemblages at 51 study sites in six Gauteng nature reserves derived from cluster analysis of a similarity matrix using the non-metric Bray Curtis similarity coefficient and the agglomerative clustering technique, group average linking.

land on flat or rolling terrain with a few patches of very open *Burkea* woodland that were, presumably, more extensive in the past. The isolated rocky outcrops on the hilltops are dominated by open *Acacia* woodland at lower altitude with other tree species including *Protea* sp. dominating at slightly higher altitude. Trapping was restricted to the eastern end of the reserve with two sites each at lower altitude in grassland (1338–1389 m) and on isolated *Acacia* woodland rocky outcrops (1379–1383 m), and one site each at slightly higher altitude in grassland (1419 m) and on a wooded rocky outcrop characterized by *Protea* sp. (1452 m). Dung type diversity is high as the reserve is stocked with many large mammalian herbivores including Nguni cattle (an indigenous breed), white rhinoceros, Burchell's zebra, blue and black wildebeest, giraffe, eland, waterbuck, red hartebeest, gemsbok, blesbok, springbok, impala, and also omnivores including, chacma baboon and vervet monkeys. The Gauteng municipality of Bronkhorstspruit administers the reserve.

Abe Bailey Nature Reserve (area: 4197 ha, alt.: 1496–1541 m, mean annual rainfall: 655–668 mm, surveyed 13–14 December 2002). This upland reserve comprises primarily grassland on sandy loam with a relict patch of mostly severely degraded open woodland near the main southern entrance that was, presumably, greater in extent during the past. Three trapping sites were placed in the open woodland (one in denser woodland near the dam, the other two in the severely thinned out area) and another six at intervals across the grassland along the east–west axis of the reserve. The reserve is stocked with large mammalian herbivores (Burchell's zebra, black wildebeest, red hartebeest, springbok) and predators (brown hyaena, aardwolf, black-backed jackal, Cape fox).

Higher-lying reserve

Suikerbosrand Nature Reserve (area: 11500 ha extended to 18000 ha in 2003, Altitude: 1631–1930 m, Average annual rainfall: 706–733 mm, surveyed 13–14 December 2001). The reserve comprises an isolated ridge lying up to 300 m higher than the surrounding highveld. It is dominated by grassland with sizeable patches of open woodland on the warmer north-facing slopes all on finer-grained soils. Three trapping sites were placed in each of the three habitat types, montane grassland (1888–1930 m), highveld grassland (1631–1685 m) and open woodland (1637–1699 m). The reserve is stocked with large mammalian herbivores including Burchell's zebra, eland, black wildebeest, red hartebeest, kudu, springbok, blesbok, as well as omnivores and predators including, chacma baboon, black-backed jackal, and brown hyaena.

Data analysis

Diversity. Faunal variation between and within reserves was assessed using the simple measures of species richness and abundance together with the Shannon Wiener diversity index (Magurran 1987). Completeness of the species richness measurement was assessed by comparing observed species numbers with those predicted using the Abundance-based Coverage Estimator (ACE) method of Chadzon *et al.* (1998), which is included in the EstimateS computer package of Colwell (1997). In order to assess the completeness of the Gauteng species record, the survey species list was compared with that from the reference collection of the CSIRO Dung Beetle Research Unit (DBRU), which is now part of the National Collection of Insects in Pretoria. Biogeographical composition across the reserves was summarized using a simple classification into savanna/widespread or highveld-centred species (see Appendix).

Reserve similarity versus *distinctiveness.* The species abundance data matrix of 153 species/varieties by 51 study sites was fourth-root transformed and standardized by dividing each abundance value by the site (column) mean. This, respectively, normalized and centred data distribution before analysis. It also emphasized the distribution of the moderately abundant species that characterize biogeographical patterns more strongly than common widespread species. Principal trends were determined using three different multivariate analytical methods. These were cluster analysis, using PRIMER version 4 (Plymouth Marine Laboratory 1994), and two ordination techniques, non-metric multiple dimensional scaling (MDS) and parametric principal components factor analysis (PCFA) using STATISTICA version 5 (Statsoft Inc. 1995). For the cluster analysis, a similarity matrix was calculated from the transformed site data using the non-metric Bray Curtis similarity coefficient and this matrix was subjected to analysis by the agglomerative clustering technique, group average linking. For the ordinations, the transformed data matrix was converted to a site-by-site correlation matrix. MDS ordination was conducted at the maximum setting of nine dimensions. Although clear clusters were produced by these two analyses, the principal environmental factors were clearly oblique to the principal statistical dimensions in the MDS. In order to statistically group variables, a hierarchical analysis of oblique factors was conducted using PCFA ordination with varimax-normalized rotation (see Statsoft Inc. 1995 for an outline and Wherry 1984 for a more detailed discussion). This technique groups variables with similar but otherwise unique factor loadings. It then rotates these oblique factors to align them with the groups (clusters) of variables using a method that has the effect of maximizing between-group variance. A matrix of correlations between oblique factors is then calculated and this matrix is further factor-analysed to generate a series of extended (orthogonal) factors. These extended factors divide the variance into that which is shared between clusters (S factors – in this instance, due to species represented in different proportions in more than one cluster), or is unique to a cluster (P factors – in this instance, due to species represented in a single cluster). In a regression of extended factors on clusters, coefficients of determination are used to define the proportion of

Table 1. Dung beetle species recorded in Gauteng by the CSIRO Dung Beetle Research Unit but not re-recorded during the present survey.

Food specialization	Habitat specialization	Temporal specialization
Mycetophages	**Deep sand**	**Autumn**
Coptorhina sp. (De Wildt)[7]	*Pachylomerus opaca* (Lansberge)[4]	*Cheironitis* sp. nr *scabrosus* (F.)[7]
Coptorhina klugi Hope[7]	*Scarabaeus flavicornis* (Boheman)[3]	
	Scarabaeus zambesianus Péringuey[5]	**Late succession on dung**
Large non-ruminant droppings	*Phalops wittei* Harold[3]	*Oniticellus formosus* Chrevrolat[1]
Heliocopris andersoni Bates[4]	*Copris cassius* Péringuey[3]	
Heteronitis castelnaui (Harold)[4]	*Pedaria* sp. V[5]	**Immediately after rain**
Oniticellus egregius Klug[1]	*Onthophagus* sp. nr *pullus* (Kalahari)[3]	*Copris evanidus* Klug[2]
Carrion and deep sand	**Clay**	
Metacatharsius sp. a[3]	*Heliocopris neptunus* Boheman[7]	
Onthophagus nanus Harold[7]	*Copris denticulatus* Nguyen Phung[3]	
Scarabaeus inquisitus Péringuey[7]	*Onthophagus producticollis* d'Orbigny[3]	
Millipede remains	**Shade**	
Sceliages hippias Westwood[6]	*Sisyphus* sp. X (*sensu* Paschalidis 1974)[3]	
Sceliages difficilis zur Strassen[6]		

1: Davis (1989), 2: Davis (1995), 3: Davis (1996), 4: Davis (1997), 5: Doube (1991b), 6: Forgie *et al.* (2002), 7: A.L.V. Davis, pers. obs.

variance accounted for by each extended factor within each cluster of sites. In this analysis, the technique may align statistical and environmental factors more closely although no single environmental factor is represented by any statistical factor.

RESULTS

Diversity

The survey recorded 152 species of dung beetles (one species comprising two varieties, Appendix), of which 53 species and one variety were not recorded in Gauteng by the DBRU. However, of the 128 species recorded by the DBRU, 29 species were not re-recorded during the present survey. Most (24) of these 29 missed species show habitat, food, or temporal specializations (Table 1), which made their capture unlikely given the methods and timing of the present survey.

In general, habitat species richness (r = –0.54, P = 0.024) and diversity (r = –0.38, P = 0.133), declined from lower to higher altitude, although there were exceptions (Table 2). Species richness and diversity also declined from unshaded to shaded habitats at lower altitude and from grassland to open woodland at higher altitude but, again, there were exceptions. In most cases, observed species richness was greater than 80 % of predicted richness. Abundance showed no identifiable trend.

Biogeographical composition showed a distinct polarization (Table 3). Bushveld reserves showed extreme dominance of savanna-centred and widespread species whereas the highest-lying reserves showed a more balanced fauna of widespread and highveld-centred species. There was a strong positive correlation between proportional composition of highveld species and altitude (% richness of highveld species: $y = –143.8 + 0.11607x$, $r = 0.968$, $r^2 = 0.936$, $P < 0.001$; % abundance of highveld species: $y = –119.9 + 0.09614x$, $r = 0.952$, $r^2 = 0.907$, $P < 0.001$). There was a similar, fairly high positive correlation with average annual rainfall, which roughly paralleled the altitudinal gradient (% richness of highveld species: $y = –395.9 + 0.639x$, $r = 0.879$, $r^2 = 0.773$, $P < 0.001$; % abundance of highveld species: $y = –348.5 + 0.55616x$, $r = 0.925$, $r^2 = 0.855$, $P < 0.001$).

Reserve similarity *versus* distinctiveness

As cluster analysis (Fig. 2), and MDS ordination (Fig. 3) group the sites for each reserve, between-reserve variation is clearly greater than within-reserve variation. In general, percentage similarity between reserves decreases from lower to higher altitude (Fig. 2) and statistical distance increases (Fig. 3). However, qualitative assessments of axes for regional (altitude, rainfall) and local habitat

Table 2. Mid-rainy season, dung beetle species richness, abundance and diversity at six Gauteng nature reserves.

Reserve	Average abundance/ trap	Number of species[1]		% species observed	Diversity[2] (H')	Number of traps
		Observed	Predicted			
A. ENTIRE RESERVE						
Tswaing	352.2	74	76.0	97.4	3.11	45
Leeuwfontein	966.5	79	82.3	96.0	2.61	45
Roodeplaat	147.4	59	65.7	89.8	2.46	45
Ezemvelo	441.8	59	68.3	86.4	1.94	30
Abe Bailey	1013.6	65	72.9	89.2	2.22	45
Suikerbosrand	52.7	48	51.0	94.2	2.64	45
B. HABITATS						
Tswaing						
Open woodland	522.1	64	72.1	83.2	2.96	15
Modified woodland	301.8	64	71.9	89.0	3.03	15
Grassland (unnatural)	226.8	57	59.6	95.6	3.16	10
Thicket	244.2	34	51.5	66.0	2.13	5
Leeuwfontein						
Loamy sand	1226.5	71	75.2	94.4	2.67	15
Sandy loam	619.0	59	61.6	95.8	2.72	15
Stony sandy loam	1054.0	53	70.1	75.7	2.14	15
Roodeplaat						
Grassland	177.6	45	54.7	82.3	2.36	15
Open woodland	196.2	44	51.7	85.1	2.31	15
Thicket	53.8	27	33.7	80.2	2.11	15
Ezemvelo						
Grassland	589.9	50	57.5	87.0	1.59	15
Open woodland	293.7	45	54.3	82.9	2.10	15
Abe Bailey						
Grassland	921.4	59	65.4	90.2	2.40	30
Open woodland	1197.8	48	54.7	87.7	1.63	15
Suikerbosrand						
Montane grass	24.1	25	34.6	75.3	2.48	15
Highveld grass	68.9	34	38.1	89.3	2.30	15
Open wood	65.0	30	36.5	82.2	1.89	15

1: number of species predicted using the ACE method of Chadzon *et al.* (1997) available in the estimateS computer package (Colwell 1997).
2: Shannon-Wiener diversity index.

variables (soil, vegetation) are clearly oblique to statistical axes (Fig. 3). In general, the oblique altitudinal axis is parallel to the rainfall and vegetational axes, particularly at higher altitude, whereas the soil type gradient is at right angles to this axis and parallel to the lower altitude vegetational axis. Even so, altitude and rainfall were more strongly correlated with MDS dimension one values (altitude: $r = 0.94$, $r^2 = 0.88$, $P < 0.001$; rainfall: $r = 0.92$, $r^2 = 0.85$, $P < 0.001$) than with PCFA factor values (altitude: $r = 0.84$, $r^2 = 0.71$, $P < 0.001$; rainfall: $r = 0.63$, $r^2 = 0.40$, $P < 0.001$) after varimax-normalized rotation, which aligns statistical factors with clusters of faunal and reflected environmental similarity (Table 4, Fig. 4). Although the PCFA ordination superimposes some statistically defined clusters in the plot of Factor 1 against Factor 2 (Fig. 4), Table 4 shows clear separation of loadings for all clusters along at least one of the seven oblique factors. Correlations between these clusters (Table 5) shows greater similarity between lower altitude reserves and lower similarity between higher altitude reserves as in the cluster analysis (Fig. 2). Factor analysis of the correlation matrix between the clusters / oblique factors yields nine extended factors (Table 6). Correlations between the clusters and the extended factors, divides the variation into

Table 3. The distribution of savanna/widespread and highveld-centred species across six Gauteng nature reserves (data collated from the Appendix).

	Number of species					
	Tswaing	Leeuwfont.	Roodeplaat	Ezemvelo	Abe Bailey	Suikerbos.
Savanna-centred spp.	73	77	59	52	39	16
Highveld-centred spp.	1	2	0	7	26	32
% Highveld-centred	1.4	2.5	0.0	11.9	40.0	66.7
	Mean abundance / trap					
Savanna-centred spp.	352.16	966.41	147.40	417.93	801.87	22.82
Highveld-centred spp.	0.04	0.09	0.00	23.87	211.73	29.88
% Highveld-centred	0.01	0.009	0.00	5.40	20.89	56.70
Mean altitude (m)	1148	1262	1263	1393	1513	1767
Mean rainfall (mm)	627	618	657	627	661	719

three values for each reserve (Table 6). Along extended Factor S1, clusters show high coefficient of determination values for lowland reserves (Table 6), moderate values for intermediate altitude reserves (Ezemvelo, Abe Bailey) and extremely low values for the highland reserve (Suikerbosrand). Along extended Factor S2, clusters show fairly high coefficient of determination values for the highland reserve, low values for the next highest reserve (Abe Bailey) and for Roodeplaat where the fauna of cool thickets overlapped with those at higher altitude (Fig. 4), and extremely low values for all other reserves. Correlations for each of the remaining seven shared and primary extended factors were unique to a single cluster at six places of decimals. This essentially unique variance was highest at intermediate altitude and lowest at the altitudinal extremes.

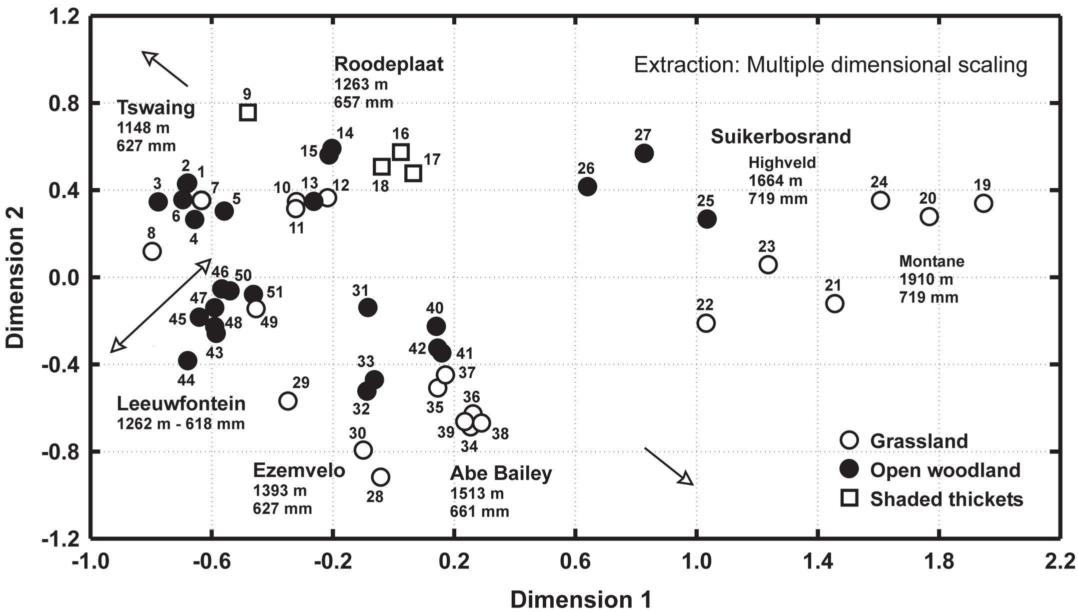

Fig. 3. MDS (multiple dimensional scaling) ordination plot of the first two dimensions (out of nine) showing the distances between the species abundance composition of dung beetle assemblages at 51 study sites in six Gauteng nature reserves (analysis conducted on a site × site correlation matrix with 300 iterations and a stress of 0.016 in the best iteration, arrows depict orientation of environmental gradients).

Table 4. Average oblique factor values for clusters of sites with unique loadings generated during varimax normalized rotation of a PCFA ordination conducted on a on a site-by-site correlation matrix for dung beetle species abundance.

Cluster	Nature reserve	Average factor loadings						
		Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7
Cluster 1	Tswaing	**0.786**	0.118	–0.064	0.084	0.294	0.310	0.035
Cluster 2	Abe Bailey	0.121	**0.878**	0.055	0.138	0.168	0.161	0.084
Cluster 3	Suikerbosrand 1*	–0.035	0.132	**0.738**	0.035	0.039	–0.031	0.214
Cluster 4	Ezemvelo	0.096	0.181	–0.004	**0.806**	0.136	0.242	0.041
Cluster 5	Roodeplaat	0.327	0.204	0.022	0.137	**0.737**	0.203	0.130
Cluster 6	Leeuwfontein	0.360	0.210	–0.044	0.259	0.187	**0.773**	0.037
Cluster 7	Suikerbosrand 2*	0.034	0.150	0.261	0.044	0.291	0.075	**0.752**
Eigenvalue		22.7	6.7	4.6	3.5	2.7	1.3	1.1
Proportion of variance (%)		44.6	13.1	9.0	6.8	5.2	2.6	2.2

*Suikerbosrand 1 = grassland sites plus open wood 1, Suikerbosrand 2 = open wood 2 and 3.

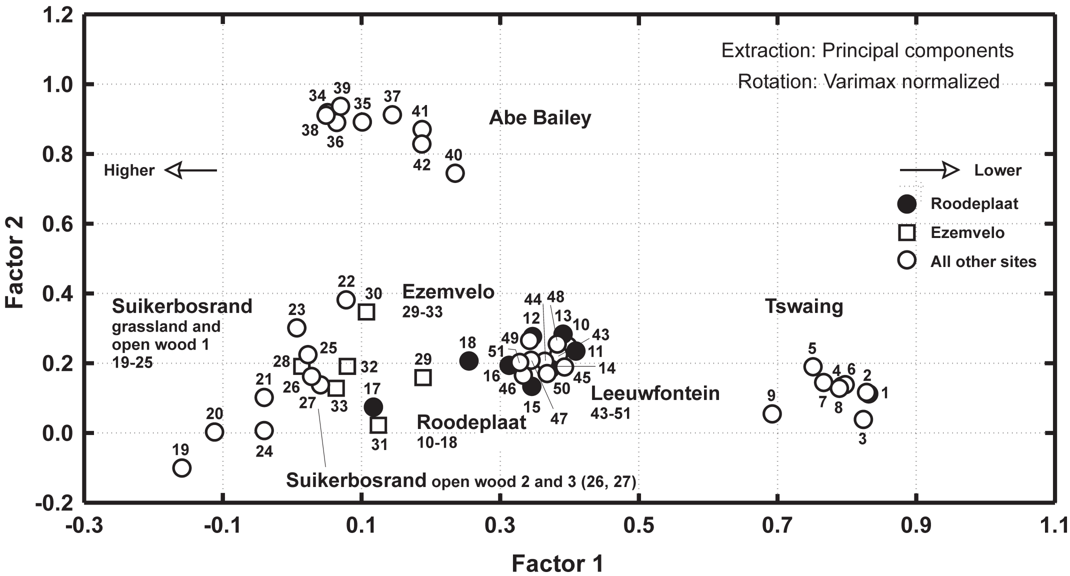

Fig. 4. PCFA (principal components factor analysis) ordination plot of the first two factors, after varimax normalized rotation, showing the distances between the species abundance composition of dung beetle assemblages at 51 study sites in six Gauteng nature reserves.

DISCUSSION

Validity of data

Although trapping was conducted on only a single 24-hour occasion in each reserve, this is considered to have been sufficient to record major spatial differences in species representation and species abundance composition. This claim is supported by the high percentage values of observed *versus* predicted species richness that were mostly >80 % both for the faunas of reserves and included habitats. Most values were based on data from 15 or more traps. It has been shown that 15 traps are sufficient to record as many as 95 % of the dung beetle species present at study sites in Mediterranean regions (Lobo *et al.* 1998).

Diversity

Species richness is influenced by regional climatic variables such as temperature and rainfall (Kirk & Ridsdill-Smith 1986; Davis 1997, 2002), and modified by local variables such as habitat diversity, edaphic characteristics, and microclimatic differences induced by vegetation cover. Thus,

Table 5. Correlation matrix for clusters of sites with unique loadings derived from varimax normalized rotation of a PCFA ordination conducted on a on a site-by-site correlation matrix for dung beetle species abundance.

	Pearson's *r* correlation coefficient						
Cluster (nature reserve)	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7
Cluster 1 (Tswaing)	1.00						
Cluster 2 (Abe Bailey)	0.36	1.00					
Cluster 3 (Suikerbosrand 1*)	–0.07	0.24	1.00				
Cluster 4 (Ezemvelo)	0.35	0.42	0.08	1.00			
Cluster 5 (Roodeplaat)	0.72	0.50	0.13	0.43	1.00		
Cluster 6 (Leeuwfontein)	0.74	0.48	–0.02	0.60	0.60	1.00	
Cluster 7 (Suikerbosrand 2*)	0.21	0.35	0.57	0.20	0.50	0.23	1.00

*Suikerbosrand 1 = grassland sites plus open wood 1, Suikerbosrand 2 = open wood 2 and 3.

Table 6. Correlations between clusters of sites with unique oblique factor loadings[2] and extended (orthogonal) factors derived from analysis of the correlation matrix between the oblique factors (S = secondary factors comprising variance shared between clusters, P = primary factors comprising variance unique to a single cluster).

	Coefficient of determination, r^2 (correlation coefficient, *r*)						
Extend. factor	Cluster 1 Tswaing	Cluster 2 Abe Bailey	Cluster 3 Suikerbos.[1]	Cluster 4 Ezemvelo	Cluster 5 Roodeplaat	Cluster 6 Leeuwfontein	Cluster 7 Suikerbos.[1]
S1	0.69 (0.83)	0.27 (0.52)	0.00 (–0.04)	0.34 (0.59)	0.59 (0.77)	0.74 (0.86)	0.07 (0.26)
S2	0.00 (–0.04)	0.11 (0.34)	0.46 (0.68)	0.02 (0.13)	0.10 (0.31)	0.00 (0.01)	0.53 (0.73)
S3	0.31 (0.55)	0	0	0	0	0	0
S4	0	0.62 (0.79)	0	0	0	0	0
S5	0	0	0.54 (0.73)	0	0	0	0
S6	0	0	0	0.64 0.80)	0	0	0
P-1	0	0	0	0	0.31 (0.56)	0	0
P0	0	0	0	0	0	0.26 (0.51)	0
P1	0	0	0	0	0	0	0.40 (0.63)

1: cluster 3 = Suikerbosrand grassland sites and open wood 1, Cluster 7 = Suikerbosrand open wood 2, 3.
2: generated by varimax normalized rotation of a PCFA ordination conducted on a site-by-site correlation matrix for dung beetle species abundance.

although species richness declined significantly across the altitude and rainfall gradient, it was clearly modified by local effects, which would include vegetation disturbance (see Tswaing), stone content and soil grain size (see Leeuwfontein, Roodeplaat), and temperature differences between shade and open vegetation (see Roodeplaat, Tswaing). Overall diversity declined from bushveld to upper bushveld, in concert with decline in lowland faunal influence, and also from open to more shaded habitats. However, it increased again in Suikerbosrand where an endemic highland fauna dominated. Abundance probably varied primarily according to local variables such as dung density, incidence of rainfall, edaphic and vegetative characteristics. It was highest at Abe Bailey where trapping was conducted on a warm day immediately following heavy rainfall (>100 mm).

Some species, previously recorded for the province, were not re-recorded during the survey. Most were probably missed as they show specializations (Table 1). However, four species may have been missed, since they are uncommon in Gauteng (*Heliocopris pirmal* (Fabricius), *Onthophagus aschenborni* Frey, *Scarabaeus ebenus* (Klug), *Pedaria* sp. VI (*sensu* Doube *et al.* 1991), whereas there is no obvious explanation for the lack of records for the common generalist species, *Drepanocerus patrizii* (Boucomont). It is probable that most species showing specializations would be recorded if trapping were conducted at the right time, in the right place using the right bait. However, three of the categories probably include species that are rare or locally extinct since deep sands and very large non-ruminant herbivore droppings are now poorly represented or absent from the province. Kalahari-centred species (Davis 1997) were formerly recorded in deep sand outliers (Davis 1996) that have now been converted into sand mines for the building industry. The large-bodied, *Heteronitis castelnaui*, is known from Gauteng by only a single specimen recorded in the bushveld in 1973 (DBRU reference collection, unpubl. data), although it is commonly recorded in elephant dung in savanna game reserves (Davis 1997). There is a proposal to extend the collaborative reserve of Leeuwfontein into a major regional game park that would be aimed at attracting international visitors through easy access on an improved local transport system (Gauteng News 2001). If implemented, then reintroduction of elephants and rhinoceros might increase dung beetle diversity through favouring population expansion of locally rare coarse dung specialists.

Faunal trends and reserve similarity *versus* distinctiveness

Gauteng occupies part of the transition between the bushveld woodland of the savanna biome and the open vegetation of the mostly higher lying grassland biome (Low & Rebelo 1998). In the three reserves lying between 1100 and 1300 m (Tswaing, Leeuwfontein, Roodeplaat), vegetation is dominated by woodland and although there are grassland patches, most of these clearly result from disturbance. About two-thirds of the variation was due to shared lower-lying savanna faunal influence and about one-third was unique to each reserve, although on the finer-grained soils of Roodeplaat, about 10 % represents closer relationships to highland faunas. Although the two reserves lying between 1330 and 1550 m (Ezemvelo, Abe Bailey) were dominated by grassland, there were patches of disturbed woody vegetation. Shared variance showed greater bias to savanna (one-third of the variation) than to high grassland faunal influence (about 10 % of the variation in Abe Bailey, 2 % in the lower Ezemvelo) although there was also a high proportion of unique faunal composition (about 60 % of the variation), much of which was contributed by locally abundant species with upland distribution centres (Appendix). Although the results indicate that there is substantial savanna characterization in these reserves, Low & Rebelo (1998) classify Abe Bailey as Rocky Highveld Grassland (type 34). This is partly synonymous with Acocks' (1988) Central Bankenveld (type 61b), which he suggests was once open *Acacia* woodland, perhaps cleared and ploughed by the Ndebele who were settled in the region. Suikerbosrand was also classed as Rocky Highveld Grassland or Bankenveld, but as it lay above 1600 m, the dung beetle fauna was dominated by highland faunal elements (about 50 % of the variation) with the balance represented by unique faunal variance, contributed mainly by highland-centred species (Appendix). Although grassland was dominant, the patches of natural woodland that occurred in sheltered spots and on warmer northern hillsides mostly showed faunal composition that was intermediate but distinct from the highveld grassland and the bushveld.

Shared variance along extended factors S1 and S2 (Fig. 4) is interpreted as representing savanna or highland faunal influence. This interpretation is supported by the biogeographical classification of species (Davis 1997; Davis & Dewhurst 1993; Davis *et al.* 1999) in the Appendix. Species recorded primarily in lower to intermediate altitude reserves are mostly widely distributed in tropical Africa or southern African savannas. Species recorded primarily in higher to intermediate altitude reserves comprise many southern African highland specialists. In addition to variance shared between reserves, there was also much unique variance in each reserve. Some of this unique variance results from widespread species that were recorded in low abundance in single reserves. However, some results from uncommon specialist species with restricted regional and local distributions. Some distinctive characteristics of each reserve are briefly discussed below.

Tswaing. although there is a high degree of similarity between the faunas of the three low-lying reserves, Tswaing also shows some distinctiveness that may reflect a faunal bias to hotter dryer savanna. There is a clear disturbance gradient from high similarity between natural open woodland sites to lower similarity to disturbed open woodland sites and least similarity to sites where vegetation has been converted to grassland. When the survey was conducted, the reserve was only stocked with Nguni cattle.

Leeuwfontein. The grouping of sites reflects consistent faunal differences across the soil type gradient from stony sandy loam to sandy loam to loamy sand in the south. There is a strong southerly bias in the distribution of sand specialists such as *Pachylomerus femoralis, Gymnopleurus aenescens, Pedaria* sp. b, *Catharsius tricornutus* and a northerly bias in the distribution of the finer soil specialist, *Garreta nitens.* Some of the reserve distinctiveness may be due to the incidence of relatively good numbers of the coarse-fibred, non-ruminant dung specialists, *Proagoderus loricatus* and *Onitis granulisetosus,* which show restricted game-reserve distributions (Davis 1997). Their presence may reflect the high density of zebra dung on sandy soils. The observations emphasize the importance of sands (threatened by mining) and large non-ruminant mammals (locally extinct before reintroduction) for a complete provincial dung beetle fauna.

Roodeplaat. The development of many thickets supporting shade specialist species (also recorded in crater rim thicket in Tswaing) may be associated with the finer-grained soils. These finer-grained soils may be responsible for some faunal distinctiveness for the reserve. Although thicket faunas grouped together, there was some overlap between faunas in the dominant open wood and those in disturbed patches reduced to grassland, particularly with Grassland 3, which was an island in the woodland.

Ezemvelo. The high faunal distinctiveness was probably related to the sandy soils. These are uncommon at higher altitude and probably account for the occurrence of the uncommon and patchily distributed upland endemic, *Scarabaeus heqvisti,* and that of *Onthophagus* sp. (granular), which has otherwise been recorded only from high-rainfall deep sands on the east coast. Both species were primarily recorded in higher altitude grassland above 1400 m. The sandy nature of the soils would also account for the occurrence of savanna- and Kalahari-centred sand specialists such as *Pachylomerus femoralis* and *Proagoderus sappharinus* that were otherwise only recorded in the sandy south of Leeuwfontein. There were clear distinctions between grassland and wooded hilltop faunas with *Scarabaeus rusticus* particularly characteristic of the latter.

Abe Bailey. Although the shared savanna faunal influence was much greater than shared highland faunal influence, the high faunal distinctiveness probably owes much to the high relative or unique abundance (Appendix) of three species centred in the drier southwestern parts of the highveld, *Onthophagus fritschi, O. asperulus,* and the melanic variety of *O. aeruginosus.* All three of these species or varieties were more abundant in grassland than in disturbed open woodland. The higher altitude, moderate rainfall, sandy loams and high density of antelope and their pellet droppings may be responsible for the records of three uncommon *Scarabaeus* species not or hardly represented in the other reserves. Although the woodland was extremely opened out and degraded, woodland and grassland faunas showed clear and consistent separation. Extremely high abundance resulted from the heavy rain (>100 mm) preceding the survey.

Suikerbosrand. As this reserve occurs at relatively high altitude in a higher rainfall regime, and the survey was conducted in cool conditions after heavy rainfall, the fauna was characterized by low abundance and strong highland faunal influence both in shared and unique variance. Mixed site relationships reflected differences in proximity, altitude and aspect. Two extensive open woodland patches showed distinct faunal characterization intermediate to that of highland grass and lower-lying woodland. The fauna of another woodland patch (site 1) was close to those of highveld grassland on north facing slopes both faunistically and geographically. The fauna of highveld grassland on cooler south-facing slopes (site 3) was closer to that of montane grassland. Along with Abe Bailey, this reserve protects *Epirinus gratus,* a rarely encountered species, centred in southwestern North West Province and northeastern Northern Cape.

Conservation recommendations

The Gauteng reserve system includes much of the provincial dung beetle fauna (Appendix). However, a number of species were not re-recorded during the present survey (Table 1). Greater than a half of these missed species are range-restricted specialists on particular dung and soil types that are poorly represented by the current reserve system. It is probable that diversity of the represented faunas would be enhanced by the reintroduction of very large non-ruminant (monogastric) mammals that drop large coarse-fibred dung. It is also probable that enhanced species richness would result from incorporating any surviving areas of deep bushveld sands and highveld clays into the reserve system.

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REFERENCES

ACOCKS, J.P.H. 1988. *Veld types of South Africa.* 3rd Edition. Botanical Research Institute and Department of Agriculture and Water Supply, Pretoria, South Africa.

CAMBEFORT, Y. 1982. Les coléoptères Scarabaeidae *s. str.* de Lamto (Côte d'Ivoire): structure des peuplements et rôle dans l'écosystème. *Annnals de la Société Entomologique de France* (N.S.) **18**: 433–459.

CHADZON, R.L., COLWELL, R.K., DENSLOW, J.S. & GUARIGUATA, M.R. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier, F. & Comiskey, J.A. (Eds) *Forest Biodiversity Research, Monitoring and Modelling: Conceptual Background and Old World Case Studies.* 285–309. Parthenon Publishing, Paris.

COLWELL, R.K. 1997. *EstimateS: Statistical estimation of species richness and shared species from samples. Version 5.* User's guide and application published at: http://viceroy.eeb.uconn.edu/estimates (accessed 1 June 2004).

DAVIS, A.L.V. 1989. Nesting of Afrotropical *Oniticellus* (Coleoptera, Scarabaeidae) and its evolutionary trend from soil to dung. *Ecological Entomology* **14**: 11–21.

DAVIS, A.L.V. 1994. Associations of Afrotropical Coleoptera (Scarabaeidae, Aphodiidae, Staphylinidae, Hydrophilidae, Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *Journal of Natural History* **28**: 383–399.

DAVIS, A.L.V. 1995. Daily weather variation and temporal dynamics in an Afrotropical dung beetle community (Coleoptera: Scarabaeidae). *Acta Oecologica* **16**: 641–656.

DAVIS, A.L.V. 1996. Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). *Pedobiologia* **40**: 260–280.

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. 2002. Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. *African Entomology* **10**: 53–65.

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., VAN AARDE, R.J., SCHOLTZ, C.H. & DELPORT, J.H. 2002. Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. *Global Ecology and Biogeography* **11**: 191–209.

DAVIS, A.L.V. & DEWHURST, C.F. 1993. Climatic and biogeographical associations of Kenyan and north Tanzanian dung beetles (Coleoptera: Scarabaeidae). *African Journal of Ecology* **31**: 290–306.

DOUBE, B.M. 1991a. Dung beetles of southern Africa. In: Hanski, I. & Cambefort, Y. (Eds) *Dung Beetle Ecology.* 133–155. Princeton University Press, Princeton.

DOUBE, B.M. 1991b. Appendix B8. In: Hanski, I. & Cambefort, Y. (Eds) *Dung Beetle Ecology.* 383–387. Princeton University Press, Princeton.

FINCHER, G.T., STEWART, T.B. & DAVIS, R. 1970. Attraction of coprophagous beetles to feces of various animals. *Journal of Parasitology* **56**: 378–383.

FORGIE, S.A., GREBENNIKOV, V.V. & SCHOLTZ, C.H. 2002. Revision of *Sceliages* Westwood, a millipede-eating genus of southern African dung beetles (Coleoptera: Scarabaeidae). *Invertebrate Systematics* **16**: 931–955.

GAUTENG NEWS (2001) *Speed train on track.* Published at: http://www.gpg.gov.za/publications/index.html (accessed 29 October 2004).

JAY-ROBERT, P., LOBO, J.M. AND LUMARET, J-P. 1997. Altitudinal turnover and species richness variation in European montane dung beetle assemblages. *Arctic and Alpine Research* **29**: 196–205.

KIRK, A.A. & RIDSDILL-SMITH, T.J. 1986. Dung beetle distribution patterns in the Iberian Peninsula. *Entomophaga* **31**: 183–190.

LOBO, J.M., LUMARET, J.P. AND JAY-ROBERT, P. 1998. Sampling dung beetles in the French Mediterranean area: effects of abiotic factors and farm practices. *Pedobiologia* **42**: 252–266.

LOW, A.B. & REBELO, A.G. 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs and Tourism, Pretoria.

MAGURRAN, A.E. 1987. *Ecological Diversity and its Measurement.* Croom Helm, London.

NEALIS, V.G. 1977. Habitat associations and community analysis of south Texas dung beetles (Coleoptera: Scarabaeinae). *Canadian Journal of Zoology* **55**: 138–147.

PASCHALIDIS, K.M. 1974. The genus *Sisyphus* Latr. (Coleoptera: Scarabaeidae) in southern Africa. M.Sc. thesis, Rhodes University, Grahamstown.

PLYMOUTH MARINE LABORATORY 1994. PRIMER, version 4. Plymouth.

STATSOFT, INC. 1995. *STATISTICA for Windows Computer Programme Manual.* Tulsa, OK.

WHERRY, R.J. 1984. *Contributions to Correlational Analysis.* Academic Press, New York.

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Appendix. Quantitative species inventory for six Gauteng nature reserves (average numbers per trap, spaces separate groups of species with similar patterns of occurence.).

	Tswaing	Leeuw.	Rood.	Ezem.	Abe B.	Suiker.	Biog.[1]	Habitat[2]	
								Soil	Veg.
Mainly savanna centred									
Onthophagus lamelliger Gerstaecker	2.63	0.00	0.00	0.00	0.00	0.00	EA	?	?
Catharsius philus Kolbe	0.91	0.00	0.00	0.00	0.00	0.00	Ssav	F	GOW
Onthophagus trinodosus Fahraeus	0.61	0.00	0.00	0.00	0.00	0.00	Ssav	?	?
Onitis uncinatus Klug	0.27	0.00	0.00	0.00	0.00	0.00	EA	F	OWG
Pedaria sp. c (*sensu* Davis 1996)	0.27	0.00	0.00	0.00	0.00	0.00	Ssav	F	OWG
Copris elphenor Klug	0.13	0.00	0.00	0.00	0.00	0.00	EA	S	OWG
Scarabaeus galenus (Westwood)	0.09	0.00	0.00	0.00	0.00	0.00	Ssav	?	?
Oniticellus planatus Castelnau	0.04	0.00	0.00	0.03	0.00	0.00	PA	?	?
Onthophagus sp. C	0.03	0.00	0.00	0.00	0.00	0.00	?	?	?
Onitis granulisetosus Ferreira	0.00	2.60	0.00	0.00	0.00	0.00	Ssav	?	?
Gymnopleurus aenescens Wiedeman	0.00	0.29	0.00	0.00	0.00	0.00	Ssav	S	GOW
Heliocopris atropos Boheman	0.00	0.22	0.00	0.00	0.00	0.00	EA	?	?
Cleptocaccobius convexifrons (Raffray)	0.00	0.18	0.00	0.00	0.00	0.00	EA	S	OWG
Heliocopris faunus Boheman	0.00	0.07	0.00	0.00	0.00	0.00	Ssav	?	?
Caccobius sp.	0.00	0.04	0.00	0.00	0.00	0.00	?	?	?
Heliocopris japetus Klug	0.00	0.02	0.00	0.00	0.00	0.00	EA	S	Gen
Onthophagus sp. g	0.00	0.02	0.00	0.00	0.00	0.00	?	?	?
Sisyphus goryi Harold	17.30	34.51	3.42	0.00	0.00	0.00	PA	G	OW
Onthophagus flavolimbatus Klug	4.26	1.96	0.00	0.00	0.00	0.00	EA	S	GOW
Onitis fulgidus Klug	2.76	7.13	0.02	0.00	0.00	0.00	Ssav	F	SOW
Drepanocerus kirbyi (Kirby)	1.08	0.18	0.07	0.00	0.00	0.00	PA	G	OWS
Euoniticellus intermedius (Reiche)	0.94	0.04	0.02	0.00	0.00	0.00	PA	G	OWG
Phalops boschas Klug	0.53	0.62	0.00	0.00	0.00	0.00	Ssav	?	?
Caccobius sp. 4 (*sensu* Davis *et al.* 2002)	0.47	0.22	0.02	0.00	0.00	0.00	?	?	?
Neosisyphus calcaratus Klug	0.43	0.13	0.00	0.00	0.00	0.00	Ssav	?	?
Phalops smaragdinus Harold	0.34	0.04	0.00	0.00	0.00	0.00	Ssav	S	OW
Copris vilhenai Ferreira	0.31	0.11	0.00	0.00	0.00	0.00	Ssav	S	SOW
Phalops ardea Klug	0.27	0.96	0.00	0.00	0.00	0.00	Ssav	?	?
Phalops flavocinctus Klug	0.09	0.04	0.00	0.00	0.00	0.00	Ssav	F	GOW
Proagoderus loricatus Klug	0.07	0.31	0.00	0.00	0.00	0.00	EA	?	?
Onthophagus sp. a (*sensu* Davis 1996)	16.44	0.13	9.84	0.00	0.45	0.00	?	S	SOW
Onthophagus albipodex d'Orbigny	0.74	0.00	0.20	0.00	0.07	0.00	EA	S	G
Sisyphus impressipennis Lansberge	0.51	0.11	0.07	0.03	0.00	0.00	EA	?	S
Onthophagus aequepubens d'Orbigny	0.43	0.00	0.07	0.00	0.00	0.00	Ssav	S	S
Neosisyphus fortuitus Péringuey	0.35	0.00	0.02	0.00	0.00	0.00	EA	G	SOW
Onthophagus sp. nr *lacustris* Harold	0.24	0.00	0.29	0.00	0.00	0.00	?	G	S
Sisyphus gazanus Arrow	0.14	0.00	0.11	0.00	0.00	0.00	PA	?	S
Onthophagus sp.	0.04	0.00	0.07	0.00	0.00	0.00	?	?	?
Onitis alexis Klug	0.02	0.00	0.09	0.00	0.00	0.00	PA	G	GOW
Onthophagus sp. e (*sensu* Davis 1996)	0.02	0.00	0.24	0.00	0.00	0.00	Ssav	F	OWG
Onthophagus interstitialis Fahraeus	0.00	0.00	0.29	0.00	0.00	0.00	Shv	F	G
Copris amyntor Klug	0.00	0.00	0.22	0.00	0.00	0.00	Ssav	F	OW
Onitis viridulus Boheman	0.00	0.00	0.09	0.00	0.00	0.00	EA	F	Gen
Onthophagus verticalis Fahraeus	0.00	0.04	0.04	0.00	0.00	0.00	Ssav	S	SOW
Onthophagus rasipennis d'Orbigny	25.68	49.18	0.09	1.00	0.00	0.00	Ssav	G	OW
Onthophagus stellio Erichson	9.49	22.80	0.02	7.83	0.00	0.00	Ssav	S	GOW
Anachalcos convexus Boheman	1.13	1.36	1.89	1.47	0.00	0.00	PA	G	SOW
Caccobius ferrugineus Fahraeus	0.62	2.38	0.00	0.47	0.00	0.00	PA	S	G
Tiniocellus spinipes (Roth)	0.22	12.11	2.51	5.13	0.00	0.00	PA	G	OW
Caccobius nigritulus Klug	0.18	20.20	0.18	0.13	0.00	0.00	EA	S	OWS
Kheper subaeneus (Harold)	0.16	0.16	0.27	0.27	0.00	0.00	PA	?	?
Drepanocerus laticollis Fahraeus	0.99	0.51	0.00	0.17	0.00	0.00	PA	S	OW

Continued on p. 15

	Tswaing	Leeuw.	Rood.	Ezem.	Abe B.	Suiker.	Biog.	Habitat	
								Soil	Veg.
Mainly savanna centred									
Pedaria sp. b (*sensu* Davis 1996)	1.56	5.73	0.04	0.27	0.00	0.00	SA	S	GOW
Metacatharsius troglodytes Boheman	1.59	0.58	0.00	0.73	0.00	0.00	Ssav	S	G
Onthophagus pallidipennis Fahraeus	5.42	1.07	0.07	0.10	0.00	0.00	Ssav	S	OW
Gymnopleurus virens Erichson	42.84	10.56	6.56	0.70	13.07	0.00	PA	F	OWG
Garreta nitens (Olivier)	31.63	34.18	4.29	0.00	9.83	0.00	PA	F	OWS
Euonthophagus sp. nr *carbonarius* Klug	17.44	155.27	3.78	0.17	2.63	0.00	Ssav	F	GOW
Onthophagus vinctus Erichson	13.21	13.84	6.51	226.50	0.03	0.00	PA	S	SOW
Kheper nigroaeneus (Boheman)	10.41	1.22	1.09	0.00	0.63	0.00	Ssav	?	?
Cleptocaccobius viridicollis (Fahraeus)	9.07	2.87	0.36	0.00	1.17	0.00	EA	G	OWG
Allogymnopleurus thalassinus Klug	2.76	2.22	0.00	2.07	0.38	0.00	Ssav	S	G
Catharsius tricornutus de Geer	2.67	7.47	0.04	0.80	0.70	0.04	SA	S	Gen
Liatongus militaris (Castelnau)	1.86	0.04	0.02	0.27	6.20	0.00	EA	F	GOW
Onthophagus sp. nr *pullus* Roth	1.63	114.64	0.07	23.67	17.98	0.00	Ssav	G	OWG
Scarabaeus ambiguus (Boheman)	1.53	57.71	0.27	3.83	25.10	0.00	Ssav	F	G
Neosisyphus ruber (Paschalidis)	1.41	6.93	0.42	0.90	0.37	0.00	SA	F	GOW
Scarabaeus bohemani Harold	0.96	0.38	0.18	0.00	6.60	0.00	SA	F	G
Phalops dregei Harold	0.56	11.07	0.02	2.07	7.85	0.00	SA	G	GOW
Hyalonthophagus alcedo (d'Orbigny)	0.42	4.36	0.09	0.10	0.13	0.00	Ssav	S	OW
Drepanocerus fastiditus Péringuey	0.18	0.02	0.00	0.03	0.03	0.00	PA	G	GOW
Digitonthophagus gazella (Fabricius)	0.11	0.07	0.07	2.43	0.87	0.00	PA	G	G
Onthophagus sp. d (*sensu* Davis 1996)	0.07	4.16	0.04	0.00	10.88	0.00	?	F	SOW
Onthophagus sp. B	0.05	0.02	0.00	0.00	0.03	0.00	?	?	?
Onthophagus quadrinodosus Fahraeus	0.00	0.78	0.00	0.23	0.65	0.00	Ssav	S	SOW
Onthophagus apiciosus d'Orbigny	0.00	0.24	0.04	0.10	0.05	0.00	Ssav	?	?
Catharsius sesostris Waterhouse	0.00	0.13	0.24	0.83	0.03	0.00	PA	S	SOW
Catharsius pandion Harold	0.00	0.11	0.00	0.00	0.87	0.00	Ssav	?	?
Pedaria sp. II (*sensu* Doube 1991)	0.00	0.02	0.00	0.00	1.08	0.00	Ssav	?	?
Onthophagus sp. nr *sugillatus* Klug (3)	24.85	264.36	46.78	63.17	466.90	11.53	SA	G	OWS
Onthophagus aeruginosus Roth (green)	33.47	42.69	18.36	22.00	37.22	5.18	EA	G	OWS
Onthophagus obtusicornis Fahraeus	19.04	31.20	20.84	0.30	171.53	0.73	Ssav	F	GOW
Onthophagus fimetarius Roth	16.09	20.58	4.18	3.13	46.08	0.71	PA	S	Gen
Sarophorus costatus Fahraeus	20.95	1.11	4.33	0.03	0.00	0.44	SA	G	SOW
Sisyphus alveatus Boucomont	0.16	0.76	0.78	0.00	0.07	1.80	SA	F	OWG
Scarabaeus rusticus (Boheman)	0.00	0.60	0.02	17.33	0.10	0.53	Ssav	?	?
Odontoloma louwi Howden & Scholtz	0.02	0.13	2.00	0.00	5.28	0.38	Ssav	F	Gen
Onthophagus pilosus Fahraeus	0.18	1.71	0.53	0.23	10.15	0.36	SA	S	G
Onthophagus ebenus Péringuey	0.18	0.20	1.20	0.03	1.48	0.16	Ssav	G	Gen
Onthophagus pugionatus Fahraeus	0.93	0.00	3.71	0.00	1.05	0.16	Ssav	G	S
Copris mesacanthus Harold	0.00	0.02	0.36	0.03	0.02	0.11	Ssav	F	OWG
Onthophagus deterrens Péringuey	0.04	0.00	0.02	0.00	0.27	0.07	SA	?	?
Pachylomerus femoralis (Kirby)	0.00	5.78	0.00	3.90	0.00	0.00	Ssav	S	OWG
Scarabaeus goryi Castelnau	0.00	1.29	0.00	0.27	0.00	0.00	PA	S	Gen
Proagoderus sappharinus Péringuey	0.00	1.04	0.00	3.30	0.00	0.00	Kal	S	OWG
Kheper lamarcki (M'Leay)	0.00	0.84	0.00	0.03	0.02	0.00	Ssav	S	OW
Heliocopris hamadryas (Fabricius)	0.00	0.58	0.00	0.00	0.03	0.00	PA	S	SOW
Onitis deceptor Péringuey	0.00	0.11	0.00	0.03	0.00	0.00	Ssav	S	OWS
Pedaria sp. a (*sensu* Davis 1996)	0.00	0.07	0.00	0.10	0.00	0.00	Kal	S	G
Onthophagus signatus Fahraeus	0.00	0.02	0.00	0.67	0.00	0.00	Ssav	S	OWG
Proagoderus brucei Reiche	0.00	0.00	0.00	0.87	0.00	0.00	PA	?	?
Onthophagus cribripennis d'Orbigny	0.00	0.00	0.04	0.33	0.00	0.00	Ssav	?	?
Onthophagus sp. t	0.00	0.00	0.00	0.03	0.00	0.00	?	?	?
Drepanocerus sp.	0.00	0.00	0.00	0.03	0.00	0.00	?	?	?
Onthophagus croesulus Bates	0.00	0.00	0.00	0.20	0.00	0.00	Ssav	?	?
Onthophagus bicavifrons d'Orbigny	0.00	0.00	0.00	0.10	0.00	0.00	EA	?	?
Onthophagus depressus Harold	0.00	0.00	0.00	0.07	0.00	0.00	EA	?	?

Continued on p. 16

	Tswaing	Leeuw.	Rood.	Ezem.	Abe B.	Suiker.	Biog.	Habitat	
								Soil	Veg.
Mainly highland centred									
Onthophagus sp. w	0.00	0.00	0.00	12.40	0.00	0.02	?	?	?
Onthophagus sp. (granular)	0.00	0.00	0.00	5.27	0.00	0.00	?	?	?
Scarabaeus heqvisti zur Strassen	0.00	0.00	0.00	1.80	0.00	0.00	?	?	?
Onthophagus cyaneoniger d'Orbigny	0.00	0.00	0.00	22.37	68.12	0.20	Shv	?	?
Onthophagus fritschi d'Orbigny	0.00	0.00	0.00	0.00	57.52	0.02	Shv	?	?
Onthophagus parumnotatus Fahraeus	0.00	0.00	0.00	0.37	39.38	0.29	SA	?	?
Onthophagus aeruginosus Roth (black)	0.00	0.00	0.00	0.00	23.95	0.00	Shv	?	?
Onthophagus asperulus d'Orbigny	0.00	0.00	0.00	0.00	11.03	4.67	Shv	?	?
Copris obesus Boheman	0.00	0.00	0.00	0.00	2.85	0.04	EA	?	?
Sisyphus caffer Boheman	0.00	0.07	0.00	1.10	2.83	0.00	Shv	?	?
Epirinus gratus Péringuey	0.00	0.00	0.00	0.00	2.10	0.11	Shv	?	?
Gymnopleurus leei (Fabricius)	0.00	0.00	0.00	0.00	1.57	0.20	Shv	?	?
Copris antares Ferreira	0.00	0.00	0.00	0.00	1.05	0.00	Shv	?	?
Onthophagus monodon Fahraeus	0.00	0.00	0.00	0.00	0.38	0.00	Shv	?	?
Cyptochirus ambiguus (Kirby)	0.00	0.00	0.00	0.00	0.33	0.09	PA	?	?
Scarabaeus ?interstitialis (Boheman)	0.04	0.00	0.00	0.00	0.18	0.00	?	?	?
Euoniticellus triangulatus (Harold)	0.00	0.00	0.00	0.00	0.17	0.09	EA	?	?
Scarabaeus sp.	0.00	0.00	0.00	0.00	0.10	0.00	?	?	?
Cheironitis hoplosternus (Harold)	0.00	0.00	0.00	0.03	0.10	0.00	SA	?	?
Onthophagus sp. nr *sugillatus* Klug	0.00	0.00	0.00	0.00	0.05	0.00	?	?	?
Metacatharsius latifrons Harold	0.00	0.00	0.00	0.00	0.03	0.00	Kal	S	?
Onitis picticollis Boheman	0.00	0.00	0.00	0.00	0.02	0.00	SA		
Scarabaeus satyrus (Boheman)	0.00	0.00	0.00	0.00	0.02	0.00	Arid	?	?
Scarabaeus funebris (Boheman)	0.00	0.00	0.00	0.00	0.02	0.00	Ssav	?	?
Proagoderus lanista Castelnau	0.00	0.00	0.00	0.00	0.00	11.00	Shv	?	?
Onthophagus sp. nr *fimetarius* Roth	0.00	0.00	0.00	0.00	0.00	2.40	?	?	?
Onthophagus binodis Thunberg	0.00	0.00	0.00	0.00	0.00	2.24	Shv	?	?
Pedaria sp. (highveld)	0.00	0.00	0.00	0.00	0.00	1.98	Shv	?	?
Onthophagus sp. x	0.00	0.00	0.00	0.00	0.00	1.58	?	?	?
Garreta unicolor (Fahraeus)	0.00	0.00	0.00	0.00	0.08	1.36	SA	?	?
Catharsius sp. (highveld)	0.00	0.00	0.00	0.00	0.05	1.24	Shv	?	?
Sisyphus costatus Thunberg	0.00	0.00	0.00	0.00	0.00	0.80	Shv	?	?
Onthophagus nr cribripennis d'Orbigny	0.00	0.00	0.00	0.00	0.00	0.56	Shv	?	?
Copris fidius Olivier	0.00	0.00	0.00	0.00	0.00	0.36	SA	?	?
Drepanocerus sp. nr *laticollis* Fahraeus	0.00	0.00	0.00	0.00	0.00	0.29	Shv	?	?
Onitis caffer Boheman	0.00	0.00	0.00	0.00	0.20	0.27	SA	?	?
Onthophagus cinctipennis Quedenfeldt	0.00	0.02	0.00	0.00	0.03	0.20	SA	?	?
Onthophagus sp nr *absyrtus* Balthasar	0.00	0.00	0.00	0.00	0.00	0.09	Shv	?	?
Onthophagus obtutus Péringuey	0.00	0.00	0.00	0.00	0.00	0.09	Shv	?	?
Onitis tortuosus Houston	0.00	0.00	0.00	0.00	0.02	0.07	SA	?	?
Onthophagus lugubris Fahraeus	0.00	0.00	0.00	0.00	0.00	0.04	Shv	?	?
Euoniticellus africanus (Harold)	0.00	0.00	0.00	0.00	0.00	0.04	Shv	?	?
Onthophagus sp. z	0.00	0.00	0.00	0.00	0.00	0.04	?	?	?
Onthophagus sp. v	0.00	0.00	0.00	0.00	0.00	0.02	?	?	?
Copris jacchoides Nguy. Phung & Camb.	0.00	0.00	0.00	0.00	0.00	0.02	Shv	?	?
Caccobius obtusus Fahraeus	0.00	0.00	0.00	0.00	0.00	0.02	EA	?	?

1: biogeographical distribution pattern: PA = Pan-African savanna distribution, EA = distribution centred on southern to East Africa savannas or highlands, Ssav = distribution centred on southern African savannas mainly in the east, SA = distribution centred on southeast African savannas and highlands, Shv = distribution centred on southeast African highlands, Kal = distribution centred on the southern Kalahari, Arid = distribution centred on the arid southwest of southern Africa. Assessment from Davis (1997) and Davis & Dewhurst (1993).

2: habitat association in the Gauteng bushveld (associations are specific in some, vary regionally in others). Soil: S = sandy soil bias, F = finer-grained soil bias, G = soil generalist. Vegetation: G = grassland, Gen = generalist, OW = open woodland, S = shaded thicket (categories mostly combined. Assessment from Davis (1996).

3: species identified by letters but without citations are unidentified species and are only cited in the present manuscript.