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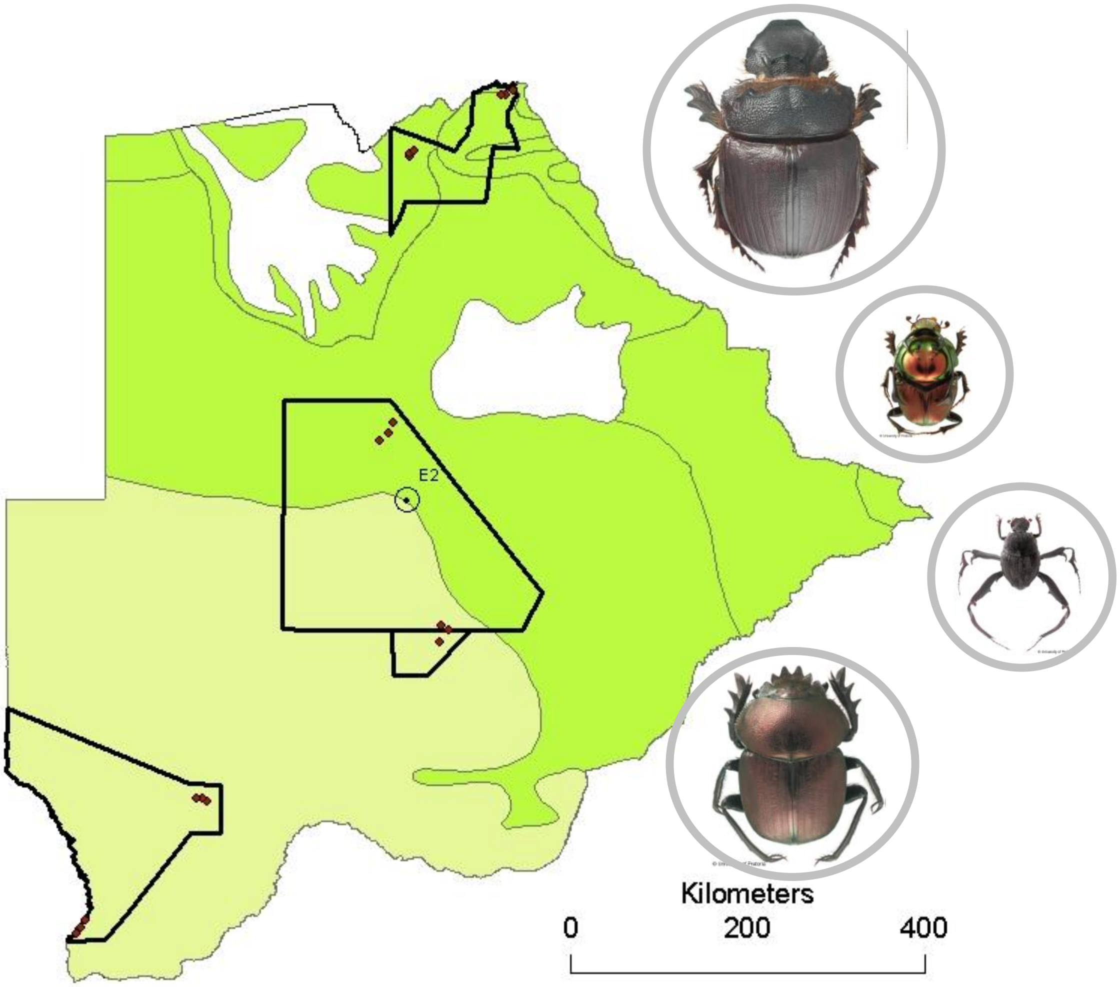
Local and regional factors influencing dung beetle assemblage structure across an environmental gradient in Botswana



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Local and regional factors influencing dung beetle assemblage structure across an environmental gradient in Botswana

By

Balatlhane Power Tshikae

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DEDICATION

To my late father-Kelobilwe, brother-Kelopemang and sister-Masefako

To all my teachers and mentors with love……….

“I ‘m glad I have run the course to the finish”

Abstract

The taxonomic composition, structure, and diversity of current local species assemblages results from an interacting complex of historical, regional ecological and local ecological factors. Structural differences between such current species assemblages are primarily determined by changing ecological conditions across spatial gradients. These conditions may change abruptly or they may represent a gradual divergence. Across the Botswana Kalahari basin there is a gradual northeast-southwest aridity and dung type gradient, which was demonstrated to strongly influence dung beetle assemblage structure at six study sites from Chobe National Park to the Central Kalahari Reserve to the Kgalagadi Transfrontier Park using carrion and four dung types as bait (pig, elephant, cattle, sheep). Regional patterns were primarily influenced by climate (rainfall) while dung type mainly showed a local influence on patterns of variation. Four distinct biogeographical groups were defined for the study region comprising widespread, northeast/widespread, northeast, and arid southwest Kalahari-centred species. Biogeographical diversity was higher in the more mesic NE than the arid SW but varied somewhat between bait types. In the SW, Kalahari endemics dominated all bait types. In general, abundance and species richness declined along the aridity gradient although the pattern was uneven due to low numbers in the north of the Central Kalahari Game Reserve. Species showed high turnover (beta – diversity), particularly between the moister NE and the Kalahari/Savanna ecotone. Hierarchical Analysis of Oblique Factors showed statistically distinct separation between assemblage structure at the six study sites and that the proportion of mesic NE shared influence on assemblage composition declined towards the SW where there was an increase in Kalahari endemics. Similarly the proportion of arid SW shared influence declined towards the NE. Plotting these results onto a map showed that the point of intersection between shared NE or SW influence lay very close to the ecotone between SW (Kalahari Xeric Savanna) and NE-centred ecoregions (*Acacia-Baikiaea* Savanna) defined for the area by Olson et al. (2001). In terms of dung type diversity, increasing aridity across the Kalahari represents a gradient of diminishing resources with the loss of large dung types to the SW and increasing dominance of dung pellets. Several different patterns of response were shown using different methods. Four principal patterns of bait type association were indicated by one method. Another method showed that, rather than diminishing numbers of competing species leading to widening niche widths to the

SW, niche widths were narrowest at the Kalahari / mesic Savanna ecotone. Using several other multivariate techniques, three different patterns of dung type resource partitioning were demonstrated that paralleled the aridity gradient, one common to the NE and two to the SW. The historical, regional and local ecological factors influencing these patterns of dung beetle assemblage structure are discussed as well as implications and recommendations for conservation.

Keywords: *Acacia-Baikiaea*, beetles, biogeographical patterns, Botswana, carrion, dung association, ecotone, environmental gradient, Kalahari-basin, local factors, regional factors, Scarabaeinae, xeric savanna.

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DECLARATION

I, **Balatlhane Power Tshikae** declare that the thesis/ dissertation, which I here by submit for the degree of **Doctor of Philosophy in Entomology** at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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CHAPTER 1 GENERAL INTRODUCTION

The taxonomic composition, structure, and diversity of current local species assemblages results from an interacting complex of historical, regional ecological and local ecological factors (Ricklefs, 1987; Blackburn & Gaston, 2001; Lobo & Davis, 1999; Koleff & Gaston, 2002; Bonte *et al.*, 2003; Summerville & Crist, 2003, Hoeinghaus *et al.*, 2007a). Structural differences between such current species assemblages are primarily determined by changing ecological conditions across spatial gradients (Mykra *et al.*, 2007; McCauley, 2007; Davis *et al.*, 2008). These conditions may change abruptly or they may represent a gradual divergence (Strayer *et al.*, 2003).

In the Northern Cape, South Africa, local dung beetle assemblage structure has been shown to vary in response to interacting climatic and edaphic factors operating at several spatial scales (Davis *et al.*, 2008). At regional scales of organization, assemblage structure shows clear and relatively abrupt changes across the ecotone separating the more mesic deep Kalahari sands and the more arid, often stony, Nama Karoo (Davis *et al.*, 2008). Furthermore, because of conditions unique to the region lying to the south of the River Orange (Gariep), similar structural differences are also observed at local scales of organization across the habitat boundary between an isolated Kalahari sand dune and the stony Nama Karoo matrix (Davis & Scholtz, 2004).

The current study extends work conducted in the Northern Cape by examining regional and local patterns in the dung beetle fauna across the deep sands of the Botswana Kalahari Basin in central southern Africa to the northeast of the Nama Karoo ecotone. The geological and climatic evolution of this region has probably produced a further ecotone between the more arid savanna in the southwest and the more mesic savanna in the northeast. This hypothesis is tested by pattern analyses of dung beetle species richness, diversity, assemblage structure, and food type association at six localities across this environmental gradient. The study also discusses the conservation implications for dung beetles amidst recent anthropogenic changes across the Botswana Kalahari.

The Kalahari Basin of southern Africa constitutes the southern part of the Mega-Kalahari Basin that extends northwards to West Central Africa. It is geographically extensive, biologically diverse, and is dominated by a swathe of Tertiary (Cenozoic) sands (Tyson 1986; Haddon & McCarthy, 2005). From the northeast to the southwest, it spans two ecoregions (Olson *et al.*, 2001) and three climatic regions according to the classification of Walter & Leith (1964). Responses to this climatic variability across the basin lead to regional spatial gradients in flora and the natural indigenous mammal fauna (Ringrose *et al.*, 2002; Skinner & Chimimba, 2008). However, the regional distribution patterns and biogeographical composition of its local invertebrate assemblages are poorly studied. The present work examines how the dung beetle fauna in this basin responds to spatial gradients comprising both climatic and ecological factors. An understanding of the current assemblage patterns within the southern Kalahari Basin requires information on both its history and current physical setting including (1) geology, (2) climatology and (3) the history of mammal distribution relative to climatic and vegetation zones. It is hypothesized that principal influences on dung beetle assemblage structure would be the increasing regional aridity to the southwest and local differences in the availability of different dung resources.

1.2 Geological history and current setting

A comprehensive overview of the geological formations, time scale and climatic changes in the southern Africa subcontinent, including the Mega-Kalahari basin, are available in Tyson (1986), Stokes *et al.*, (1998), Key & Ayres (2000), and Haddon & McCarthy (2005).

The Mega-Kalahari Basin is a term generally applied to the world’s most extensive mantle of aeolian sands that extends from South Africa, north of the Orange River through Botswana covering the eastern to the north part of Namibia with its eastern boundary in the western part of Zimbabwe including the southwestern tip of Zambia through Angola into the west of the Democratic Republic of Congo. In Botswana, the Kalahari sand system covers greater than 75 % of the landmass from the northeast to the southwest (Perkins & Shaw, 1996) (Fig. 1.1).

Despite a comprehensive overview of the geological formations (Key & Ayres, 2000), the exact period of origin and formation of the Mega-Kalahari Basin is still a moot point. However the geological history of the Mega-Kalahari can be traced from the Cretaceous (Stokes *et al.*, 1998; Haddon & McCarthy, 2005). The geological development has been multifaceted, and punctuated by numerous forces that actively shaped the geomorphology across the basin. This included the down-warp of the interior of southern Africa that led to the formation of the Botswana basin in the Late-Cretaceous and early Tertiary. This down warping and uplift along epeirogenic axes not only back-tilted the rivers into the newly formed large basin but also led to the deposition of the Kalahari Group sediment (Haddon & McCarthy, 2005).

Further Late Miocene – Pliocene uplift along the epeirogenic axes in the east was followed by erosion of the exposed sandstone with sands carried into the basin by the inward draining rivers and deposited over the lithified earlier Kalahari Group sediments. Geological evidence also demonstrates that the deposition of sediments was followed by alternating periods of more arid and more humid conditions (Cooke, 1980; Stokes *et al.*, 1998). During the drier periods in the Late-Quaternary (Stokes *et al.*, 1998), possibly in the Pleistocene, considerable reworking of Kalahari deep sands by aeolian processes (wind action) produced dune fields across the basin, particularly in the southwest.

The Mega-Kalahari basin is currently characterized by scattered outcrops of Pre-Cambrian and Karoo rocks within a sand matrix (Cooke, 1980). There are, however, deep sands and dune fields over most of Botswana with depressions around the lowest points in the Mababe and Makgadikgadi Depressions in which edaphic character may differ. Even so, there is evidence that a variety of sand accumulations occur on many of the present-day pan surfaces (Cooke, 1980). Although the basin is filled with geological formations of Late Tertiary ages, which are of aeolian, lacustrine, and fluviatile origin, the accumulation of unconsolidated sand and dune field formation is a considerably more recent event.

Since the dominance of sand is a comparatively recent phenomenon so is the faunal setting. Although the maximum age of origin of dung beetles is estimated at 90 Mya (upper Cretaceous) (Chin & Gill, 1996), fossil evidence and molecular dating of most extant genera that are widespread on Kalahari sand are from the Miocene (Forgie *et al.*, 2006; Krell, 2007; Davis *et al.*, 2008). If arid conditions are partly accountable for the accumulation of unconsolidated sand, and aridity of the Mega-Kalahari Basin is no older than the middle Miocene (ca 15 Mya), there can be no doubt that dung beetle adaptation to the Kalahari deep sand are more recent than this era.

1.2 Recent climatic history and current physical setting

A synopsis of the historical climatic changes experienced in the subcontinent is provided by Tyson (1986). The development of southern polar glaciations is believed to be responsible for both the generation of cold upwelling of the Benguela Current on the west coast and the Pliocene northward shift of climatic belts. This resulted in the replacement of the early Cenozoic savanna climate by a possibly much drier climate, especially in the southwest of the subcontinent. More recent intensification of the upwelling perhaps resulted in the intensification of the climatic patterns.

The current climatic system is the result of three cells of air currents. A cell of dry air over the cold Benguela upwelling is the result of a current that emanates from glacial regions by “creeping” along the sea bed and surfacing on the south west coast of Africa. This dry air cell expands over most of southern Africa in the cool dry season, hence dry winter conditions. It shifts southwards in summer to bring dry summers to the winter rainfall region.

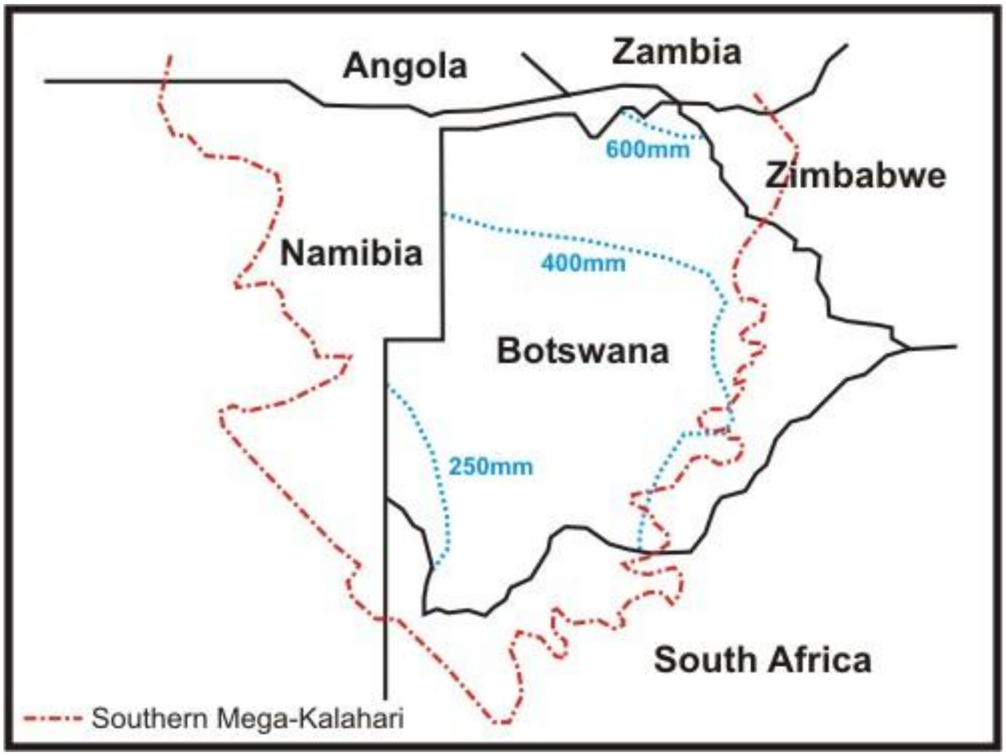


Figure 1.1 **Rainfall isohyets for Botswana and the boundary of southern Mega-Kalahari basin, with western, southern and eastern edges in Namibia, South Africa and Zimbabwe (after Barker, 1993).**

A cell of westerly winds expands north-eastwards from the southern Atlantic in winter to bring winter rainfall to the Western Cape whereas a cell of easterly winds expands south-westwards from the Indian Ocean across southern Africa in summer to bring summer rainfall to the rest of Southern Africa. In summer, there is a sequential expansion of the easterlies across the region so that the northeast (NE) of Botswana receives rainfall earlier and the southwest (SW) much later in summer, with the result that the NE receives more rain than the SW, hence the rainfall gradient from NE to SW.

The rainfall gradient has in turn influenced the vegetation physiognomy and mammal herbivore distribution patterns from NE to SW. There is no doubt that the nature of climatic regimes that characterize the Kalahari Basin, especially the rainfall events, have far reaching implications for the diversity of species and natural history strategies espoused by the region‘s dung beetle fauna.

1.3 Mammals and radiation of dung beetles

Dung beetles of the subfamily Scarabaeinae show a relatively long evolutionary history of specialization to feeding and breeding in dung, particularly in warmer climates (Hanski & Cambefort, 1991; Davis & Scholtz, 2001). During the Cenozoic, climatic changes gave rise to diverse open habitats that were exploited by many radiating mammals. Because of the diversification of mammals during the Cenozoic, there was an increase in dung types, dung size and densities that perhaps triggered a shift from saprophagy or mycetophagy to coprophagy (Hanski & Cambefort, 1991; Scholtz & Chown, 1995). Hence, increased mammal diversity is often invoked as a precursor to the radiation of dung beetles species. Even though dung dominates as a food resource for scarabaeinae, there are nevertheless several other documented trophic and behavioural specializations such as mycetophagy, necrophagy, millipede and ant association (Bornemissza, 1971; Krell, 1999; Philips & Scholtz, 2000; Forgie, 2003).

Dung beetle food associations have mostly diversified according to the history of diversification of mammals and their dung types. Dung types differ according to their physico-chemical characteristics. These are related to dropping size which in turn is related to mammal body size (e.g. pellets vs. boluses), water content, fibre content, plus chemical make-up stemming from diet, and digestive systems (e.g. carnivore or herbivore – ruminant or non-ruminant herbivore see Edwards, 1991; Paetel, 2002). Most species arrive at the dung resource by flight except for a few flightless species, e.g. *Circellium bacchus* associated with dense vegetation on deep coastal sands in the Fynbos Biome of South Africa (Kryger *et al.*, 2006) and the southwest African desert-inhabiting *Pachysoma* (Harrison & Philips, 2003; Sole *et al.*, 2005; Scholtz & Holm, 2008). Most dung beetles detect carrion and dung odours during cruising flights and dung is located by a well-developed olfactory sense with a selective response to particular volatiles allowing identification of preferred dung types (Inouchi & Shibuya, 1986; Mulla & Ridsdill-Smith, 1986; Dormont *et al.*, 2004; 2007; Flechtmann *et al.*, 2009). Some empirical (dung type association) and experimental work (odour response by olfactory sensillae) has been done in support of this hypothesis (Mulla & Ridsdill-Smith, 1986; Schmitt *et al.*, 2004).

Modern dung beetle assemblages are associated primarily with mammalian dung and the regional diversity of their dung types (Davis & Scholtz, 2001) with several physical factors also playing an important role, especially climatic (Davis, 1987; 1997), edaphic (soil type), and physiognomic (vegetation shade or lack of it; see Davis *et al.*, 1988; Davis, 1996c). This has led to different groups of species some with a restricted distribution, others widespread. Today some modern dung beetles have a forest distribution, nonetheless many are more abundant in shrubland and grasslands (savanna) habitats (Halffter & Matthews, 1966) where a diversity of dung types has existed since the Oligocene (35 Mya).

1.4 Recent mammal history relative to vegetation and climatic zones of Botswana

Climate is generally considered as the most important dynamic element and the most obvious independent variable that shapes the distribution patterns of vegetation and mammals at local and regional scales (Cowling *et al.,* 2003). The Botswana Kalahari Basin straddles two ecoregions which include a considerable diversity of ecotypes. These different ecotypes support different mammal species composition across the basin due to a climatic gradient of increasing aridity. There are three climatic zones from NE to SW across the Kalahari Basin according to Walter & Lieth (1964). These climatic types are: II3g (dry savanna), II4c (xeric Kalahari), and II(III)a) (arid SW)). There can be no doubt that over the millennia the development of these climatic zones has influenced the composition and structure of vegetation which in turn influenced mammal distribution patterns.

Most of the Botswana Kalahari Basin is covered by woodland / shrubland of different types that vary according to the rainfall gradient and edaphic factors. From the NE to SW, vegetation changes from open savanna woodland merging into arid zone shrubland and grassland where total annual rainfall is low (Ringrose *et al.*, 2003). There is no surface water in the vast centre and southwest Kalahari. Consequently, mammal response to the climatic gradient and lack of surface water is characterized by the absence from the South west Kalahari of large indigenous mammals that drink regularly, in particular elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*). As a result, large coarse fibred droppings of elephant and large moist fine fibred pads produced by buffalo are now restricted to the NE whereas pellets dominate in the SW, thus creating an ecological difference across the Kalahari basin.

The Kalahari was once a migratory system from watered centres in the SW (arid-adapted fauna with NE movement during the rains) and the NE (savanna fauna with SW expansion during the rains to the limits of permanent water; in the past, possibly beyond Lake Ngami, which is now dry). The seasonal migratory systems allowed ungulates the use of the best habitat-types at the right time between adjacent eco-regions. Furthermore it allowed ungulate prey escape from predator regulation and thus the seasonal environment provided favourable ground for juveniles to grow outside the range of their main predators (Verlinden, 1995).

Fencing, infrastructure development and settlement, now fragment the natural Kalahari system into three large isolated conservation areas with national park or game reserve status. These developments impose severe limitations on migratory patterns so that the reserves in the SW, Centre and NE comprise primarily resident populations of indigenous mammals supported by the provision of drinking water within conservation areas. The largest protected areas within the basin are Chobe National Park and Central Kalahari Game Reserve in Botswana, and the Kgalagadi Transfrontier Park shared by Botswana and South Africa. These main reserves straddle two of the major climatic regions (Davis, 1997), two ecoregions (Cowling *et al.*, 2003) and three of the 25 climatic types described by Walter & Lieth (1964). Chobe National Park including Savuti reserve in NE savanna (II3g) and Central Kalahari Game Reserve (II4c) are situated in the *Acacia-Baikiaea* Savanna region, while Khutse Game Reserve (II4c), and Kgalagadi Transfrontier Park including Mabuasehube in SW (II(III)a) are situated in the Kalahari Xeric Savanna region (Olson *et al.*, 2001).

Although the dynamics of the Kalahari basin, including its mammals and vegetation zones, have been the focus of many scientific studies (Ben-shahar, 1993; Rutina *et al.*, 2004; Omphile *et al.*, 2006), the invertebrate faunas, especially the dung beetle assemblages, have not received the same amount of attention. Yet clear associations with different climate (Davis, 1990; 1997), vegetation and dung types have been shown for species of Scarabaeidae in southern Africa (Davis, 1994; 1996c; 2001; van Rensburg *et al.*, 1999; Botes *et al.*, 2006).

1.5 Objectives and thesis outline

During the last three decades knowledge of scarabaeinae ecology and biogeography in the subcontinent has strongly increased due to research carried out primarily in South Africa (Tribe, 1976; Davis, 1987; 1989; 1994a; 1997; Davis & Scholtz, 2004; Davis *et al.*, 2008). Notwithstanding this extensive advancement, the dung beetle fauna of the complex sand systems of the southern Mega-Kalahari Basin is still much less well understood and this is more so in countries like Botswana where there has been more limited research on invertebrates.

The goal of the present study is to examine the influence of the climatic and mammal dung diversity gradient in structuring the Botswana Kalahari dung beetle assemblages (Scarabaeinae: Scarabaeidae) in three conserved, now disjunct, natural regions (separated by settled regions and game fences - See Fig. 2, Chapter 2). Ideally, this work would have compared data collected before and after the migratory system was interrupted by settlements and fencing, but only an “after the event” study is possible now. However, the present dung beetle assemblages will reflect past history to an extent (Davis & Scholtz, 2001).

Therefore the study examines the effect of the climatic gradient across the current reserve system relative to present local mammal faunas, which also change relative to the gradient. Trends in dung type distribution may greatly influence the distribution patterns of dung beetle fauna. Inspired by this and the information about changes in climate and vegetation physiognomy the following hypotheses were formulated. These hypotheses were tested using data collected between December 2005 and April 2006 from three conserved areas across the Botswana Kalahari.

(1) Species richness will decline from NE to SW, possibly related to fewer dung types and less suitable climatic conditions. Species richness may be limited by fewer rainfall events, fewer dung types, and lower vegetation heterogeneity.

(2) Niche separation (dung type specificity) will be reduced across the climatic gradient leading to more niche overlap, possibly owing to harsher conditions favouring less selectivity between a reduced number and density of dung types (reduction in available resources) with fewer competitors (lower species richness).

(3) Dung type associations will change from NE to SW to reflect local dung type availability.

(4) Carrion assemblages will change from NE to SW reflecting changes in density of scavenging mammals and reductions in climatic suitability.

(5) Greater endemism to the unique conditions of the SW will lead to distinct patterns of species turnover from the filtered out non-psammophilous savanna fauna in the NE (beta diversity) with no net change in local alpha diversity values due to arid adaptation of the SW endemic species.

(6) Distinct differences in species assemblage structure will result from this turnover to reflect the climatic and ecoregion classification for the area.

In addition to the introduction (Chapter 1) and description of the study area and methodological approach (Chapter 2), this thesis comprises five chapters on the contribution of regional and local spatial factors to dung beetle distribution patterns across the climatic gradient in the Botswana Kalahari. It examines the biogeographical distribution and composition of the Botswana Kalahari dung beetle fauna (Chapter 3). It considers changes in species and functional diversity with increasing aridity (Chapter 4). It determines how species abundance composition changes with increasing aridity and how well it corresponds to ecoregion classification (Chapter 5). It also determines patterns of species bait-type association and examines if they change with increasing aridity (Chapter 6). The closing chapter (7) discusses the overall contribution of historical, regional and local ecological factors to the results and their implications for regional conservation management. The appendices consist of a paper published in *Environmental Entomology* that emanates from preliminary work undertaken in the first year of the study (Tshikae *et al.*, 2008) as well as a number of summaries of raw data and expanded results for statistical analyses.

CHAPTER 2 STUDY AREA, TRAPPING METHODS AND HYPOTHETICAL APPROACH

2.1 Study region

The study was restricted to the deep sands of the southern Kalahari Basin, which lie at >930 m above sea level. Within Botswana, the area stretches from the northeast to the southwest of the country across a climatic, vegetation and dung type gradient. The gradient straddles three climatic regions (Walter & Lieth, 1964; Davis, 1997), and two ecoregions (Olson *et al.*, 2001; Cowling *et al.*, 2003) each with differing mammal compositions. The gradsect also traverses three large reserve complexes, now isolated by farming activities, comprising Chobe National Park (NP), Central Kalahari Game Reserve (CKGR) and Kgalagadi Transfrontier Park (Fig. 2.1). The reserves are located in different annual rainfall regimes along the climatic gradient. The gradsect commenced in Chobe NP in the higher rainfall region of the northeast (600-700 mm p/a), traversed the CKGR (400-450 mm p/a), and ended in the Kgalagadi Transfrontier Park in the lower rainfall region of the southwest (150-300 mm p/a) (Botswana Meteorological Services Department unpubl. data). Six study areas were chosen along the survey transect, two in each reserve complex. Three study sites were selected in each study area.

The study region is an important wildlife conservation and management area with anthropogenic activities dominating the landscape between and around the reserves, primarily pastoral farming (Moleele & Mainah, 2003, Astrom, 2003). Mammal diversity and densities vary between different reserves. Most mammals across the study region have a wide habitat tolerance, yet distribution is mainly dictated by availability of surface water. Accessibility to surface water, or the lack of it, has historically influenced the mammal distribution and migratory patterns within and between reserves (Verlinden, 1995) and consequently the relative availability of principal dung types across the region.

The principal dung types may be summarized as 1) large fairly-dry coarse-fibred droppings of large non-ruminant herbivores, 2) large moist fine-fibred pads of large ruminant herbivores, 3) small dry pellets from small and medium sized herbivores, and 4) small, strongly-odoured droppings from omnivores and carnivores. Recent census data support a NE / SW bias in the availability of these dung types (Table 2.1). In the mesic NE, Chobe NP harbours a greater diversity of mammals than any other reserve in Botswana and all dung types are represented. This includes large coarse droppings or large moist pads dropped by high populations of water dependent taxa such as elephant or buffalo (Botswana Wildlife and National Parks Department, 2004 unpubl. data). There is also representation by pellets dropped by antelope or small strong smelling droppings dropped by omnivores such as baboon. However, from the central to the arid southwest Kalahari, the mammal composition changes to one dominated by the less water dependent antelope, thus making pellets the dominant dung type with some carnivore dung also present. Summary information on mammal distribution and density is provided in Table 2.1.

Several studies carried out in Africa (Davis, 1994; Tshikae *et al.*, 2008), Europe (Martin Piera & Lobo, 1996) and South America (Peck & Howden, 1984) showed that dung beetle display selectivity between different dung types. Therefore absence or loss of particular dung types is likely to influence diversity and spatial patterns of distribution (e.g. Davis, 1997). Differences in dung beetle assemblage structure may also be induced by differences in the amounts of dung dropped by different animals, as was the case in France where a change from sheep to cattle caused a 300% increase in the amount of dung, thus inducing a 300% increase in dung beetle abundance (Lumaret *et al.*, 1992). There is also the effect on assemblages of differences in the frequency of dung (higher diversity where there are concentrations of dung versus lower diversity where dung is more scarce) (Lobo *et al.*, 2006). Thus differences in the relative availability of different dung types would be expected to trigger changes in the dung beetle community across the climatic gradient in Botswana.

Habitat constraints and competitive ability are also important factors that can greatly influence trends in dung beetle community organization (Davis, 1996a). The interactive effect of these constraints is manifest in body size and dung exploitation behaviour especially on different soil types. For example near Pretoria, on sand the principal groups were typified by large ball rollers and large fast burying tunnellers while, on clay, groups were typified by large and small rollers plus small tunnellers (Davis, 1996a). The Kalahari basin, however, is dominated by a continuous swathe of Cenozoic sands which makes the habitat influence in particular soil type an important factor in community organization across the gradient. Hence both abiotic and biotic interactions would be expected to explain dung beetle community organization across the Kalahari basin.

2.1.1 Description of study areas

Chobe NP is situated in the northernmost part of Botswana with its northern boundary defined by the Chobe River (Fig. 2.1). It extends south-westwards to encompass the currently dry Savuti channel along which water used to drain towards the Mababe depression. Chobe NP lies within the mid-summer rainfall region and is subject to climate type II3g (Walter & Lieth, 1964; Davis, 1997). One study area was situated in the north on the fringes of the Chobe River at 893.9 m above sea level with mean annual temperatures exceeding 28 ^{o}C and mean annual rainfall of 652.3 mm. The rainy season commences in October reaching its seasonal peak in December/ January. Although most sites were covered by trees and shrubs, in which the dominant tree species was *Baikiaea plurijuga* (Table 2.3), the three sites were selected to reflect the range in tree cover from the most to least dense. Chobe NP is particularly noted for its high populations of elephant, buffalo, zebra, impala, and many other species of antelope (Table 2.1). At Chobe NP all of the principal dung types are present (Davis & Scholtz, 2001; Tshikae *et al.*, 2008).

A second study area was situated in the Savuti channel on the fringes of the Mababe depression (Table 2.3) nearly 200 km southwest of the Chobe River at Kasane. Savuti lies within the same climate type as the Chobe River study area and annual rainfall averages 592.3 mm. Although most of Savuti now lacks surface water, some areas become marshy for a few months in the rainy season. The two main vegetation types were *Colophospermum mopane* dominated woodlands and mixed shrubland dominated by *Combretum* spp.

Generally Savuti features similar dung types to those available on the Chobe River (Table 2.1).

In the Kalahari Game Reserve (CKGR), there were two study areas selected, one in the north (NC-Kalahari) and another in the south (Khutse). The northern study area formed part of the historical range of elephants (Smithers, 1971) at the fringes of the Makgadikgadi Depression although their southernmost limit is now in the southern part of the Chobe park complex at Moremi Game Reserve. The NC-Kalahari sites lay 165 Km southeast of the now dry Lake Ngami a historically important habitat for wildlife including large indigenous mammals. The lake dried up completely during a severe drought in 1965-66. Although abundant rains subsequently filled it again, it dried up once more in the 1980s (Encyclopaedia Britannica, 2009). Despite being occasionally filled by abundant seasonal rains, it has now shrunk in expanse and is currently subjected to grazing by cattle, horses and other livestock (Magole, 2009). The northern study area is characterized by an undulating topography comprising a number of small dry pans surrounded by deep sand. Although tall grass dominates the landscape, there are small patches of *Acacia*, *Lonchocarpus nelsii* and *Grewia* shrubs on dunes. The annual rainfall ranges from 300 – 362 mm. The dominant mammals, at the present time, are gemsbok and springbok, making pellets the dominant dung type.

The study area in the south was situated within Khutse Game Reserve in the southernmost part of CKGR. The annual rainfall, though variable and unpredictable, averages 376.7 mm mostly in the summer months of September – April with a seasonal peak in January (Fig. 2.3). Khutse lies within the mid-summer rainfall climate type (II4c). It is arid with no surface water. The dominant woody plant species were *L. nelsii* and *Terminalia sericea*. Dominant mammals were gemsbok and springbok, again, making pellets the dominant principal dung type.

In the southwest region, two study areas were situated in the Kgalagadi Transfrontier Park, one in the north in the former Mabuasehube Game Reserve, and one in the southwest near Two-Rivers, within the dunefield of the former Gemsbok National Park. Mabuasehube is an arid grassland-dominated landscape that includes *Acacia* shrubs widely dispersed within the grassland matrix. At Two-Rivers (SW-Kalahari), the extensive dunes are mostly well vegetated and relatively stable. The lower slopes are characterized by patches of *Acacia haematoxylon* and *Rhigozium* species. The upper slopes comprise mostly grassland except for a few dune tops that are bare and rolling. The region is arid with long-term average annual rainfall of 284.7 mm in Mabuasehube and 193.3 mm in the former Gemsbok National Park. Both study areas lie in the late summer rainfall region, with seasonal peaks in precipitation shifting towards March and April, particularly in the southwest (Fig. 2.3b). The study area has no persistent surface water and is in climate type II(III)a at the southern edge of the Kalahari region, beyond which lies the hyper-arid Nama/Karoo. Dominant mammals' include gemsbok and wildebeest (Table 2.3) thus making pellets the dominant dung type.

2.1.2 Trapping sites

Whilst every attempt was made to standardize the conditions at study sites, their selection was dictated by logistics and habitat availability. With regard to logistics, the three trapping sites in each of the six study areas were at the maximum possible distance from one another that could be travelled within the short time allotted for processing the catch (about 2-3 hours). This was dependent on road conditions (mostly sandy tracks), travelling regulations (time), and distance from designated camping facilities. These regulations also meant that the study sites were primarily near the borders of conserved regions.

Vegetation and soil type has a strong influence on species abundance structure of dung beetle assemblages (Davis, 1996b; Davis *et al.*, 2002). Therefore, vegetation and soils were standardized as far as possible but there were some unavoidable differences across the climatic gradient (Tables 2.2., 2.3.). In general, study sites were restricted to deep Kalahari sands where there was a heavy presence of wildlife. In four study areas continuous expanses of aeolian sand deposits dominated the landscape (Chobe Khutse, Mabuasehube and SW-Kalahari) (Table 2.2) interrupted by a few pans in the southwest. However Savuti, was centred in the Mababe Depression that represents a fossil lagoon while NC-Kalahari was centred at the edge of the Makgadikgadi Depression and comprised a mosaic of parabolic dunes within the bed of a fossil lagoon. Here, trapping sites were placed 7–12 km apart in pockets of deep sand that stretched for 2-3 km adjacent to and between the many patches of lagoon bed of differing sizes.

Three soil samples were taken from a depth of 20-25 cm at each study site, one at each end and one in the centre of each trap line. These were analysed for proportions of silt, clay and sand grains, and one –way analysis of variance was used to test for differences in soil composition. The results indicate that there were significant differences in soil composition between some study areas (Table 2.2) although all sites comprised from 94.0% to 99.5% sand.

Various measurements were made to determine vegetation density at selected study sites. Although most of the gradsect comprised open shrubland or grassland vegetation, Chobe was mostly densely wooded (Table 2.3). The three sites were selected to represent a range from the most open to the most closed vegetation. At wooded study sites, the height of five selected trees and/or shrubs was estimated by eye. Shrubs were classified as up to 4.5m tall and trees as over 4.5m. For each selected tree or shrub, the distance was measured from its centre to the centre of the four nearest neighbouring trees or shrubs in the cardinal directions of north, east, south, and west, with permitted deviation up to ±45°. In the case of a tree, further measurements were made from the trunk to the edge of its canopy, then to the edge of the nearest neighbour’s canopy and then to its trunk. In the case of shrubs with multiple stems, measurements were taken from the central stems. These measurements of woody vegetation were used to generate cover density data (Table 2.3, Appendix A1). Density of grass and herbaceous surface cover were measured at each of the 18 study sites by walking transects of 100 steps (Davis, *et al.*, 2002). Surface cover was scored as present or absent depending on whether or not grass or herbs made contact with the boot tip at each pace. All results were expressed as percentages.

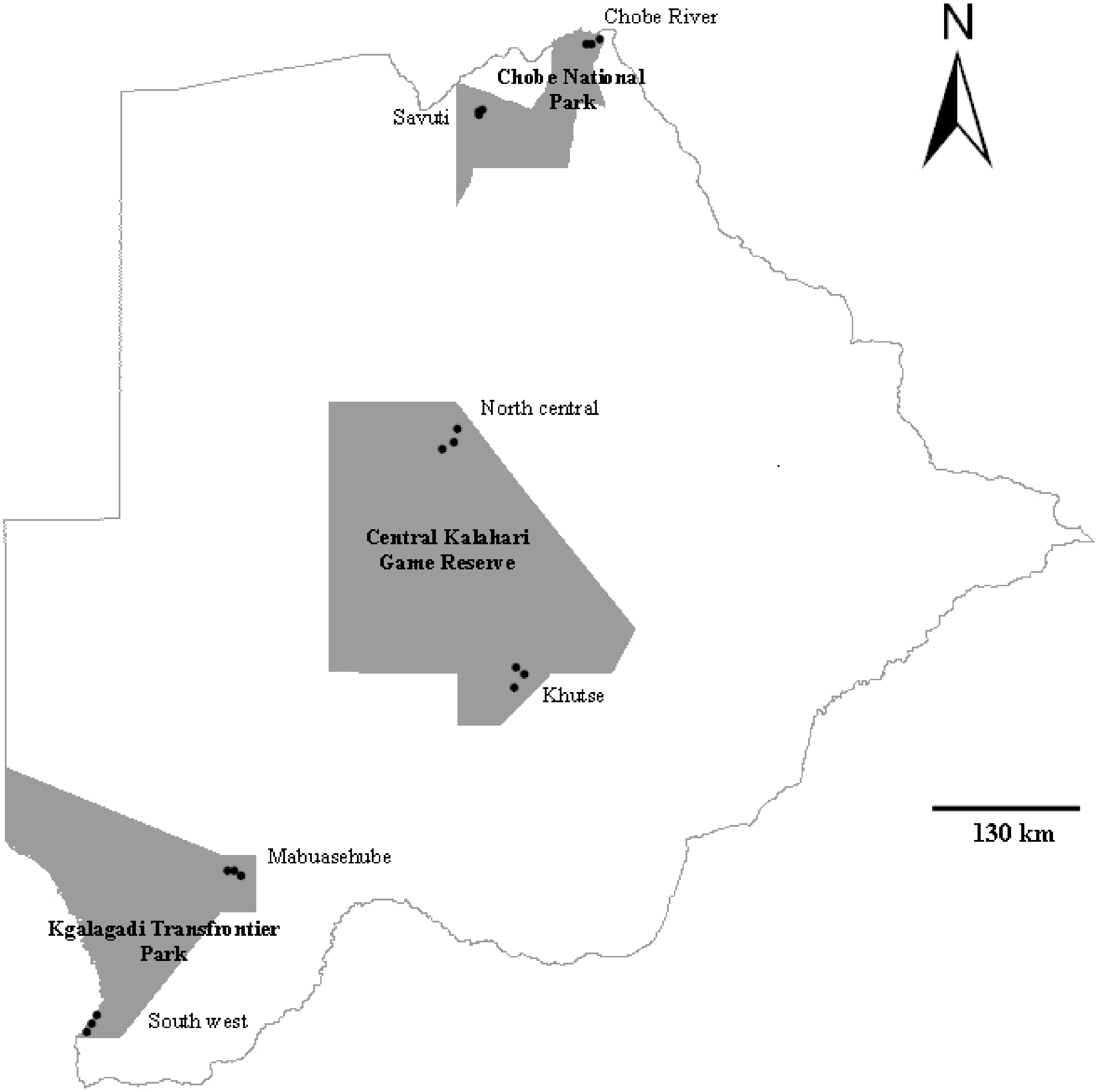


Figure 2.1 Map of Botswana showing principal conservation areas (Grey) and the location of trapping sites (●)

Table 2.1. Estimated density per 100 Km^2 of mammals in major conservation areas in Botswana Kalahari Basin (Department of Wildlife & National Parks, Census Report 2004, Botswana)

	Density per 100 km^2					
Indigenous mammals	Chobe NP 10589 km^2	CKGR 52800 km^2	Khutse 2500 km^2	K Trans Park 28000 km^2	Dung type[1]	Unit Mass (kg)[2]
Elephant	304.7	0.0	0.0	0.0	Monogastric	1725
Zebra	10.9	0.0	0.0	0.0	Monogastric	313
Warthog	1.6	0.2	0.0	0.0	Monogastric	79
Buffalo	100.1	0.0	0.0	0.0	Pads	450
Giraffe	9.9	2.2	6.2	0.0	Pellet	1192
Eland	2.1	15.8	2.0	14.8	Pellet	840
Roan antelope	0.2	0.0	0.0	0.0	Pellet	270
Waterbuck	1.7	0.0	0.0	0.0	Pellet	260
Gemsbok	0.0	58.0	25.7	109.2	Pellet	240
Sable	1.1	0.0	0.0	0.0	Pellet	230
Kudu	4.1	10.9	6.2	1.2	Pellet	228
Lechwe	1.9	0.0	0.0	0.0	Pellet	192
Hartebeest	0.0	10.8	29.8	28.1	Pellet	165
Wildebeest	1.4	2.9	7.8	9.0	Pellet	134
Impala	15.5	0.0	0.0	0.0	Pellet	55
Springbok	0.0	7.4	4.1	8.8	Pellet	41
Duiker	0.0	1.0	2.0	0.3	Pellet	21
Steenbok	0.9	6.8	2.0	15.2	Pellet	11
Baboon	2.7	0.0	5.8	0.0	Omnivore	31.8
Lion	0.9	0.4	2.0	0.2	Carnivore	190
Hyena(spotted)	0.1	0.3	2.0	0.7	Carnivore	59
Cheetah	0.9	0.3	6.2	0.6	Carnivore	54
Hyena (brown)	0.7	0.05	44.0	3.9	Carnivore	47
Jackal	0.0	0.2	0.0	0.5	Carnivore	8
Bat-eared Fox	0.0	0.0	0.0	0.5	Carnivore	4
Domestic Livestock						
Cattle	0.0	0.0	12.3	2.9	Pads	270
Sheep + Goats	0.0	0.0	0.0	7.5	Pellet	27.5

[1] Dung type classification is according to Davis & Scholtz, 2001; Omnivore, small, strongly-odoured dung dropped primarily by primates; Carnivore, small, strongly-odoured dung dropped primarily by predators and scavengers; Pellets, pellets dropped by both large and small herbivores, some also known to drop small pats when eating exceptionally wet diet; Pads, fine-fibred dung dropped by large ruminant herbivores (e.g. cattle and buffalo); Monogastric, coarse-fibred dung of non ruminant herbivores (elephant, zebra, horse, rhinoceros, donkeys). *Predators are mostly nocturnal; hence population size has not been effectively estimated from daytime aerial surveys (Botswana Central Statistics organisation, 2005). The cited information on predators has been extracted from other gross published estimates in the northern and southern zones (Botswana Central Statistics Organisation, 2005). [2] Wild mammal average mass according to The Mammals of Southern African Subregion (Skinner & Chimimba, 2005)

Table 2.2. Soil grain-size analysis between study areas and descriptions of land region and land systems at each study areas across the climatic gradient

	Soil grain analysis			
	% silt	% Clay	% sand[1]	Description of land Region and land Systems[2]
Chobe River	1.87	2.32	94.54^{a}	Aeolian sand deposits with almost flat to gently undulating plain
Savuti	0.63	1.87	96.18^{ab}	Depression with almost flat fossil lagoon
NC-Kalahari	0.90	2.23	95.80^{a}	Depression with undulating parabolic dune system and flat fossil lagoon
Khutse	0.00	1.00	99.24^{b}	Aeolian sand deposits with flat calcrete patches
Mabuasehube	1.95	1.05	98.57^{b}	Aeolian sand deposits with almost flat plain with few pans
Sw-Kalahari	0.30	2.52	96.51^{ab}	Aeolian sand deposits with undulating to rolling longitudinal dune system

[1] In the % sand column, values that are followed by different letters are significantly different ($P < 0.05$, Tukey's HSD).
[2] Descriptions of land regions and land systems were taken from the Land Systems Map of Botswana; soil mapping and advisory services project, AG: DP/BOT/ 85/ 011, by Wit & de Bekker, 1990; accessed at (http://eusoils.jrc.ec.europa.eu/esdb_archive/eudasm/africa/lists/cbw.htm)

2.1.3. Trap description and data collection

At each site, 20 pitfall traps were arranged in a 10 x 2 grid (Fig. 2.2.). Each neighbouring pitfall trap was separated by 50 m as recommended by Larsen & Forsyth (2005). Each consisted of a 5-litre plastic bucket buried into the sand up to its rim with a little soapy water at its base to immobilize the catch (Davis *et al.*, 2002). Baits were wrapped in chiffon that allowed the spreading out of volatiles yet excluded dung beetles. Baits were placed in wrapped lumps on wires across the buckets. Traps were baited in non-random sequence with one of four different mammal dung types of similar size, *c.*250 ml, or with a small carrion bait of *c.*100 ml. The baiting sequence was, pig, cattle, elephant, carrion and sheep dung repeated four times along the grid.

Although the study was conducted in conservation areas, it was difficult to collect sufficient dung for baits in the field. Therefore, the dung of domesticated pig, cattle, and sheep, were used as surrogates for indigenous omnivore, large ruminant, or pellet-dropping mammals represented in both past and present faunas across the study region. These were readily available around Pretoria. Baits of pig, cattle and sheep dung, or carrion (rotten chicken livers), were prepared, deep frozen, and thawed before use. Elephant dung becomes unattractive to dung beetles following freezing. Therefore, fresh dung was collected at Chobe, Savuti, or at Pretoria Zoo and baits were freshly made in the field.

Table 2.3. Summary description of vegetative cover at study sites across the Botswana Kalahari Basin (see Appendix A1)

		Percentage Cover (Mean ± SD)		
Locality	**Vegetation description**	**Grass**	**Shrubs**	**Trees**
Chobe River	*Baikiaea* woodland, few shrubs and sparse grass	**38.00 ± 5.29**	**38.43 ± 4.99**	**60.39 ± 9.78**
Savuti	*Mopane* shrubland and short sparse grass tufts	**33.92 ± 11.11**	**62.47 ± 16.84**	
NC-Kalahari	Grassland with open *Acacia* woodland and sparse shrubs	**65.50 ± 10.13**	**37.38 ± 10.97**	**38.23 ± 25.23**
Khutse	Sparse shrubs and short grass tufts	**59.25 ± 24.65**	**34.85 ± 6.59**	
Mabuasehube	Grassland with sparse shrubs	**58.08 ± 5.30**	**26.00 ± 9.42**	
SW-Kalahari	Sand dunes, few sparse trees, shrubs, herbs and grass	**22.25 ± 8.79**	**13.83 ± 3.27**	**17.81 ± 6.51**

In each study area, trapping was conducted for a single 48 hour period. These trapping occasions were spread from December 2005 till April 2006 (Fig. 2.2.) to coincide with the seasonal peaks in activity by dung beetles in the mid- and late-summer rainfall regions of Southern Africa (Davis, 1996; 1997; Fig. 2.3). Traps were baited in the early morning and rebaited every 12 hours (late afternoon or early morning) to present fresh dung to both diurnal and nocturnal dung beetle species. Trap catches were collected after 24 hours and 48 hours and preserved in 97.6% ethanol. Material from this study, including voucher specimens, has been deposited in the reference collection of the Department of National Museum, Monuments and Art Gallery in Botswana.

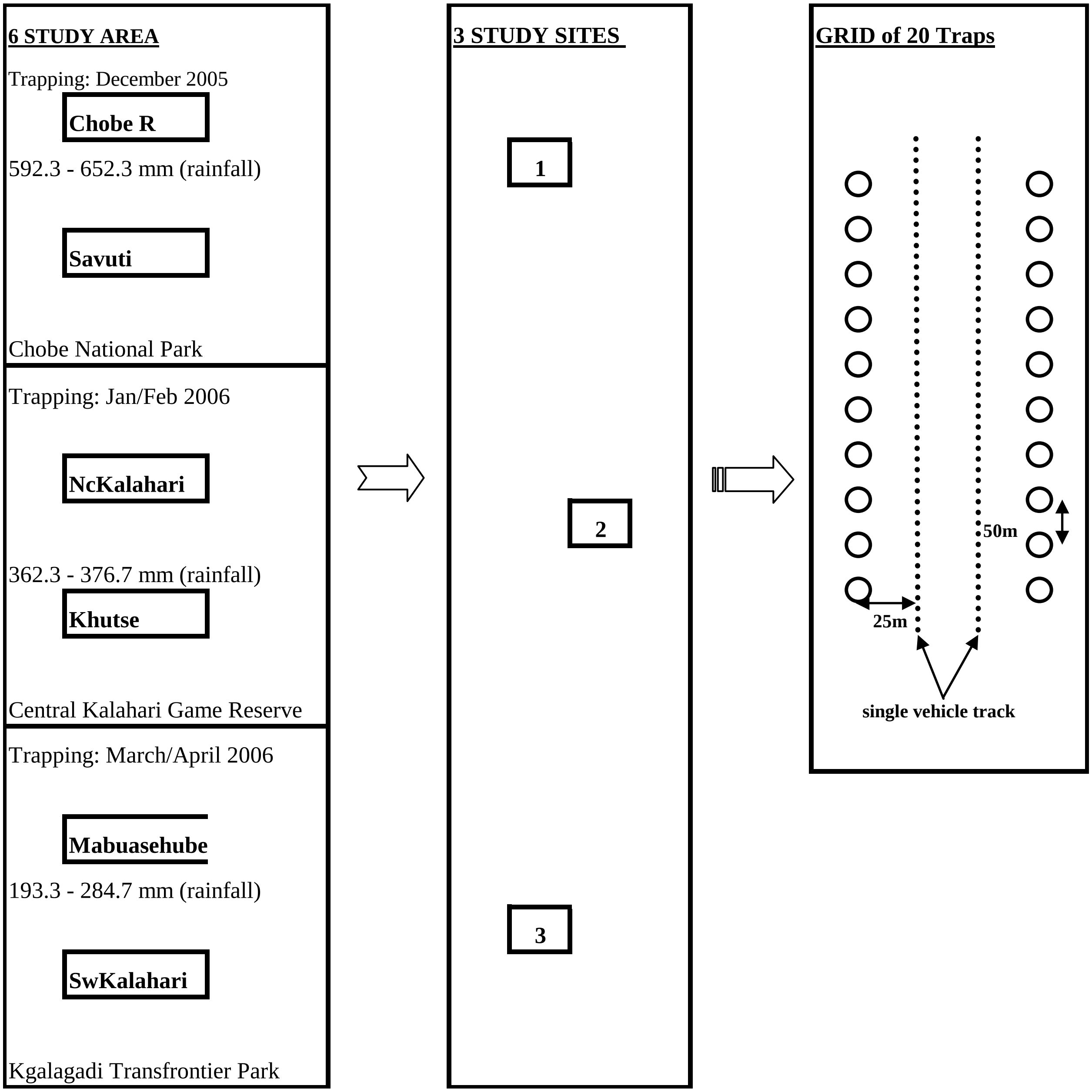


Figure 2.2. **Schematic diagrams showing the 6 study areas, 3 sites in each study area and grid of 20 traps at each study site 10 on either side of the vehicle track (this diagram is not according to scale)**

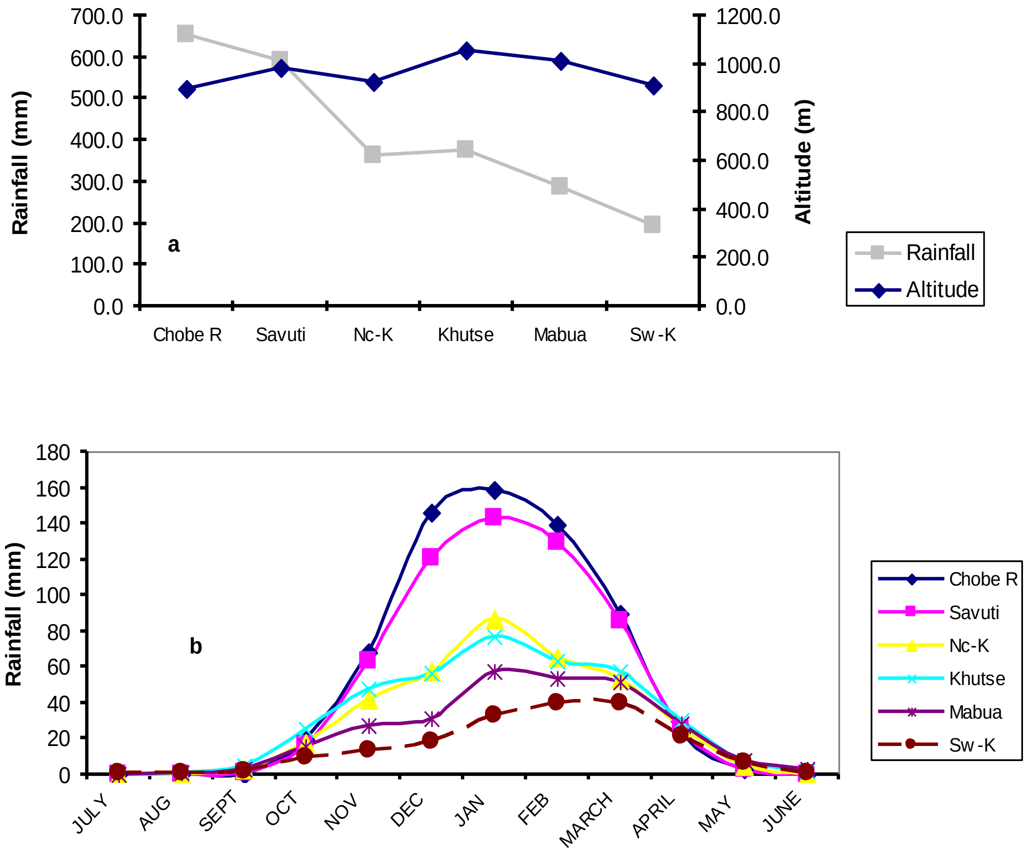


Figure 2.3. **Altitude and average seasonal rainfall (a) and the average monthly seasonal rainfall (b) in each study area**

2.2. Hypothetical approach

2.2.1. Overview

The dung beetle fauna of the study area was examined at a series of different scales from sub-continental (southern Africa south of 15^{o} S), to regional (Botswana Kalahari Basin), to local represented by each of the 6 study areas (Figs. 2.1., 2.2).

As the Botswana Kalahari represents a centre of endemism (Davis, 1997), particularly to the southwest, a study was made to determine if there were clear biogeographical patterns shown by the recorded dung beetle species (Chapter 3). As the study region also showed a clear climatic gradient across three climate types (Walter & Lieth, 1964) and two ecoregions (Olson *et al.*, 2001), various statistical methods were used to test for continuous ecological patterns or patterns of faunal division across the gradient (Chapters 4, 5). The Botswana Kalahari once supported a migratory system from arid SW and mesic NE centres. It was hypothesized that resource partitioning might be more developed in the mesic NE, where a wider range of food types was present. Therefore the results were tested to determine if niche widths increased and resource partitioning decreased towards the SW where the presented dung types comprised a mixture of those still present and those never or no longer present after dryer climate developed in the Pliocene and the rivers dried up. This was combined with a study on dung type associations of the recorded species (Chapter 6).

CHAPTER 3 BIOGEOGRAPHICAL DISTRIBUTION PATTERNS OF THE BOTSWANA DUNG BEETLE FAUNA IN SOUTHERN AFRICA AND THE LOCAL BIOGEOGRAPHICAL COMPOSITION OF ASSEMBLAGES ACROSS THE BOTSWANA KALAHARI

Introduction

The geological processes and climatic oscillations during the Pliocene and Pleistocene have substantially influenced the African fauna and flora (Vrba, 1985; Linder, 2003). Chapters 1 and 2 have provided background information on the development of the Kalahari sands as a physical barrier and the aridity as a filter of savanna elements centred in the moist regions (Wright, 1978). The increasing aridity to the SW Kalahari is paralleled by changes in vegetation physiognomic structure (Scholes *et al.*, 2004; Ringrose *et al.*, 2002) and mammal assemblages that in turn would have affected other species that depend on them through changes in available resources. The present Kalahari basin environmental setting of the xeric and mesic ecoregions (Olson *et al.*, 2001) has potential effects on past lineage turnover (Vrba, 1985) and the current biogeographical patterns may reflect this past history.

Dung beetles are essentially good indicators of biogeographical patterns (Davis, 1997; Davis & Scholtz, 2001). They have a long history of association with mammal dung (Davis, 2001; Davis & Scholtz, 2002) and respond to microhabitat variations (Davis, 1996). In southern Africa there are *ca*.582 species of dung beetles occurring south of 15° S (Doube, 1991; Davis, 1997). Most species have broad distributions in a wide range of habitats (Davis *et al.*, 2009; Scholtz *et al.*, 2009) and a few species have restricted distributions (Davis, 2002). A substantial body of evidence has linked these distribution patterns to gradients in climate, altitude, soil and vegetation type or indigenous large mammal diversity and distribution (Davis, 1997; Davis & Scholtz, 2001, Scholtz *et al.*, 2009). Although several recent studies have documented faunal biogeographical compositions across the Kalahari basin (Barker, 1993; Davis, 1997; Prendini, 2005) and along the Karoo/Kalahari ecotones

(Davis & Scholtz, 2004; Davis *et al.*, 2008) some of these studies were undertaken with limited data for Botswana faunas (Davis, 1997; Prendini, 2005).

The present study examines biogeographical composition of dung beetle assemblages surveyed within the Kalahari basin across a climate gradient using an improved data set. It was hypothesized that the species distributions would classify into two major groups, NE savanna and SW Kalahari centred taxa (Davis, 1997; Davis & Scholtz, 2004; Davis *et al.*, 2008). It was expected that the results would provide some support for the hypothesis that the Kalahari deep sands act as a geographical barrier to many non-psammophilous savanna species and as filter for those psammophilous species intolerant of increasingly more arid conditions. This would account for the species turnover (Chapter 4) and endemism to the southwest demonstrated by Davis (1997).

3.2. Analytical Methods

3.2.1. Biogeographical composition of the Botswana dung beetle fauna

Multivariate techniques were used to determine the biogeographical distribution patterns shown by 140 dung beetle species recorded across the Botswana Kalahari basin. A data matrix was constructed using unpublished Southern African data from the former collection of the Australian CSIRO Dung Beetle Research Unit (now part of the National Collection of Insects, Pretoria, South Africa) and published records (Scholtz & Howden, 1987; Steenkamp & Chown, 1996; Davis *et al.*, 2003). The data matrix comprised 140 species by the number of degree squares occupied by each species in 25 southern African climate types (Fig 3.1). Before analysis for biogeographical patterns, the 140 x 25 data matrix was fourth-root-transformed to normalize the data and converted to a correlation matrix for 140 species. The matrix was subjected to factor analysis by STATISTICA release 9 (StatSoft Inc., 1994 - 2005) using principal components as the method of factor mining. Biogeographical clusters of species were defined at the default factor loading of 0.7 or greater.

Hierarchical analysis of oblique factors was conducted on the principal components factor analysis. The technique first rotates ordination axes through defined clusters, which has the effect of increasing the coalescence of data points around each factor and maximizing between cluster variance. A second ordination is conducted on the resulting ordinate values for the defined clusters. This generates primary factors (variance unique to a cluster) and secondary factors (variance shared between clusters). Regressions of these extended orthogonal factors on the original oblique factors generate a Pearson's r correlation coefficient. Multiplying these r values generate r^2 values (coefficient of determination), which represent the decimal proportion of variance accounted for by each extended factor within each cluster.

A further ordination technique, multi-dimensional scaling (MDS) (Primer v.5) was used to determine if similar results are obtained using a different analytical method.

The Proportional biogeographical composition of species abundance was determined for each of the five bait types for the six study areas. Cross-tabulation tables with goodness of fit tests (http://home.ubalt.edu/ntsbarsh/Business-stat/otherapplets/Catego.htm) were used to determine any significant difference between the biogeographical compositions of different study areas.

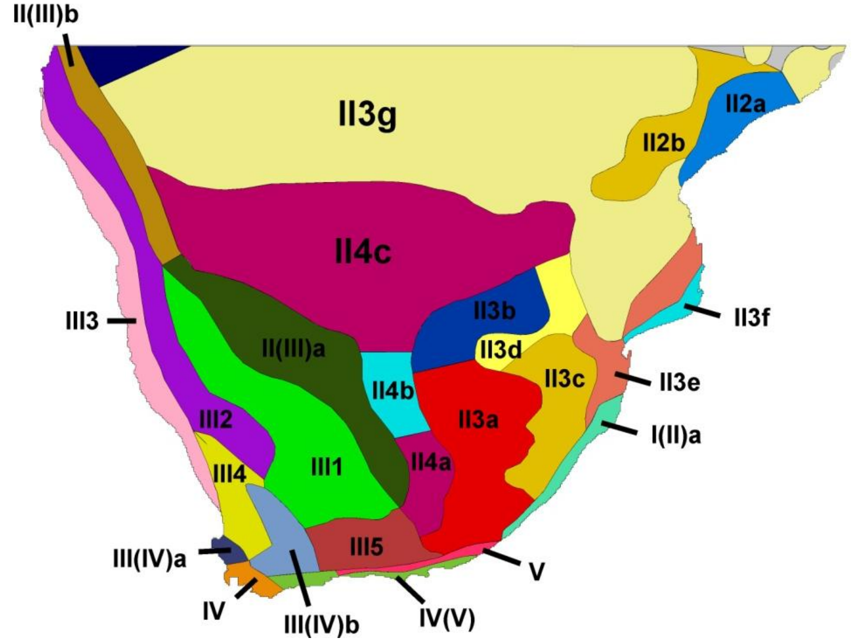


Figure 3.1. A map of southern Africa showing 25 Climate types defined by Walter and Lieth (1964)

3.3. Results

3.3.1. Influence of sub continental-scale factors on the species recorded in the survey area

Both ordination analyses yielded similar patterns of species group separation (Figs 3.2, 3.3). Four principal biogeographical groups were defined using factor analysis, plus one other group that comprised poorly recorded species (Fig. 3.2). This group classification was imposed on the MDS ordination plot to demonstrate the similarity in patterns (Fig. 3.3). The mostly high coefficient of determination values (r^2) for the correlation between oblique factors and the shared extended factor in Table 3.1., suggest a great deal of overlap between most clusters except cluster 2. The higher r^2 value for the correlations between oblique factor 2 and extended primary factor 2 indicates a more strongly defined unique character of biogeographical separation for that cluster. This cluster group contributes by far the greatest proportion of individuals to the faunas in the southwest of Botswana (Table 3.2.).

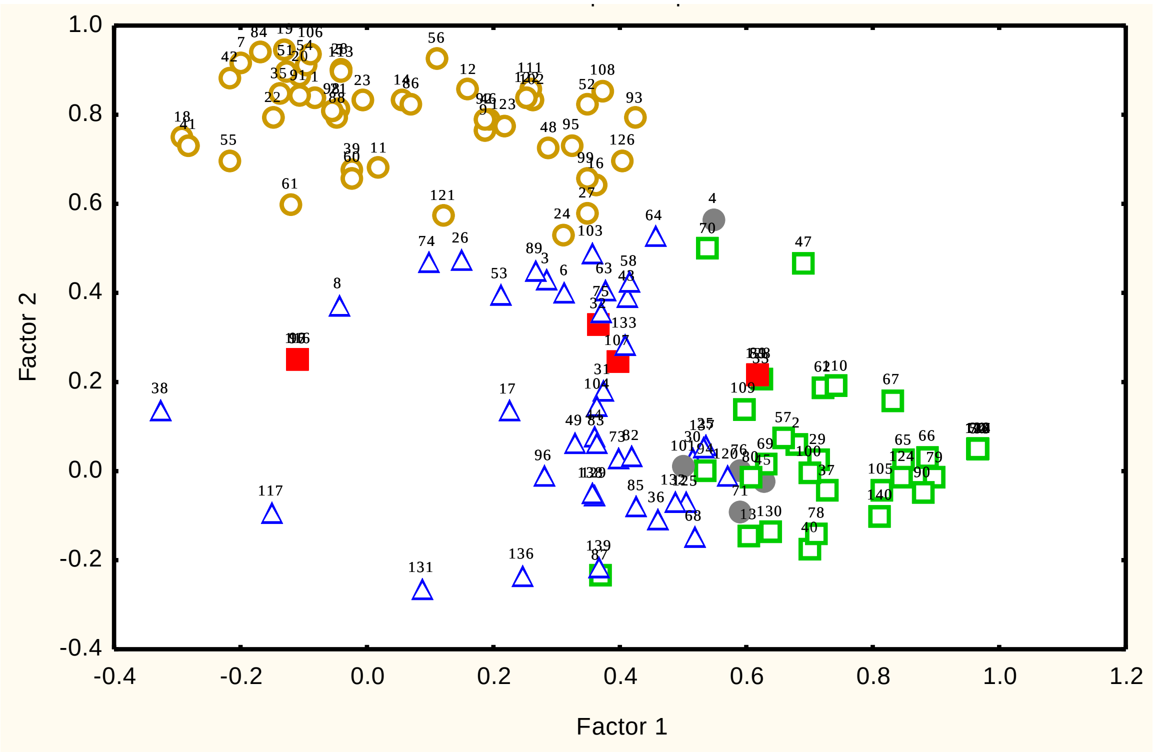


Figure 3.2. **Ordination plot of species distributions in southern Africa derived from Factor Analysis (Cluster 2 = southwest bias (open circle), Cluster 4 = widespread/northeast (closed circle), Cluster 3 = widespread (triangle), Cluster 1 = northeast bias (open square), Cluster 5 = poorly recorded (closed square) (See Appendix A4 for key to species numbers)**

The maps of overall distribution pattern of each species group in southern Africa, mostly suggest a great deal of spatial overlap (Fig. 3.4.). This is implicit in the results shown by Table 3.1 (see high r^2 values for correlations between oblique factors and the shared extended orthogonal factor in 3 out of 4 cases). Only Cluster 2 is shown to have a more clearly defined biogeographical character by the high r^2 for the correlation between the oblique and primary extended factor P2. In the maps, the relative centring of the cluster groups are probably obscured as some data points represent only one species record whereas others represent many species. The ordination plots, however, show clear group separations (Figs 3.3., 3.4.). The relative positioning of these cluster groups reflect their biogeographical pattern centred either to the northeast or southwest with widespread species occupying the intervening ordinal space.

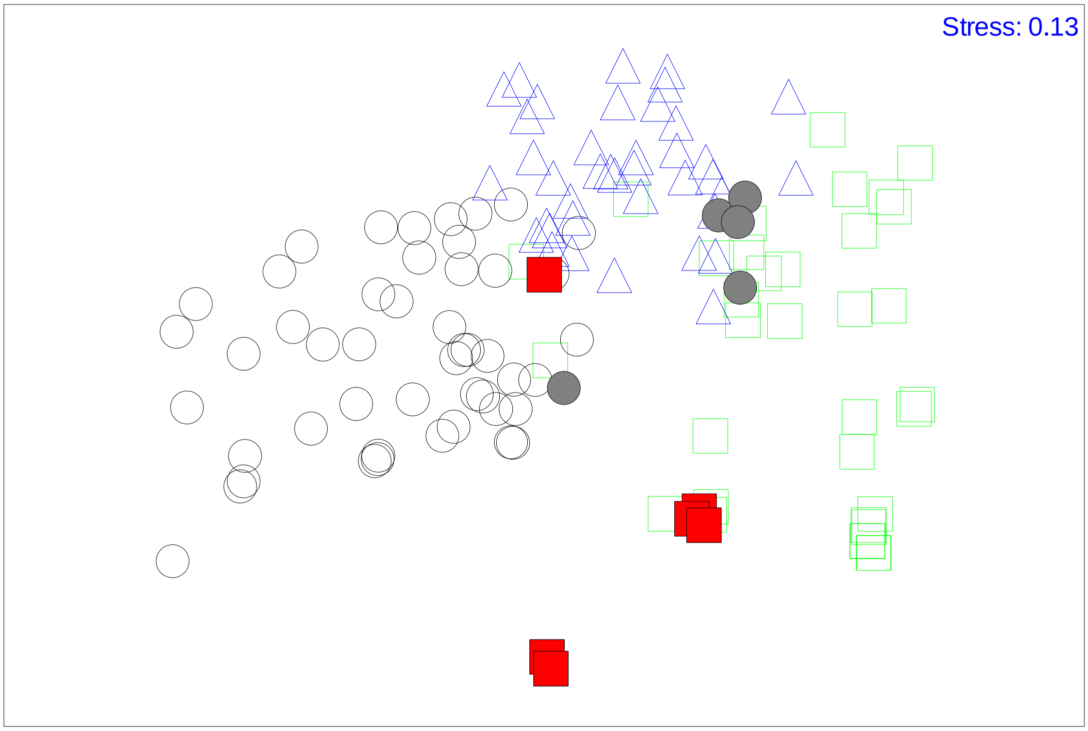


Figure 3.3. **MDS ordination plot for five biogeographical clusters of species (Cluster 2 = southwest bias (open circle), Cluster 4 = widespread/northeast (closed circle), Cluster 3 = widespread (triangle), Cluster 1 = northeast bias (open square), Cluster 5 = poorly recorded (closed square)**

The clusters of species showing widespread, northeast, or southwest biogeographical bias showed contrasting patterns of proportional representation across the sampling sites in the Kalahari. Species with a widespread / northeast or northeast bias showed a sharp decline in proportional abundance to the southwest whereas species with a southwest bias steadily increased (Table 3.2.). The proportional abundance of widespread species was high in the northeast savanna (Chobe) and in the transitional zone (northeast edge of the Kalahari at Khutse) (Table 3.2.).

The proportional biogeographical compositions of species attracted to each bait type largely reflected the general trends across the study areas (Table 3.2.) although there was a great deal of variation to the northeast (Table 3.3., Appendix 3.3). In terms of proportional abundance, species showing widespread/northeast or northeast biogeographical bias were, again, principally centred in the more mesic northeast savanna (Chobe, Savuti). Those showing southwest biogeographical bias were well represented from the arid southwest to the southwest of the more mesic savanna (SW-Kalahari to Savuti) but mostly declined in representation to the northeast (Table 3.3). Those showing widespread biogeographical distribution were centred in the northeast of the savanna and northeast of the Kalahari (Chobe, Khutse). Also there was a slight variation in biogeographical composition between bait types in the NE although Kalahari endemics dominated all bait types in the SW (typified by low S.D.). Three to four patterns were well represented in Chobe and Savuti, two in NC-Kalahari and Khutse, and only one in Mabuasehube and SW-Kalahari, thus showing reduction in biogeographical diversity to the SW (Tables 3.2, 3.3).

Table 3.1. Correlations between oblique factor loadings (varimax-normalized rotated) and extended factors derived from hierarchical analysis of oblique factors from the biogeographical analysis (results for Cluster 5 omitted = poorly recorded species)

	Correlation coefficient r and coefficient of determination (r^2)			
	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Extended factors	Northeast -bias	Southwest - bias	Widespread	widespread/northeast
Shared factor (S1)	0.78 (0.61)	0.49 (0.24)	0.85 (0.72)	0.73 (0.54)
Primary factor (P1)	0.62 (0.39)	0.0	0.0	0.0
Primary factor (P2)	0.0	0.87 (0.76)	0.0	0.0
Primary factor (P3)	0.0	0.0	0.53 (0.28)	0.0
Primary factor (P4)	0.0	0.0	0.0	0.68 (0.46)

Table 3.2. Overall proportional biogeographical composition (species clusters defined in Fig. 3.1.) at the six study areas in Botswana

	Percentage abundance					
Biogeographical group	**Chobe River**	**Savuti**	**NC-Kalahari**	**Khutse**	**Mabuasehube**	**SW-Kalahari**
Widespread/northeast	**33.84**	**11.99**	4.91	0.02	0.05	0.0
Widespread	**32.62**	**11.31**	**11.14**	**31.48**	1.06	0.71
Northeast - bias	**19.92**	**35.06**	2.98	1.28	0.07	0.0
Southwest - bias	**13.59**	**41.44**	**80.87**	**66.79**	**98.71**	**99.29**
Poorly recorded	0.03	0.21	0.10	0.43	0.11	0.0
Total abundance	44446	13980	6949	26316	18819	12987

values > 10 % highlighted

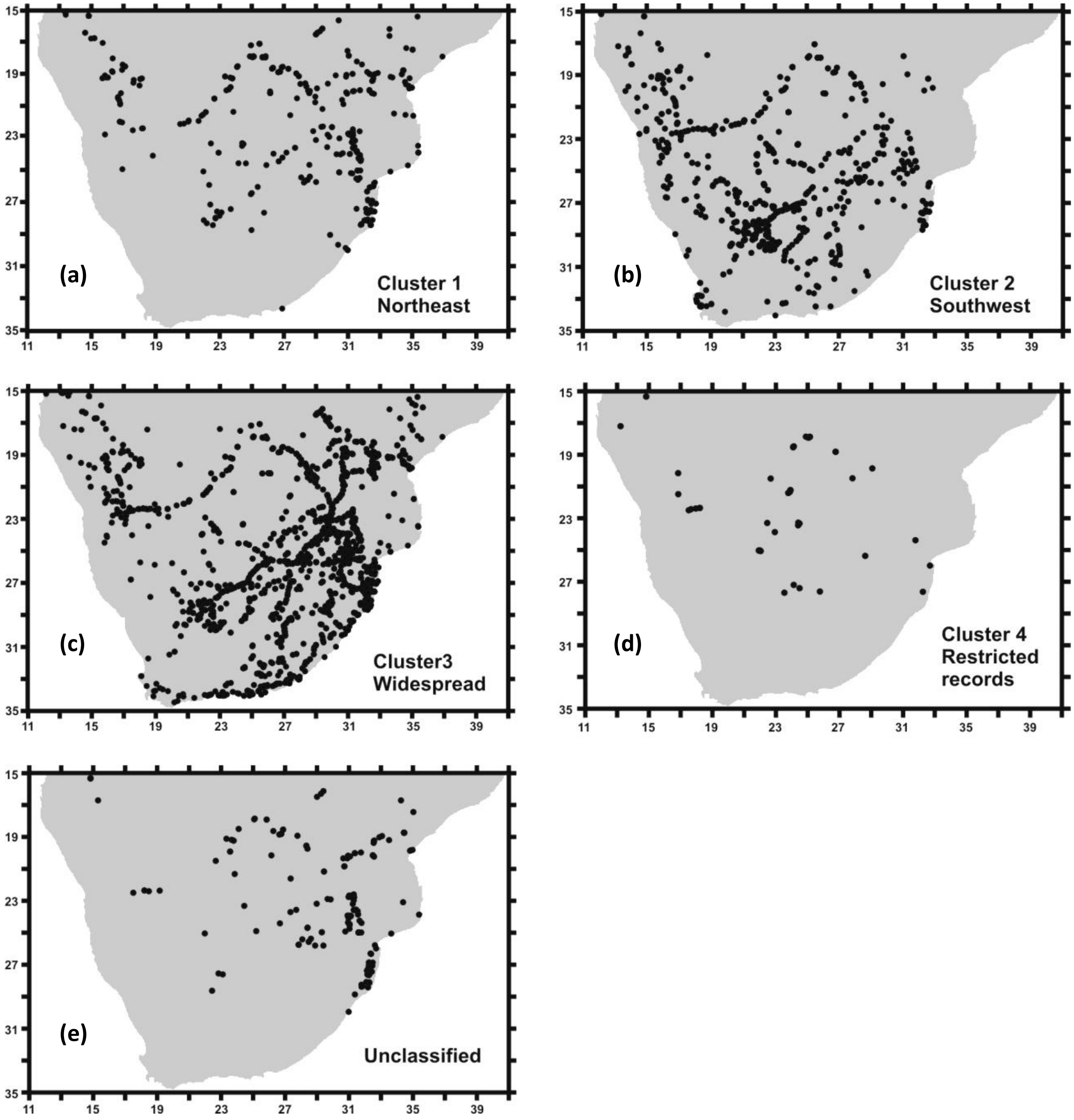


Figure 3.4. (a – e). Spot distribution for restricted/poorly recorded, unclassified and three biogeographical groups or sub groups of dung beetles defined in the ordination plot (see figure 3.2)

Table 3.3. Variation across bait types (carrion, pig, elephant, cattle and sheep dung) for proportional biogeographical composition (species clusters defined in Fig. 3.1.) at the six study areas in Botswana

	Mean percentage abundance of five bait types ± SD								
	Mid-summer rainfall			Arid late summer rainfall					
Biogeographical area	**Chobe River**	**Savuti**	**NC-Kalahari**	**Khutse**	**Mabuasehube**	**SW-Kalahari**	**Chi-square(χ^2)**	**P**	**r**
Widespread/northeast	26.12 ± 10.81	6.74 ± 8.55	8.49 ± 6.89	0.02 ± 0.04	0.04 ± 0.06	0.00	36.46	0.01	0.30
Widespread	32.36 ± 4.56	13.33 ± 7.28	10.41 ± 8.47	39.05 ± 20.58	1.09 ± 0.80	0.62 ± 0.21	37.62	0.01	0.24
Northeast - bias	24.35 ± 8.18	42.33 ± 18.88	3.54 ± 3.80	0.97 ± 0.55	0.06 ± 0.07	0.00	11.83	0.92	0.15
Southwest - bias	17.11 ± 6.52	37.35 ± 15.68	77.39 ± 10.14	59.25 ± 20.08	98.56 ± 0.78	99.38 ± 0.21	62.02	0.00	0.18
Poorly recorded	0.05 ± 0.04	0.25 ± 0.25	0.16 ± 0.19	0.72 ± 0.64	0.26 ± 0.47	0.00	0.41	1.00	0.05

3.4. Discussion

The present SW Kalahari region is considered to be the SW end of an arid corridor that connected NE and SW Africa in the glacial periods of the Pleistocene (Lamoral, 1978; 1979). This arid corridor has been recently cut by increasing rainfall in central Africa creating an aridity gradient from NE –SW in southern Africa.

As previously noted by Davis (1993, 1997), this climatic history has resulted in equivalently strong NE / SW patterns in the biogeography of dung beetles in southern Africa due to differences in both the periodicity and amounts of seasonal rainfall. Such distinct faunal differences between NE regions with higher mid-summer rainfall peaks and SW regions with lower late summer rainfall peaks are supported by the current results showing distinct differences in biogeographical composition between the more mesic NE savanna and the arid Kalahari in the SW.

Within Botswana, the increasing aridity to the SW has presumably acted as a filter for psammophilous NE moist savanna species with a limited tolerance of increasingly arid conditions leading to high species turnover (Chapter 4) between the moister NE and the NE/Kalahari transitional zones and their replacement by endemic Kalahari elements to the SW. This is also supported by the greater biogeographical diversity in the NE and severely limited diversity in the SW that is dominated in the extreme by SW biogeographical elements. Consequently the hypothesis of decreasing biogeographical diversity in the fauna and increasing endemism to the SW is supported. Although there is some variation in the proportional biogeographical composition on different bait types at each of the 6 study areas, there is no fundamental difference in biogeographical patterns across the aridity gradient on these different bait types.

The Kalahari deep sand may also constitute a barrier to some non-psammophilous invertebrates. Although no current data were recorded to determine the effect of the Kalahari deep sands on barring dung beetle species associated with finer-grained soils, there is evidence that the sand systems constitute barriers to non-psammophilous scorpions (Prendini, 2005). With regard to dung beetles, it is also likely that the Kalahari acts as a barrier to savanna species with such a habit. For example, *Onitis viridulus* is known to be widespread from southern to east Africa on finer-grained soils (A.L.V. Davis pers. comm.). However, in the present study, it was represented by only a single specimen recorded in the extreme NE on the deep sands of Chobe.

CHAPTER 4 PATTERNS OF SPECIES DIVERSITY, TURNOVER, AND FUNCTIONAL DIVERSITY ACROSS THE BOTSWANA KALAHARI

4.1. Introduction

Species diversity is influenced by historical, regional ecological and local ecological factors (Ricklefs & Schluter, 1993; Lobo & Davis, 1999). In Botswana, these include sand deposition and development of an aridity gradient (Cooke, 1985; Tyson, 1986), land system perturbations (De Wit & Bekker, 1990) and the frequency and density of available dung types (Tshikae *et al*., 2008). For millennia these factors have interacted in ways that have influenced, respectively, species composition and species diversity in the region (Davis & Scholtz, 2004).

Species distribution patterns along environmental gradients have been extensively studied with different patterns of diversity and abundance always emerging. Studies in the USA and Brazil recorded an increase in species richness of gall-inducing insects with increase in elevation and aridity gradients (Fernandes and Price, 1988; Lara and Fernandes, 1996). However a study along the border between USA and Mexico, documented a decrease in both gall-inducing insects and tree species with increasing aridity (Blanche & Ludwig, 2001). Also in Australia there was no correlation between gall-inducing insect species richness and more arid environments (Blanche *et al*., 2000). Recent studies in South Africa, at the Nama Karoo-Kalahari ecotone have also shown that dung beetle species richness declined along a gradient of increasing aridity, however decrease in diversity was associated with edaphic characteristics and drier conditions (Davis & Scholtz, 2004; Davis *et al*., 2008). Also, functional composition varied along this aridity gradient with assemblages in the mesic NE comprising high proportions of tunnellers whereas those in the southwest were dominated by ball rollers (Davis & Scholtz, 2004).

In the above cited studies from South Africa, besides climatic considerations, variations in vegetative physiognomic and edaphic characteristics have influenced species distribution patterns. The current study however was conducted in a region that provides a relatively homogeneous soil type (sand), but over a wide range of moisture regimes (Scholes *et al*., 2004), with noticeable dung resource gradients (Chapter 2). In Chapter 3, it was found that the biogeographical patterns of scarabaeinae beetles were primarily influenced by climate variability and dung type at regional and local spatial scales respectively. There was variation in biogeographical composition between bait types in the NE and decreasing diversity in biogeographical composition along the NE–SW aridity gradient. The present chapter aims to examine patterns of species richness, alpha, beta, and functional diversity and the relative influence of the climatic gradients implied by differences between study areas and trophic factors. It was hypothesized that species richness will decline from NE to SW, possibly limited by increasingly less suitable climatic and ecological conditions, such as fewer rainfall events, fewer dung types, and lower vegetation heterogeneity.

4.2. Analytical Methods

4.2.1. Validity of data

Rarefaction curves and species estimator methods were used to assess the completeness of the species record for each study area. In each area, sample-based rarefaction was calculated from a matrix of species abundance by samples for each dung type using the EstimateS 7 computer package (Colwell, 2005). Average expected species richness was calculated using five different species estimators (Chao 1 & 2, Jacknife 1 & 2 and bootstrap). Proportional completeness of the species record was cited as a percentage of observed against estimated species richness.

4.2.2. Diversity indices

Alpha and Beta diversity (species turnover) for dung beetles were examined across the climatic gradient. The Shannon-Wiener index was used to measure alpha diversity on each bait type in each study area. This index is expressed as $H' = \sum p_i \log_2 p_i$ where p_i represents the decimal proportion of the ith species. Whittaker's beta-diversity index is considered one of the best early indices (Wilson & Schmida, 1984) for comparing species diversity between ecosystems or along environmental gradients. Hence it was selected for sequential pairwise comparison of study areas across the climatic gradient. It is expressed as Beta diversity, β_w;

$$\beta = \frac{S}{\bar{\alpha}} - 1$$

Where S = the total number of species recorded in both communities (study areas) and $\bar{\alpha}$ = the average number of species found within both communities along the environmental gradient.

4.2.3. Factors influencing species diversity

A GLM repeated measures ANOVA analysis was performed to determine the influence of spatial (6 study areas each with 3 study sites), trophic (5 bait types) and temporal factors (2x24 h sampling days) on total species richness, diversity, and abundance across the climatic gradient using Statistica, version 6.0 (Statsoft, 2008). Trap data on each sampling day were treated as repeated measures. Tukey's HSD post hoc tests were also conducted to determine which subjects are responsible for any significantly different variance that is detected.

4.2.4. Functional Diversity

The Kalahari basin dung beetle species were classified according to their behavioural patterns, comprising four principal functional groups defined by Doube (1990). The major functional groups comprise *ball-rollers* which roll a portion of dung away from the original dung pat before it is buried, *tunnellers* which provision tunnels made under the original dung pat with piece meal(dung balls), *kleptocoprids* which utilize dung buried by other dung beetles, and *endocoprids* which breed within the original dropping *in situ* (see Davis & Scholtz, 2001). In the present study, only the first 3 functional groups were recognized given that scarabaeinae endocoprids tend to be relatively uncommon compared to other functional groups (see Doube, 1990; Davis, 1996c; Davis & Scholtz, 2001). This allowed for an assessment of the proportional representation of ball rollers, tunnellers, and kleptocoprids across the climatic gradient. For each study area the proportion of species in each functional group was expressed as a percentage of all species present in the study area.

4.2.5. Species abundance patterns

Dung beetle assemblages from the six study areas were compared using non-metric multidimensional scaling (MDS). Analyses were conducted on combined data for carrion and dung assemblages and on dung assemblages only. Ordination plots were used to display dung beetle assemblage relationships among the six study areas to reveal the differences in dung beetle community structure. In this case assemblages in areas or samples with higher similarity are placed closer to one another and the less similar assemblages are placed further apart.

Cluster analysis was used to both define dung beetle community divisions in relation to study areas across the climatic gradient and to support the ordination analysis. The same data were arranged as a matrix of mean species abundance per site per bait type. These data were fourth-root transformed before analysis and the nonmetric Bray-Curtis similarity coefficient was used to compute a similarity matrix. This matrix was subjected to the agglomerative clustering technique, group average linking, using the multivariate analytical computer package PRIMER Version 5.0 (Clarke & Warwick, 2001). Multiple paired comparisons of community clusters were conducted using ANOSIM, a subroutine of this package.

4.3. Results

4.3.1. Completeness of the species record

Almost all the rarefaction curves were near asymptote, suggesting that most species were sampled with each bait type (Fig. 4.1). Sampling of the study region can be considered representative as observed species richness of most bait types is greater than 70% of the predicted species. Furthermore predictions of local species richness for each bait type using 5 non-parametric estimators showed that species record was fairly complete (Table 4.1). Species richness was prominent in pig bait in all study areas except Savuti and Mabuasehube. Cattle dung bait lacked consistency across the study region while sheep bait attracted a high number of species in Mabuasehube and Sw-Kalahari. Carrion was lower everywhere except in north central Kalahari where it comes above some dung baits, perhaps due to opportunistic feeding of some species (see *Pachylomera femoralis*, Appendix A4).

4.3.2. Species richness, alpha and beta diversity patterns

A total of 123 497 individuals was trapped comprising 139 species. Both study areas and bait type had strong effects on diversity and species richness (Table 4.2). Chobe NP showed greater overall species richness and abundance than CKGR and KTP (Appendix A4). There was a decline in species numbers from Chobe then an increase at Khutse followed by decline (Appendix A4, Fig. 4.2). The same general pattern is shown by overall abundance and overall alpha diversity (Appendix A4). For detailed species richness, the above pattern is repeated in many cases (Table 4.3) with some exceptions (e.g. sheep & cattle to the SW). Detailed alpha diversity shows no such consistency in pattern (Table 4.4). Beta diversity patterns showed a peak in turnover between Savuti and NC-Kalahari followed by a decrease to the SW (Fig. 4.2).

Mean species numbers showed a decreasing trend from the mesic northeast to arid southwest (Fig. 4.2.). On the other hand pairwise turnovers (Beta diversity) in species composition across the environmental gradient were high between Savuti and NC-Kalahari and also between NC-Kalahari and Khutse (Fig. 4.2). Intermediate beta diversity values were recorded between sites in Chobe River and Savuti and as well as between sites located in Khutse and Mabuasehube (Fig. 4.2). The dendrogram shows that Chobe River and Savuti assemblages grouped together separately from the Central and Southwest Kalahari assemblages (Fig. 4.3). Within the central-southwest Kalahari cluster, NC-Kalahari and Khutse were outliers to Mabuasehube and SW-Kalahari group, suggesting that though very similar and distinct from Chobe–Savuti assemblages, are nonetheless different from one another

4.3.3. Factors influencing diversity, abundance and species richness

Diversity, abundance and species richness were significantly different between study areas and bait type (Table 4.2). Tukey's HSD test showed significant differences in diversity between study areas with no clear regional patterns. However differences in bait types were primarily between dung and carrion baits (Table 4.4). In species richness, significant differences among study areas were mainly between NC-Kalahari and all study areas and also between SW-Kalahari and all study areas ($P<0.05$). For bait types, post hoc tests showed that species richness differed significantly between carrion, omnivore, non-ruminant herbivore and ruminant baits ($P < 0.05$)(Table 4.4).

4.3.4. Species abundance patterns

The MDS ordination based on fourth-root transformation of a relative abundance matrix indicated carrion samples as scattered between assemblages from different study areas (Fig. 4.4a). A new analysis was performed with carrion samples removed and a new MDS plot with a lower stress value and distinct assemblages in each study area supported removal of carrion samples (Fig. 4.4b). Carrion samples were characterized by a few common species in particular *Scarabaeus flavicornis,* across the study region.

4.3.5. Cluster analysis results

Analysis of similarity (ANOSIM) indicates great variability in species composition between study areas (ANOSIM, Global R = 0.855, P < 0.01). Marked differences (ANOSIM, Global R = 1, P < 0.01) were found between study sites located in moister savanna (Chobe National Park) and arid Kalahari (Kgalagadi Transfrontier Park). Central Kalahari Game Reserve (CKGR) faunas were less similar (Figs 4.3 and 4.4b) than were Chobe NP and Kgalagadi Transfrontier Park (KTP) faunas suggesting more internal consistency between the faunas of Chobe NP and KTP than those within CKGR.

4.3.6. Functional patterns

Trends in functional group structure varied across the study region (Fig. 4.5). Kleptocoprids comprised the greatest proportion of dung beetles across the Kalahari basin. There was an increase in kleptocoprids from Chobe then a sharp decline at Khutse followed by an increase (Fig. 4.5). The proportion of ball rollers showed a decreasing trend from Chobe to NC-Kalahari that peaked sharply at Khutse and steadily decreased toward the arid SW while remaining proportionally higher than in the moister NE savanna. The proportion of tunnellers increased from Chobe to Savuti then steadily declined to Mabuasehube followed by slight increase to the arid SW-Kalahari (Fig. 4.5).

Table 4.1. (a) Observed species richness. (b) Mean estimated richness from 5 non-parametric estimators (Chao 1 & 2, Jacknife 1 & 2 and Bootstrap. (c) Percentage of estimated richness in five bait types across six study areas

	Observed richness					
	Chobe River	**Savuti**	**NC-Kalahari**	**Khutse**	**Mabuasehube**	**SW-Kalahari**
(a)						
Carrion	33	25	14	28	19	14
Pig	53	45	32	51	32	31
Elephant	47	50	27	47	28	23
Cattle	35	49	19	25	21	29
Sheep	52	35	12	22	38	31

	Mean (±SD) estimated richness from five nonparametric estimators					
	Chobe River	**Savuti**	**NC-Kalahari**	**Khutse**	**Mabuasehube**	**SW-Kalahari**
(b)						
Carrion	40.3 (3.3)	34.3 (4.3)	20.2 (2.6)	28.6 (1.1)	19.2 (0.9)	16.9 (1.2)
Pig	77.0 (16.4)	55.5 (6.1)	60.5 (20.7)	61.4 (3.8)	39.0 (4.0)	31.7 (0.9)
Elephant	61.2 (11.1)	63.5 (5.9)	35.0 (3.5)	52.9 (2.1)	31.5 (1.2)	26.1 (1.1)
Cattle	40.2 (4.2)	57.6 (4.0)	26.0 (3.6)	28.5 (1.6)	28.9 (4.7)	32.2 (1.2)
Sheep	93.5 (36.1)	39.4 (1.4)	16.5 (2.2)	27.7 (2.1)	63.7 (19.3)	41.5 (6.7)

	Percentage of estimated species richness					
	Chobe River	**Savuti**	**NC-Kalahari**	**Khutse**	**Mabuasehube**	**SW-Kalahari**
(c)						
Carrion	81.89	72.89	69.31	97.90	98.96	82.84
Pig	68.83	81.08	52.89	83.06	82.05	97.79
Elephant	76.80	78.74	77.14	88.85	88.89	88.12
Cattle	87.06	85.07	73.08	87.72	72.66	90.06
Sheep	55.61	88.83	72.73	79.42	59.65	74.70

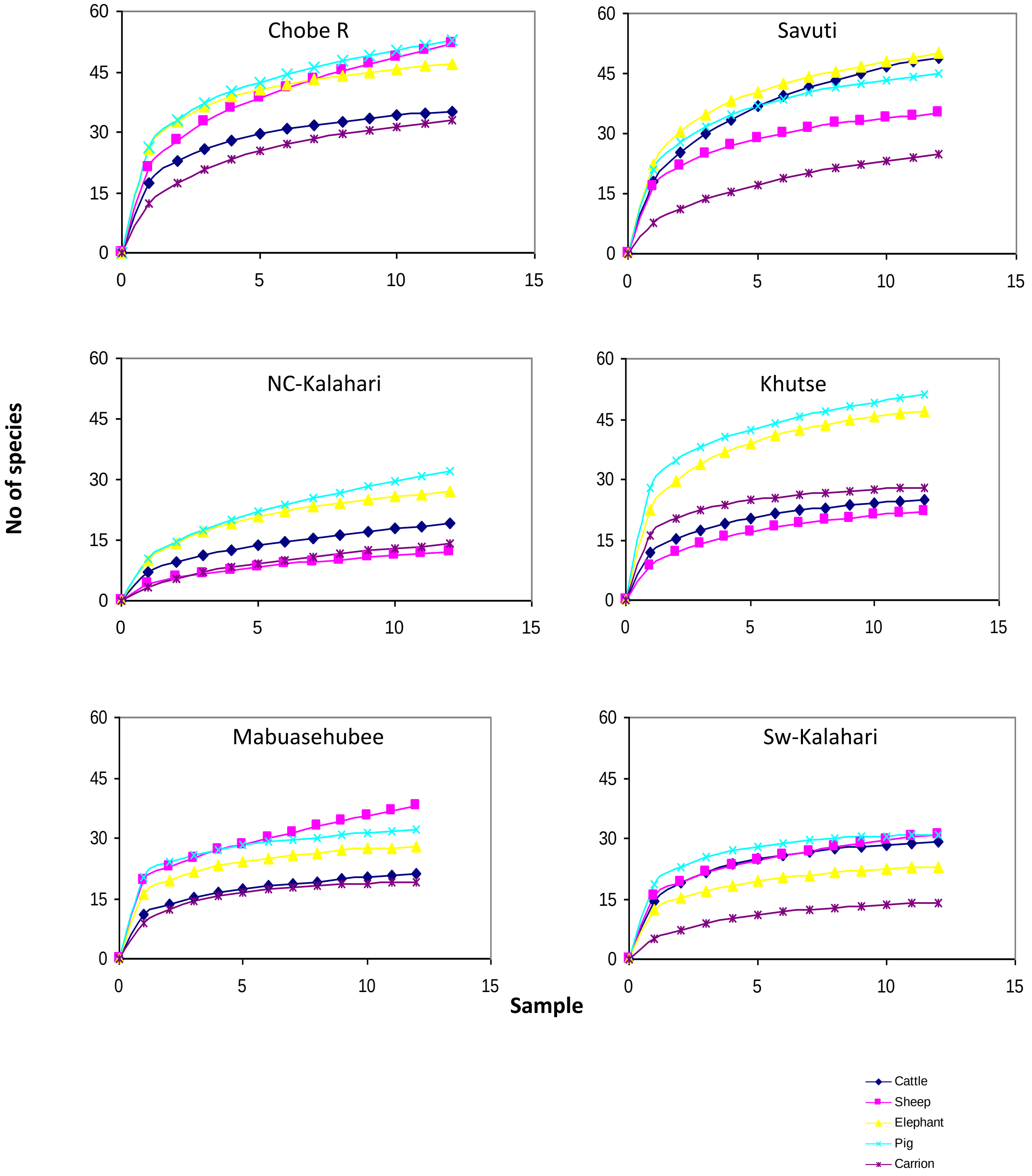


Figure 4.1. **Sample based rarefaction curves for species on five different bait types in all six study areas**

Table 4.2. Results for a General Linear Model (GLM) of factors influencing diversity, species richness and abundance of dung beetles across the Kalahari in Botswana

	F - value	DF	P- value
Diversity (Shannon-Wiener)			
Place (Study area)	71.81	5	***
Bait type	33.80	4	***
Place * Bait type	11.17	20	***
Day	0.38	1	NS
Day * Place	11.89	5	***
Day * Bait type	1.05	4	NS
Day * Place * Bait type	2.68	20	***
Observed species (S)			
Place (Study area)	65.00	5	***
Bait type	91.26	4	***
Place * Bait type	11.39	20	***
Day	0.74	1	NS
Day * Place	16.46	5	***
Day * Bait type	1.44	4	NS
Day * Place * Bait type	5.35	20	***
Abundance (N)			
Place (Study area)	24.29	5	***
Bait type	49.16	4	***
Place * Bait type	7.89	20	***
Day	0.02	1	NS
Day * Place	1.86	5	NS
Day * Bait type	0.26	4	NS
Day * Place * Bait type	1.04	20	NS

*** *P* <0.001; NS, not significant

Table 4.3. Distribution of mean diversity and species richness of dung beetles in five bait types across the Kalahari in Botswana

	Carrion	Pig	Elephant	Cattle	sheep
Mean diversity / trap ± S.D.					
Chobe River	1.45 ± 0.69^{de}	1.46 ± 0.65^{ab}	1.57 ± 0.85^{bc}	1.82 ± 0.53^{bc}	1.83 ± 0.67^{a}
Savuti	1.29 ± 0.30^{ce}	1.90 ± 0.13^{cd}	1.98 ± 0.30^{ac}	1.99 ± 0.37^{b}	2.07 ± 0.30^{a}
NC-Kalahari	0.52 ± 0.41^{a}	1.12 ± 0.43^{a}	1.29 ± 0.34^{b}	1.04 ± 0.30^{a}	0.65 ± 0.52^{b}
Khutse	1.90 ± 0.30^{bd}	1.89 ± 0.64^{cd}	2.07 ± 0.25^{ac}	1.69 ± 0.32b^{c}	0.95 ± 0.47^{b}
Mabuasehube	1.22 ± 0.43^{ef}	1.98 ± 0.22^{c}	1.85 ± 0.17^{c}	1.66 ± 0.24^{c}	2.08 ± 0.15^{a}
Sw-Kalahari	0.89 ± 0.37^{af}	1.60 ± 0.46^{bd}	1.53 ± 0.26^{bc}	1.75 ± 0.24^{bc}	1.93 ± 0.27^{a}
One-way ANOVA results	$F_{(5, 138)}$ = 35.52***	$F_{(5, 138)}$ = 17.95***	$F_{(5, 138)}$ = 9.56***	$F_{(5, 138)}$ = 16.59***	$F_{(5, 138)}$ = 34.97***
Mean species richness / trap ± S.D.					
Chobe River	7.38 ± 4.80^{c}	18.00 ± 8.86^{bc}	15.04 ± 11.21^{c}	12.38 ± 5.62^{b}	15.42 ± 8.18^{b}
Savuti	5.67 ± 2.06^{cd}	16.08 ± 4.83^{c}	15.54 ± 4.92^{c}	13.38 ± 5.11^{b}	13.17 ± 4.22^{b}
NC-Kalahari	2.33 ± 1.13^{bd}	7.33 ± 3.31^{a}	7.42 ± 2.41^{a}	5.13 ± 1.48^{a}	2.75 ± 1.54^{a}
Khutse	12.71 ± 4.44^{a}	22.21 ± 7.97^{b}	16.38 ± 5.74^{c}	8.54 ± 2.64^{c}	5.83 ± 2.08^{a}
Mabuasehube	5.75 ± 1.75^{cd}	16.33 ± 2.06^{c}	12.71 ± 2.20^{bc}	8.50 ± 2.30^{c}	15.63 ± 4.11^{b}
Sw-Kalahari	3.46 ± 1.67^{d}	13.88 ± 3.79^{c}	9.33 ± 2.51^{ab}	10.88 ± 2.69^{bc}	12.83 ± 3.17^{b}
One-way ANOVA results	$F_{(5, 138)}$ = 23.04***	$F_{(5, 138)}$ = 12.19***	$F_{(5, 138)}$ = 9.04***	$F_{(5, 138)}$ = 20.21***	$F_{(5, 138)}$ = 40.95***

*P < 0.05; **P < 0.001; ***P < 0.0001.In each column; values followed by a different letter differed significantly (Tukey’s HSD).

Table 4.4. Overall mean diversity and species richness in all bait types and across study areas

Bait type	Overall (H')	Overall(spp)
Carrion	1.20 ± 0.62^{a}	6.22 ± 4.46^{a}
Pig	1.66 ± 0.55^{b}	15.64 ± 7.19^{b}
Elephant	1.70 ± 0.52^{b}	12.74 ± 6.58^{c}
Cattle	1.65 ± 0.45^{b}	9.80 ± 4.52^{d}
Sheep	1.57 ± 0.72^{b}	10.94 ± 6.57^{d}
Places		
Chobe River	1.63 ± 0.11^{bd}	13.64 ± 2.58^{b}
Savuti	1.85 ± 0.09^{c}	12.77 ± 1.26^{be}
NC-Kalahari	0.92 ± 0.09^{a}	4.99 ± 0.88^{a}
Khutse	1.67 ± 0.11^{bd}	13.13 ± 2.39^{bc}
Mabuasehube	1.74 ± 0.13^{bc}	11.78 ± 0.93^{ce}
Sw-Kalahari	1.53 ± 0.10^{d}	10.08 ± 0.79^{d}

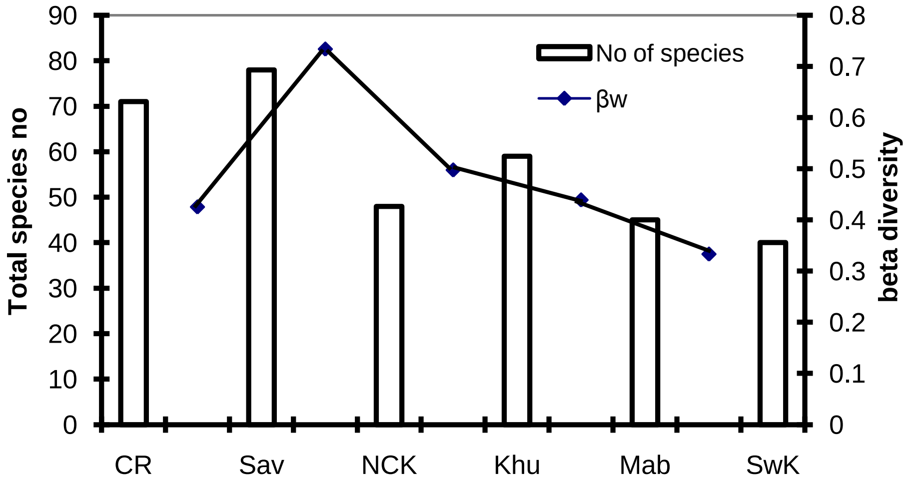


Figure 4.2. **Observed total number of species and pairwise turnover in species composition between study areas along an aridity gradient. (CR) Chobe River; (Sav) Savuti; (NCK) North Central Kalahari; (Khu) Khutse; (Mab) Mabuasehube; (SwK)- Southwest Kalahari**

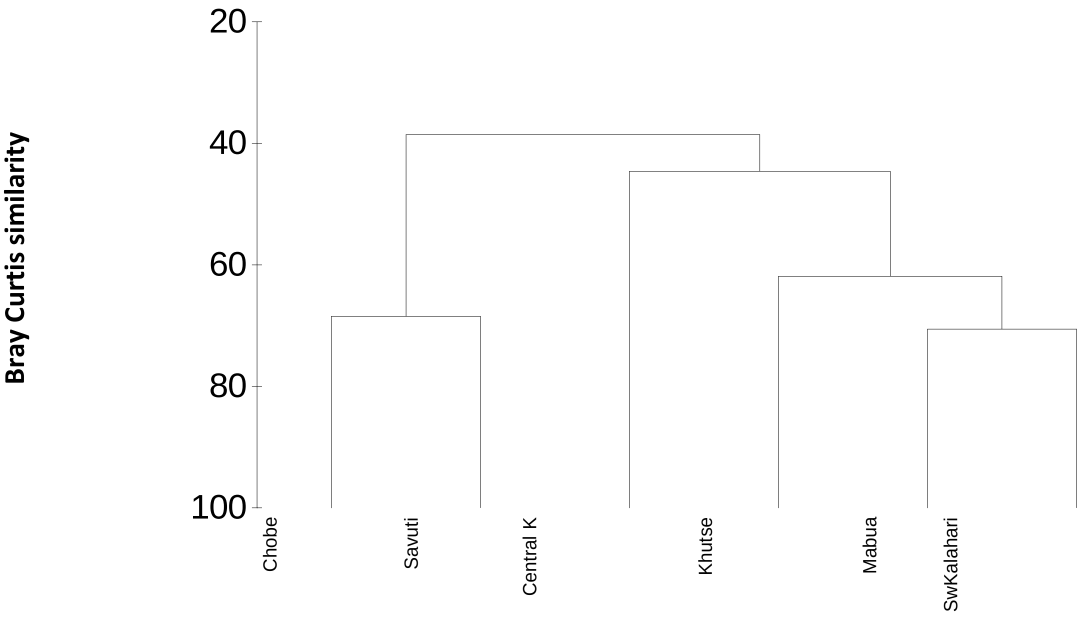


Figure 4.3. **Dendrogram showing percentage similarity between dung beetle assemblages along the aridity gradient in the Botswana Kalahari (Central-K: North Central Kalahari; Mabua: Mabuasehube; Sw-K: Southwest Kalahari)**

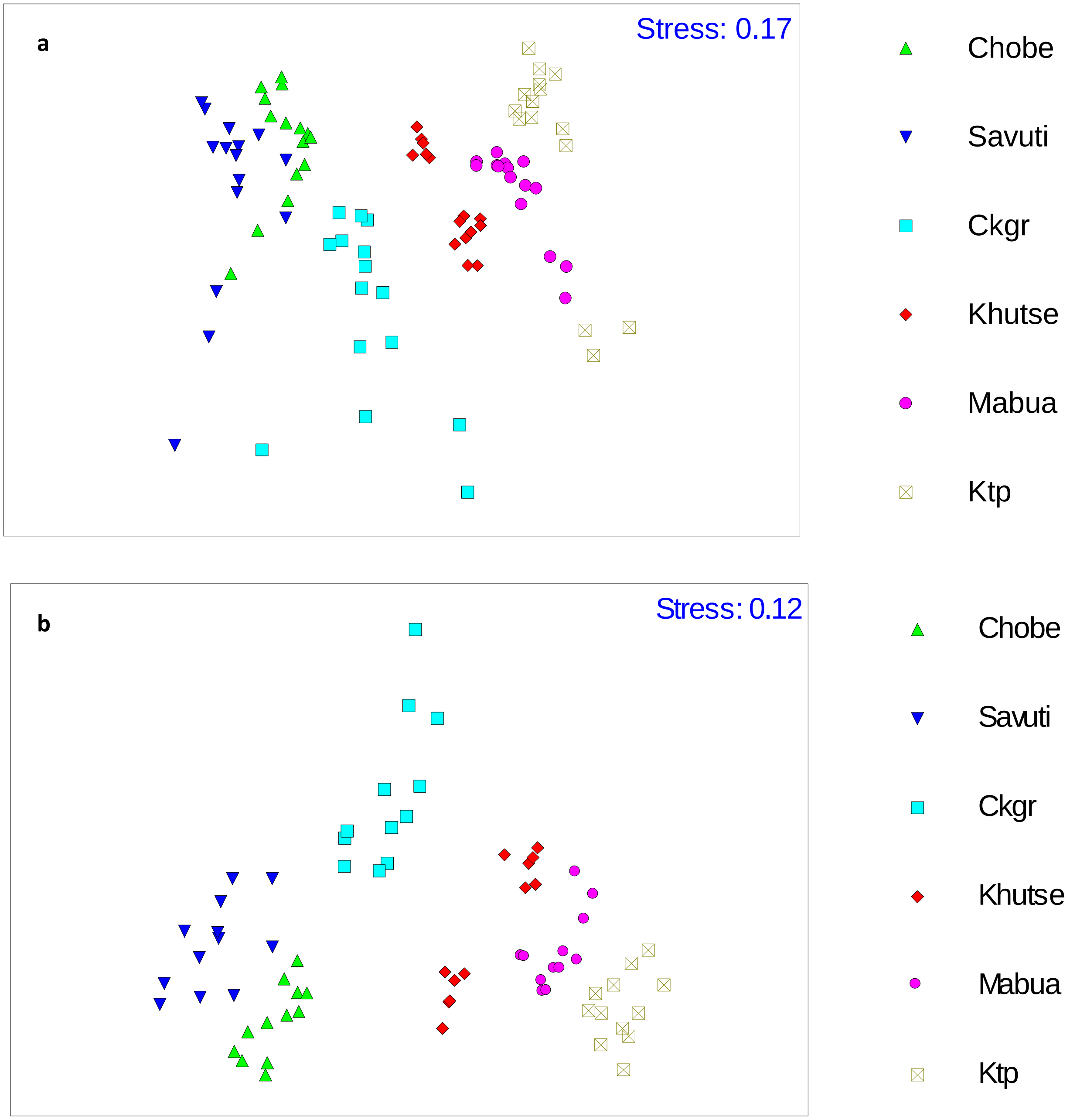


Figure 4.4. Non-metric Multidimensional Scaling (MDS) ordination of species abundance for dung beetles trapped to (a) dung and carrion baits and (b) dung baits only, in six study areas.

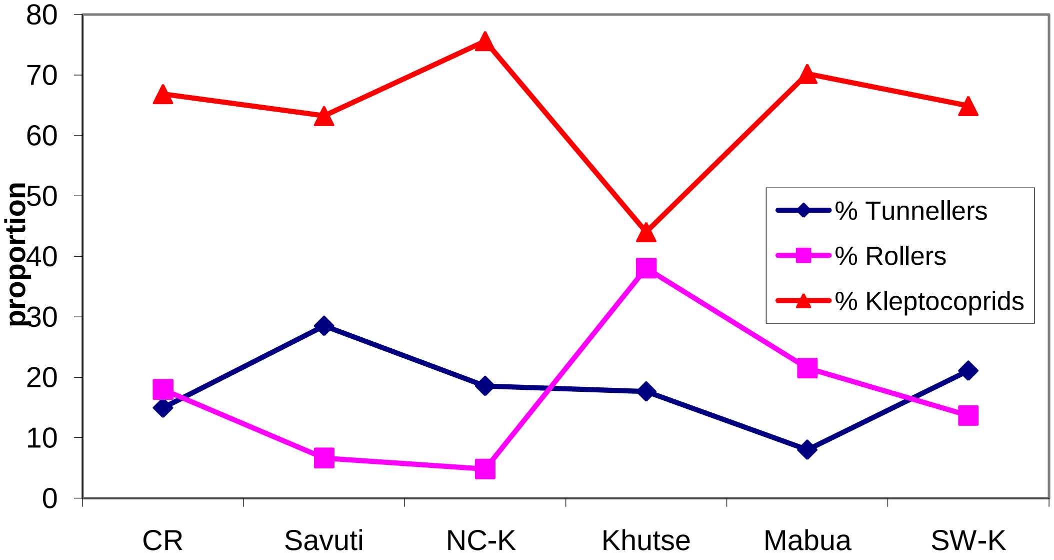


Figure 4.5. **Proportion of the three common functional groups in six study areas (see Fig 4.3 for key of study areas).**

4.4. Discussion

It is widely known that the Kalahari basin is characterized by climatic and physiognomic variability from the mesic northeast to the arid southwest (Davis, 1987; Davis, 1997; Cowling *et al*., 2003). This gradual change in the climate and vegetation has greatly influenced the distribution of the grasshopper (Barker, 1993) and herpetofauna (Haacke, 1984). Dung beetles are by no means an exception (Davis & Scholtz, 2004). Several studies have demonstrated that environmental gradients and ecological changes involving quantity and quality of dung types produce changes in species composition, abundance and other attributes, including functional diversity (Lumaret *et al.*, 1992; Davis, 1994a; Carpaneto, 2005).

The results of this study show patterns of dung beetle assemblage structure that could be linked to the influence of the aridity gradient and perhaps mammal diversity. This was demonstrated by the great overall species richness, abundance, high turnover and differences in community patterns between the six study areas. It was also exemplified by the greater overall abundance and species richness in sites located at Chobe River and Savuti where there is higher rainfall and a full range of dung types. While both attributes plummeted at NC-Kalahari before slightly peaking at Khutse and then levelling off towards the SW-Kalahari sites where a single dung type (pellets), in particular, dominates. The fact that overall species richness and abundance in NC-Kalahari were lower than in Khutse could imply that the local environmental conditions (habitat heterogeneity) between these two areas are different, as highlighted by a higher concentration of pans in NC-Kalahari than in Khutse. Apart from habitat heterogeneity it appears that mammals in these two areas also utilized habitats differently. Throughout the study, animal herds in NC-Kalahari were mostly seen on the pan and pan edges. This may have been to avoid long grass in sandy habitats in order to have a clear view of predators. While in Khutse animal herds, in particular gemsbok (*Oryx gazella*), were mostly seen on sandy habitats where the grass was short and predators could be seen from a distance. Thus, the relatively low averages of dung beetles in NC-Kalahari most likely reflect differences in mammal and therefore dung density between places.

Despite the relatively species rich dung beetle communities within the Kalahari basin, community composition varies greatly over several scales, with an exceptionally high (c. 0.73) species turnover (Beta-diversity) between some study areas along the aridity gradient. This high species turnover, especially between Savuti and NC-Kalahari, would be due to species lost through lower species richness in NC-Kalahari. It may also be consistent with the abrupt changes in climate and vegetation physiognomic features as well as changes in dung types. However, more interesting is the beta diversity between NC-Kalahari and Khutse. Turnover between NC-Kalahari and Khutse perhaps demonstrates differences in local environmental conditions rather than vegetation and dung type which remain similar in these two localities. NC-Kalahari is at the edge of the Makgadikgadi depression and has a high concentration of pans with patches of deep sand stretching 3-4 Km between them. Possibly the species area relationships effect (Gaston & Lawton, 1990) due to smaller and fewer sand pockets as compared to extensive pans. In addition it could mean that Khutse is drier than NC-Kalahari, being a transitional zone to proper Kalahari, lying within the 350 mm isohyet. The presence of *Pachylomera opacus* and *Scarabaeus proboscideus*, arid specialists, in Khutse gives emphasis to this claim (see Davis, 1997). Furthermore, the high turnover values possibly indicate the proximity of cattle posts to the Khutse Game Reserve boundary hence to sampling sites (approximately, 17 Km) which perhaps locate them within the flight ranges of such large ball rollers as *P. femoralis* and *Kheper lamarcki* which were present and more abundant in Khutse while absent in NC-Kalahari. These are likely to be supported by copious amount of domestic animal dung especially cattle and horse.

In this study, a clear trend in the proportion of functional groups especially in the roller taxa occurs between the moister and arid areas. Ball rollers are proportionally more abundant in the arid Kalahari than in the moister savanna. However, tunnellers were also found to be proportionally more abundant than rollers in the SW-Kalahari, a habitat that is dominated by pellet dung. This proportional pattern, particularly in ball rollers is also observed in the Kalahari / Nama-Karoo ecotone, where there are climate and habitat gradients (Davis & Scholtz, 2004; Davis *et al.*, 2008). Ball rollers were proportionally higher in the Nama-Karoo which is hyper-arid and characterized by stony Karoo sands than in the much moister Kalahari deep sands. In another study carried out in South Africa under similar rainfall conditions proportions of ball rollers increased from clay to sandy habitats in Gauteng and the reverse in Mkuze (Davis, 1996c). In above studies it is clear that functional group structure responds to habitat differences (Davis, 1996c; Davis & Scholtz, 2004). However, proportional functional groups showed no consistent relationship with any particular habitat type.

CHAPTER 5 REGIONAL AND LOCAL SPATIAL PATTERNS ACROSS THE BOTSWANA KALAHARI

5.1. Introduction

Geographical patterns are the result of changing abiotic conditions across space and the changing effects of biotic interaction (Fjeldså, 1994; Fjeldså & Lovett, 1997; Martin, 2001). In dung beetles, geographical patterns result principally from different climates, in particular, temperature and rainfall (Davis & Dewhurst, 1993; Davis, 1997; Andresen, 2005); from edaphic characteristics either sand or clay, or stony versus deep soils (Davis, 1996a; Davis & Scholtz, 2004; Davis *et al.*, 2008); from different vegetation physiognomy due to its effect on microclimate (Davis, 1994b; Davis, 1996c; Davis *et al.*, 2002; Boonrotpong *et al.*, 2004; Botes *et al.*, 2006); and from food type, both food type diversity and availability (Davis 1994, Estrada *et al.*, 1999; Tshikae *et al.*, 2008; Davis *et al.*, 2010). The interactive effects of abiotic and biotic factors vary between local and regional scales and also with the specific attributes of the geographical region (Davis *et al.*, 2008).

In Botswana, there are limited soil and vegetation differences except for woodland in Chobe versus less shaded sparse shrubland elsewhere (Lumbile *et al.*, 2007; Ringrose *et al.*, 2003; Scholes *et al.*, 2004). The Kalahari deep sand covers 75% of the land mass. Conversely there are strong northeast-southwest rain and dung gradients (Chapters 2 & 3). These gradients span two climatic (Davis, 2002) and two ecoregions (Olson *et al.*, 2000; 2001), which divide the Botswana Kalahari Basin into mesic and xeric savanna, also suggested by the biogeographical analysis in Chapter 3. The increasing harsh ecological conditions to the SW may also influence distribution patterns of dung beetles due to rapid desiccation of pellet dung that forms the major diet and microhabitat for adults.

In the Northern Cape, which constitutes part of the southwest, dung beetle studies showed strong differences across the Nama Karoo and Kalahari ecotone (Davis *et al.*, 2008). Clear regional groups and patterns of separation were identified either side of the major ecotone between the Nama Karoo and Xeric Kalahari Savanna to the SW. At subregional scales climatic patterns, either annual temperature or annual rainfall, had a strong effect on faunal divisions whereas at local scales noticeable separation were due to edaphic characteristics (Davis *et al.*, 2008). Despite several studies carried out in South Africa, a study examining similar group patterns and separation across and either side of the xeric and mesic savanna ecotone has never been attempted in Botswana. This study may be slightly different to the Northern Cape work as there is less edaphic variation and only rainfall variation with limited temperature variation. Also no work has been done on dung effects across the Nama Karoo and Kalahari ecotone in Northern Cape. Therefore the present study examines the influence of the Kalahari aridity gradient on assemblage composition and whether the ecotone between the xeric and mesic savanna (Olson *et al.*, 2001) is readily identified by dung beetle spatial patterns. It was hypothesized that greater endemism to the unique conditions of the SW will lead to distinct patterns of species assemblage structure that reflect the climatic and ecoregion classification for the area.

5.2. Analytical methods

5.2.1. Spatial patterns across the climatic gradient of Botswana

Patterns of species abundance across the environmental gradient of Botswana were compared using ordination analyses. The data matrix comprised 140 species x 90 combined spatial and trophic variables composed of data for 5 bait types x 3 trapping sites x 6 study areas. The data matrix was fourth-root-transformed to normalize the data and converted to a correlation matrix for 140 x 90 combined spatial and trophic variables. The matrix was subjected to factor analysis by STATISTICA release 8 (StatSoft Inc., 1994 - 2005) using principal components as the method of factor extraction. Combined analysis of dung and carrion data showed some overlap between study areas. Thus, separate factor analyses were conducted on dung and carrion data. Both dung (131 x 72) and carrion (60 x 18) data matrices were fourth-root transformed before analysis. Hierarchical analyses of oblique factors were conducted on each Factor Analysis to generate extended factors (see description of method in Chapter 3: Analytical methods). For each analysis, the correlation coefficients (r values) for regressions of extended orthogonal on oblique factor values were used to calculate coefficients of determination (r^2 values), which define the proportional contribution of each extended factor to variance within each ordination cluster (either unique to a cluster – primary extended factors; or shared between clusters – secondary extended factors). Further regressions tested for correlations between oblique factors from the dung analysis (overall and separately) and variation in rainfall across the environmental gradient.

5.2.2. Relationships between ordination results and the environmental gradient

Assemblage response to climatic and ecological factors were analysed using analysis of variance (2-way ANOVA), and multiple regressions were used to determine the effect of rainfall and dung type on oblique factor loadings in the ordination of species abundance data recorded in traps baited with dung.

5.2.3. Ecotone between the Kalahari Xeric Savanna and *Acacia-Baikiaea* Savanna

The r^2 values for shared secondary extended factors derived from the ordination analysis of dung data were plotted on a linear spatial scale to determine the point of intersection between SW Kalahari and NE more mesic Savanna influence represented respectively by secondary factors S1 and S2. This point was plotted on the Botswana portion of a map of global ecoregions (Olson *et al.*, 2001) to determine how well it fitted to that classification.

5.3. Results

Combined ordination analysis of dung and carrion faunas produced clear separation between some clusters along factors 1 and 2 comprising data points for single study areas at the extremes of the aridity gradient (Fig. 5.1.), but less obvious separation for data points representing intervening study areas and for most of those representing carrion-baited traps. Separate analyses for dung and carrion data produced much clearer separation between study areas or regions with different patterns shown by each (Figs. 5.2., 5.3.). Similar results were obtained using a different ordination technique in Chapter 4.

5.3.1. Dung fauna only

The dung data ordination suggests that the regional climatic gradient has a stronger effect on assemblage structure than dung type association as the data points for assemblage structure at each of the six study areas were well separated in ordinal space (Figs. 5.2., 5.3.) and followed the same sequence as the geographical gradient in Fig. 5.2. As the data points for each spatial cluster represent assemblages attracted to the same four different dung types, food selection thus had only a local influence. There was a distinct separation between all study areas except NC-Kalahari and Khutse in the ordination plot for Factors 1 and 2. On the contrary there is a clear separation between all places. The separation between Khutse and NC-Kalahari is obscured in Fig. 5.2. Therefore, a plot of factor 1 against factor 3 was used to demonstrate the clear separation between the NC-Kalahari and Khutse faunas in ordinal space (Fig. 5.3.).

Rainfall showed a strong significant effect on overall factorization (Table 5.1.) in the ordination of dung data ($F_{(6, 12)} = 457.2$; $P < 0.001$) with dung type also having a significant but much weaker effect on these factors ($F_{(6, 18)} = 5.3$; $P < 0.001$). There was also a significant but relatively weak interaction between rainfall and dung ($F_{(6, 36)} = 1.5$; $P < 0.05$). Multiple regressions also emphasized that the effect of rainfall was strong on overall factorization (Table 5.3.). However, regressions on individual factors show that rainfall was strongly correlated with those factors with high loadings for study areas at the extremes of the environmental gradient but weakly correlated with those in the middle near the ecotone of the Kalahari Xeric and Acacia-Baikiaea Savannas (Table 5.3).

5.3.2. Carrion fauna only

The carrion data ordination shows more limited separation across the regional aridity gradient than that of the dung data ordination. Those in the northeast were mostly distinct from one another in different study areas (Chobe, Savuti, NC-Kalahari) except for the wooded site 3 in NC-Kalahari that clustered with the Savuti sites. However, those sites at Khutse, Mabuasehube and Sw-Kalahari were all together in a single cluster (Table 5.2., Fig.

5.4.). The four different patterns defined from carrion analysis accounted for >78 % of total variance and showed relatively low proportions of shared variance across shared factor S1 with relatively high values for unique variances P1-4 (Table 5.2a, b).

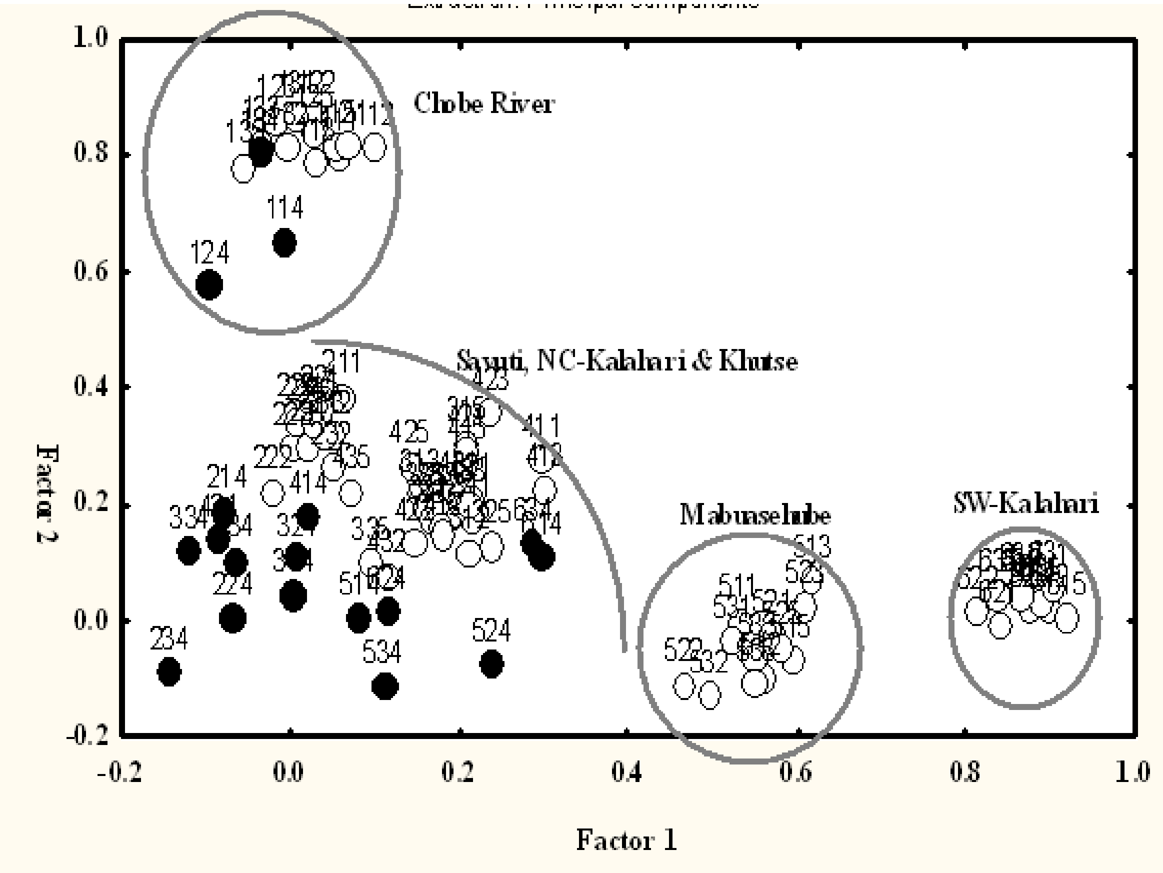


Figure 5.1. **Ordination plot showing clusters of data points for dung beetle assemblages attracted to different bait types across the Botswana Kalahari basin (open circle: dung bait; closed circle: carrion bait); {numbers: the first digit = study area; 1 = Chobe, 2 = Savuti, 3 = NC-Kalahari, 4 = Khutse, 5 = Mabuasehube 6= SW-Kalahari, second digit = site(1, 2, 3) and third digit = bait type (1 =pig, 2 = cattle, 3 = elephant, 4= carrion, 5 = sheep)}**

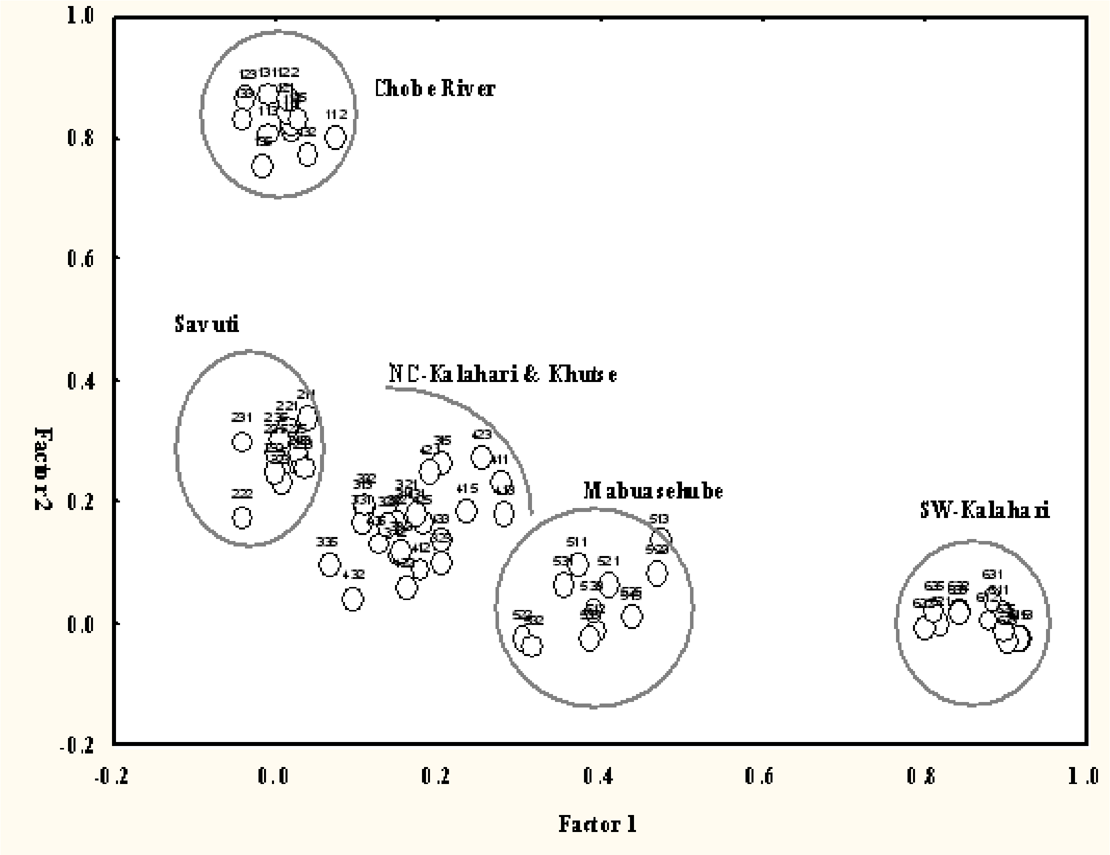


Figure 5.2. Ordination plot showing clusters of data points representing dung beetle assemblages on different dung baits only (Key to numbers see Fig. 5.1.)

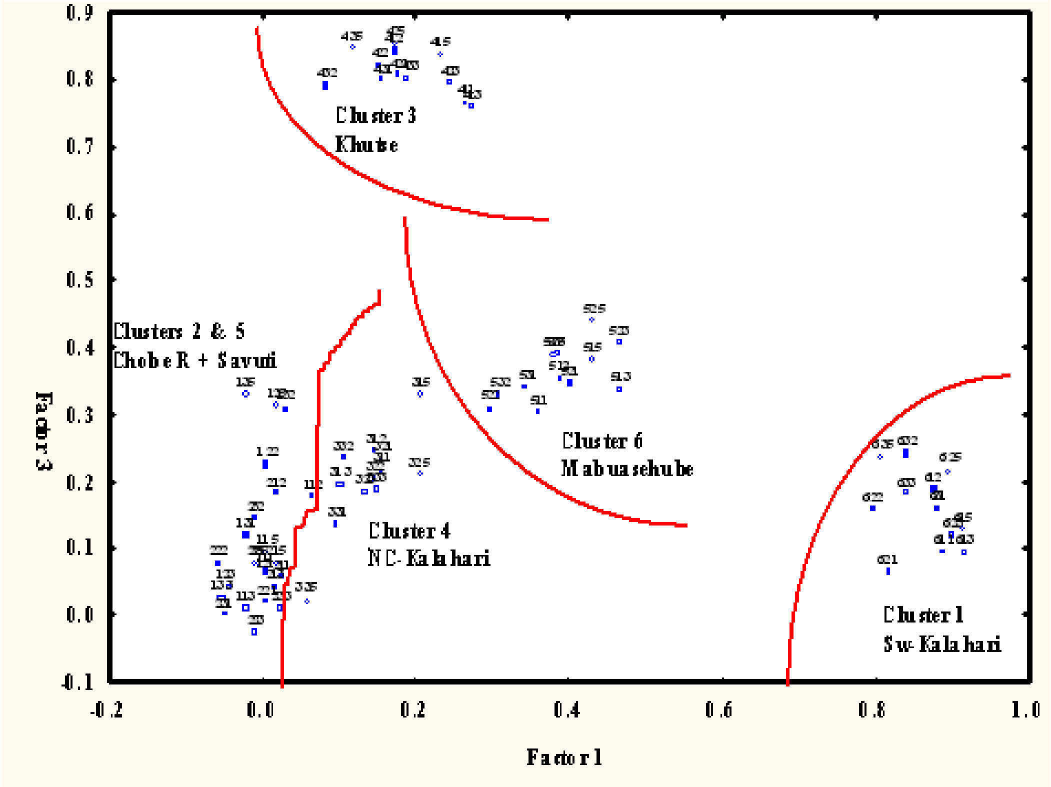


Figure 5.3. Ordination plot showing wide separation between NC-Kalahari and Khutse clusters for dung beetle assemblages attracted to different dung baits only (Key numbers see Fig. 5.1.)

Table 5.1. (a) Correlations between oblique factor loadings and extended factors (b) Eigen values and proportional contribution to variance for each factor derived from hierarchical analysis (Fig. 5.2.)

	Corelation coefficient (r) and coefficient of determination (r2)					
(a)	Sw-Kalahari	Chobe River	Khutse	NC-Kalahari	Savuti	Mabuasehube
Extended factors	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6
Shared factor S1-SW	0.71(0.51)	0.10(0.01)	0.70(0.49)	0.46(0.21)	0.08(0.01)	0.88(0.77)
Shared factor S2-NE	-0.01(0.0)	0.73 (0.54)	0.35 (0.12)	0.60 (0.36)	0.77 (0.59)	0.17 (0.03)
Primary (P1)	0.70 (0.49)	0.0	0.0	0.0	0.0	0.0
Primary (P2)	0.0	0.67 (0.45)	0.0	0.0	0.0	0.0
Primary (P3)	0.0	0.0	0.62 (0.39)	0.0	0.0	0.0
Primary (P4)	0.0	0.0	0.0	0.65 (0.43)	0.0	0.0
Primary (P5)	0.0	0.0	0.0	0.0	0.63 (0.40)	0.0
Primary (P6)	0.0	0.0	0.0	0.0	0.0	0.45 (0.20)

	Eigen value and proportional contribution of each factor		
(b)	Eigen Value	%Total variance	Cumulative %
Cluster 1	29.88	41.50	41.50
Cluster 2	14.62	20.31	61.81
Cluster 3	5.40	7.50	69.30
Cluster 4	4.59	6.37	75.67
Cluster 5	3.19	4.43	80.10
Cluster 6	2.30	3.19	83.29

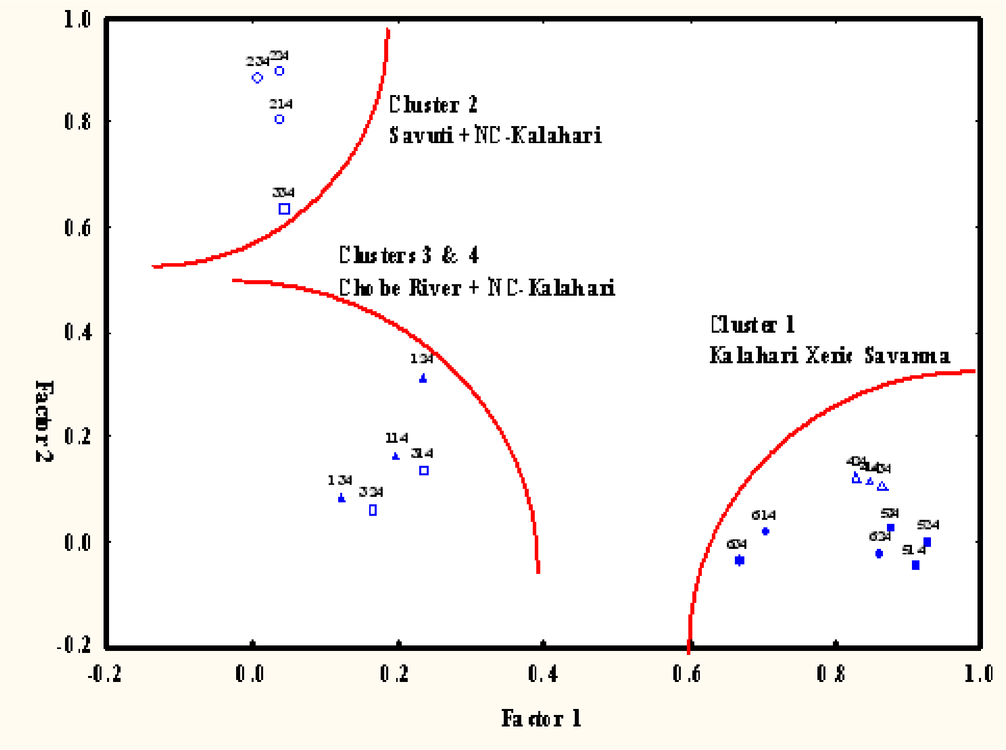


Figure 5.4. **Ordination plot showing clear separation between carrion assemblages across the study region (Sites Key: open triangle = Chobe River, closed triangle = Khutse, open circle = Savuti, closed circle = Sw-Kalahari, open square = NC-Kalahari, closed square = Mabuasehube)**

Table 5.2. (a) Correlations between oblique factor loadings and extended factors (b) Eigen values and proportional contribution to variance for each factor derived from hierarchical analysis of carrion only assemblage

	Correlation coefficient (r) and coefficient of determination (r^{2}			
(a) Extended Factors	Khu, Mabua & Sw-K, Cluster 1	Savuti/NC-K (site3) Cluster 2	Chobe River Cluster 3	NC-Kalahari Cluster 4
Shared factor (S1)	-0.60(0.36)	-0.49(0.24)	-0.61(0.37)	-0.58(0.38)
Primary (P1)	0.80(0.64)	0.0	0.0	0.0
Primary (P2)	0.0	0.87(0.76)	0.0	0.0
Primary (P3)	0.0	0.0	0.79(0.63)	0.0
Primary (P4)	0.0	0.0	0.0	0.81(0.66)

	Eigen value and proportional contribution for each factor		
(b)	Eigen value	%Total variance	Cumulative %
Cluster 1	7.70	42.78	42.78
Cluster 2	3.28	18.20	60.98
Cluster 3	1.60	8.89	69.87
Cluster 4	1.55	8.63	78.50

Table 5.3. Results of multiple regression showing correlations between ordination factors from the dung analysis (Fig. 5.2., Table) and rainfall patterns across the Botswana Kalahari

	Spatial regression values		
	R^2	$F_{(1,70)}$	P
Rainfall vs Factor 1 (Sw-Kalahari)	0.72	179.60	**
Rainfall vs Factor 2 (Chobe River)	0.59	104.00	**
Rainfall vs Factor 5 (Savuti)	0.49	67.45	**
Rainfall vs Factor 6 (Mabuasehube)	0.32	32.80	**
Rainfall vs Factor 3 (Khutse)	0.044	4.34	*
Rainfall vs Factor 4 (NC-Kalahari)	0.003	0.19	NS
Rainfall vs All Factors	0.67	142.78	**

* $P < 0.05$, ** $P < 0.01$ and NS = not significant

5.3.3. Savanna vs. Kalahari influence on dung fauna

There were six different patterns defined from the dung fauna analysis. The six patterns accounted for more than 83 % of the total variance and showed different patterns of shared and unique variance (Table 5.1a, b). Faunal structure showed almost equally high proportions of unique variance at each extreme of the climatic gradient in Chobe and the Sw-Kalahari. The unique variance at intervening places was only marginally lower except in Mabuasehube where there was a very high shared southwest character of the fauna (Table 5.1a). Shared northeast character was relatively high at Chobe, Savuti, and NC-Kalahari but declined steeply to the southwest. Shared southwest character was relatively high in the Sw-Kalahari, Mabuasehube and Khutse but declined to the northeast, particularly beyond NC-Kalahari (Table 5.1a). Plotting the proportions of shared variance for SW and NE bias in faunal structure on a linear spatial scale showed a point of intersection lying between NC-Kalahari and Khutse (Fig. 5.5.). Geographically, this point lay only 6 km from the edge of two major ecoregions defined for the southern Kalahari Basin and mapped by Olson *et al.*(2001) (Fig. 5.6). These were the *Acacia-Baikiaea* Savanna ecoregion to the northeast and the Kalahari Xeric Savanna ecoregion to the southwest.

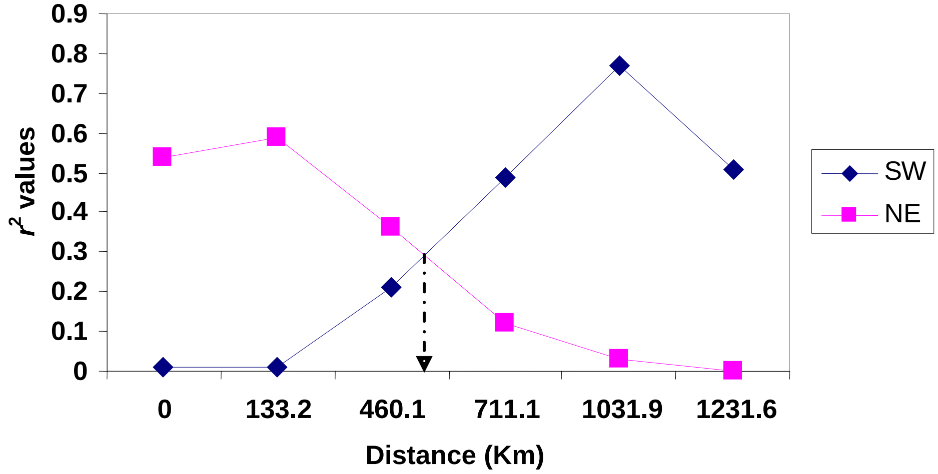


Figure 5.5. Plot of r^2 values showing the point of intersection between SW Kalahari Xeric versus NE mesic savanna influence on dung beetle species abundance composition as defined by shared secondary factors from ordination (S1 = SW bias, S2 = NE bias – see Table 5.1). On a linear scale the arrow is 88 km from the NC-Kalahari towards the Khutse sites. Cumulative distances are shown between the six study areas: Chobe R = 0; Savuti = 133.2; NC-Kalahari = 460.1; Khutse = 711.1, Mabuasehube = 1031.9; Sw-Kalahari = 1231.6.

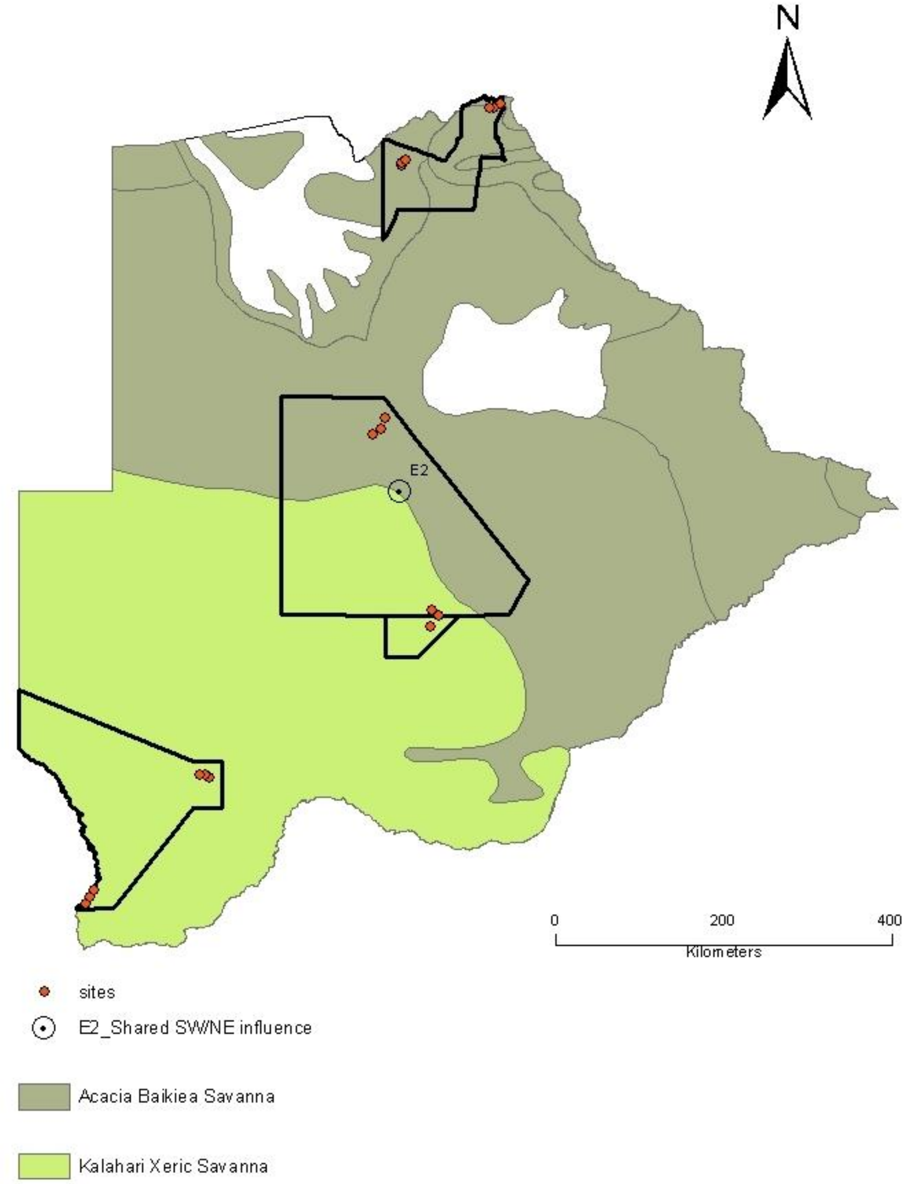


Figure 5.6. **Map showing the ecotone between the *Acacia-Baikiaea* Savanna and Kalahari Xeric Savanna ecoregions (Olson *et al.*, 2001) and E2 - the point of intersection between shared SW versus shared NE influence (see Fig. 5.5.).**

5.4. Discussion

The scarabaeinae sand faunas of the Botswana Kalahari show clear ecological patterns across the aridity and trophic gradient. Major differences in patterns are shown by the carrion and dung faunas. Of the several factors that might shape assemblage structure, a major influence appears to be rainfall variability. The dung fauna was strongly influenced by regional rainfall gradient but relatively little by dung types. This is clear because study areas were sufficiently far apart for each to support distinctly different dung faunas in terms of statistical separation, which is an important consideration for conservation. Factorization of the structure of each dung fauna has provided an appreciation of the relative uniqueness of the fauna at each study area and the relative import of two major influences SW Kalahari vs NE savanna interpreted from the two shared factors in an ordination of the species abundance data from dung baited traps. These influences overlap to different degrees across the ecotone between the Kalahari Xeric and *Acacia-Baikiaea* Savanna ecoregions (Olson *et al.*, 2001) but the point of intersection between factors on a linear scale for distance almost exactly coincides with the mapped ecotone providing impressive support for its accuracy despite the irregularity in the path that it follows (Fig. 5.6.).

The carrion fauna is also statistically separated between study sites in the NE of the study region although those in the Kalahari (SW) all cluster together suggesting less variability than for the dung fauna. Carrion distribution effects may have influenced local spatial patterns. The Kalahari Basin in particular is an area of abundant vertebrate scavengers and perhaps low carrion density (Scholtz *et al.*, 2009). Thus, from long ago these led to popular assumptions that carrion feeding is uncommon in Afro-tropical savanna (Halffter & Matthews, 1966). While this may sound logical in view of the scavengers and predator population that roam most Afro-tropical savannas (Scholtz *et al.*, 2009), it is not supported by the observation of this study. It seems there is a well developed community of carrion species across the Kalahari basin. In Chobe NP, particularly the Savuti area, since 1970’s there has been increasing occurrence of lion predation on young elephants (*Loxodonta africana*) which may take several days to finish (Power & Compion, 2009). In CKGR two (*c*.1 week old) unfinished gemsbok (*Oryx gazella*) carcases were found in the vicinity of the study sites (personal obs.). It is not known if the currently observed incidents were prevalent historically or isolated cases, whatever the case might be this indicates that there has been a good chance for the development of a carrion feeding assemblage.

Besides climatic, mammal and trophic considerations, effects of landscape patterns and habitat structure may also be influential in separating faunal structure from place to place (Davis *et al*., 2000). The vegetation physiognomy varied between and even within study areas. For instance, Chobe River was characterized by *Baikiaea* woodland with some local influence of shade versus unshaded sites, also Savuti where *Colophospermum mopane* shrubs were dominant. Mabuasehube was predominantly sparse *Acacia* shrubs while Sw-Kalahari was mostly grass on dunes. These local variations in microhabitats and other environmental cues are known to influence species composition and structure (Davis *et al.*, 1999). Thus, some species in Chobe River to Savuti, comprised shade tolerant species (*Mimonthophagus anomalus*) that were filtered out to the southwest, whereas some species centred in the SW-Kalahari dunefield comprised specialists on dunes (e.g. *Drepanopodus costatus*) (see Appendix A4).

CHAPTER 6 REGIONAL AND LOCAL PATTERNS OF FOOD ASSOCIATION ACROSS THE BOTSWANA KALAHARI

6.1. Introduction

There is a limited body of evidence on dung type associations of Afrotropical dung beetles (Davis, 1994; Botes *et al.*, 2006, Davis *et al.*, 2010), which variously show specialization or generalization in selectivity for different dung types. A recently published work has examined trophic associations of dung beetle species occurring in the northeast Kalahari Basin (Tshikae *et al.*, 2008). However, none has investigated dung effects on dung beetles across the entire Botswana Kalahari basin, which crosses an ecotone between the mesic and xeric savanna (Chapter 5) and also represents a gradient of diminishing dung resources.

The probable resource gradient across the Botswana Kalahari appears to be primarily driven by decreasing rainfall to the southwest. This generates decreasing dung beetle species richness to the southwest (Chapter 3), which may be related to the gradual disappearance of large, fast rollers and tunnellers as a result of the decreasing size and diversity of dung types (Appendix A4; Chapter 2,) due to the restriction of large ruminant and monogastric herbivores to the northeast (although cattle have now been introduced into the SW). Greater dung type diversity and dung beetle species packing in the northeast (Chapter 4; Tshikae *et al.*, 2008) might be expected to result in greater dung type specialization and narrower niche widths as documented elsewhere (Sowig & Wassmer, 1994; Gittings & Giller, 1998). To the contrary, the combined effect of fewer species and both lower amounts and lower diversity of dung types in the southwest might result in lower competition, less dung type selectivity, and wider niche widths in the southwest.

In this chapter, three different sets of analyses have been considered to examine regional and local patterns of dung type association. One simultaneously analyses regional and local patterns of spatial and bait type association. The other two examine local bait type associations and then determine how the ecological patterns that they describe vary across the entire region. These analyses were designed to examine the effect of the Kalahari aridity gradient on partitioning of diminishing trophic resources. It was hypothesized that niche separation (dung type specificity) will be reduced across the climatic gradient leading to more niche overlap, possibly owing to harsher conditions favouring less selectivity between a reduced number and density of dung types (reduction in available resources) with fewer competitors (lower species richness). Also, that dung type associations will change from NE to SW to reflect local dung type availability.

6.2. Analytical methods

6.2.1. Hierarchical Analysis of Oblique Factors

Multivariate techniques were used to determine the overall trophic and spatial patterns. Firstly, dung beetle species with a total abundance of <10 were removed, leaving 91 species. Secondly, a data matrix of 91 species x 30 combined study regions (6) and bait types (5) was created to determine bait type association across the different reserves and sites. The matrix was 4th root transformed before analysis to normalize the data. An ordination analysis was performed with a maximum of 10 factors based on two ecoregions and five bait types offered across the environmental gradient. Varimax normalized rotation of factor axes was used to align factors with clusters of study areas showing similar patterns of distribution or assemblage structure. A Hierarchical Analysis of oblique factors was conducted on the principal components factor analysis to determine relative contribution of shared spatial variance (secondary factors) and unique faunal composition (primary factors) to spatial distribution patterns (see Chapter 3 Analytical methods). The coefficient of determination (r^2 values) for each cluster was calculated from Pearson’s r values as this translates into the proportional influence of shared and unique variance in each cluster. Spatial associations and food associations of dung beetles were determined from the species classification provided by the factors generated in the factor analysis.

6.2.2. Niche width analysis

The relative generalization or specialization in food associations across the 6 study areas was quantified using the generalization/specialization index (GSI) method outlined by Davis (1996c). This was achieved by first calculating a food niche width index for each species in the six study areas. This simply utilized the calculation of the Shannon-Wiener index that is expressed as $H' = \Sigma p_{ij} \ln p_{ij}$ where p is the decimal proportion of total abundance of the ith species trapped to bait type j. The species indices were standardized to a scale from 0 (specialist) to 1 (generalist) by dividing each index value by -1.609 which represents the most generalist value generated by the current data set. Secondly, the abundance values for each species attracted to each bait type were standardized by conversion to a percentage scale. In each of the six study areas for each bait the GSI for bias to extreme generalist (100) or extreme specialist (0) food association was calculated using the formula $GSI = \Sigma(Wp)_i$ where W is the niche width value and p the percentage proportion of the ith species (Davis, 1996c). From these GSI values the mean +/- SD index value for dung baits only were obtained for each study area. GSI values for dung baits only were compared between six study areas using one-way analysis of variance. Tukey's HSD analysis was used to determine means that were different from one another.

6.2.3. Canonical Correspondence Analysis

The computer program CANOCO vs. 4.5 (ter Braak & Smilauer, 2006) was used to perform canonical correspondence analysis (CCA) on species relative abundance data. CCA is an ordination technique that associates species relative abundance to environmental variables and is considered a robust method for pitfall data analysis (Palmer, 1993). CANOCO recognizes both measured and dummy environmental variables (ter Braak, 1995; Palmer, 1993). In this study the five bait types (carrion, pig, elephant, cattle and sheep dung) were treated as dummy environmental variables. They were coded as 1 for presence or 0 for absence. At each study, traps 1 to 20 were treated as unit samples. All abundance data were 4^{th} root transformed before analysis to reduce the effect of species with extremely high abundances. A Monte Carlo statistical test was used to test for significance of assemblage patterns. Environmental variables were represented by arrows. The relatively long arrow positioned close to an axis indicates a strong relationship with that axis (ter Braak, 1996; Palmer, 1993). Dung beetles situated along or close to the arrows have a strong association with that variable. The eigenvalues of the Canonical Correspondence Analysis (CCA) measure the proportion of the total variation in dung beetle abundance described by each axis (ter Braak & Verdonschot, 1995).

A protractor was used to measure angles between all of the possible paired combinations of vectors representing different environmental variables (dung types). Cross-tabulation was used to test for similarity or dissimilarity between the patterns that emerged.

6.3. Results

6.3.1. Hierarchical Analysis of Oblique Factors

Ten different patterns were defined from the combined analysis of the spatial and trophic data for the more abundant species (Figs 6.1 to 6.4., Tables 6.1., 6.2.). These could be reduced to four main patterns of trophic association (Figs 6.4. to 6.6.). One pattern was dominated by dung type generalists (Fig. 6.5. Cluster A) and comprised five groups with differing spatial centres across the entire environmental gradient of Botswana (Fig. 6.2.). A second pattern was variously dominated by bias to carrion, pig and elephant dung (Fig. 6.5. Cluster B) (see discussion below), and comprised three groups with greatest proportional abundance centred on the Savanna / Kalahari transition (see Chapter 5). The other two patterns comprised carrion (F8) or elephant dung (F7) specialists centred in the extreme northeast. In conclusion, all four main trophic patterns were represented in the northeast whereas only two were represented in the southwest.

The ten patterns accounted for >88 % of the total variance and showed various patterns of shared and unique variance (Tables 6.1., 6.2.). Species grouped in Patterns 2, 5, and 6, show high shared variance across shared factor S1 and are characterized by spatial centring to the southwest, particularly Khutse and Mabuasehube (Figs 6.2., 6.3.). S1 correlation values are positive for Pattern 2 (Pig / elephant dung bias) and negative for Patterns 5 (carrion / pig dung bias)) and 6 (dung generalists). Species grouped in Patterns 1, 4, 7 and 9 are characterized by high shared variance across shared factor S2. Patterns 1, 4, and 9 show similar dung generalization but are centred on different northeast reserves (Figs 6.2., 6.4.). Pattern 7 shows a negative S2 correlation value and elephant dung specialization in Savuti whereas the relatively high unique (P1) correlation for Factor 1 characterizes species found primarily in the woodland of Chobe. Species grouped in Patterns 3, 6, and 8, show high shared variance across shared factor S3, for which there is no obvious explanation. The species of Pattern 8 show a positive S3 correlation with strong carrion specialization centred on Chobe and Savuti (Fig. 6.4). Those of Patterns 3 and 6 are dung generalists showing negative S3 correlations and southwest spatial bias centred on the southwest Kalahari or Mabuasehube / Khutse, respectively (Fig. 6.2.). Species grouped in Patterns 10 showed high shared variance across shared factor S4 characterized by occurrence in Chobe and North Central with an elephant, pig dung and carrion bias (Fig. 6.3.). Only three species remained unclassified to any one of the ten patterns.

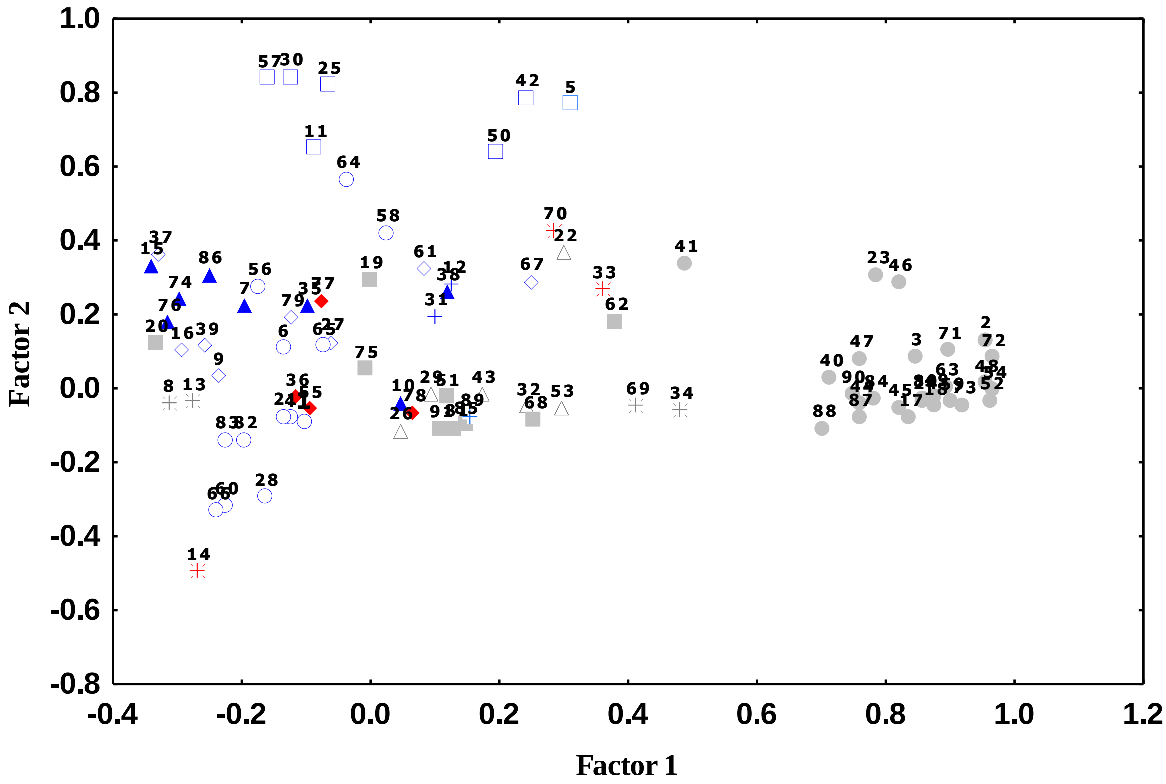


Figure 6.1. Two-dimension ordination plot showing the statistical distance between 91 species of dung beetles divided into 10 groups based on analysis of species abundance on five bait types at six study sites across the Botswana Kalahari (see appendix A3 for key to species code and relative abundances; Factors: 1= filled circle, 2 = open square, 3 = open circle, 4 = filled square, 5 = filled triangle, 6 = open diamond, 7 = open triangle, 8 = filled diamond, 9 = blue star, 10 = grey star,11 = red star(unclassified species).

Table 6.1. Eigen values derived from the hierarchical analysis of oblique factors (Fig. 6.1.).

Factors	Eigen value	% Total variance	Cumulative %
1	26.99	29.66	29.66
2	12.92	14.19	43.86
3	10.90	11.98	55.84
4	10.00	10.99	66.82
5	5.41	5.95	72.77
6	4.26	4.68	77.45
7	3.19	3.51	80.96
8	2.49	2.74	83.70
9	2.18	2.40	86.10
10	1.96	2.16	88.25

Table 6.2. Correlations between oblique factor loadings and extended factors derived from hierarchical analysis of oblique factors (see Fig. 6.1.).

	Coefficient of determination (r^2)									
	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7	Cluster 8	Cluster 9	Cluster 10
Spatial bias	Ch	Kh	SW	Sav	Kh/Mab	Kala	Sav	Ch/Sav	Sav/Kh	Ch/NC
Trophic bias	Dung	Pig/Ele	Dung	Dung	Pig/Car	Dung	Ele	Car	Dung	Pig/Ele
Secondary factors										
S1-SW	0.00^	**0.54**	0.01	0.01^	**0.51^**	**0.30^**	0.01	0.00	0.01	0.06
S2- NE	**0.24**	0.01	0.06	**0.60**	0.06	0.04	**0.53**	0.05	**0.44**	0.01
S3 - NE/SW	0.01^	0.00	**0.31^**	0.00	0.01	**0.33^**	0.00	**0.38**	0.01	0.01
S4 - NE	0.10	0.00	0.16	0.00^	0.11	0.09	0.00^	0.00	0.00^	**0.50^**
Primary factors>	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
	0.64	0.45	0.46	0.39	0.32	0.24	0.45	0.56	0.53	0.43

^negative correlations

Ecological bias represented by highlighted r^2 for extended factors interpreted from empirical data

S1 = shared SW bias on dung: Khutse (Kh), Mabua (Mab), and (Kala) = previous two plus SW

S2 = shared NE bias on dung: mainly Chobe (Ch) and Savuti (Sav)

S3 = shared carrion bias to NE (Chobe / Savuti = Ch/Sav) with strong negative correlation to SW (Kala)

S4 = shared Chobe / North Central bias (Ch/NC)

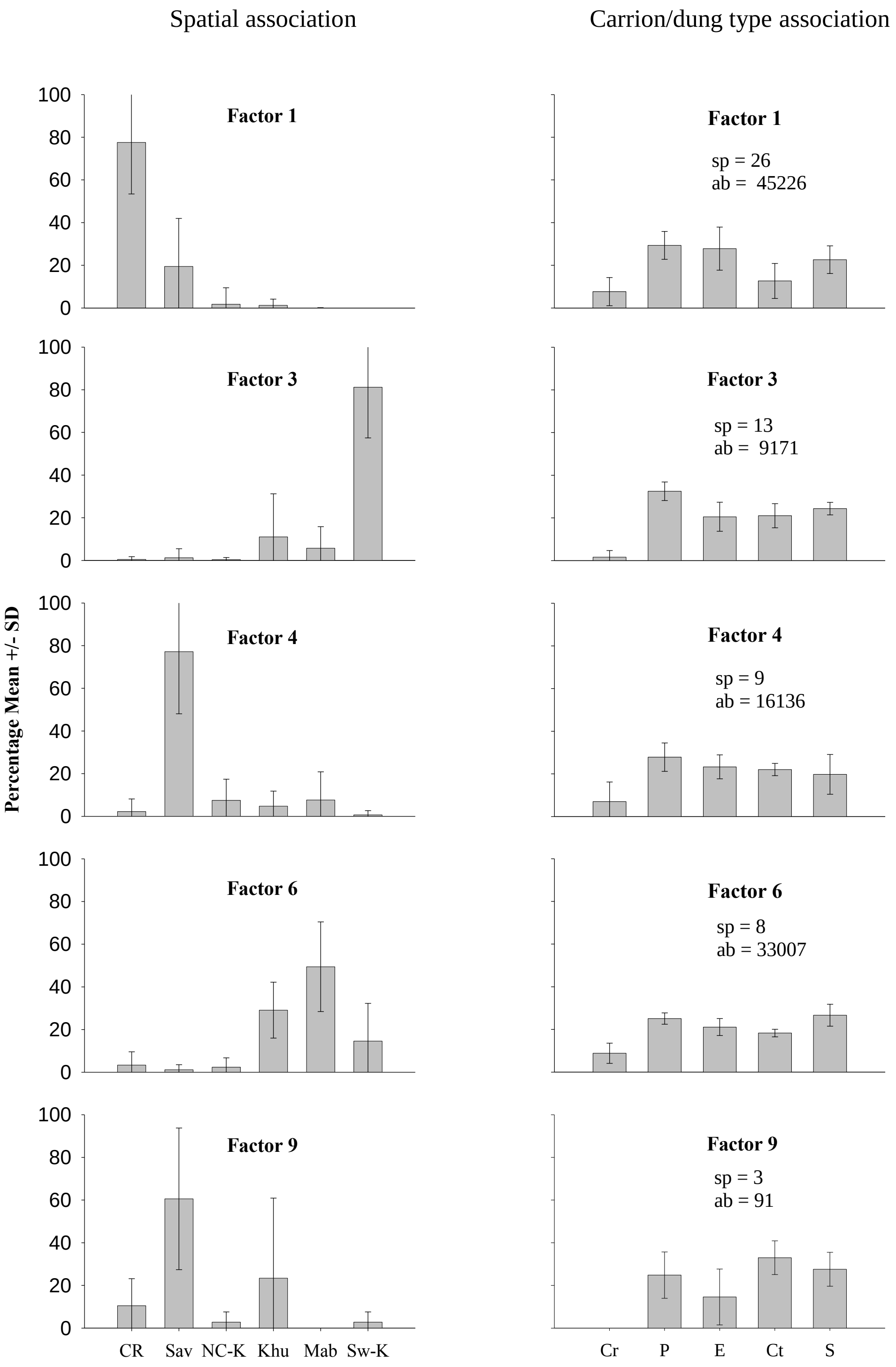


Figure 6.2. **Bar diagrams showing mean ± SD spatial and trophic associations of dung beetle species constituting factors 1, 3, 4, 6 and 9 in the hierarchical factor analysis.**

Fig. 6.3.

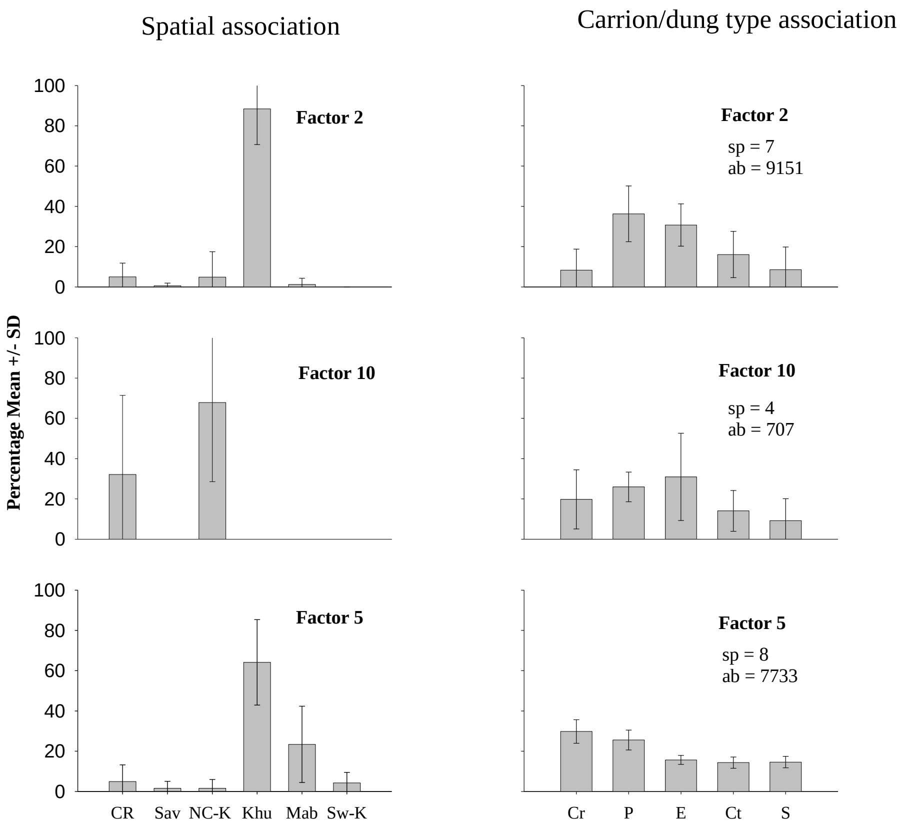
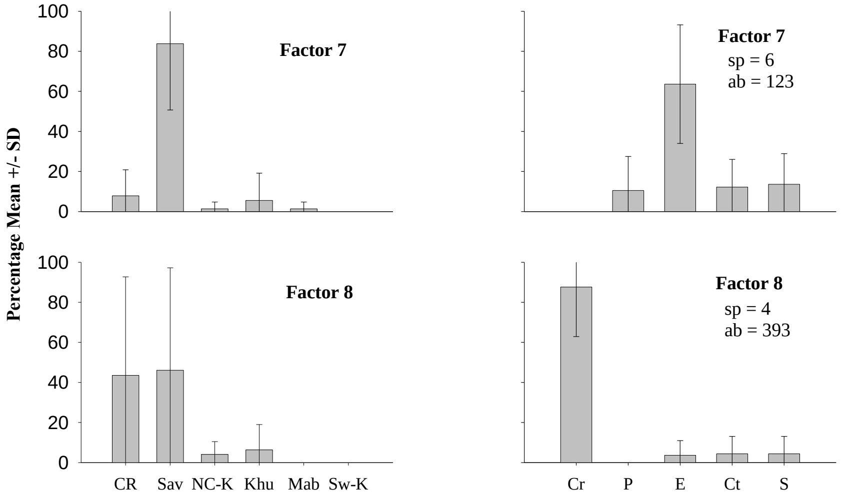


Fig. 6.4.



Figures 6.3., 6.4. **Bar diagrams showing mean ± SD spatial and bait associations of dung beetle species constituting factors 2, 10, 5, (Fig. 6.3.) and 7, 8 (Fig. 6.4.) in the hierarchical factor analysis.**

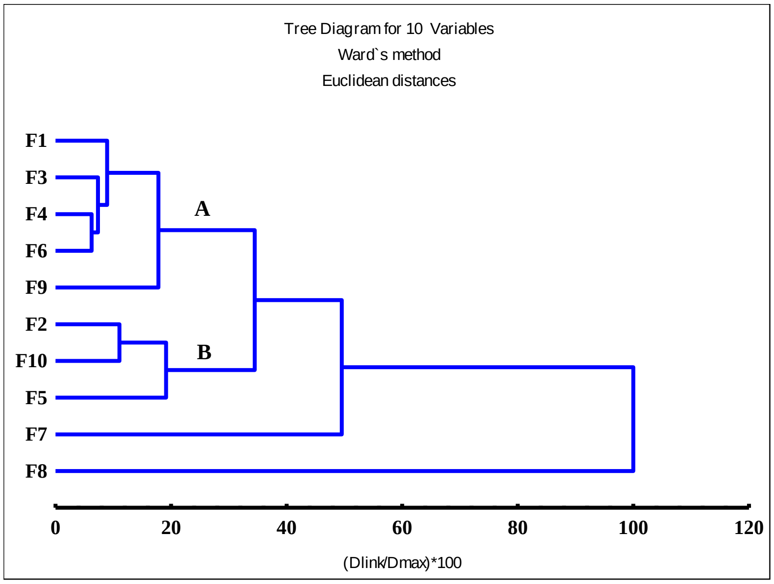


Figure 6.5. Dendrogram summarizing similarities in trophic association between groups of dung beetles defined on the basis of both spatial distribution and bait type association. Cluster A. Dominated by dung type generalists with differing spatial biases across the entire study region (see Figs. 6.2., 6.6.), Cluster B. Variously dominated by bias to carrion, pig, and elephant dung across the Kalahari / Savanna transition (see Figs. 6.3., 6.6.), F7, F8. Specialists on elephant dung (F7) or carrion (F8) in the northeast savanna region (see Fig. 6.4.).

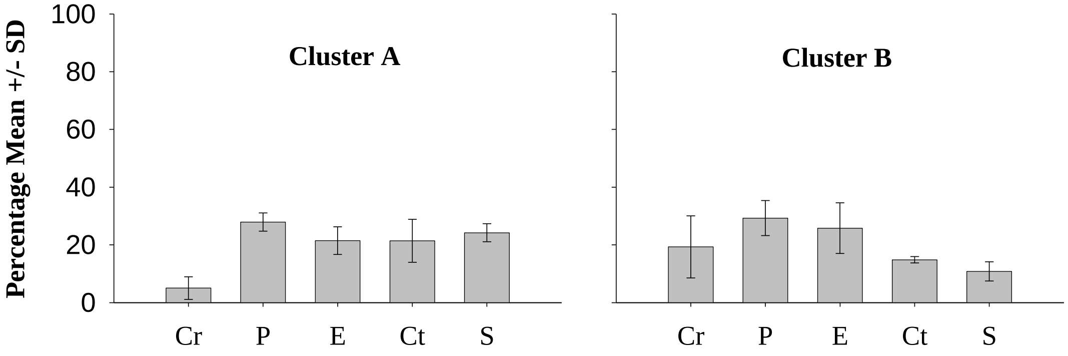


Figure 6.6. Bar diagrams showing mean ± SD bait associations of the species representing two major clusters in Fig. 6.5.

6.3.2. Niche width

The niche widths of all species were marginally narrower across the transition zone between the mesic *Acacia-Baikiaea* savanna and the Kalahari xeric savanna (Table 6.3.). A similar pattern was shown by the mean values for a generalization / specialization index on the four dung types. Although the values in the transitional region indicated only a marginally more specialist fauna, there was a significant difference (Analysis of variance, $F = 7.70$, d.f. = 5, 18, $P < 0.001$). Index values for carrion showed a shallow decline from more generalist in the northeast to more specialist in the southwest.

Table 6.3. Relative specialization or generalization of all dung beetle species between carrion or dung types across the Botswana Kalahari region and mean trophic niche width.

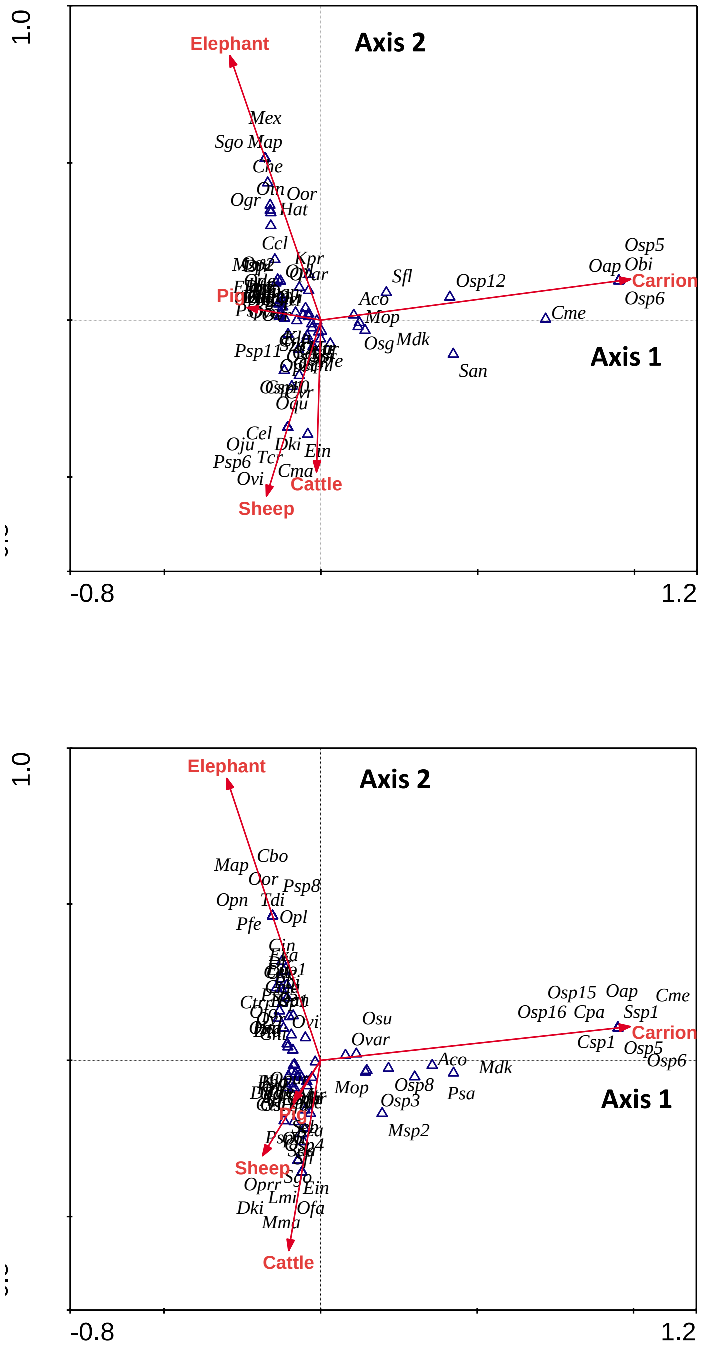
	Species niche width Mean± SD	Generalization / specialization index (GSI)					GSI Mean ± SD for 4 dung types
		Carrion	Pig	Elephant	Cattle	Sheep	
Chobe River	0.48 ± 0.32	66.23	65.39	68.59	72.76	70.2	69.24 ± 3.09^{bc}
Savuti	0.37 ± 0.30	55.37	66.21	67.04	73.89	72.29	69.86 ± 3.80^{bc}
NC-Kalahari	0.26 ± 0.29	50.82	61.79	63.57	60.7	66.24	63.08 ± 2.42^{ab}
Khutse	0.38 ± 0.24	51.47	55.44	56.71	61.92	67.58	60.41 ± 5.54^{a}
Mabuasehube	0.41 ± 0.32	50.81	64.61	72.14	74.45	69.14	70.09 ± 4.25^{bc}
Sw-Kalahari	0.51 ± 0.29	47.22	76.06	77.93	75.29	71.08	75.09 ± 2.89^{c}

* Values followed by a different letter differed significantly ($P < 0.05$, Tukey's HSD)

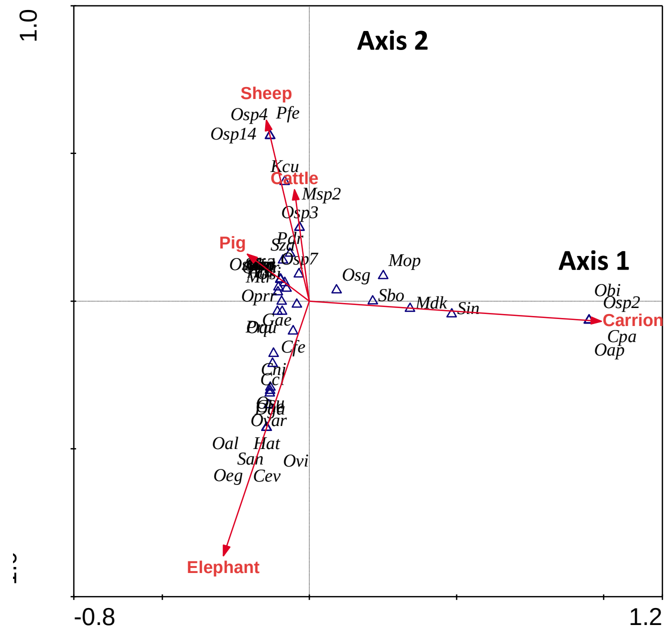
6.3.3. Canonical Correspondence Analysis

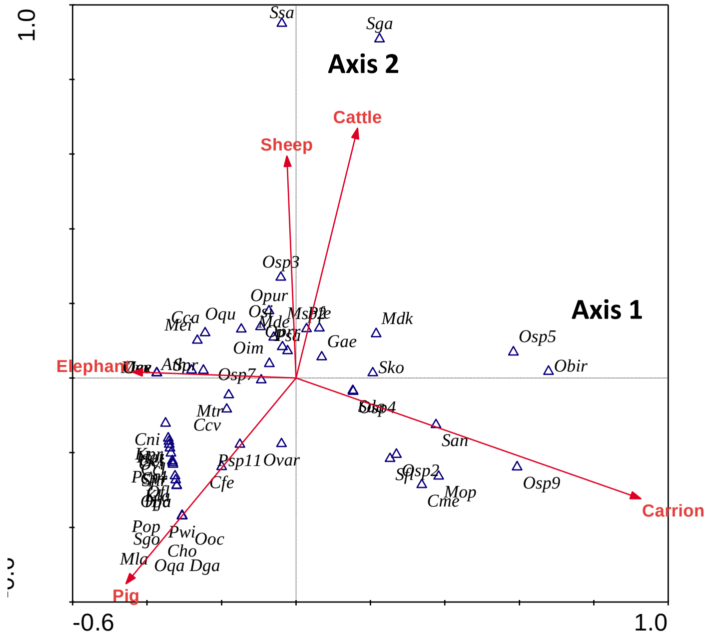
For CCA analyses at each of the six study areas across the Botswana Kalahari, tests of Monte Carlo permutations for all canonical axes detected significant patterns of association between species variables and environmental variables (bait-types) (Table 6.4.). In the study areas located in the NE and SW respectively the eigenvalues for the first and the second axes together accounted for greater than 31-60% and 24-47% of the variance in species environment relationships (Table 6.4.). In each analysis, there was a clear and fairly similar pattern of separation along axis 1 between carrion (positive loadings) and dung fauna (mostly negative loadings) (Figs. 6.7. to 6.12.). In general, patterns of separation between dung types extended along axis 2.

Comparison of biplots for axis 1 and 2 from each area revealed both differences and similarities in patterns of bait type association (Figs. 6.7. to 6.12.). Measurements of angular separation between environmental vector lines quantified these differences in patterns of association between dung types (Table 6.5.). They differed significantly (6 x 6 contingency test: $\chi^2 = 992.5$; d.f. 5, $P < 0.001$). Cluster analysis of the angular separation data showed three principal patterns of exploitation of dung across the rainfall gradient of Botswana (Fig. 6.13.). These were the northeast savanna region (Chobe, Savuti, NC-Kalahari), the northeast of the arid Kalahari region (Khutse, Mabuasehube) and the arid SW-Kalahari. The savanna group pattern showed close relationships between ruminant faunas of pads and pellets with a wide separation from that of pig (not Savuti) and an even wider separation from that of elephant. The northeast Kalahari group pattern showed similar close relationships between ruminant faunas of pads and pellets with a wide separation from that of elephant and an even wider separation from that of pig. The southwest arid pattern was quite different with a close similarity between the faunas of pig and cattle dung which were widely separated from those of sheep and elephant dung. In the savanna and southwest, associations with pig dung were weakly defined as they were represented by short vector lines. Although the angle of separation was similar between the two most distant vector lines for dung type in each CCA analysis (153-164^{o}), mean angle of separation between pairs of lines declined across study areas from southwest to northeast with the exception of Chobe (Table 6.5.).

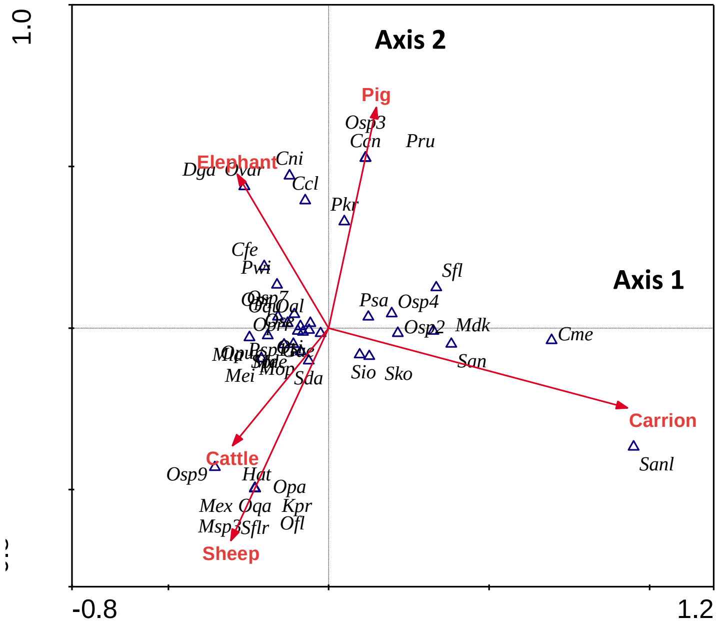


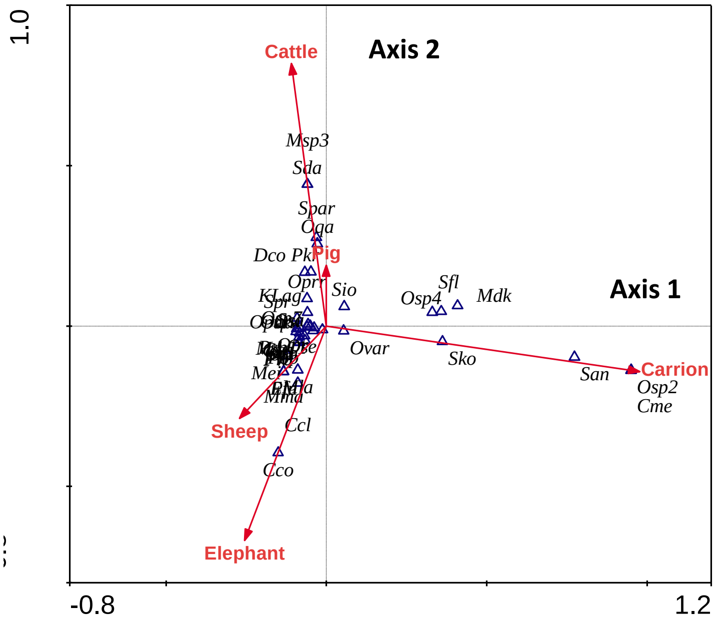
Figures 6.7., 6.8. **Biplots of dung beetle abundance distribution in pitfall traps baited with different types of dung and carrion in Chobe and Savuti. CCA ordination diagram with dung beetle species (△) and environmental variables (arrows).**





Figures 6.9., 6.10. **Biplots of dung beetle species abundance distribution in pitfall traps baited with different types of dung and carrion in CKGR (North Central and Khutse). CCA ordination diagram with dung beetle species (△) and environmental variables (arrows).**





Figures 6.11., 6.12. **Biplots of dung species beetle abundance distribution in pitfall traps baited with different types of dung and carrion in Kgalagadi Transfrontier Park (Mabuasehube and Sw-Kalahari). CCA ordination diagram with dung beetle species (△) and environmental variables (arrows).**

Table 6.4. Statistics for species-environmental relationships derived from CCA ordinations (Figs. 6.7.-6.12.).

	Axis				Cumulative Eigen values axes 1& 2	Monte Carlo Test of all canonical axes	
	1	2	3	4			
	Eigen values					F	P
Chobe River	0.23	0.08	0.05	0.03	0.31	3.75	0.002
Savuti	0.41	0.17	0.10	0.06	0.58	3.51	0.002
NC-Kalahari	0.40	0.19	0.14	0.07	0.60	2.82	0.002
Khutse	0.17	0.10	0.05	0.05	0.27	3.92	0.002
Mabuasehube	0.18	0.06	0.05	0.04	0.24	3.53	0.002
Sw-Kalahari	0.41	0.06	0.05	0.04	0.47	7.05	0.002
	Correlation coefficients						
Chobe River	0.98	0.96	0.92	0.87			
Savuti	0.99	0.99	0.96	0.92			
NC-Kalahari	0.99	0.99	0.95	0.86			
Khutse	0.99	0.98	0.96	0.90			
Mabuasehube	0.99	0.97	0.87	0.85			
Sw-Kalahari	0.99	0.97	0.95	0.90			

Table 6.5. Degrees of separation between vector lines representing average association with dung type in each study area.

	Chobe River	Savuti	NC-Kalahari	Khutse	Mabua-sehube	SW-Kalahari
Cattle / Sheep	15°	22°	6°	16°	15°	130°
Cattle / Pig	98°	24°	46°	155°	153°	7°
Cattle / Elephant	159°	153°	155°	102°	110°	152°
Sheep / Pig	83°	2°	40°	139°	164°	137°
Sheep / Elephant	144°	131°	149°	86°	124°	23°
Pig / Elephant	62°	129°	109°	53°	43°	160°
Mean (± SD)	93.5°(53.2°)	76.8°(67.6°)	84.2°(62.2°)	91.8°(52.2°)	101.5°(60.1°)	101.5°(68.0°)
Range end to start	159°	153°	155°	155°	164°	160°

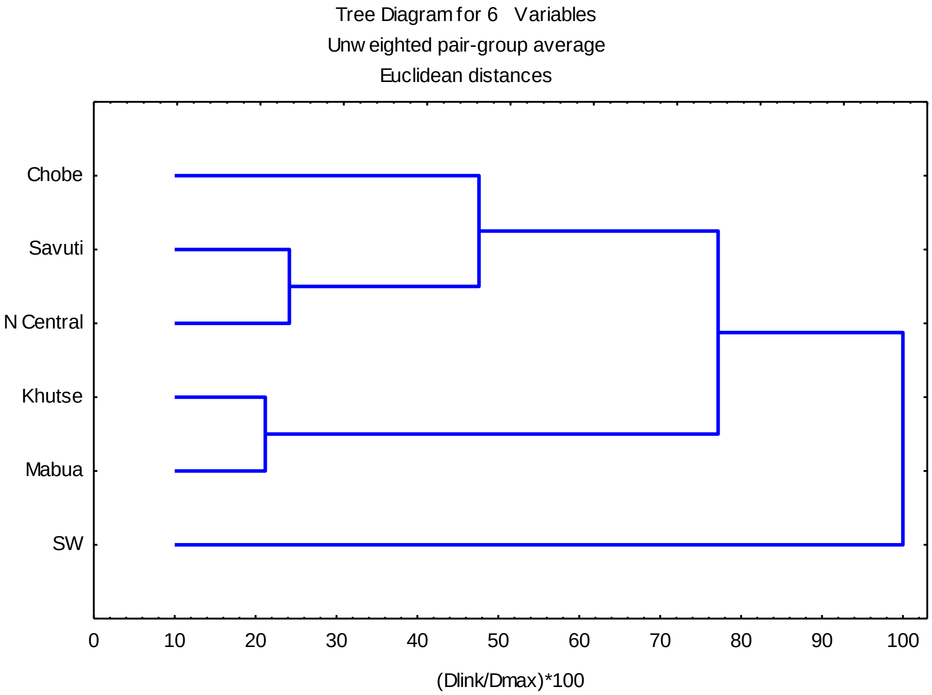


Figure 6.13. **Dendrogram showing the proportional similarity or dissimilarity between patterns of dung association across the environmental gradient of the Botswana Kalahari (from analysis of data in Table 6.5.).**

6.4. Discussion

The hierarchical analysis reflects both the patterns of spatial distribution and dung type association. It shows that some general patterns of association are repeated across the environmental gradient although different species are involved in the association reflecting the species turnover described in Chapter 4. There are probably a number of variables involved including the increasing aridity to the southwest and changes in the availability of different dung types. Slightly greater variability of associations in the Savanna faunas (elephant, carrion, dung generalist, pig/elephant) compared to the Kalahari (dung, pig/carrion, pig/elephant) provides weak support to the hypothesis of greater trophic specialization in the moister savanna. However, the niche width and generalization / specialization indices do not support this hypothesis. There are similar degrees of relative generalization of dung faunas at either extreme of the environmental gradient with a slight but significant increase in specialization at the Kalahari / savanna transition zone. This pattern does not readily lend itself to an explanation.

The CANOCO analysis shows that patterns of dung type association change from the savanna to the Kalahari. The change from closer similarity of cattle and sheep faunas to those of pig in the savanna to their closer similarity to those of elephant in the northeast Kalahari could reflect some quality related to the absence of elephants from the local mammal faunas to the southwest. The six patterns also equate to the overall manner of partitioning of the dung resource by dung beetles. Three principal patterns have been demonstrated and in sequence, these parallel increasing aridity across the environmental gradient. However, the increase in mean separation between dung association vector lines in the southwest would suggest greater specialization or less overlap between faunas in the Kalahari. This analysis does not therefore support the main hypothesis which predicts greater specialization to dung types in the savanna to the northeast. Overall, one analysis provides some support for greater species specialization in the savanna whereas two do not. Those suggest greater separation to the southwest or at the savanna / Kalahari transition. Therefore, no clear conclusions may be drawn.

CHAPTER 7 DISCUSSION AND CONCLUSION

7.1. Effects of the environmental gradient across the Botswana Kalahari

The Botswana Kalahari has been edaphically biased by sand deposition and climatically characterized by an aridity gradient leading to primarily open vegetation (with exception of some parts of Chobe NP) and diminishing diversity of dung resources (amounts and types reduced) due to reduced mammal diversity that taper to the arid southwest Kalahari from 19 species in Chobe NP through 15 in the Central Kalahari down to 14 species in the Transfrontier National Park. The dung beetle species accumulation curves have shown a shift in species richness from the NE to SW. Although biased by edaphic and climate characteristics, overall species richness match those recorded in other Afrotropical savannas (Hanski & Cambefort, 1991). The species accumulation curves and non-parametric estimators indicate that the present study has successfully sampled most species of dung beetles present in Chobe NP, CKGR and Kgalagadi Transfrontier Park.

The Kalahari aridity gradient may have influenced biogeographical patterns across the Kalahari basin. The ordination analysis (Chapter 3) suggests that the Botswana Kalahari basin comprises four biogeographical groups that overlap along the aridity gradient. These are identified as the northeast, northeast/widespread, widespread and the southwest. However the only two centres with major influence on dung beetle regional distribution are at the extremes of the gradient. These are the moist NE and arid SW Kalahari (Davis, 1997). The two centres are congruent to climate, patterns in particular rainfall, thus the present biogeographical patterns of dung beetles clearly attest to the contributions of both geological and climatic history within the Kalahari basin. Although there are no data collected to support this claim, variable climate and the accumulation of Kalahari deep sand (Chapters 1 & 2), appears to have barred non-psammophilous dung beetles species as shown by scorpion taxa (Prendini, 2005). In dung beetles, fauna separation of close relatives to the SW and NE has been documented (Davis *et al*., 2008) resulting from a historical process of separation between drier SW and moister NE centres followed by Pliocene - Pleistocene climatic change so that now there is overlap in distribution across the aridity gradient whilst still showing distributions centred on arid SW or moister NE centres.

The present study's results have also shown some variation in biogeographical composition between bait types in NE while those in the SW were dominated by Kalahari endemics highly adapted to pellet dung. Biogeographical diversity declined from the NE to SW, thus, supporting the hypothesis for a decline in biogeographical composition and diversity to the arid SW Kalahari. Similarly Barker (1993) found that biogeographical composition patterns of grasshoppers in the same survey region decreased from NE to the SW as a result of decreasing rainfall and that endemism was higher in the SW.

The Kalahari aridity gradient may have also influenced species richness and diversity. Generally, dung beetle species richness and abundance declined to the SW, but in a zigzag fashion. Species richness and abundance were low at NC-Kalahari which is situated at the edge of the Makgadikgadi Depression. Dung beetles are known to respond to rainfall and several other ecological variables (Klein, 1989; Estrada *et al*., 1993; Andresen, 2005; Horgan, 2005; Numa *et al*., 2009; 2011). Thus there are several possible explanations for assemblage structural differences between study areas. Initially land-systems perturbations (depressions and pans) appear to be a plausible explanation, however, it is unlikely to be the underlying factor because it doesn't have a similar effect at Savuti which is also in the vicinity of the Mababe Depression. Although changes in dung types (lack of large, fine and fibrous dung pats) seems to be an alternative causal factor influencing species richness, this seems far fetched in view of the complex situation in Khutse where such dung types do not occur yet species patterns are high. Functional diversity showed no consistency with the aridity gradient. Kleptocoprids were dominant over tunnellers and rollers from NE to SW. Their widespread dominance is perhaps related to natural history (small body size) which makes physiological sense, rather than causal relationship between guilds and diminishing resources.

Several regional and local factors are known to influence dung beetle assemblage structure (Davis & Scholtz, 2001), for instance rainfall, vegetation, landscape patterns and dung types

(Davis, 1990; 1994a; 1996c; Davis & Scholtz, 2004; Davis *et al.*, 2008; 2010). In this study soil type was essentially similar across the gradient thus regional spatial patterns were primarily influenced by variability in climate. It should be noted that the regional climatic gradient which is essentially related to decreasing rainfall has a strong correlation with vegetation structure (Ringrose & Chanda 2000; Privette *et al.*, 2004; Scholes *et al*., 2004) and mammal distribution including the diversity and density of their dung types which in turn influenced dung beetle patterns. Climate has been identified as the overriding factor influencing dung beetle assemblage structure. This is supported by the plotting of shared variance obtained from hierarchical analysis of oblique factors, which showed that species centred in the NE decline in representation and abundance to the SW where the SW centred species are dominant. Although there were effects of depressions, dunes and pans to consider, significant spatial variances for which soil was responsible were not recorded across the study region. These factors, however, are likely to have a local effect which influenced the occurrence of some species independently of the climatic gradient.

On the other hand, local spatial patterns might have been influenced primarily by landscape patterns, habitat structure and differences in dung types (Chapters 5 and 6). For example, the land systems analysis (Chapter 2) shows that Savuti and NC-Kalahari study areas were located on the fringes of depressions. The striking features in these two study areas is the rarity of *Kheper lamarcki* and *Pachylomera femoralis*, species that are widespread and most abundant in sandy savannas characterized by mid-summer rainfall climatic regime. Another example, is that species centred on the southwest Kalahari comprised primarily sand dune specialists (Davis & Scholtz, 2004; Davis *et al* 2008; 2010). Vegetation is greatly influenced by soil type which in turn influences dung beetle patterns (Davis *et al*., 2010). In terms of vegetation structure, some species in Chobe NP comprised shade specialists. Mammalian dung constitutes an important breeding and feeding resource for dung beetles (Hanski & Cambefort, 1991; Scholtz *et al.*, 2009). Thus, a strong natural gradient of dung types possibly influenced local occurrence of certain species. Some species within Chobe NP comprised primarily specialists on the coarse-fibred dung of non-ruminant herbivores such as elephant (Davis, 1994a; 1997). These local factors may have affected overall patterns of abundance, species richness and species occurrence differently at each study area (Davis, 1994a; 1996c; 1997).

In conclusion, the Botswana Kalahari Basin dung beetle fauna was strongly influenced by historical, regional and local factors. The dung beetle assemblage of the Botswana Kalahari comprises fauna centred in the northeast and southwest Kalahari regions, which coincide respectively with mid-summer and late-summer rainfall regions. These two centres strongly influenced the regional distribution of dung beetles along the northeast–southwest rainfall gradient. In terms of trophic associations there were two major groups, the dung fauna and the carrion fauna. Changes in ecological factors (i.e. landscape patterns, vegetation and dung types) only had a local effect on assemblage patterns. This was more pronounced in dung beetle abundance and species richness. Exceptionally high abundance and species richness values were congruent with high rainfall, dung type diversity and vegetative physiognomic structure shade *vs*. unshaded situations.

Of the several hypotheses tested in this study most were supported. Some of the hypotheses were strongly supported whereas some were weakly supported. A few were disproved or had no obvious support. However some hypotheses were not entirely disproved yet not strongly supported. Only one hypothesis was rejected; one which predicted a change in species abundances distribution between food types. Further research including several parallel transects along the aridity gradient would be useful in accurate elucidation of the patterns displayed by dung beetles in the Botswana Kalahari basin. The ecoregion boundary is not straight thus its edge effect may vary from one transect to another. Due to lack of invertebrate studies along the aridity gradient, parallels can be drawn only from a vegetation studies transect (Privette *et al*., 2004; Scholes *et al*., 2004) which lies further south of the dung beetle transect.

7.2. Implications of the results for regional conservation and management strategies

There are four main eco-climatic regions defined for southern Africa (Davis, 1997). The Botswana Kalahari straddles the borders of two of these centres with major protected areas in each. This work has shown that dung beetle assemblages in these protected areas are statistically distinct. However, existing information remains inadequate for the development of effective and efficient conservation and management strategies (Davis, 2002). This also limits the ability to predict accurately, how assemblage structure would respond to the ever changing environment (Thomas, 2005).

Efforts to conserve and manage ecosystems and the services they provide are often hindered by insufficient understanding of the functional dynamics of the systems (Hoeinghaus *et al.*, 2007b). This is true of the Botswana Kalahari basin which harbours three important conservation areas. Chobe NP in particular is a home to thousands of elephants, which are well documented for changing habitat structure across southern Africa (Ben-shahar, 1993; 1998; Cumming *et al*, 1997; de Beer *et al*., 2006) yet there has never been an objective study of the biogeographical and trophic structure of the widely accepted “indicator taxa” in conservation and biodiversity management (Davis *et al*., 2001; McGeoch *et al.*, 2001).

This study was conducted in conserved areas where all biota inside the reserve are considered protected. Species ranges, however, may extend beyond the reserve boundaries into inhospitable environment where such protection is not guaranteed. There was also strong edge effect between Moister northeast and Savanna/Kalahari ecotones shown by decline in abundance and species richness. The sensitivity of dung beetles to environmental factors and specialization to mammalian dung makes them useful as indicators of changes across a climatic and ecological resource gradient (Jankielsohn *et al*., 2001; Errouissi *et al.*, 2004; Davis *et al*., 2004) which may have importance in conservation and nutrient recycling studies. The integrity of many semi-natural areas is also threatened by the advancing front of many kinds of anthropogenic disturbances (Foxcroft & Richardson, 2003; Foxcroft *et al.*, 2007). Over the last 50 years anthropogenic activities for example cattle rearing (Perkins, 1996) have expanded deeper into the Kalahari basin to reach even the boundaries of some protected areas that were once dominated by indigenous mammals and this has raised concerns over conservation of habitat and the resident faunas (Melton, 1985; Dougill *et al.*, 1999). This view is exemplified by the changed spatial patterns reflected by some species in other taxa such as birds (Herremans, 1998; Herremans & Herremans-Tonnoeyr, 2000). This is particularly the case in management areas surrounding protected areas. These conservation concerns also signal the significance of ecological data in understanding the dynamics of the semi-arid Kalahari basin.

Also it should be remarked that empirical research has shown that various current conservation networks are insufficient to conserve dung beetle biodiversity (Nichols *et al.*, 2008). This being the case even in countries such as Costa Rica that have continuous strong conservation efforts, where changes in assemblage structure in the past 35 years were characterized by overall loss of dung beetle species (Scholtz *et al*., 2009). Globally anthropogenic activities both direct and indirect with dire consequences for dung beetles have been profiled (Didham *et al*., 1998; Andresen, 2003; 2008; Davis & Philips, 2005; 2009; Shahabuddin *et al*., 2005). Anthropogenic activities (Cattle grazing) create landscape patterns and habitat structure that are so different to those inside reserves (Jankielsohn *et al*., 2001; Jay-Robert *et al*., 2008; Navarrete & Halffter, 2008; Jacobs *et al*., 2010). In view of the results of the present research such patterns may induce local effects on dung beetle assemblages. Dung beetles assemblages showed a strong relationship with vegetation physiognomy and dung types, but many threat variables for dung beetles faunas stem from habitat destruction and considerable reduction in trophic resources. Most conservation areas across the Kalahari basin don't have a perimeter fence thus they remain accessible to domestic livestock. Domestic livestock are not only synonymous with bush encroachment but their dung may also contain chemicals with deleterious effect on dung beetles (Kruger *et al*., 1999; Bang *et al*., 2007). Consequently there is a greater need to expand conservation frontiers of vulnerable organisms to include both commercial and communal agricultural landscapes. There is a greater need for policy makers' to outline clear and effective management strategies, so as to curb farming practices that have dire consequences for dung beetles and the environment. Moreover, infrastructure development should consider the broader picture which embraces taxa with specific needs. Long term support for dung beetle research and maintenance of research sites (Escobar et al., 2008) would contribute to clear understanding and refined conservation strategies on the focal taxon for biodiversity conservation.

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APPENDICES

Appendix A1 (Chapter 2) Brief description of vegetative cover at study sites across the Botswana Kalahari Basin; the percentage cover of each vegetation category (trees, shrubs and grass) are each independent measurements

Locality and site	GPS Grid Reference	Vegetation description	%Tree canopy cover	% Shrub cover	% surfaceCover
Chobe N P					
Chobe River site 1	S17 54 52.4 E25 01 09.4	Dense canopy *Baikiaea* woodland, few shrubs and sparse grass	68.74	36.20	40
site 2	S17 54 36.9 E25 01 08.1	Open and sparse *Baikiaea* woodland	49.62	34.94	42
site 3	S17 54 57.4 E25 03 48.4	Dense *Baikiaea* woodland	62.82	44.14	32
Savuti					
site 1	S18.53092 E24.08378	Shrubland and short sparse grass tufts		58.71	27.5
site 2	S18.50264 E24.08978	Shrubland and short grass tufts		47.82	46.75
site 3	S18.47368 E24.12659	shrubland and few short sparse grass tufts		80.87	27.5
Central Kalahari G.R.					
Nc-Kalahari site 1	S21.22689 E23.91247	Tall grass and sparse shrubs		27.01	65.25
site 2	S21.33407 E23.86986	Tall grass and sparse shrubs		36.27	75.75
site 3	S21.40508 E23.77819	Open *Acacia* woodland, short sparse grass	38.23	48.86	55.5
Khutse					
site 1	S23.27663 E24.40434	Sparse shrubs and short grass tufts		28.86	60.5
site 2	S23.33220 E24.48308	few shrub and medium height grass tufts		41.91	83.25
site 3	S23.44818 E24.39556	Shrubland, short sparse grass tufts		33.79	34
Kgalagadi Trans. Park					
Mabuasehube site 1	S25.06566 E22.03332	Grassland sparse shrubs		21.40	53.25
site 2	S25.02857 E21.98819	Tall grass few shrubs		19.75	57.25
site 3	S25.03126 E21.92641	Shrubland short grass		36.84	63.75
Sw-Kalahari					
site 1	S26 24 29.4 E20 42 32.7	Dune slope grassland, very few shrubs		10.35	21.25
site 2	S26 20 34.4 E20 45 02.8	Dune slope grassland, few tall herbs and shrubs		16.84	31.5
site 3	S26 15 47.4 E20 48 11.2	Dune slope, few sparse trees, shrubs, herbs and no grass	17.81	14.32	14

Appendix A2 (Chapter 3) (a – e) Proportional biogeographical composition of dung beetle assemblages in each bait-type across a climatic gradient in Botswana

a) Widespread/northeast

Bait type	Chobe	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari
Carrion	16.18	0.00	19.72	0.00	0.00	0.00
Pig	44.18	20.23	3.43	0.01	0.06	0.00
Elephant	27.13	10.23	6.44	0.09	0.14	0.00
Cattle	21.24	1.21	2.88	0.00	0.00	0.00
Sheep	21.89	2.03	10.00	0.00	0.01	0.00

b) Widespread

Bait type	Chobe	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari
Carrion	25.87	12.05	0.94	29.39	0.47	0.27
Pig	29.91	5.10	6.73	32.46	0.41	0.66
Elephant	33.62	17.53	22.73	18.22	2.39	0.62
Cattle	34.75	8.54	6.85	42.80	1.00	0.73
Sheep	37.63	23.44	14.81	72.36	1.16	0.84

c) Northeast - bias

Bait type	Chobe	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari
Carrion	36.06	75.27	9.86	1.24	0.00	0.00
Pig	15.29	33.23	3.02	1.35	0.03	0.00
Elephant	28.14	27.88	3.68	1.45	0.17	0.00
Cattle	18.58	36.01	0.79	0.19	0.00	0.00
Sheep	23.69	39.27	0.37	0.60	0.08	0.00

d) Southwest - bias

Bait type	Chobe	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari
Carrion	21.78	12.05	69.01	69.01	98.43	99.73
Pig	10.62	41.15	86.73	65.96	99.36	99.34
Elephant	11.01	44.31	67.10	79.25	97.30	99.38
Cattle	25.40	53.98	89.29	55.28	99.00	99.27
Sheep	16.76	35.26	74.81	26.75	98.70	99.16

e) Poorly recorded

Bait type	Chobe	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari
Carrion	0.10	0.63	0.47	0.36	1.10	0.00
Pig	0.01	0.29	0.08	0.21	0.14	0.00
Elephant	0.09	0.06	0.05	0.99	0.00	0.00
Cattle	0.03	0.26	0.20	1.73	0.00	0.00
Sheep	0.03	0.00	0.00	0.30	0.05	0.00

Appendix A3 (Chapter 5.)

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Factor 1																
Kheper lamarcki	2	115	3176	985	571	479	0	139	9	5	5	0	0	0	0	0
Kheper prodigiosus	3	2	44	132	3	5	0	17	11	23	12	0	0	0	0	0
Scarabaeus zambesianus	17	8	321	253	114	384	1	8	1	19	59	0	11	1	4	2
Anachalcos convexus	18	51	85	42	22	83	4	5	0	0	2	0	0	0	0	0
Heliocopris japetus	23	0	16	23	5	7	0	5	2	6	3	0	0	0	0	0
Pedaria sp. (humped)	24	0	3	9	0	5	0	0	1	0	0	0	0	0	0	0
Metacatharsius opacus	40	176	162	100	109	141	136	161	28	106	68	1	2	0	1	0
Metacatharsius troglodytes	41	21	148	131	104	296	2	10	25	36	166	0	222	393	66	36
Onitis granulisetosus	44	0	10	15	0	0	0	0	0	0	0	0	0	0	0	0
Onitis orthopus	45	0	15	76	0	1	0	0	4	0	0	0	0	0	0	0
Caccobius cavatus gp	46	9	693	462	376	1568	2	55	82	145	223	0	0	0	0	0
Caccobius ferrugineus	47	16	1020	887	109	424	2	850	248	270	427	1	104	61	6	0
Caccobius nigritulus	48	72	9659	1485	696	2173	0	1228	297	17	27	0	1	1	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Cleptocaccobius convexifrons	49	33	820	142	281	1927	0	0	0	0	0	0	0	0	0	0
Euonthophagus sp. ??1	52	6	263	90	18	73	0	13	18	2	0	0	0	0	0	0
Onthophagus anomalus	54	7	1059	112	19	245	0	2	3	0	0	0	0	0	0	0
Onthophagus plebejus	59	2	71	23	0	13	0	0	2	0	0	0	0	0	0	0
Onthophagus sp. nr *pullus* (horned)	63	0	15	1	0	5	0	1	0	0	0	0	0	0	0	0
Onthophagus verticalis	71	0	63	71	10	36	0	1	16	1	1	0	0	0	0	0
Onthophagus vinctus	72	15	2244	621	52	589	1	25	46	5	6	0	0	4	0	0
Onthophagus virescens	73	2	343	58	12	142	0	127	48	2	3	0	0	0	0	0
Onthophagus sp. (4 spot)	80	1	35	6	17	7	5	6	1	2	0	0	0	0	0	0
Proagoderus bicallosus	84	0	7	2	1	2	0	5	18	1	0	0	0	0	0	0
Drepanocerus ?freyi	87	0	1	11	0	5	0	1	9	0	1	0	0	0	0	0
Drepanocerus laticollis	88	1	20	97	4	82	0	61	383	21	102	0	0	0	0	0
Euoniticellus sp.	90	0	4	1	0	1	0	3	12	0	0	0	0	0	0	0
Factor 2																
Pachylomerus femoralis	5	23	220	63	163	583	0	0	1	0	0	0	0	0	0	1

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Scarabaeus sp. nr flavicornis	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedaria sp. IV	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copris cassius	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Metacatharsius sp. (minute)	42	0	2	3	1	1	1	1	0	2	0	0	0	0	1	0
Cleptocaccobius viridicollis	50	0	1	0	1	0	0	0	0	0	0	0	4	0	0	0
Onthophagus impressicollis	57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Factor 3																
Drepanopodus costatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kheper sp. (La Grat)	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachylomerus opacus	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnopleurus asperrimus	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pycnopanelus krikkeni	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus flavimargo	56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus pallidipennis	58	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus probus	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Onthophagus quadraticeps	64	0	9	0	4	14	0	10	1	1	1	0	1	1	1	0
Onthophagus quadrinodosus	65	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Onthophagus semiflavus	66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalops rufosignatus	82	0	0	0	0	0	0	0	0	0	0	0	7	1	0	0
Phalops wittei	83	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Factor 4																
Allogymnopleurus thalassinus	19	0	1	0	0	0	0	29	9	21	74	0	14	5	3	2
Gymnopleurus aenescens	20	0	0	0	0	0	3	247	16	117	55	2	154	35	68	0
Digitonthophagus gazella	51	0	1	0	0	0	0	4	19	21	48	0	1	5	0	0
Onthophagus sp. nr *pullus* (sp. a)	62	16	1110	238	349	543	8	2025	1215	638	270	1	2141	800	417	143
Onthophagus suffusus	68	0	7	1	0	0	213	842	391	153	25	0	2	4	0	0
Onthophagus sp. *A2*	75	0	0	0	0	0	3	17	1	2	0	0	0	0	1	0
Phalops boschas	81	0	0	0	0	0	0	15	4	9	2	0	0	0	0	0
Proagoderus loricatus	85	0	0	0	0	0	0	21	3	2	3	0	0	0	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Oniticellus formosus	91	0	0	0	0	0	0	1	16	2	3	0	0	0	0	0
Factor 5																
Scarabaeus anderseni	7	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Scarabaeus flavicornis	10	35	29	9	3	1	0	1	0	2	0	0	0	0	0	0
Scarabaeus kochi	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Catharsius melancholicus	35	58	0	0	6	0	1	0	0	0	0	0	0	0	0	0
Metacatharsius dentinum (Karoo)	38	74	66	11	25	59	15	9	0	3	0	125	16	7	11	0
Onthophagus sp. A	74	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Onthophagus sp. B	76	0	0	0	0	0	0	3	0	4	0	0	0	0	0	2
Proagoderus sappharinus	86	0	0	0	0	0	3	1	1	4	0	0	0	0	0	0
Factor 6																
Scarabaeus damarensis	9	0	0	0	0	0	0	9	0	16	2	0	0	0	0	0
Scarabaeus proboscideus	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedaria sp. (Kalahari)	27	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Metacatharsius dentinum	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Metacatharsius exiguiformes	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp. nr *probus* (granular)	61	1	205	11	40	174	0	0	0	1	0	0	9	2	2	0
Onthophagus signatus	67	20	566	137	295	546	0	111	32	153	256	1	405	307	110	33
Onthophagus sp. k (granular)	79	3	74	11	47	86	0	0	0	0	0	3	367	59	283	21
Factor 7																
Heliocopris atropos	22	0	0	3	0	1	0	0	1	1	0	0	0	1	0	0
Pedaria sp. ?V	26	0	0	0	0	0	0	0	27	2	8	0	0	0	0	0
Copris bootes	29	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0
Copris macer or vilhenai	32	0	0	0	0	1	0	0	9	2	0	0	0	0	0	0
Chironitis indicus	43	0	0	0	0	0	0	4	23	0	0	0	0	0	0	0
Milichus apicalis	53	0	0	1	0	0	0	0	17	0	0	0	0	0	0	0
Factor 8																
Catharsius pandion	36	0	0	0	0	0	68	0	0	0	0	2	0	0	0	0
Onthophagus apiciosus (check)	55	5	0	0	0	0	117	0	0	0	0	19	0	0	0	0
Onthophagus sp. (Boek)	77	107	0	0	0	0	2	0	0	0	0	0	0	0	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Onthophagus sp. (green/black)	78	35	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Factor 9																
Scarabaeus goryi	12	0	0	1	0	0	0	0	0	5	1	0	0	0	0	0
Copris elphenor	31	0	0	0	0	1	0	0	10	20	25	0	0	0	0	0
Euoniticellus intermedius	89	0	0	0	2	1	0	0	0	6	1	0	1	0	0	0
Factor 10																
Scarabaeus bohemani	8	0	0	0	0	0	0	0	0	0	0	5	6	2	1	1
Scarabaeus inquisitus (=sp 5)	13	0	0	0	0	0	0	0	0	0	0	9	1	1	2	0
Catharsius heros	34	0	1	15	0	0	0	0	0	0	0	0	1	3	0	0
Onthophagus sugillatus	69	82	56	35	24	123	0	0	0	0	0	42	123	118	29	27
Factor 11(unclassified)																
Scarabaeus inopportunus	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Catharsius calaharicus	33	0	13	28	0	3	0	0	3	0	2	0	4	5	0	0
Onthophagus sp. *variegatus* group	70	2	16	9	3	8	46	134	182	69	32	0	1	18	0	0
Factor 1																

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Kheper lamarcki	2	0	21	2	0	0	0	0	0	0	0	0	0	0	0	0
Kheper prodigiosus	3	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Scarabaeus zambesianus	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anachalcos convexus	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heliocopris japetus	23	0	7	2	0	0	0	0	0	0	0	0	0	0	0	0
Pedaria sp. (humped)	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Metacatharsius opacus	40	10	2	3	0	0	0	1	0	0	4	0	0	0	0	0
Metacatharsius troglodytes	41	2	66	87	0	6	0	0	0	0	0	0	0	0	0	0
Onitis granulisetosus	44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onitis orthopus	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caccobius cavatus gp	46	3	147	50	0	4	0	0	0	0	0	0	0	0	0	0
Caccobius ferrugineus	47	3	58	10	0	0	0	1	5	0	2	0	0	0	0	0
Caccobius nigritulus	48	0	1	3	0	0	0	4	4	0	0	0	0	0	0	0
Cleptocaccobius convexifrons	49	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Euonthophagus sp. ??1	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Onthophagus anomalus	54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus plebejus	59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp. nr pullus (horned)	63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus verticalis	71	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus vinctus	72	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus virescens	73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp. (4 spot)	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proagoderus bicallosus	84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocerus ?freyi	87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocerus laticollis	88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euoniticellus sp.	90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Factor 2																
Pachylomerus femoralis	5	1126	4911	705	444	718	0	0	0	0	0	0	0	0	0	1
Scarabaeus sp. nr flavicornis	11	0	10	1	0	0	0	0	0	0	1	0	0	0	0	0
Pedaria sp. IV	25	0	17	4	0	0	0	0	0	0	0	0	0	0	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Copris cassius	30	0	2	24	2	0	0	0	0	0	0	0	0	0	0	0
Metacatharsius sp. (minute)	42	14	21	42	17	3	0	0	0	0	0	0	0	0	0	0
Cleptocaccobius viridicollis	50	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus impressicollis	57	1	4	3	2	0	0	0	0	0	0	0	0	0	0	0
Factor 3																
Drepanopodus costatus	1	0	0	0	0	0	0	0	0	0	0	0	42	0	19	4
Kheper sp. (La Grat)	4	0	0	0	0	0	0	0	0	0	0	0	31	1	3	8
Pachylomerus opacus	6	0	1	0	0	0	0	0	0	0	0	0	27	3	1	6
Gymnopleurus asperrimus	21	0	0	0	0	0	0	0	0	0	0	0	55	16	8	52
Pycnopanelus krikkeni	28	0	0	0	0	0	0	5	0	0	1	0	2	2	5	1
Onthophagus flavimargo	56	0	13	3	0	0	0	0	0	0	1	0	58	52	11	25
Onthophagus pallidipennis	58	0	10	1	0	0	0	0	0	0	1	0	5	2	1	2
Onthophagus probus	60	0	0	0	0	0	0	40	22	7	65	2	504	206	192	274
Onthophagus quadraticeps	64	3	582	142	35	8	0	10	5	1	23	0	182	65	55	138
Onthophagus quadrinodosus	65	0	3	0	0	0	0	0	0	0	1	0	4	0	3	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Onthophagus semiflavus	66	0	0	0	0	0	2	155	65	49	126	8	2372	935	764	1002
Phalops rufosignatus	82	0	0	0	0	0	0	2	0	0	0	0	92	34	9	74
Phalops wittei	83	0	1	0	0	0	0	4	3	1	2	0	182	74	7	101
Factor 4																
Allogymnopleurus thalassinus	19	0	3	9	1	0	0	0	0	0	0	0	0	0	0	0
Gymnopleurus aenescens	20	54	222	38	23	5	4	195	79	45	229	0	0	0	0	0
Digitonthophagus gazella	51	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Onthophagus sp. nr pullus (sp. a)	62	5	455	319	75	46	0	117	212	102	525	0	64	111	170	404
Onthophagus suffusus	68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp. A2	75	0	1	0	1	0	0	9	0	0	0	0	0	0	0	0
Phalops boschas	81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proagoderus loricatus	85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oniticellus formosus	91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Factor 5																

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Scarabaeus anderseni	7	299	34	3	7	0	17	6	2	0	15	6	1	0	0	0
Scarabaeus flavicornis	10	494	214	11	9	0	329	1404	28	0	23	214	225	0	18	2
Scarabaeus kochi	15	134	61	22	21	1	11	10	4	7	17	3	3	0	0	1
Catharsius melancholicus	35	215	31	6	0	0	14	7	0	0	1	9	0	0	0	0
Metacatharsius dentinum (Karoo)	38	505	36	68	37	24	42	15	11	1	9	103	9	0	11	1
Onthophagus sp. A	74	307	110	7	1	1	7	50	3	2	17	4	0	0	0	0
Onthophagus sp. B	76	421	513	41	12	4	132	483	60	7	35	10	24	0	2	0
Proagoderus sappharinus	86	6	31	8	4	2	5	16	3	1	5	0	0	0	0	0
Factor 6																
Scarabaeus damarensis	9	55	111	11	16	0	8	221	10	144	295	0	0	0	1	0
Scarabaeus proboscideus	16	0	180	34	3	5	1	43	60	30	471	0	29	21	130	706
Pedaria sp. (Kalahari)	27	2	112	13	1	0	3	24	69	11	86	1	21	11	11	29
Metacatharsius dentinum	37	27	1167	897	65	35	2	110	122	26	874	0	90	337	299	527
Metacatharsius exiguiformes	39	0	11	11	0	5	0	3	20	5	137	0	0	2	3	2
Onthophagus sp. nr probus (granular)	61	74	2756	804	145	41	6	1084	790	393	1793	0	6	0	4	3

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Onthophagus signatus	67	17	1870	616	107	65	7	632	520	142	1095	1	143	119	153	226
Onthophagus sp. k (granular)	79	25	1812	433	10	24	2	1602	812	92	1766	1	197	61	118	282
Factor 7																
Heliocopris atropos	22	0	2	2	0	0	0	0	0	0	1	0	0	0	0	0
Pedaria sp. ?V	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copris bootes	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copris macer or vilhenai	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chironitis indicus	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Milichus apicalis	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Factor 8																
Catharsius pandion	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus apiciosus (check)	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sp. (Boek)	77	32	0	1	2	2	0	0	0	0	0	0	0	0	0	0
Onthophagus sp. (green/black)	78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Dung beetle Species		Chobe River					Savuti					NC-Kalahari				
Names	Code	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She	Car	Pig	Ele	Cat	She
Factor 9																
Scarabaeus goryi	12	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0
Copris elphenor	31	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Euoniticellus intermedius	89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Factor 10																
Scarabaeus bohemani	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scarabaeus inquisitus (=sp 5)	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Catharsius heros	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus sugillatus	69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Factor 11(unclassified)																
Scarabaeus inopportunus	14	0	0	0	0	0	38	99	12	30	160	3	48	1	34	51
Catharsius calaharicus	33	0	48	13	0	0	0	12	6	0	1	0	7	7	0	1
Onthophagus sp. variegatus group	70	19	177	87	0	1	0	0	1	0	0	5	106	27	12	7

Appendix A4 (All chapters): Abundances of 139 dung beetles species recorded in Chobe National Park, Central Kalahari Game Reserve and Kalahari Transfrontier Park.

		Chobe National Park		Central Kalahari Game Reserve		Kgalagadi Transfrontier Park		
Species	Species abbreviation.	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari	Functional Group
Drepanopodus costatus Wiedeman	Dco	0	0	0	0	0	65	*R*
Kheper cupreus Castelnau	Kcu	0	0	2	0	0	0	*R*
Kheper lamarcki M'Leay	Kla	5326	158	0	23	0	0	*R*
Kheper prodigiosus Erichson	Kpr	186	63	0	2	1	0	*R*
Kheper sp. 1 = kalaharicus	KLag	0	0	0	0	0	43	*R*
Pachylomera femoralis Kirby	Pfe	1052	1	1	7904	0	1	*R*
Pachylomera opacus Lansberge	Pop	0	0	0	1	0	37	*R*
Scarabaeus ambiguus Boheman	Sam	0	0	1	0	0	0	*R*
Scarabaeus ?lucidulus	San	2	0	1	343	40	7	*R*
Scarabaeus sp. nr *anderseni*	Sanl	0	0	0	0	9	0	*R*
Scarabaeus bohemani Harold	Sbo	0	0	15	0	0	0	*R*
Scarabaeus damarensis Janssens	Sda	0	27	0	193	678	1	*R*
Scarabaeus ebenus Klug	Seb	0	4	0	0	0	0	*R*
Scarabaeus flavicornis Boheman	Sfl	77	3	0	728	1784	459	*R*
Scarabaeus sp. nr *flavicornis*	Sflr	0	0	0	11	1	0	*R*
Scarabaeus galenus Westwood	Sga	0	0	0	2	0	0	*R*
Scarabaeus goryi Harold	Sgo	1	6	0	14	0	0	*R*
Scarabaeus inquisitus Péringuey	Sin	0	0	13	0	0	0	*R*
Scarabaeus inopportunus Ferreira	Sio	0	0	0	0	339	137	*R*
Scarabaeus kochi Ferreira	Sko	0	0	0	239	49	7	*R*
Scarabaeus parvulus Boheman	Spar	0	0	0	0	0	6	*R*
Scarabaeus proboscideus Guérin	Spr	0	0	0	222	605	886	*R*
Scarabaeus satyrus Boheman	Ssa	0	0	3	1	0	4	*R*
Scarabaeus zambesianus	Sza	1080	88	18	0	0	0	*R*

		Chobe National Park		Central Kalahari Game Reserve		Kgalagadi Transfrontier Park		
Species	Species abbreviation.	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari	Functional Group
Péringuey								
Anachalcos convexus Boheman	Aco	283	11	0	0	0	0	*R*
Allogymnopleurus thalassinus Klug	Ath	1	133	24	13	0	0	*R*
Gymnopleurus aenescens Wiedemann	Gae	0	438	259	342	552	0	*R*
Gymnopleurus asperrimus Felsche	Gas	0	0	0	0	0	131	*R*
Gymnopleurus ignitus Klug	Gig	1	0	0	0	0	0	*R*
Sisyphus goryi Harold	Sgr	0	3	0	0	0	0	*R*
Coptorhina sp.	Csp1	0	2	0	0	0	0	*T*
Heliocopris atropos Boheman	Hat	4	2	1	4	1	0	*T*
Heliocopris japetus Klug	Hja	51	16	0	9	0	0	*T*
Pedaria sp. VIII	Psp8	17	1	0	0	0	0	*K*
Pedaria sp. IV	Psp4	0	0	0	21	0	0	*K*
Pedaria sp. V	Psp5	0	37	0	0	0	0	*K*
Pedaria sp. VI	Psp6	1	1	0	0	0	0	*K*
Pedaria sp. X1	Psp11	4	0	0	128	193	73	*K*
Pycnopanelus krikkeni Cambefort	Pkr	0	0	0	0	6	10	*K*
Copris bootes Klug	Cbo	0	17	0	0	0	0	*T*
Copris cassius Péringuey	Cca	0	0	0	28	0	0	*T*
Copris cornifrons Boheman	Cco	0	0	0	0	0	1	*T*
Copris elphenor Klug	Cel	1	55	0	2	0	0	*T*
Copris evanidus Klug	Cev	0	0	5	3	0	0	*T*
Copris vilhenai Ferreira	Cma	1	11	0	0	0	0	*T*
Catharsius calaharicus Kolbe	Ccl	44	5	9	61	19	15	*T*
Catharsius heros Boheman	Che	16	0	4	0	0	0	*T*
Catharsius melancholicus Boheman	Cme	64	1	0	252	22	9	*T*
Catharsius pandion Harold	Cpa	0	68	2	0	0	0	*T*
Catharsius sp. nr *tricornutus*	Ctrr	0	6	0	0	0	0	*T*
Metacatharsius exiguiformis Ferreira	Mde	0	0	0	2191	1134	1253	*T*

		Chobe National Park		Central Kalahari Game Reserve		Kgalagadi Transfrontier Park		
Species	Species abbreviation.	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari	Functional Group
Metacatharsius dentinum Ferreira	Mdk	235	27	159	670	78	124	*T*
Metacatharsius exiguus Boheman	Mex	1	0	0	2	1	0	*T*
Metacatharsius sp.	Mei	0	0	0	27	165	7	*T*
Metacatharsius latifrons Harold	Mla	0	0	0	1	2	4	*T*
Metacatharsius marani Balthasar	Mma	0	3	0	0	0	6	*T*
Metacatharsius opacus Waterhouse	Mop	688	499	4	15	5	0	*T*
Metacatharsius troglodytes Boheman	Mtr	700	239	717	161	0	0	*T*
Metacatharsius sp.2	Msp2	7	4	1	97	0	0	*T*
Metacatharsius pumilioniformis Ferreira	Msp3	0	0	0	0	1	5	*T*
Cheironitis hoplosternus Harold	Cho	0	0	1	1	0	0	*T*
Cheironitis indicus Lansberge	Cin	0	27	0	0	0	0	*T*
Onitis alexis Klug	Oal	0	0	4	0	2	0	*T*
Onitis deceptor Péringuey	Ode	7	0	0	0	0	0	*T*
Onitis granulisetosus Ferreira	Ogr	25	0	0	0	0	0	*T*
Onitis inversidens Lansberge	Oin	5	0	0	0	0	0	*T*
Onitis orthopus Lansberge	Oor	92	4	0	0	0	0	*T*
Onitis viridulus Boheman	Ovi	1	0	0	0	0	0	*T*
Caccobius cavatus d’Orbigny	Ccv	3108	507	0	204	0	0	*K*
Caccobius ferrugineus Fahraeus	Cfe	2456	1797	172	71	8	0	*K*
Caccobius nigritulus Klug	Cni	14085	1569	2	4	8	0	*K*
Caccobius sp. 1	Csp1	2	0	0	0	0	0	*K*
Cleptocaccobius convexifrons Raffray	Ccn	3203	0	0	0	1	0	*K*
Cleptocaccobius viridicollis Fahraeus	Cvr	2	0	4	6	0	0	*K*
Digitonthophagus gazella	Dga	1	92	6	1	1	0	*T*

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Species	Species abbreviation.	Chobe River	Savuti	NC-Kalahari	Khutse	Mabuasehube	Sw-Kalahari	Functional Group
Fabricius								
Euonthophagus sp.1	Esp1	450	33	0	0	0	0	*T*
Hyalonthophagus alcyon d'Orbigny	Hal	1	2	0	0	0	0	*T*
Milichus apicalis Fahraeus	Map	1	17	0	0	0	0	*T*
Mimonthophagus anomalus Klug	Oan	1442	5	0	0	0	0	*K*
Mimonthophagus flavimargo d'Orbigny	Ofl	0	0	0	16	1	146	*T*
Onthophagus bicavifrons d'Orbigny	Obi	1	0	1	0	0	0	*T*
Onthophagus sp. nr *bicavifrons*	Obir	0	0	0	6	0	0	*T*
Onthophagus fimetarius Roth	Ofi	0	6	0	0	0	0	*T*
Onthophagus flavolimbatus Klug	Ofa	0	2	0	0	0	0	*K*
Onthophagus impressicollis Boheman	Oim	0	0	0	10	0	0	*K*
Onthophagus juvencus Klug	Oju	2	0	0	0	0	0	*T*
Onthophagus sp.	Ooc	0	0	0	1	0	0	*?*
Onthophagus pallidipennis Fahraeus	Opa	1	0	0	11	1	10	*K*
Onthophagus plebejus Klug	Opl	109	2	0	0	0	0	*T*
Onthophagus probus Péringuey	Opr	0	0	0	0	134	1178	*K*
Onthophagus sp. nr *probus*	Oprr	431	1	13	3820	4066	13	*K*
Onthophagus sp. nr *pullus (sp. a)*	Opur	2256	4156	3502	900	956	749	*K*
Onthophagus sp. nr *pullus (horned)*	Ophr	21	1	0	0	0	0	*K*
Onthophagus quadraticeps Harold	Oqu	27	13	3	770	39	440	*T*
Onthophagus quadrinodosus Fahraeus	Oqa	0	2	0	3	1	7	*T*
Onthophagus rugulipennis Fairmaire	Oru	0	0	1	0	0	0	*K*

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Onthophagus semiflavus Boheman	Ose	0	0	0	0	397	5081	*K*
Onthophagus signatus Fahraeus	Osi	1564	552	856	2675	2396	642	*K*
Onthophagus suffusus Klug	Osu	8	1624	6	0	0	0	*T*
Onthophagus sugillatus Klug	Osg	320	0	339	0	0	0	*T*
Onthophagus sp. nr *variegatus*	Ovar	38	463	19	284	1	157	*T*
Onthophagus verticalis Fahraeus	Ove	180	19	0	3	0	0	*K*
Onthophagus vinctus Erichson	Ovi	3521	83	4	3	0	0	*T*
Onthophagus virescens Harold	Ovr	557	180	0	0	0	0	*K*
Onthophagus sp. 2	Osp2	0	0	1	426	79	4	*K*
Onthophagus sp. 3	Osp3	0	23	1	2	9	0	*K*
Onthophagus sp. 4	Osp4	0	7	2	991	717	36	*K*
Onthophagus sp. 5	Osp5	107	2	0	37	0	0	*?K*
Onthophagus sp. 6	Osp6	35	1	0	0	0	0	*?K*
Onthophagus sp. 7	Osp7	221	0	733	2304	4274	659	*?K*
Onthophagus sp. 8	Osp8	66	14	0	0	0	0	*?K*
Onthophagus sp. 9	Osp9	0	0	0	5	1	0	*?K*
Onthophagus sp. 10	Osp10	2	0	0	0	0	0	*?K*
Onthophagus sp. 12	Osp12	2	0	0	0	0	0	*?K*
Onthophagus sp.13	Osp13	0	0	1	0	0	0	*?K*
Onthophagus sp.14	Osp14	0	0	1	0	0	0	*?K*
Onthophagus sp.15	Osp15	0	1	0	0	0	0	*?K*
Onthophagus sp.16	Osp16	0	1	0	0	0	0	*?K*
Phalops boschas Klug	Pbo	0	30	0	0	0	0	*T*
Phalops dregei Harold	Pdr	0	0	2	0	0	0	*T*
Phalops rufosignatus Lansberge	Pru	0	0	8	0	2	209	*T*
Phalops wittei Harold	Pwi	0	0	3	1	10	364	*T*
Proagoderus bicallosus Klug	Pbi	12	24	0	0	0	0	*T*
Proagoderus loricatus Klug	Plo	0	29	0	0	0	0	*T*
Proagoderus sappharinus Péringuey	Psa	0	9	0	51	30	0	*T*
Stiptopodius sp. (A)	Ssp1	0	1	0	0	0	0	*?*

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Tomogonus sp.	Tcr	1	0	1	0	0	0	*K*
Eodrepanus fastiditus (Péringuey)	Dfa	4	1	0	0	0	0	*T*
Ixodina freyi (Janssens)	Dfr	17	11	0	0	0	0	*T*
Drepanocerus kirbyi (Kirby)	Dki	1	2	0	0	0	0	*T*
Latodrepanus laticollis (Fahraeus)	Dla	204	567	0	0	0	0	*T*
Euoniticellus intermedius Reiche	Ein	3	7	1	0	0	1	*T*
Euoniticellus kawanus Janssens	Eka	0	3	0	0	0	0	*T*
Euoniticellus sp.	Euo1	6	15	0	0	0	0	*K*
Liatongus militaris (Castelnau)	Lmi	0	1	0	0	0	0	*T*
Oniticellus egregius Klug	Oeg	0	0	4	0	0	0	*E*
Oniticellus formosus Chevrolat	Ofo	0	22	0	0	0	0	*E*
Oniticellus planatus Castelnau	Opn	0	5	0	0	0	0	*E*
Tragiscus dimidiatus Klug	Tdi	0	1	0	0	0	0	*E*
Species richness		**71**	**78**	**45**	**59**	**48**	**40**	
Total individuals		**44512**	**13941**	**6975**	**26375**	**18867**	**13027**	
Shannon-Weiner diversity		**2.52**	**2.522**	**1.72**	**2.46**	**2.353**	**2.274**	
Total traps: N x 2 days exposure		**60 x 2**	**60 x 2**	**60x 2**	**60 x 2**	**60 x 2**	**60 x 2**	

Functional Groups; R = roller; T= tunneller; K = kleptocoprids; E = endocoprids/dwellers