

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 (Gariiep), 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 fluvial 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.

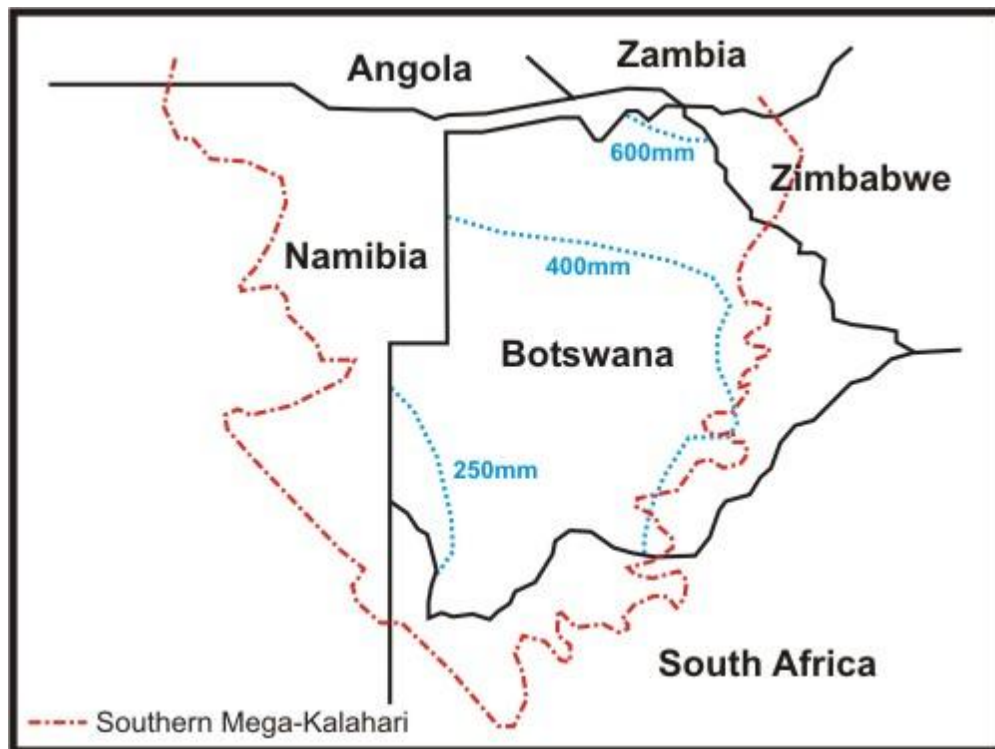


Figure 1.1 Rainfall isohyets for Botswana and the boundary of southern Mega-Kalahari basin, with western, southern and eastern edges in Namibia, South Africa and Zimbabwe (after Barker, 1993).

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 °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 $\pm 45^\circ$. 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.

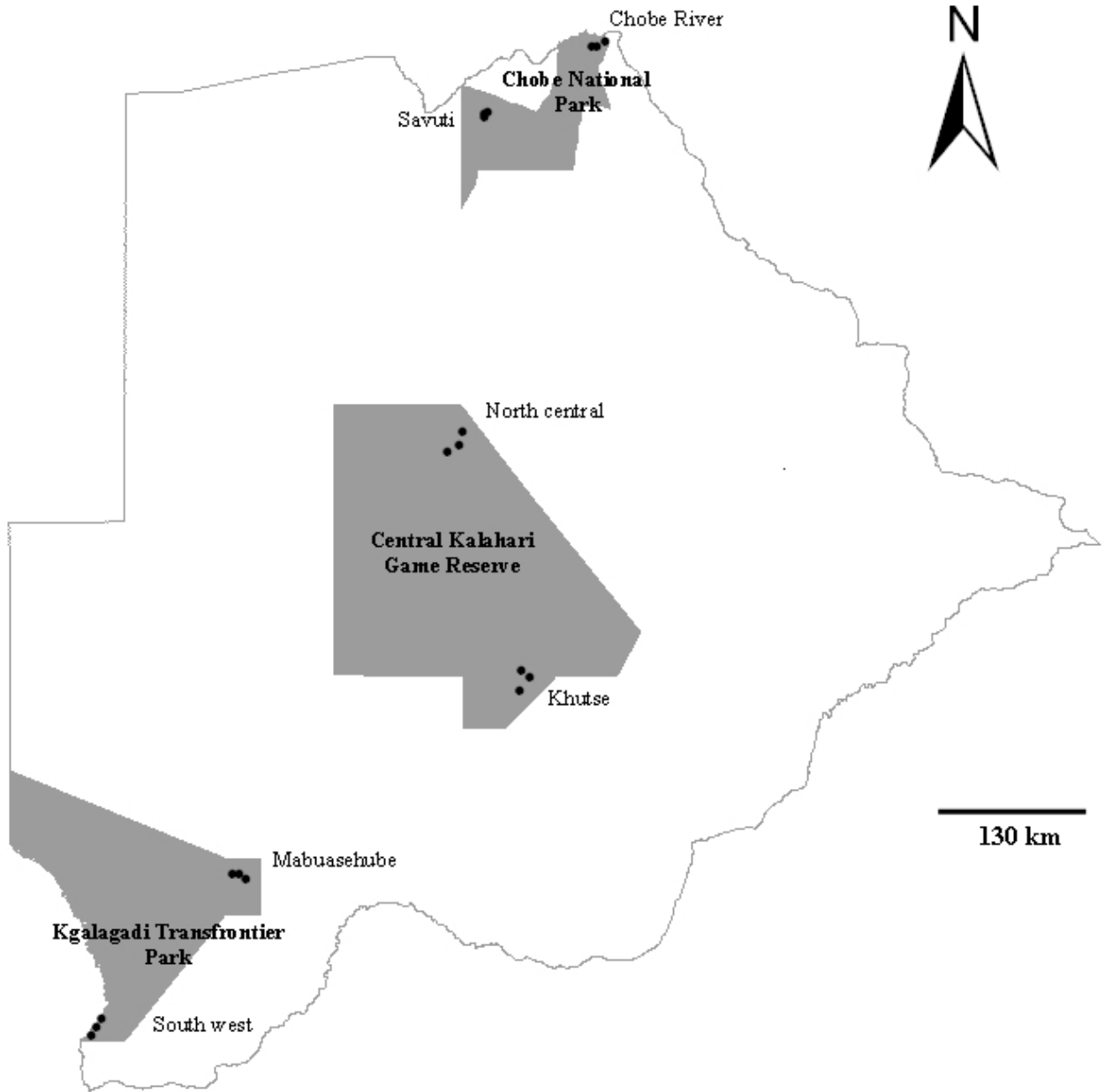


Figure 2.1 Map of Botswana showing principal conservation areas (Grey) and the location of trapping sites (●)

Table 2.1. Estimated density per 100 Km² of mammals in major conservation areas in Botswana Kalahari Basin (Department of Wildlife & National Parks, Census Report 2004, Botswana)

	Density per 100 km ²				Dung type ¹	Unit Mass (kg) ²
	Chobe NP 10589 km ²	CKGR 52800 km ²	Khutse 2500 km ²	K Trans Park 28000 km ²		
Indigenous mammals						
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

¹Dung 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). ²Wild 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			Description of land Region and land Systems ²
	% silt	% Clay	% sand ¹	
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

¹In the % sand column, values that are followed by different letters are significantly different ($P < 0.05$, Tukey's HSD).

²Descriptions 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://eussoils.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)

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

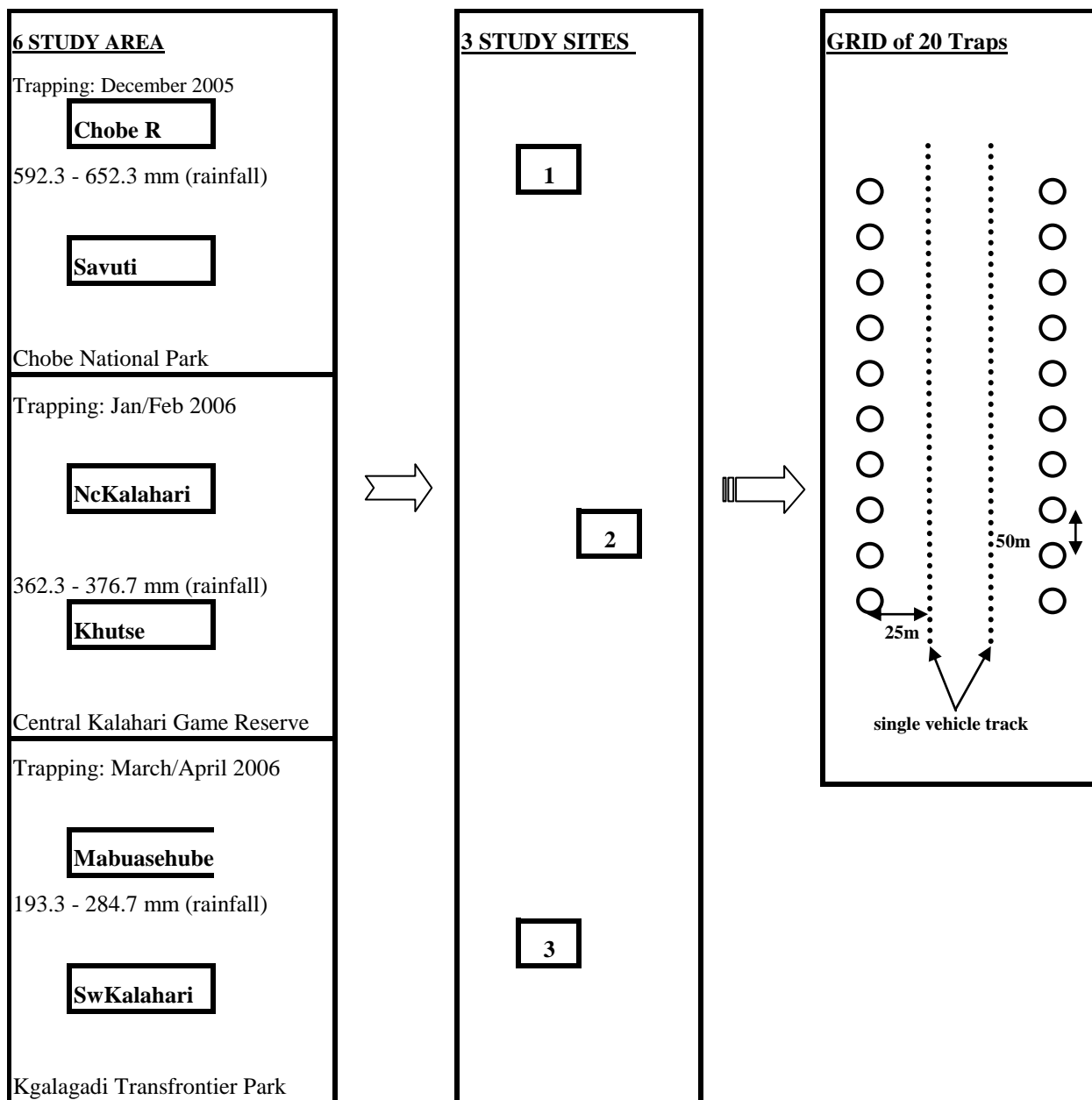


Figure 2.2. Schematic diagrams showing the 6 study areas, 3 sites in each study area and grid of 20 traps at each study site 10 on either side of the vehicle track (this diagram is not according to scale)

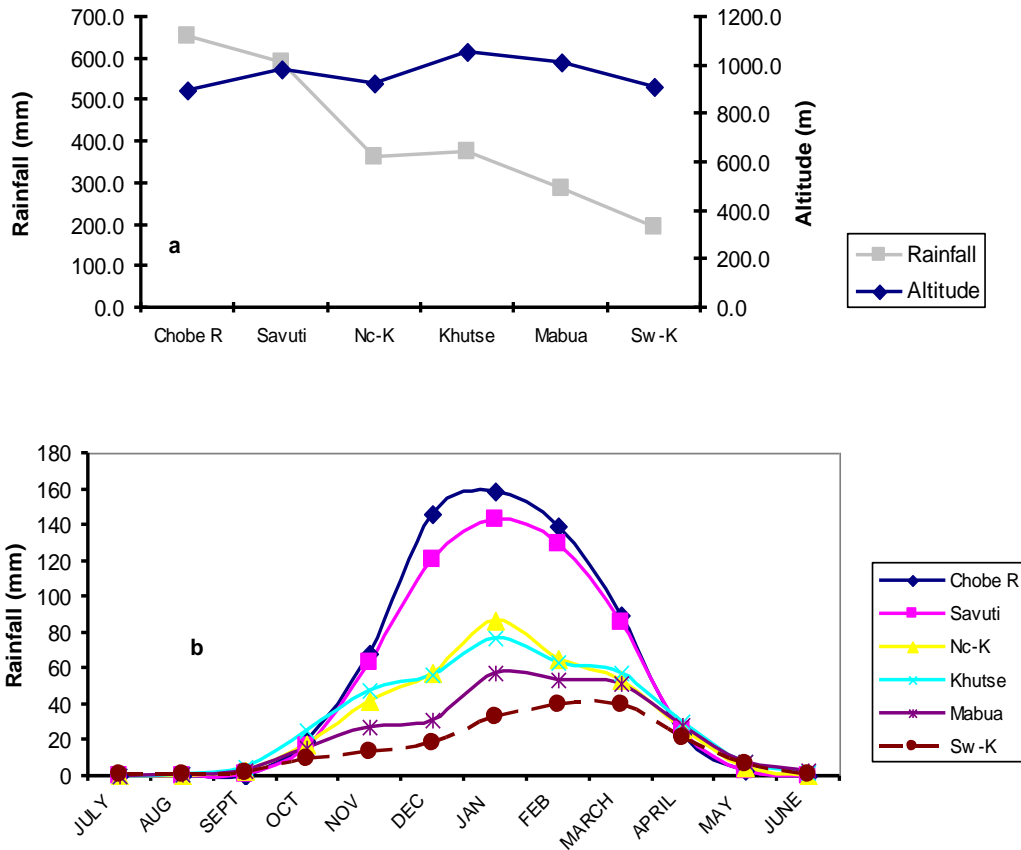


Figure 2.3. Altitude and average seasonal rainfall (a) and the average monthly seasonal rainfall (b) in each study area

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° 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).