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.