

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).

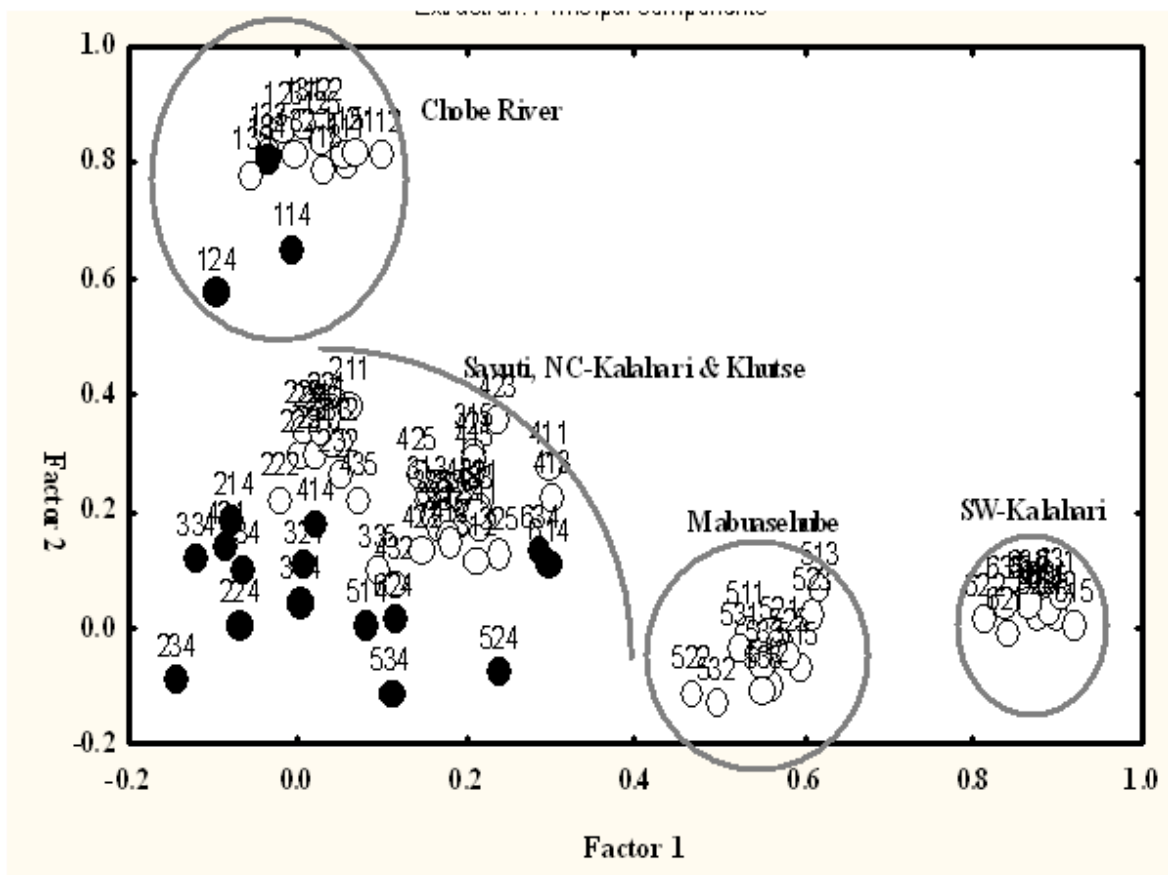


Figure 5.1. Ordination plot showing clusters of data points for dung beetle assemblages attracted to different bait types across the Botswana Kalahari basin (open circle: dung bait; closed circle: carrion bait); {numbers: the first digit = study area; 1 = Chobe, 2 = Savuti, 3 = NC-Kalahari, 4 = Khutse, 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)}

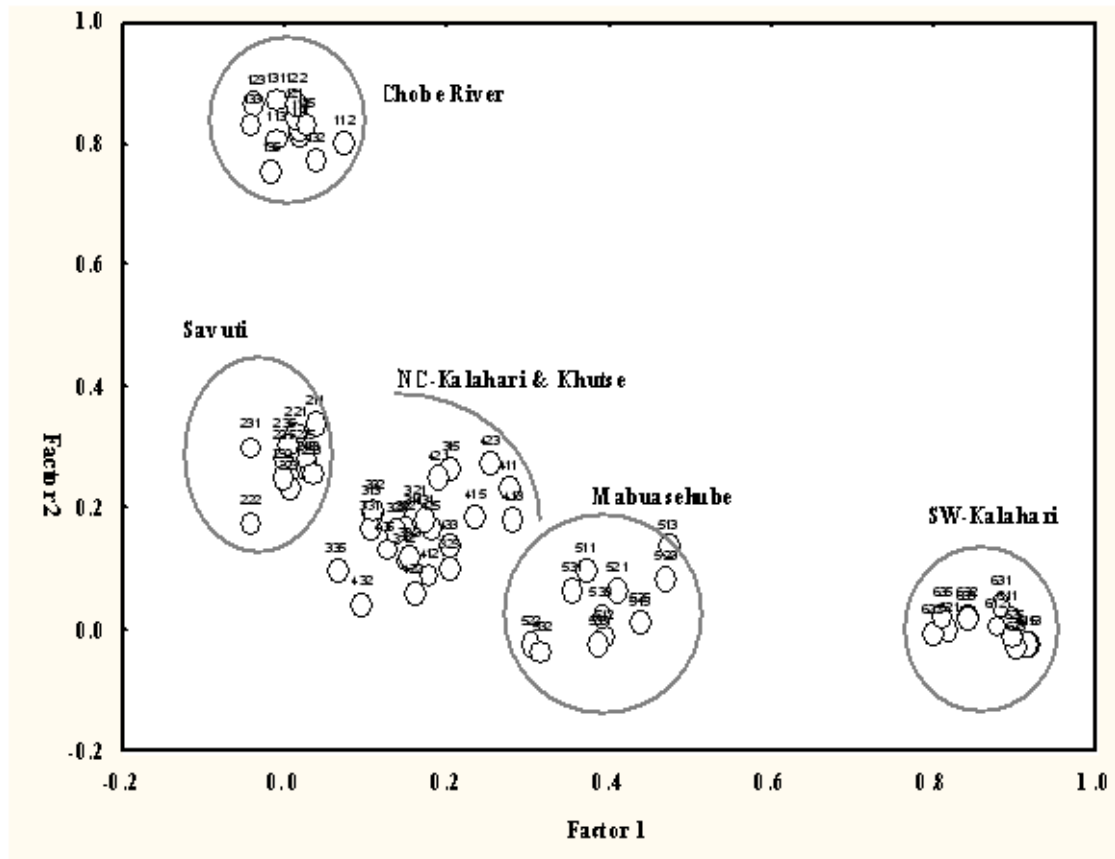


Figure 5.2. Ordination plot showing clusters of data points representing dung beetle assemblages on different dung baits only (Key to numbers see Fig. 5.1.)

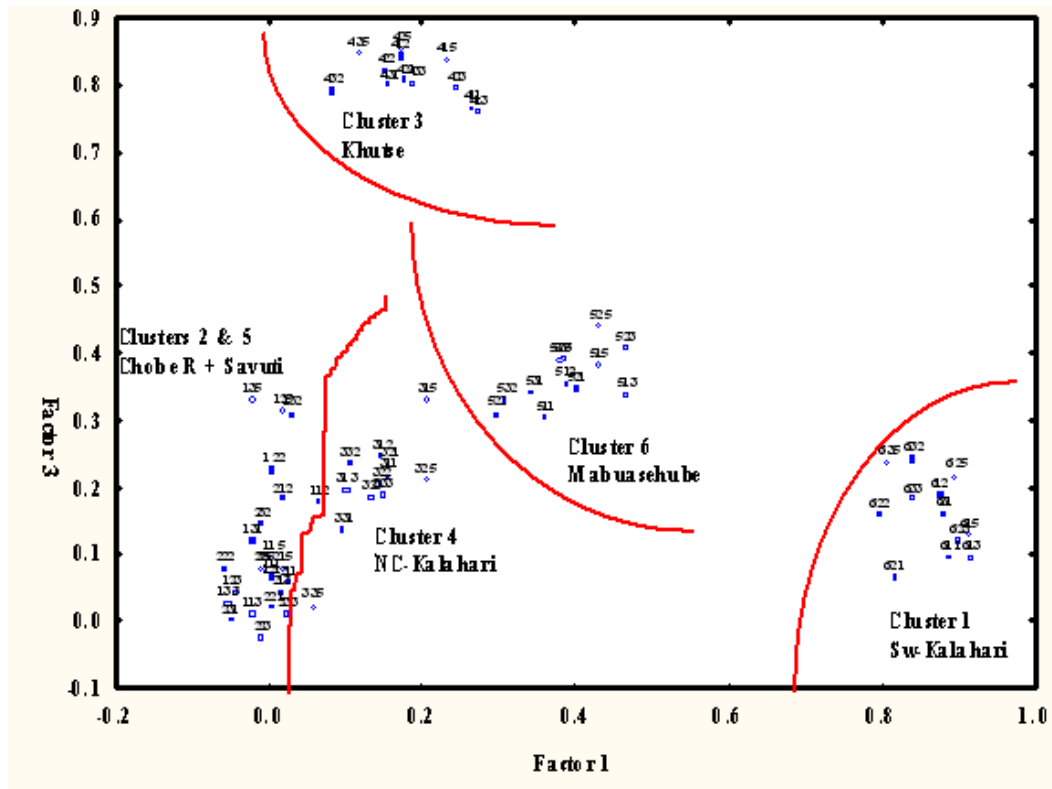


Figure 5.3. Ordination plot showing wide separation between NC-Kalahari and Khutse clusters for dung beetle assemblages attracted to different dung baits only (Key numbers see Fig. 5.1.)

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.)

(a)	Corelation coefficient (r) and coefficient of determination (r ²)					
	Sw-Kalahari Cluster 1	Chobe River Cluster 2	Khutse Cluster 3	NC-Kalahari Cluster 4	Savuti Cluster 5	Mabuasehube Cluster 6
Extended factors						
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)

(b)	Eigen value and proportional contribution of each factor		
	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

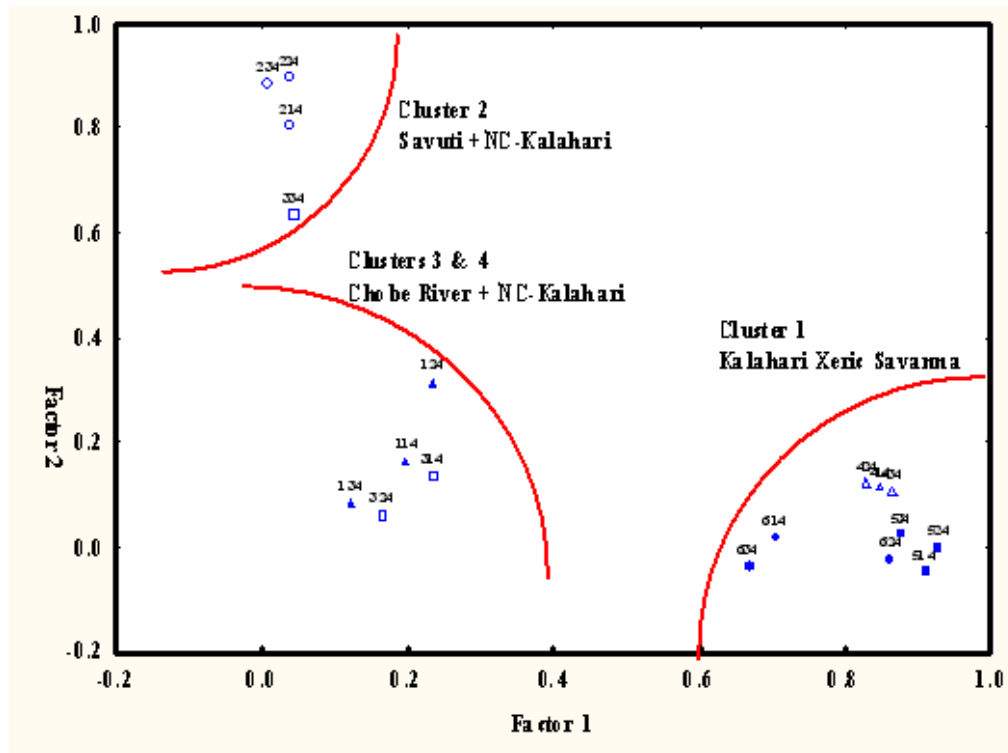


Figure 5.4. Ordination plot showing clear separation between carrion assemblages across the study region (Sites Key: open triangle = Chobe River, closed triangle = Khutse, open circle = Savuti, closed circle = Sw-Kalahari, open square = NC-Kalahari, closed square = Mabuasehube)

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

(a)	Correlation coefficient (r) and coefficient of determination (r^2)			
	Khu, Mabua & Sw-K, Cluster 1	Savuti/NC-K (site3) Cluster 2	Chobe River Cluster 3	NC-Kalahari Cluster 4
Extended Factors				
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)

(b)	Eigen value and proportional contribution for each factor		
	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.

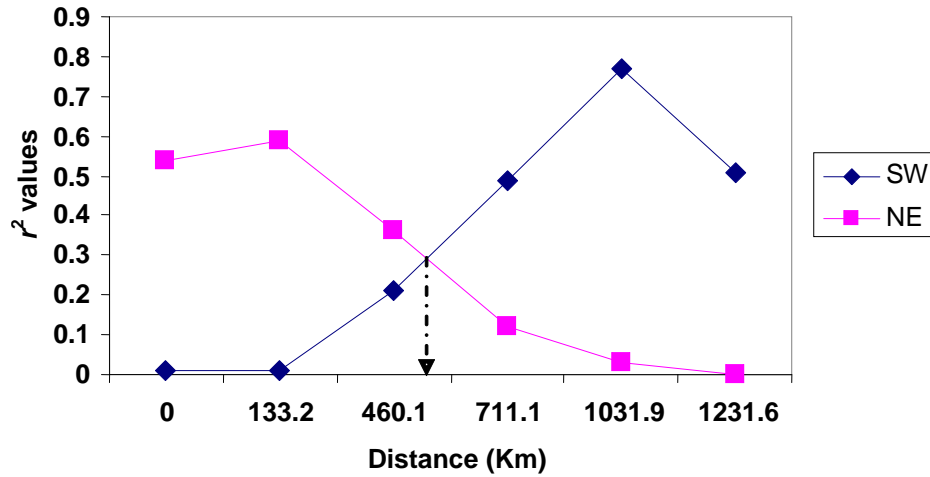


Figure 5.5. Plot of r^2 values showing the point of intersection between SW Kalahari Xeric versus NE mesic savanna influence on dung beetle species abundance composition as defined by shared secondary factors from ordination (S1 = SW bias, S2 = NE bias – see Table 5.1). On a linear scale the arrow is 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.

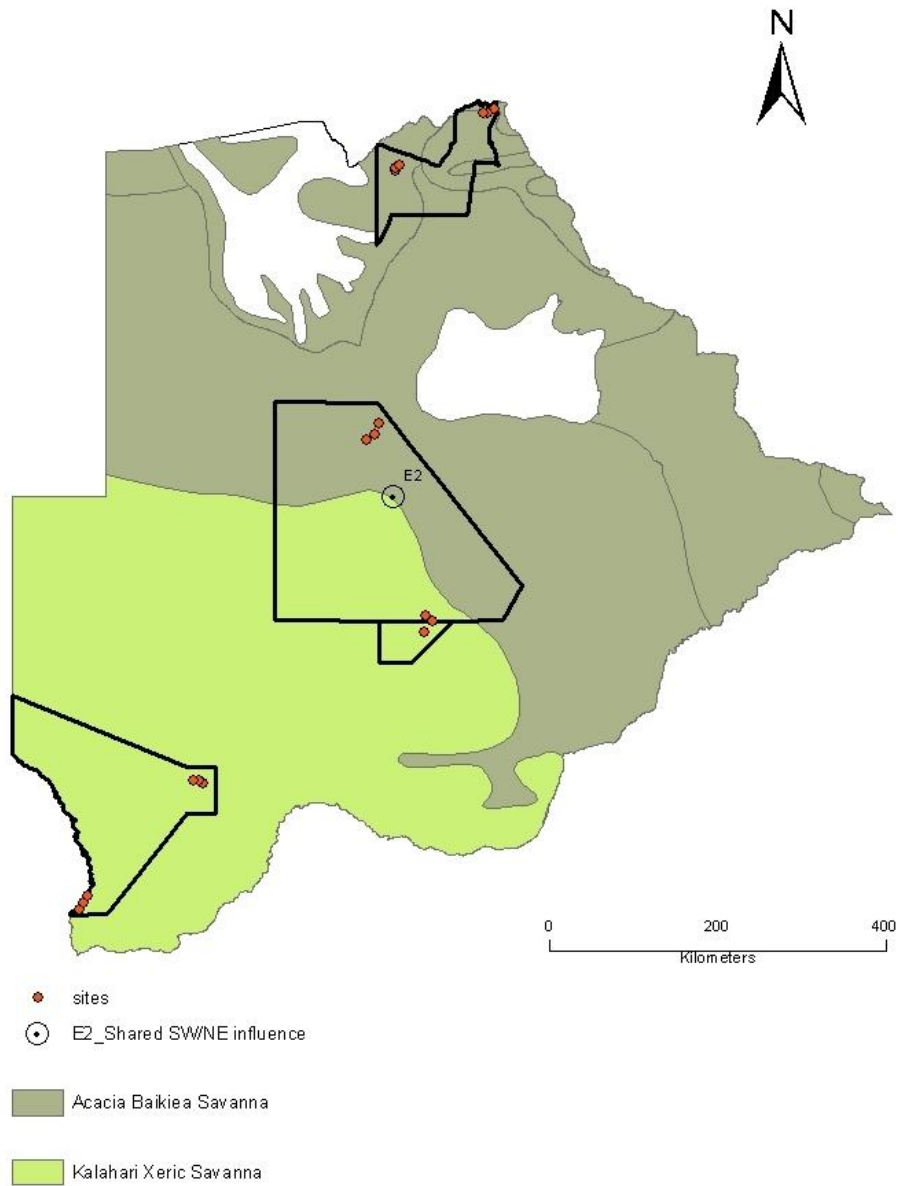


Figure 5.6. Map showing the ecotone between the *Acacia-Baikiea* Savanna and Kalahari Xeric Savanna ecoregions (Olson *et al.*, 2001) and E2 - the point of intersection between shared SW versus shared NE influence (see Fig. 5.5.).

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*) carcasses 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 $H' = \sum p_{ij} \ln p_{ij}$ where p is the decimal proportion of total abundance of the i th 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 i th 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 4th 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.

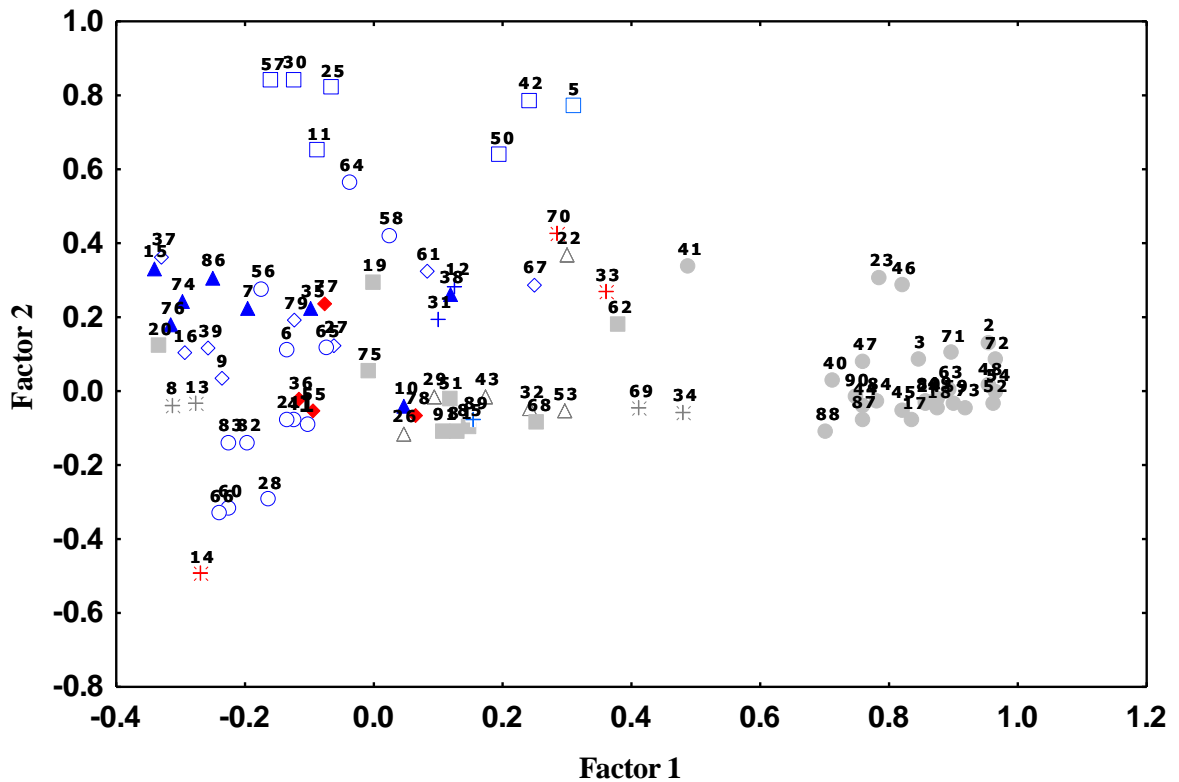


Figure 6.1. Two-dimensional ordination plot showing the statistical distance between 91 species of dung beetles divided into 10 groups based on analysis of species abundance on five bait types at six study sites across the Botswana Kalahari (see appendix A3 for key to species code and relative abundances; 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)

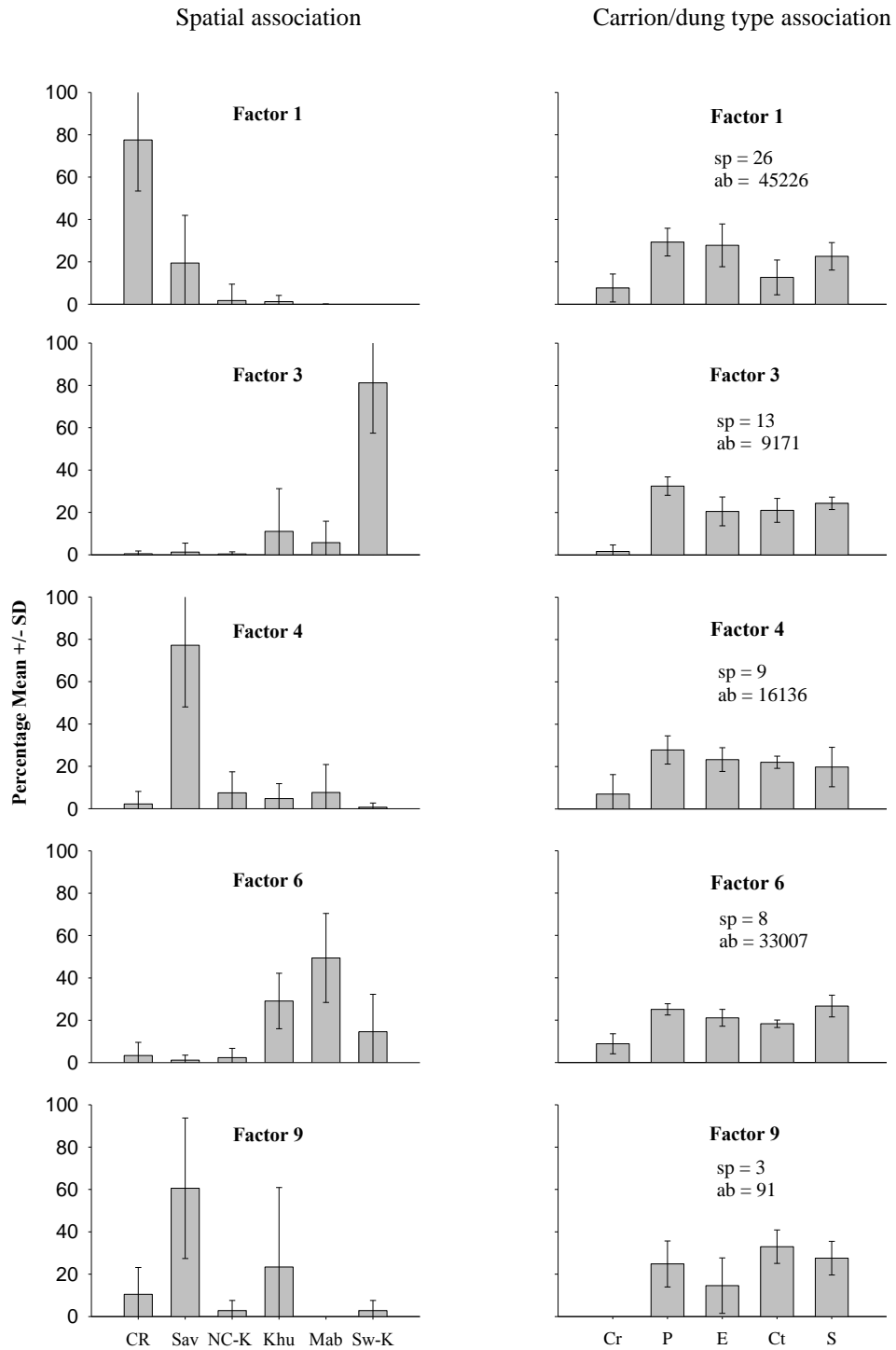


Figure 6.2. Bar diagrams showing mean \pm SD spatial and trophic associations of dung beetle species constituting factors 1, 3, 4, 6 and 9 in the hierarchical factor analysis.

Fig. 6.3.

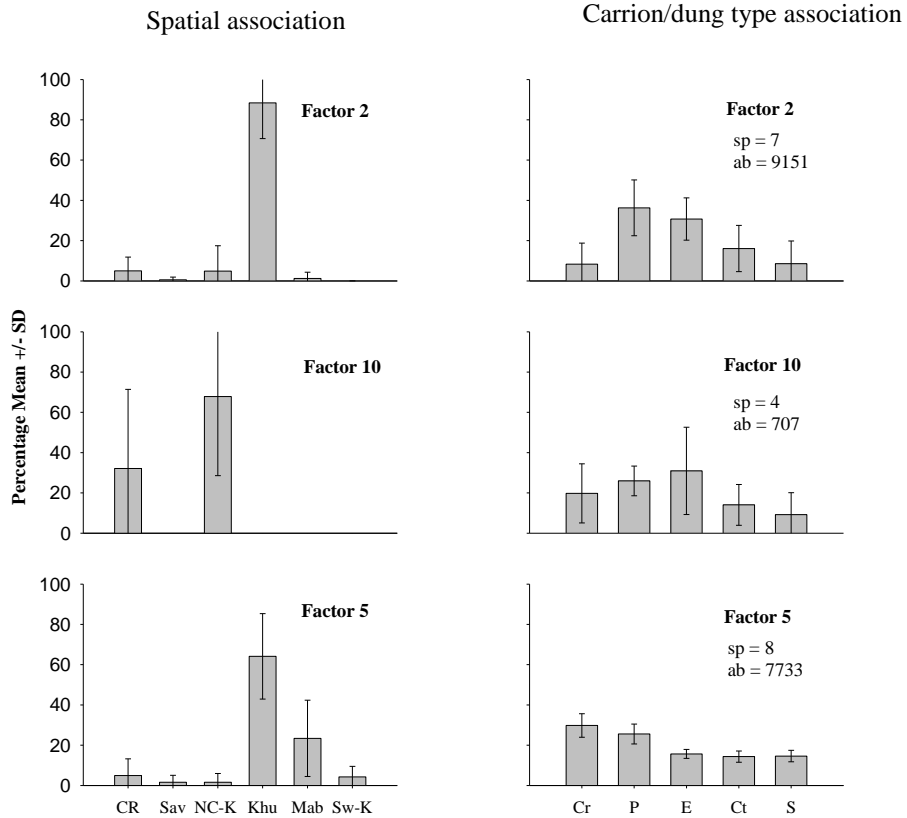
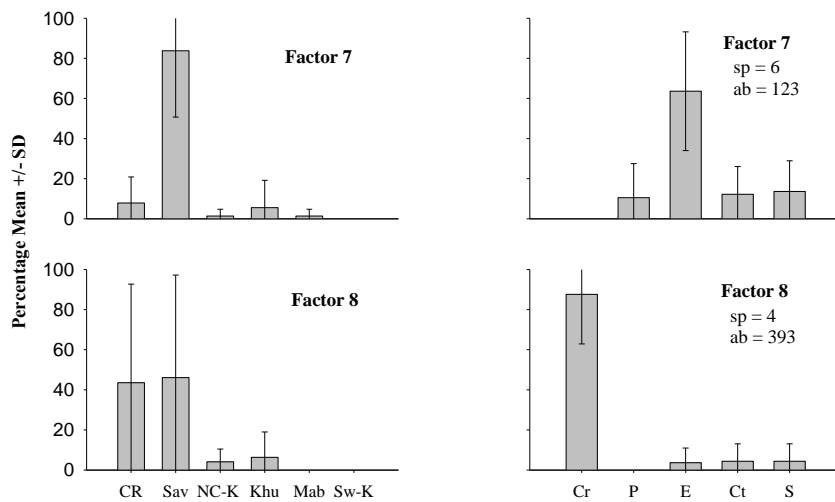


Fig. 6.4.



Figures 6.3., 6.4. Bar diagrams showing mean \pm 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.

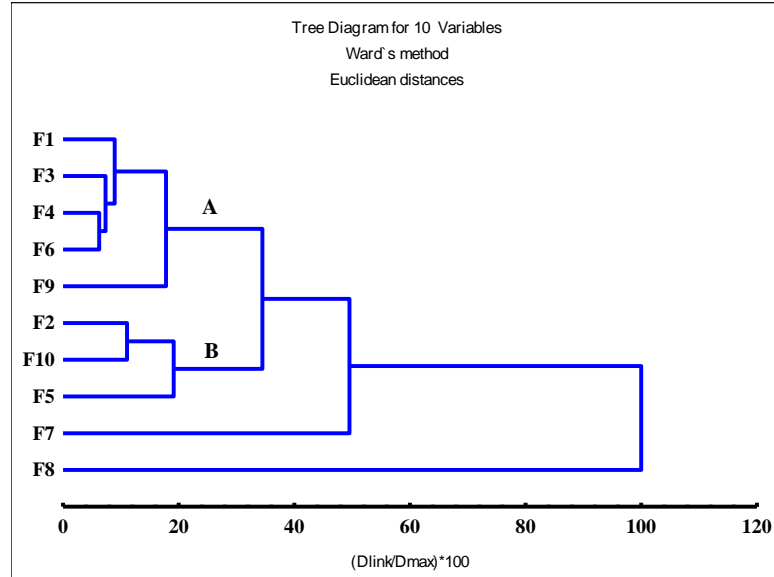


Figure 6.5. Dendrogram summarizing similarities in trophic association between groups of dung beetles defined on the basis of both spatial distribution and bait type association. Cluster A. Dominated by dung type generalists with differing spatial biases across the entire study region (see Figs. 6.2., 6.6.), Cluster B. Various 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.).

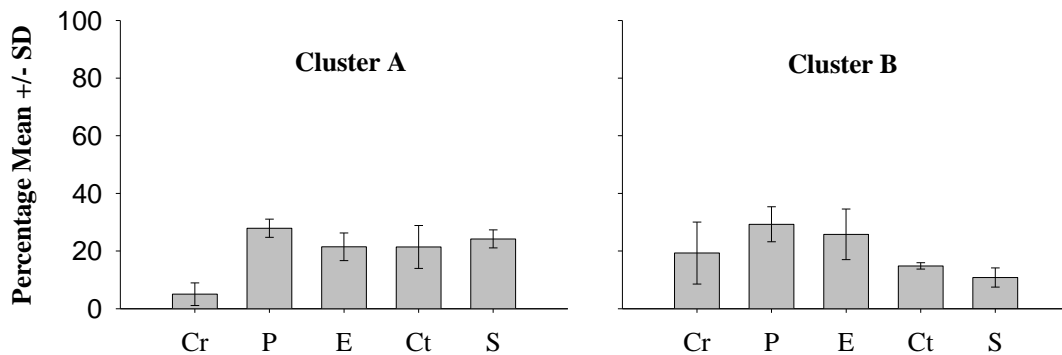


Figure 6.6. Bar diagrams showing mean \pm SD bait associations of the species representing two major clusters in Fig. 6.5.

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

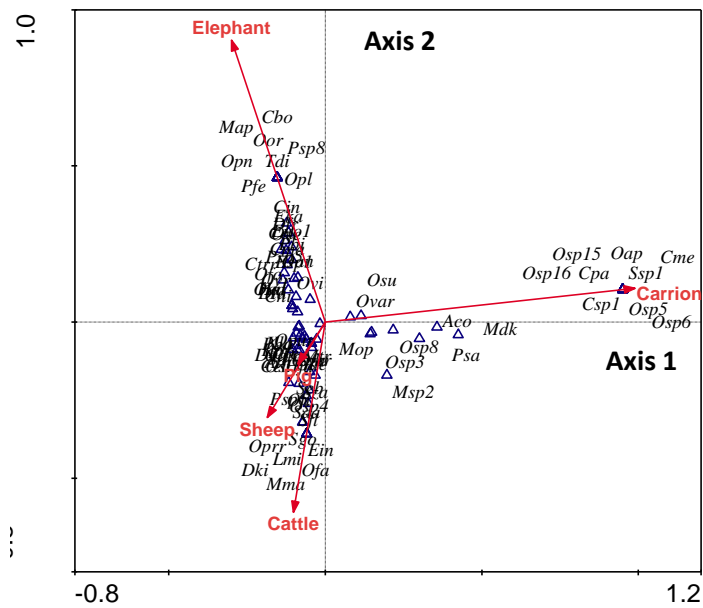
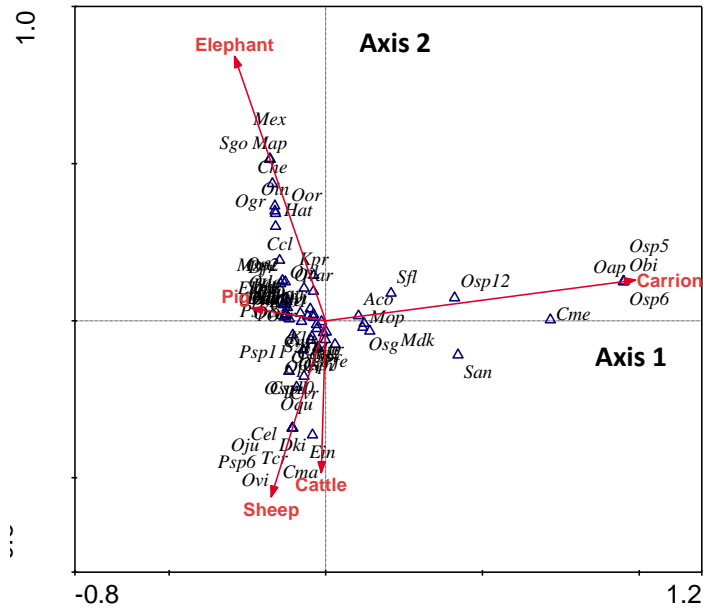
* Values followed by a different letter differed significantly ($P < 0.05$, Tukey's HSD)

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

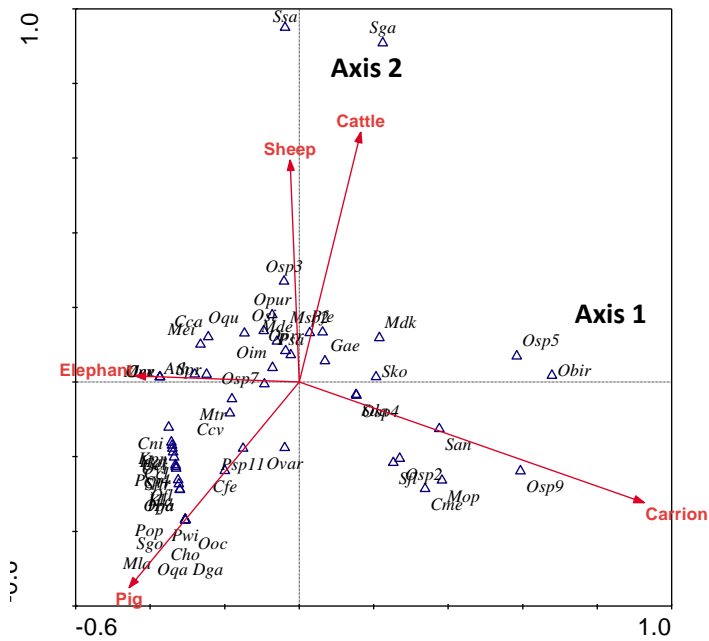
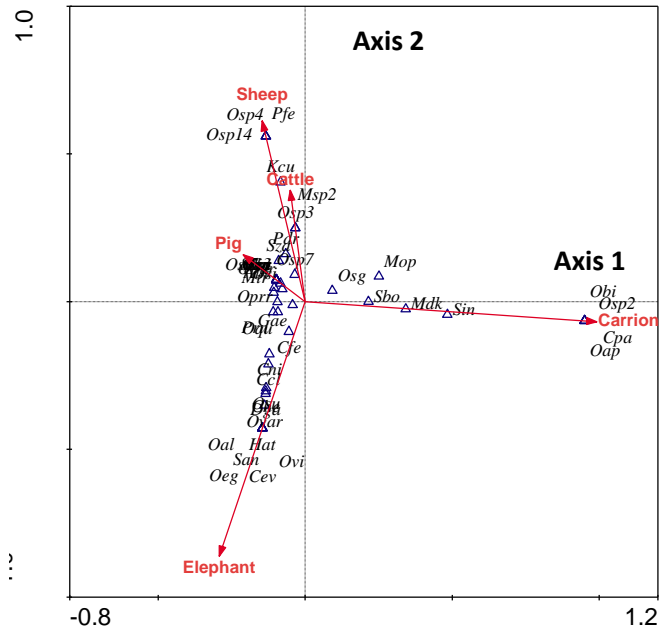
pattern of separation along axis 1 between carrion (positive loadings) and dung fauna (mostly negative loadings) (Figs. 6.7. to 6.12.). In general, patterns of separation between dung types extended along axis 2.

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°), mean angle of separation between pairs of lines declined across study areas from southwest to northeast with the exception of Chobe (Table 6.5.).

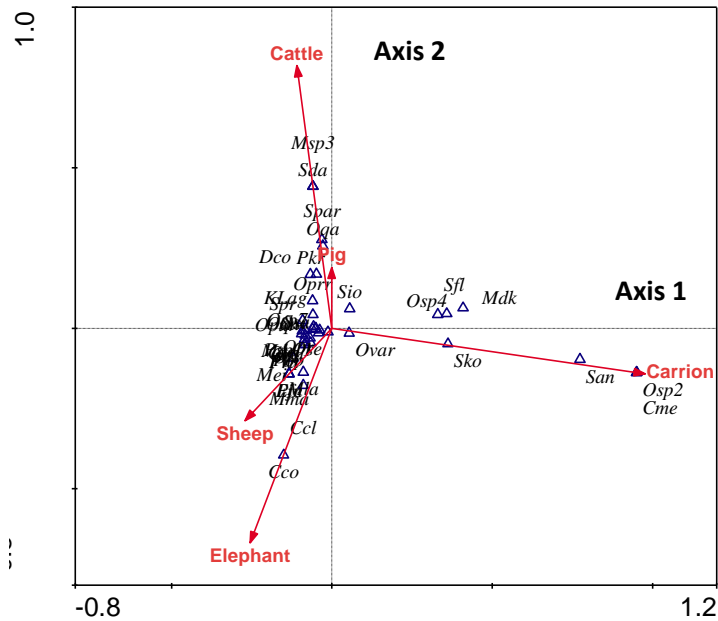
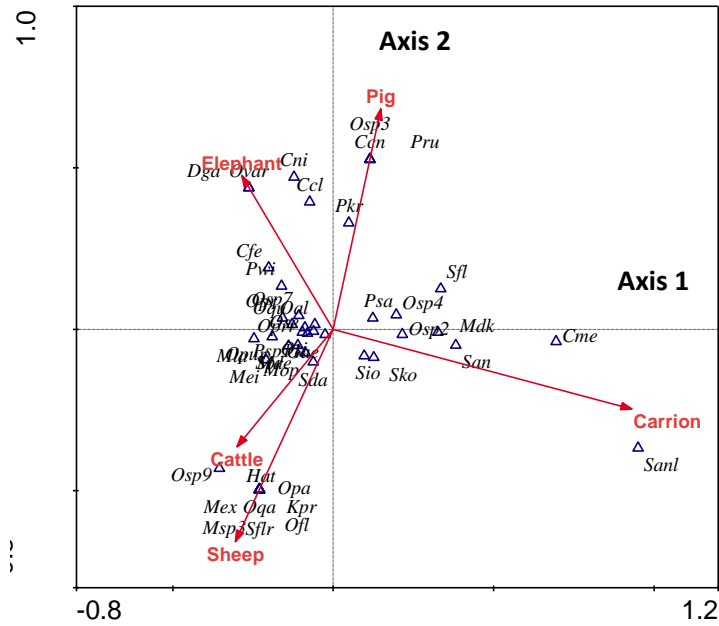


Figures 6.7., 6.8.

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 (Δ) 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 (Δ) 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 (Δ) 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		F	P
	Eigen values						
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	Mabuasehube	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°

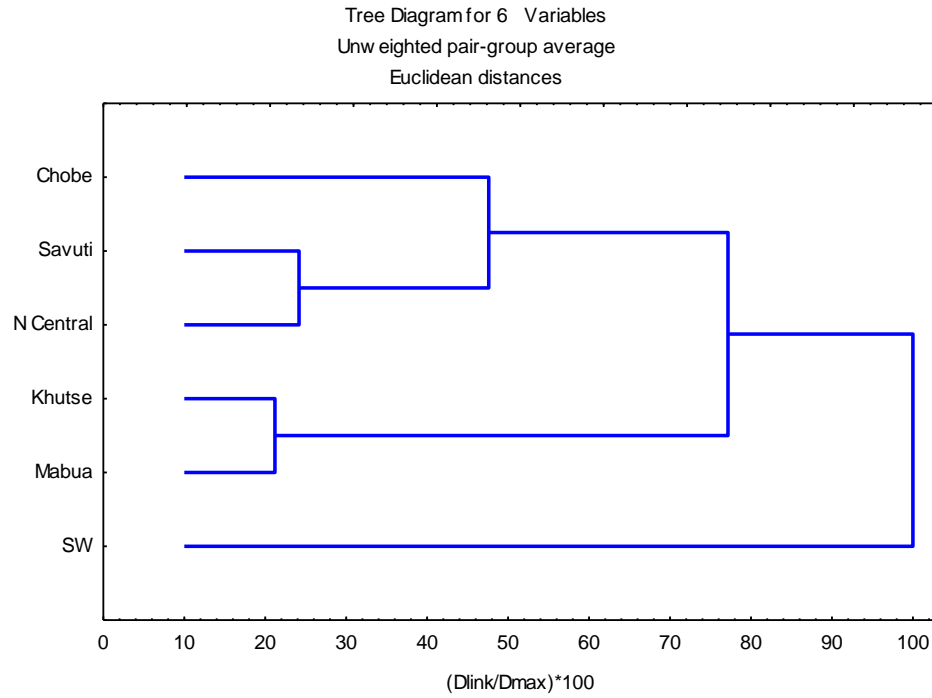


Figure 6.13. Dendrogram showing the proportional similarity or dissimilarity between patterns of dung association across the environmental gradient of the Botswana Kalahari (from analysis of data in Table 6.5).

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.