Chapter 4
SEASONAL PATTERNS OF DUNG BEETLE ASSEMBLAGES IN DIFFERENT HABITATS

4.1. INTRODUCTION

Many factors influence the distribution of dung beetles in an area. Climatic variation could have a number of effects on the distribution of dung beetle assemblages throughout the year, with dung beetle abundance fluctuating seasonally. According to Cambefort (1991) seasonality has a strong effect on dung beetle activity and Wassmer (1994) found that phenology proved to be one of the most important factors in structuring dung beetle biocoenoses. Galante *et al.* (1995) found that the distribution of dung beetle biomass was not uniform throughout the year in savanna-like woodland in western Spain. Peck & Forsyth (1982), on the other hand, found that dung beetle abundance was relatively constant through the wet and dry seasons in an Ecuadorian rain forest. The seasonal activity of dung beetle assemblages seems to be determined by the type of environment in which they occur. The more seasonal the environment, the more seasonal the occurrence of dung beetles will be. Equatorial regions, for instance, are less seasonal than temperate regions and for many organisms also more predictable (Begon *et al.* 1995). A less seasonally variable climate will allow species to be more specialized and have narrower niches. In a seasonal environment, spatial variation is more important than temporal variation of the corresponding processes because seasonality itself sets constraints on the dynamic processes and provides cues for the organisms to cope with the changing environment (Hanski, 1980a). According to Wolda (1978), seasonality in insects is controlled by three factors, i.e. resource availability, temperature and rainfall. Though several authors have reported on seasonal changes in the favourability of cattle dung as a resource for some dung-breeding insects (Macqueen *et al.* 1986; Ridsdill-Smith, 1986: Matthiessen & Hayles, 1983), the dung of large mammals is a food type that fluctuates relatively little in amount as compared with foods such as foliage of deciduous trees, fruits and seeds, flower nectar and pollen. Because of this, insects that use dung might be expected to show substantially less seasonal fluctuation in numbers than do those that use other food types in the same habitat (Janzen, 1983). The seasonal occurrence in coprophagous beetles is, however, not constrained by resources, but by other environmental factors such as temperature and rainfall. According to Hanski & Cambefort (1991a), temperature is the key factor restricting dung beetle development in northern temperate and montane regions, whilst in subtropical and tropical grasslands, rainfall is the important factor determining dung beetle activity. Jameson (1989) considers temperature the leading cause of the correlation between species numbers and time. Janzen (1983) found that in northwestern Costa Rica dung accumulates during the dry season. During the rainy season, it disappears within a few days. This seasonal variation in dung decomposition is due largely to variation in numbers of large nocturnal dung beetles. Doube (1991) also found that dung beetles are most active during the wet summer months in South Africa, and that dry periods during the wet season cause a temporary reduction in dung beetle activity. Endrödy-Younga (1982) found that dung beetle activity at Nylsvley, a semi-arid South African savanna ecosystem, was primarily during the summer months. Almost no activity was recorded during months of low rainfall and low temperature. Cambefort (1991) found two peaks of abundance in the dung beetle community in the Guinean savannas of the Ivory Coast, corresponding with two rainy seasons.

Numerous studies have shown that dung beetle activity follows a bimodal distribution depending on seasonal changes. Lumaret & Kirk (1991) found that Mediterranean dung beetles have two peaks of activity, a major one at the end of spring and another, smaller one in autumn. According to Ridsdill-Smith & Hall (1984) in areas with a Mediterranean climate, activity by native dung-feeding Scarabaeidae might be expected to be greatest in autumn and spring, restricted in mid-summer by the lack of rain, and in mid-winter by low temperatures. In western Spain, Galante *et al.* (1995) also found a major peak of species activity and biomass concentration of dung beetles attracted to cattle dung in spring and again in the Autumn.

Phenological differences between different species might influence the co-existence of dung beetle species. Certain species may be more resistant to drought and temperature fluctuations and occur during a time of the year when competition is less severe. Cambefort (1991) found that the *Gymnopleurus* species are probably inferior competitors compared to *Sisyphus*, but as the latter are abundant only after a significant amount of rain has fallen, *Gymnopleurus* may take advantage of their resistance to drought and occupy the less competitive few weeks in the beginning of the year. In southern Europe, the endocoprid *Aphodius constans*, inferior in competition to telocoprids and paracoprids, breeds during the cold winter months when the superior competitors are dormant. In the winter rainfall areas of southern Africa dung beetles are active throughout the year because of mild climatic conditions. Breytenbach & Breytenbach (1986) found that dung beetle activity in the southern Cape never ceased completely during July and Davis (1987) also observed dung beetle activity in the winter rainy season in the south-western Cape. African savannas, however, differ from the winter rainfall areas by having a distinctly seasonal climate, with clear-cut rainy and dry seasons (Cambefort, 1991). The study area, Sandveld Nature Reserve and neighbouring farms, are in a typical savanna ecosystem, which is characterised by semi-arid conditions with high daytime temperatures, distinct wet and dry seasons of varying length, with downpours alternated by extended periods of drought. The dung beetle assemblages occurring in this area is expected to be adapted to this seasonal environment showing different seasonal patterns of activity throughout the year. This will have consequences for the degradation of dung in the area with dung beetle assemblages removing dung more effectively during certain times of the year.

4.2. MATERIAL & METHODS

Sampling procedure

Seasonal patterns of dung beetle activity were recorded over a period of two years (July 1996 to June 1998). The seasonal distribution of dung beetles could then be compared for two different years. To determine seasonal differences of dung beetle assemblages in different habitats dung beetles were sampled in two different habitat types, a grassveld area and a bushveld area. In these two habitat types dung beetle assemblages in a natural habitat (Sandveld Nature Reserve) and a disturbed habitat (farms Rietvlei and Josina) were compared. The farm Rietvlei represented a grassveld area and the farm Josina a bushveld area. Three sites, spaced 1km apart, were chosen in each of the four localities. In each site three plots, spaced 50m apart, were chosen. Each plot contained four pitfall traps, spaced 1m apart. The beetles from these four traps were pooled and statistically treated as a single sample. 1l plastic pitfall traps were used for sampling. The traps were buried up to the rim and the bottom filled with salt water. A container with 200g of fresh cattle dung was put inside the trap to attract the dung beetles. This was sufficient to attract both flying and walking dung beetles. Dung beetles attracted by the dung fell into the traps and could be collected later. Fresh, insect free, cattle dung, used to bait the traps, was collected on the dairy farm Bospré, near Bloemfontein (26°00'S; 29°00'E). The dung was transported in plastic buckets and covered tightly with lids to avoid desiccation and oxidation of the dung. After baiting the traps with fresh dung they were left for 24 hours after which dung beetles in the traps were collected and preserved in 70% alcohol for later identification.

Analytical Methods

The total number of dung beetle species and individuals in each of the four habitats was calculated for each month from July 1996 to June 1998. The size range among dung-inhabiting beetles is large (Koskela & Hanski, 1977). In the present study dry mass was used as an indicator of size. The dry mass per species was obtained by calculating the mean mass of 20 specimens (10males and 10 females) of each species. These were dried at 80°C for 48 hours and were subsequently weighed on a precision balance. The biomass of beetles in each trap was calculated by summing the results derived from multiplying the abundance of each species by its mean dry mass (g) per individual.

Two major components of diversity are recognised, variety and relative abundance (evenness) of species (Magurran, 1988). In order to cover these components of the species diversity of dung beetle assemblages in the four different habitats, four different diversity indices were used, i.e. Species richness (S), Margalef (D_{mg}), Shannon (H) and

Berger-Parker (1/d). The Margalef index is calculated by Dmg=(S-1)/lnN, where S=number of species and N=total number of individuals. The Berger-Parker index is calculated from the equation $d=N_{max}/N$ where N=total number of individuals and N_{max}=number of individuals in the most abundant species. The formula for calculating the Shannon diversity index is $H'=- p_i \ln p_I$, where p_i is the proportional abundance of the i'th species=(n_i/N). Shannon evenness is calculated using the formula E=H'/lnS.

To determine significant linear relationships between biomass, abundance, Shannon diversity (H), Shannon evenness (E), Berger Parker (1/d) and Margalef (D_{mg}) indices for dung-burying beetles and physical factors (R.H., Temperature, and Rainfall) Pearson's correlation coefficient, which measures the linear association of two data sets, was used. A value of r near or equal to 0 implies little or no linear relationship exists between the two lists of numbers. A value of r near or equal to 1 or -1 indicates a very strong linear relationship.

Percentage dominance of species during each month in each habitat was calculated by $PD=100(N_{max}/N)$, where N_{max}=number of individuals in the most abundant species and N=total abundance in a habitat.

Weather data

Daily minimum and maximum temperatures and minimum and maximum relative humidity (RH) were logged with a data-logger in the bushveld and grassveld habitats. The average monthly minimum and maximum temperatures and minimum and maximum RH in the bushveld and grassveld habitats were determined from this data. Local rainfall data for the whole area were obtained from the weather station at Bloemhof (± 10 km from study area).

4.3. RESULTS & DISCUSSION

Changes in weather conditions in the study area during study period

During the sampling period the study area was characterised by high maximum temperatures during the day and lower minimum temperatures at night. There was a marked difference between the minimum and maximum temperatures (Fig 4.1.). The hottest time of the year occurred between November and February, with a peak in temperature during February 1997 and December 1998 (Fig. 4.1). There was a marked difference in temperature between the summer and winter months, with the temperature decreasing from March to July and increasing from August to October (Fig. 4.1.)

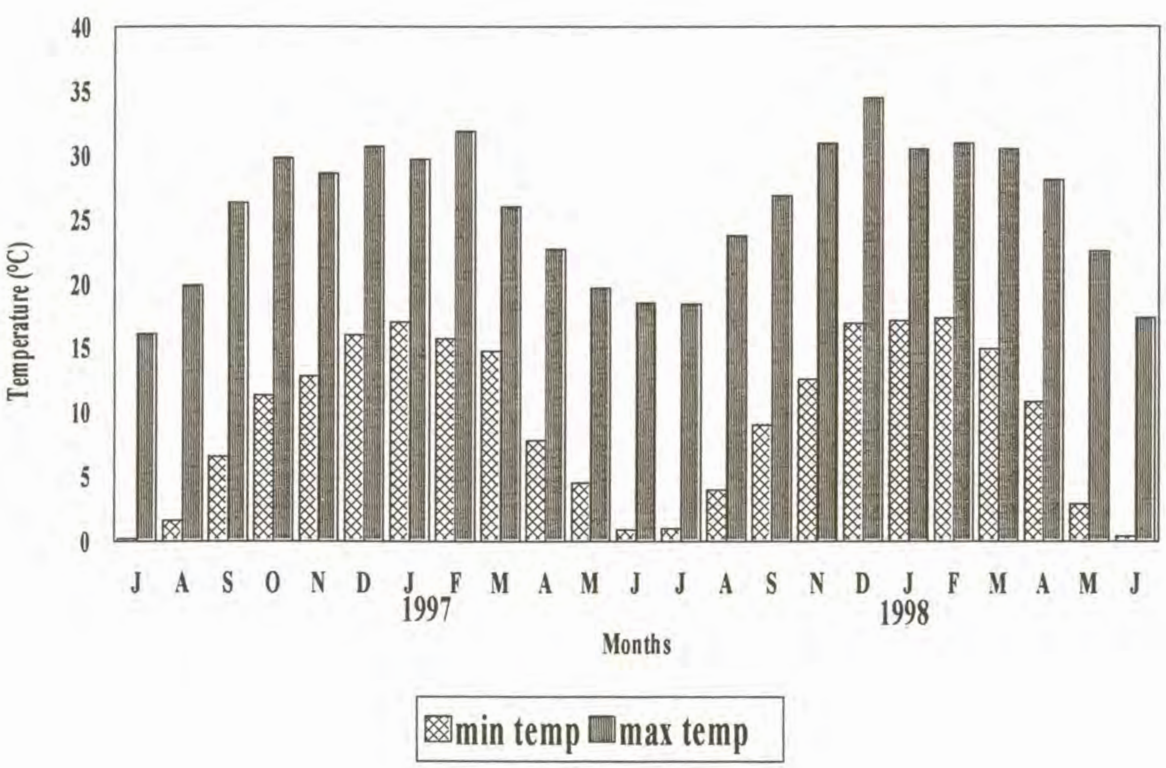


Fig. 4.1. Average monthly minimum and maximum temperatures at Sandveld Nature Reserve (July 1996 - June 1998)

During the two-year sampling period there was a wet season from November 1996 to April 1997, followed by a dry period from June 1997 to December 1997. This was again followed by a brief wet period from January 1998 to April 1998. The peak in rainfall occurred in March during both years (Fig 4.2.). There was a big difference between the minimum and maximum relative humidity, with very low minimum RH and very high maximum RH (Fig 4.2.). There was little change in RH over the seasons (Fig. 4.2.).

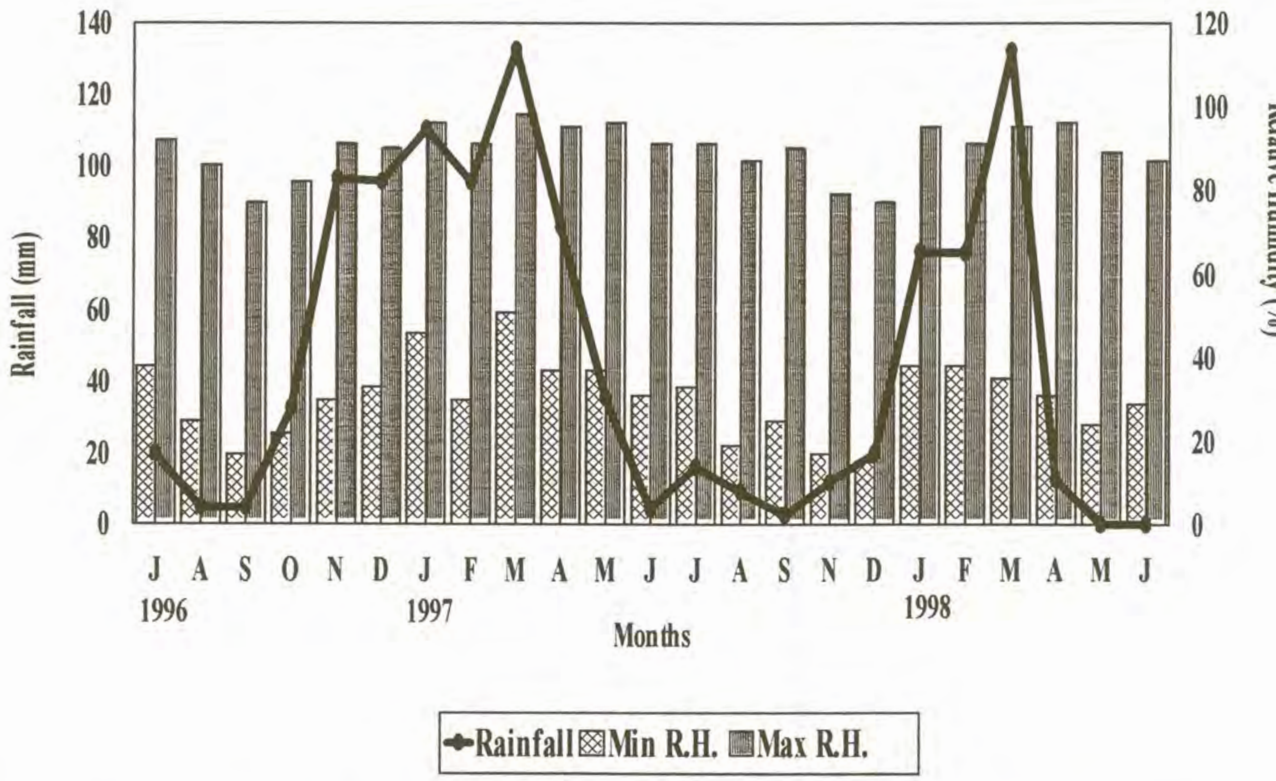


Fig. 4.2. Average monthly minimum and maximum relative humidity and average monthly rainfall at Sandveld Nature Reserve (July 1996 - June 1998).

Between-field differences in seasonal dynamics of abundance, biomass and diversity in dung beetle assemblages

In all four habitats there was a unimodal seasonal distribution in abundance of dung beetles (Fig.4.3.). In the summer rainfall areas of southern Africa the abundance of different species varies with the different seasons. According to Doube (1991) the net result of the complementary and overlapping activity patterns of species active during different seasons results in a unimodal seasonality of overall beetle activity, which contrasts sharply with the overall bimodal pattern of beetle activity in localities situated closer to the equator. There was an increase in abundance during the warmer, summer rainy season from November to March and a decrease in the colder, winter dry season from April with low abundance until September (Fig 4.3.). There was almost no dung beetle activity in the cold, dry months from May to August. Endrödy-Younga (1982) also found that dung beetles at Nylsvley were primarily active during the summer months and almost no activity was recorded during months of low rainfall and low temperature.

There were differences in the seasonal distribution of abundance in the four different habitats and also differences between the two years. In the grassveld habitats the total abundance was lower during the second year than the first year and in the natural grassveld habitat there was a peak in abundance in February during the first year and a smaller peak during November in the second year (Fig. 4.3. a.). In the disturbed grassveld habitat there was a peak in abundance during December and a smaller peak in February. In this habitat peak abundance during the second year also occurred in December, but was much lower than the first year (Fig. 4.3. b). In both the grassveld habitats the abundance peaks seemed to reflect maximum numbers of summer generations of univoltine species.

In the bushveld habitats there was no marked difference in abundance between the two years as in the grassveld habitats. In the natural habitat there was a peak in abundance during March of the first year, while during the second year the peak in abundance occurred during December (Fig. 4.3. c). In the disturbed habitat the peak in abundance was during February of the first year and December of the second year (Fig. 4.3. d).

Monthly differences in abundance of dung beetles within a habitat might be explained by differences in temperature and rainfall during the different months, with a combination of high temperature and high rainfall favouring dung beetle abundance (Fig. 4.1, Fig. 4.2). When the temperature and rainfall is to high, however, it might have a negative effect on dung beetle abundance (Fig. 4.1, Fig. 4.2). The movement of the larger herbivores might also influence abundance of dung beetles during the different months. In the nature reserve large herbivores move through a large area in search of better grazing throughout the year, while on the farms the cattle are moved between different camps. The differences in the abundance peaks between the different habitats might reflect the behaviour of the larger mammals influencing the availability of fresh dung. On the farms fresh dung will not always be available during certain months because of cattle being moved to other camps. The differences in the abundance peaks might also indicate different microclimatic conditions, influenced by a difference in vegetation, in the different habitats (Chapter 2, Table 2.1). These differences in climatic conditions will influence the rate of development of dung beetles differently in the different habitats. Jameson (1989) found that key elements of microclimate influence the quality, availability, and malleability of the dung as a nutritional resource for dung beetles. A pat of dung exposed to the sun, wind and other abiotic elements will be prone to faster desiccation and remain a viable food source for a shorter time. According to Lumaret & Kirk (1991) the activity of dung beetles at a site depends on the temperature and precipitation cycles and on the openness of the habitat. Different species might be favoured differently by these conditions and because of differences in dominance of species in the habitats there will be a difference in abundance peaks between the habitats.

Breytenbach & Breytenbach (1986) found that the samples collected during different years in the southern Cape were similar, indicating considerable seasonal constancy in species composition. This is in contrast to what was found in the present study where there were large differences between the two different years. This might indicate a more inconsistent seasonal environment in a summer rainfall area, influencing the species composition, than in the southern Cape, which is a winter rainfall area. The differences in peak abundance between the two years might be explained by variation in rainfall patterns. During the first year the wet season started earlier and lasted longer than during the second year (Fig. 4.2.). In the grassveld habitats late rain probably influenced the dung beetles and prevented them from reaching peak abundance during the second year. Floate & Gill (1998) also ascribed larger numbers of beetles trapped to variation in rainfall. Dung beetles in the bushveld habitats did not seem to be influenced by the late rain, probably due to tree cover providing more sheltered habitats compared to the open grassveld habitats. The abundance here seems to be more dependent on higher temperatures during December.

The seasonal distribution of biomass was not necessarily correlated with the distribution of abundance. In both the grassveld habitats there was a peak in biomass during January of the first year and November of the second year (Fig. 4.3. a, b). In the natural bushveld habitat there was a peak in biomass during January of both years (Fig. 4.3. c), while in the disturbed bushveld habitat the peak in biomass was also during January of the first year and November of the second year (Fig. 4.3. d). The differences in distribution of abundance and biomass can be ascribed to different seasonal patterns of species that differ in size. Climatic conditions might favour larger species at certain times of the year, while at other times the climatic conditions might be better suited for the smaller species. Although the peaks in biomass occurred at the same time in the different habitats, the peaks in biomass were higher in the natural than disturbed habitats indicating that larger species were dominant in the natural habitats and conditions were more favourable here for high abundance of these large species. Doube (1991) found that in the summer rainfall regions of southern Africa, most species emerge in abundance after the first spring rains in September-October and were most active during the wet summer months, became scarce in late autumn and rare during winter and early spring. Dung beetles in the present study followed the same general pattern and activity and biomass were highest in mid-summer, when temperatures and rainfall were highest (Fig. 4.1. & Fig. 4.2), in all the habitats. This is also in agreement with Tyndale-Biscoe (1988) who found that adult dung beetle activity at Araluen in Australia commenced in November or December and continued throughout summer until about April. The pattern of this study is, however, in contrast with Galante, *et al.* (1995) who, in western Spain, found a major peak of dung beetles in spring and again in autumn. In western Nebraska, Jameson (1989) found that prolonged temperatures above 35°C reduced activity resulting in lower abundance during the warmest months and Lumaret & Kirk (1987) state that Mediterranean dung beetles possess phenological adaptations to cope with the summer drought, and are active mostly before and after the drought resulting in two peaks of activity in spring and autumn. In the present study dung beetle biomass decreased during December (Fig. 4.3) when temperatures were highest (Fig 4.1). This might indicate that too high temperatures affect larger dung beetle species and these species might be able to survive higher temperatures by restricting their activity to months when the temperature is lower. There was a sharp decrease in abundance and biomass in the autumn (April, May) and in winter the biomass was minimal, increasing again in November in all four habitats (Fig. 4.3). It seems that low temperatures and low rainfall during the winter months influence dung beetles negatively. Galante *et al.* (1995) also found a sharp decline in dung beetle biomass during autumn and low biomass in winter. This will have consequences for the degradation of dung during the cold, dry winter months. At Rockhampton (Australia), Doube (1991) found that dung dispersal reached about 75% in the hot and wet season, but was only about 5% during the dry months.

There was a sudden drop in Shannon diversity (H) and Shannon evenness (E) from April to May in all four habitats, with low diversity and evenness from May to August and a sudden increase during September (Fig. 4.4.). The Berger Parker index, an indication of dominance, showed greater seasonal variation in the four habitats (Fig. 4.5.). The dominance in the assemblages, therefore, fluctuated widely over time. This was probably influenced by a variety of species dominating in turn, as changing conditions became suitable for each. The Margalef index, which measures species richness, showed peaks in species richness between November and March (Fig. 4.5.). Breytenbach & Breytenbach (1986) also found seasonal variation in species richness of dung beetles in the southern Cape, with distinct peaks between January and April. In general the dominance, evenness and species richness were higher in the warmer wet season than in the colder dry season, but even in the warmer wet season different species may be suited to variation in conditions causing monthly fluctuation. According to Berger *et al* (1995) more species might be expected to coexist in a seasonal environment because of different species being suited to conditions at different times of the year.

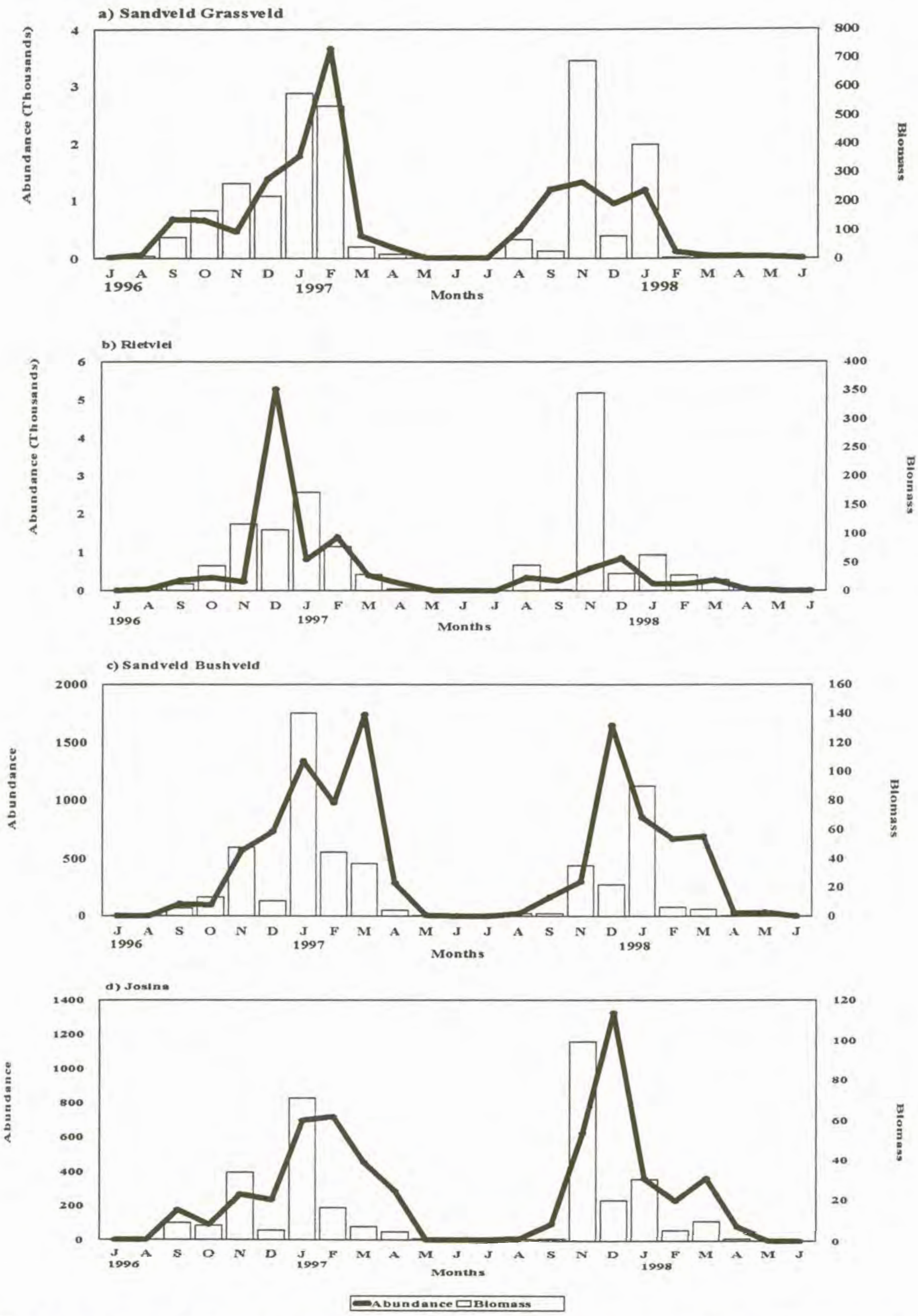


Fig. 4.3: Seasonal abundance and biomass in dung beetle assemblages over a period of two years (July 1996 - June 1998) in four different habitats.

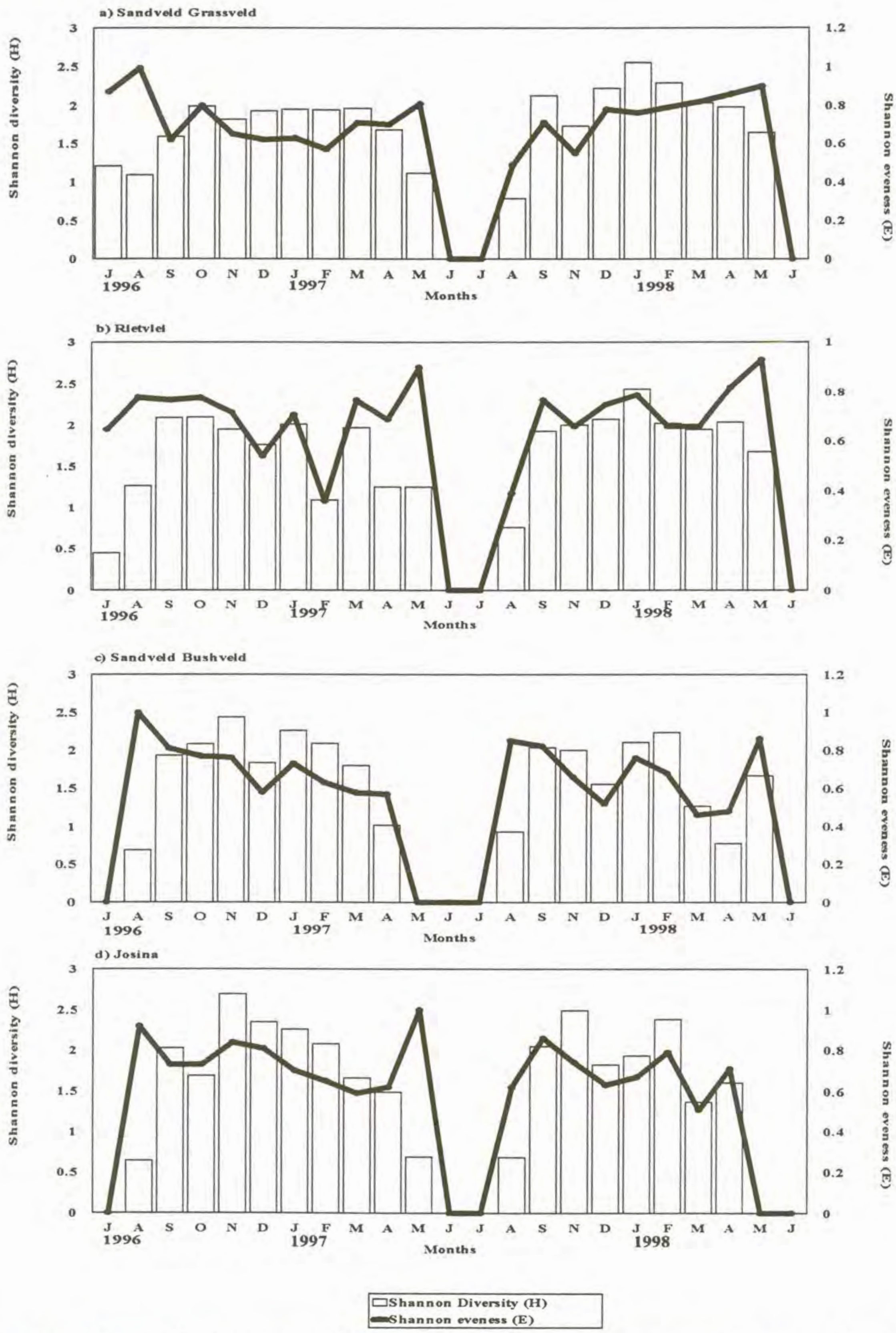


Fig. 4.4: Seasonal change in Shannon diversity and evenness for dung beetle assemblages in four different habitats.

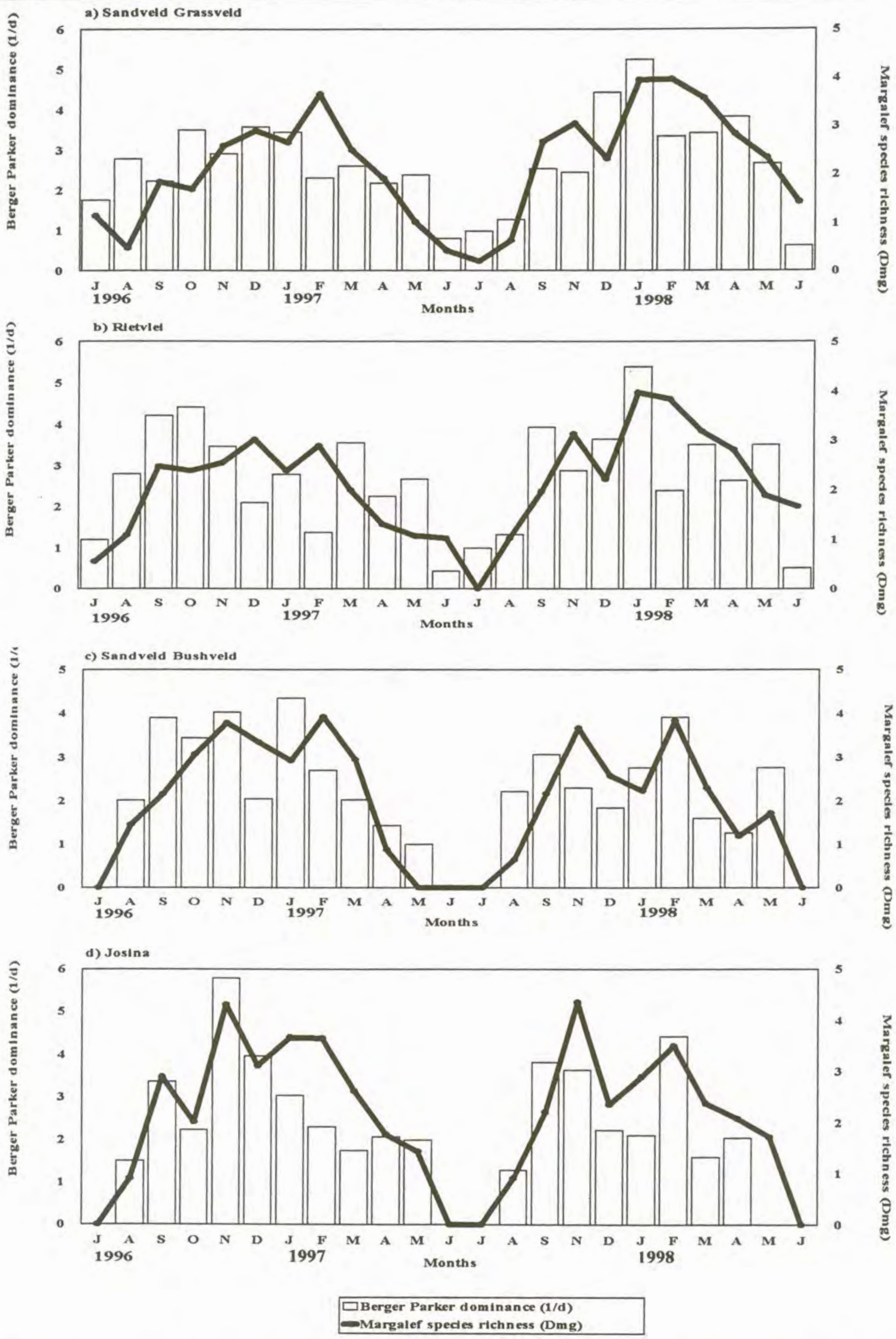


Fig. 4.5: Seasonal change in Berger Parker dominance and Margalef species richness for dung beetle assemblages in four different habitats.

Dung beetle biomass, abundance, Shannon diversity and evenness, Berger Parker dominance and Margalef species richness were all negatively correlated to relative air humidity and positively correlated to temperature and rainfall in all four habitats (Table 4.1.). Davis (1996) also found a positive correlation between beetle biomass and air temperature and also in most habitats to rainfall. According to Jameson (1989), temperature has a pronounced effect on abundance and diversity. There was a higher correlation between temperature and biomass, abundance, diversity and species richness in all four habitats than the rainfall (Table 4.1). It seems that, in the present study, temperature was the key factor regulating the distribution of dung beetle assemblages in all four habitats. Jameson (1989) argues that because temperature, directly or indirectly, is such an important factor in the system, it may be the leading cause of correlation between species numbers and time. According to Hanski & Cambefort (1991a) temperature is the key factor restricting dung beetle development in northern temperate and montane regions and in subtropical and tropical grasslands, rainfall is the important factor. This is contrary to what was found in this study. Dung beetles seemed to be negatively influenced by high relative humidity and although rainfall had an effect on seasonal distribution of dung beetles, it was less important than the temperature and cannot be considered as the key factor in seasonal distribution of the dung beetle assemblages. Tyndale-Biscoe (1988) found that excess moisture affected the females of *Onitis alexis* negatively. This species is well-adapted to semi-arid conditions. Because the study area is a semi-arid area dung beetles here are expected to be adapted to dry conditions and will be more dependent on high temperatures for development and activity than on moisture and excess moisture in fact seems to have a negative effect on their survival.

Table 4.1: Statistically significant correlation between biomass, abundance, Shannon diversity (H), Shannon evenness (E), Berger Parker (1/d) and Margalef (D_{mg}) indices for dung-burying beetles and physical factors (R.H., Temperature, and Rainfall)

	Habitat	R.H.	Temperature	Rainfall
Biomass	**S.G.**	-0.167	0.558	0.296
	Rietvlei	-0.273	0.469	0.179
	S.B.	0.226	0.538	0.506
	Josina	-0.209	0.463	0.187
Abundance	**S.G.**	-0.177	0.581	0.294
	Rietvlei	-0.071	0.412	0.322
	S.B.	0.193	0.736	0.687
	Josina	-0.236	0.724	0.36
H	**S.G.**	-0.061	0.822	0.466
	Rietvlei	-0.193	0.767	0.331
	S.B.	-0.057	0.694	0.492
	Josina	-0.176	0.873	0.331
E	**S.G.**	-0.04	0.243	0.124
	Rietvlei	-0.08	0.274	0.08
	S.B.	-0.205	0.339	0.146
	Josina	-0.154	0.533	0.238
1/d	**S.G.**	-0.06	0.74	0.347
	Rietvlei	-0.226	0.486	0.141
	S.B.	-0.269	0.605	0.273
	Josina	-0.207	0.66	0.342
D_{mg}	**S.G.**	0.041	0.883	0.587
	Rietvlei	-0.123	0.861	0.453
	S.B.	-0.244	0.853	0.507
	Josina	-0.125	0.857	0.549

*P<0.001 (S.G. – natural grassveld; Rietvlei – disturbed grassveld; S.B. –natural bushveld; Josina – disturbed bushveld)

*A value of r near or equal to 1 or -1 indicates a very strong linear relationship.

Seasonal change in Functional Group structure

The separate dung beetle communities in the bushveld and grassveld habitats showed different patterns of species biomass within functional groups while the natural and disturbed habitats showed broadly similar patterns (Fig. 4.6). There was a definite seasonal separation of functional groups in terms of biomass in the four different habitats.

In the grassveld habitats F.G. II dominated the community in terms of biomass during the winter, spring and autumn months from July to September and again from April to September with dominance of this group increasing from February to April and decreasing from November (Fig. 4.6.). There was an increase in dominance of F.G. I from October and this group was the most dominant group during summer from October to January. There was a decrease in dominance of this group from January to March when the dominance of F.G. II increased gradually (Fig. 4.6.). During December there was a slight decrease in the dominance of F.G. I, coincident with a slight increase in the dominance of F.G. II in both the natural and disturbed habitat (Fig. 4.6.). In terms of biomass the other functional groups in the grassveld areas made up a much smaller percentage of the community than F.G. I and II (Fig. 4.6). There was a clear seasonal separation between the two dominant groups in these habitats with F.G. II being less dominant in biomass while F.G. I was present.

In the bushveld habitats F.G. II was dominant in biomass during the spring months from August to October with a gradual decrease in dominance as F.G. I became more dominant during summer from November to February (Fig. 4.6.). F.G. IV gradually increased in dominance and became the most dominant group in the bushveld habitat during autumn from March to May when the other groups were either absent or less dominant (Fig. 4.6.). In these habitats there was also a clear seasonal separation of functional groups with F.G. I dominant during summer, F.G. II dominant during spring and F.G. IV dominant during autumn.

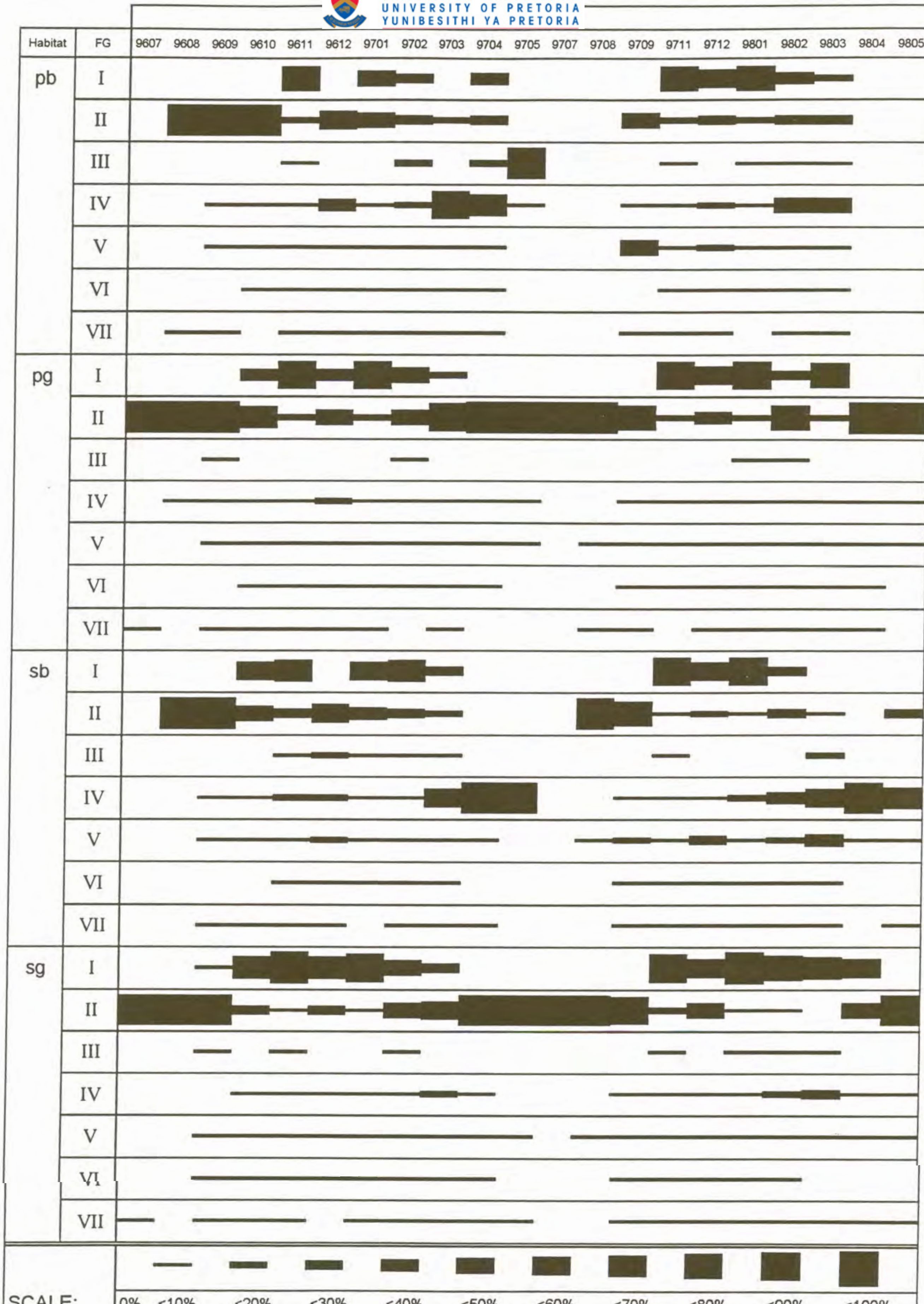


Fig. 4.6. Seasonal change in functional group (F.G.) structure, in terms of biomass, in dung beetle assemblages in different habitats (pb - disturbed bushveld, pg - disturbed grassveld, sb - natural bushveld, sg - natural grassveld)

Seasonal distribution of individual species

The most common dung beetle species in the whole study area throughout the study period was *Scarabaeus flavicornis, Pachylomerus femoralis, Onthophagus obtusicornis, Onthophagus sugillatus, Onthophagus variegatus* and *Caccobius seminulum.* The abundance of these species ranged between 1500 and 4500 individuals collected during the study period. Different seasonal patterns were observed in these species.

S. flavicornis and *P. femoralis* occurred most abundantly in the natural grassveld habitat. *S. flavicornis* showed a similar, polimodal distribution pattern in the natural and disturbed grassveld habitats, but in both the bushveld habitats the distribution was unimodal (Fig. 4.7 a). *P. femoralis* showed bimodal distribution in all the habitats (Fig. 4.7. b). *S. flavicornis* and *P. femoralis* showed peak abundance at different times of the year (Fig. 4.7. a, b). Endrödy-Younga (1982) found that at Nylsvley both these species showed peak abundance during December and March. The difference in distribution of these two species in the present study might be explained by different environmental conditions in the study area. *Onthophagus obtusicornis, O. sugillatus and O. variegatus* occurred more abundantly in the bushveld habitats than the grassveld habitats and the seasonal peaks in biomass for *Onthophagus obtusicornis* and *O. sugillatus* were higher in the natural bushveld habitat than in the disturbed bushveld habitat (Fig 4.7. c, d, e). *O. obtusicornis* and *O. sugillatus* had a bimodal distribution (Fig. 4.7. c, d), while *O. variegatus* had a unimodal distribution (Fig. 4.7. e). *Caccobius seminulum* occurred most abundantly in the disturbed grassveld habitat and showed a bimodal distribution pattern (Fig. 4.7. f.).

Although species in the natural and disturbed habitats showed similar seasonal patterns, all the species that occurred dominantly in either the bushveld or grassveld habitats were consistently more abundant in the natural than the disturbed habitats (Fig. 4.7.). This might be an indication that the microclimatic conditions, influenced by seasonal changes, in the different habitats influenced the success of species in the different habitats differently. The dominant species were much more successful in the natural habitats than in the disturbed habitats. The only exception was *Caccobius seminulum* occurring more abundantly in the disturbed grassveld habitat.

Most species showed a bimodal seasonal distribution. In most cases these patterns were recognisable between different habitats and across the years. Floate & Gill (1998) found two general seasonal patterns in dung beetle distribution, a bimodal pattern, peaking in the spring and fall and a single peak in spring to midsummer. He explains differences in seasonal activity by differences in overwintering strategy. Species in the first group overwinter as adults and emerge in spring and the autumn period of activity reflects the emergence of a new generation of adults. Species in the second group overwinter as immature stages. They complete their development in spring, then emerge as adults in late spring and summer. Species in the present study probably overwintered as adults, emerged from September to November, with new generations emerging during the summer months. The different dung beetle species are influenced differently by rainfall patterns and temperature, resulting in different distribution patterns for each species. Doube (1991) found that dry periods during the wet season cause a temporary reduction in the numbers of active beetles. In the present study *S. flavicornis* and *P. femoralis*, which occurred more abundantly in the open grassveld habitats, seemed to be more drought resistant, with their distribution patterns not necessarily influenced by rainfall patterns. During the second year the rainy season started later (Fig. 4.2.), but there was still an early peak in biomass of these two species (Fig. 4.7. a, b). There was a drop in the activity pattern of *P. femoralis* during December and although *S. flavicornis* showed an activity peak during December, this peak was much lower than in February. Temperatures probably became too high for activity of these species in the exposed grassveld habitat during December. Temperature probably influences the species in the grassveld habitat more than rainfall. *O. obtusicornis, O. sugillatus* and *O. variegatus*, which occurred more abundantly in the bushveld habitats, seemed to be influenced more by different rainfall patterns. They had a later peak in biomass during the second year, probably resulting from the later occurrence of rainfall (Fig. 4.7. c, d, e). Different species therefore seemed to be influenced differently by climatic conditions resulting in niche separation on two scales, phenological and habitat separation, enabling them to co-occur in the same area. According to Begon *et al.* (1995) balance between competing species can be repeatedly shifted and coexistence therefore fostered as a result of environmental change.

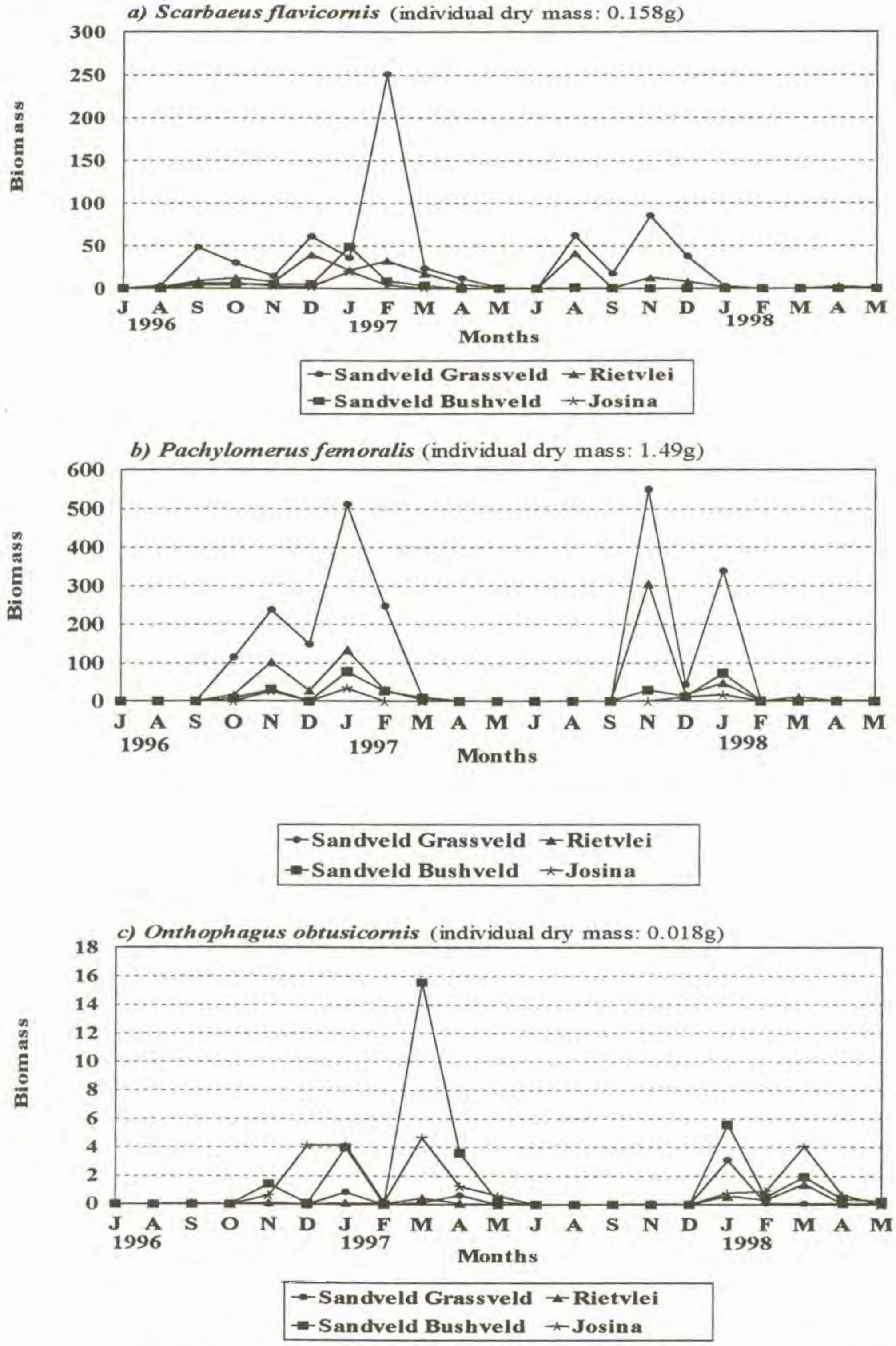


Fig. 4.7: Seasonal distribution of dominant dung beetle species from July 1996 to June 1998 at S.N.R. and neighbouring farms: a) *Scarabaeus flavicornis,* b) *Pachylomerus femoralis,* c) *Onthophagus obtusicornis*

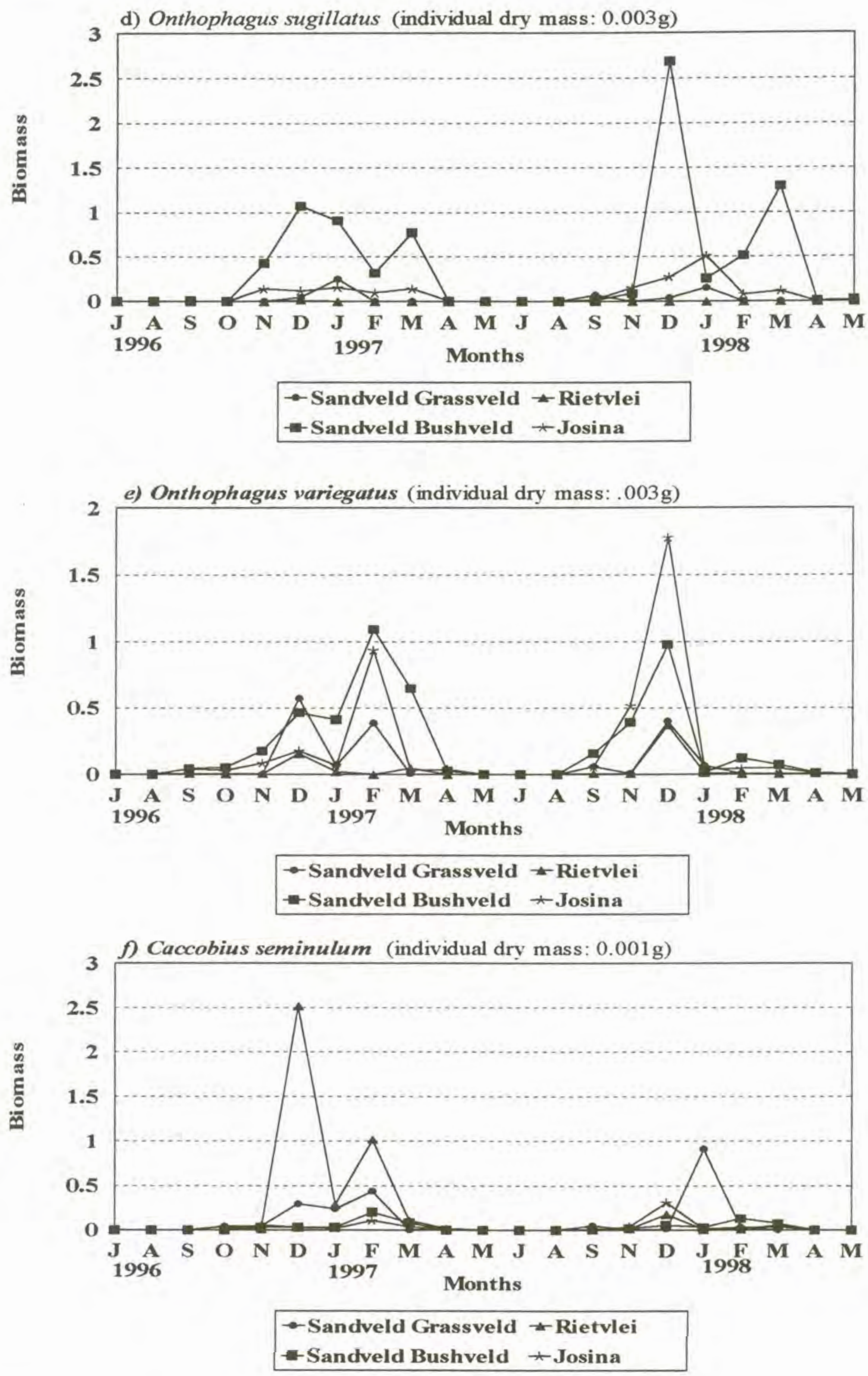


Fig. 4.7. (continued): Seasonal distribution of dominant dung beetle species from July 1996 to June 1998 at S.N.R. and neighbouring farms: d) *Onthophagus sugillatus,* e) *Onthophagus variegatus,* f) *Caccobius seminulum*

Seasonal change in species dominance

Species occurring most abundantly in the study area during the study period showed variation in their seasonal abundance. This resulted in the dominance of other species, not necessarily showing high abundance during the rest of the year in the study area, only during certain months when activity of the more abundant species was lower. According to Wassmer (1994) dominance in dung beetles species can be expressed as eudominant (>32%), dominant (10-31.9%) or subdominant (3.2-9.9%). The species in the present study were either eudominant (>32%) or dominant (10-31.9%). In the grassveld habitats dominance was highest from July to August (Fig 4.8) when the species diversity and evenness were low (Fig. 4.4.). In the natural bushveld habitat dominance was highest during April and May and in the disturbed bushveld habitat in August (Fig. 4.8). In terms of numerical abundance many different species dominated during different months of the year. *Scarabaeus anderseni* was eudominant (>32%) during the dry winter months, from July to August (Fig. 4.8.). *S. flavicornis* was dominant during most of the summer months, but there was a difference in dominance of this species between the different habitats. In the natural grassveld habitat this species was eudominant in September 1996, dominant during October 1996 and December 1996 and eudominant from February 1997 to May 1997 and again in August 1997 (Fig. 4.8.). In the disturbed grassveld habitat this species showed less frequent seasonal dominance. It was dominant during October 1996 and March 1997 and eudominant during April 1997, May 1997 and August 1997 (Fig. 4.8.). In the natural bushveld habitat this species was eudominant during September 1996, October 1996, January 1997 and dominant in August 1997 and dominant in the disturbed bushveld habitat during October 1996 (Fig. 4.8.). *Pachylomerus femoralis* was eudominant during November 1996, November 1997 and January 1998 in the natural grassveld habitat and dominant during November 1996 and November 1997 in the disturbed grassveld habitat (Fig. 4.8.). This species did not show any dominance in the bushveld habitats. The rest of the species in the natural grassveld habitat was dominant for only one month during the year. *Onthophagus quadraliceps* was dominant during January 1997, *Aphodius teter* during September 1997, *Onthophagus sp. 1* during December 1997, *Caccobius seminulum* during February 1998, *O. pilosus* during March 1998, *A. laterosetosus* during April 1998 and *S. inoportunis* during May 1998 (Fig. 4.8.).

C. seminulum was more frequently dominant in the disturbed grassveld habitat than in the natural grassveld habitat. This species was eudominant in the disturbed grassveld habitat from December 1996 to February 1997 (Fig. 4.8.). The species that were dominant in the disturbed grassveld habitat for only a month were *A. pseudolividus* during September 1996, *Onthophagus sp. 1* during December 1997, *S. inoportunis* during January 1998, *S. ambiguus* during February 1998, *O. obtusicornis* during March 1998 and *Scarabaeus sp. 1* during May 1998 (Fig. 4.8.).

O. obtusicornis occurred more frequently in the bushveld habitats than the grassveld habitats. This species was eudominant in the natural bushveld habitat from March to May 1997, during February 1997, and again from April to May 1998 and eudominant in the disturbed bushveld habitat during January, March and May 1997, dominant in February 1998 and eudominant from March to May 1998 (Fig. 4.8.). *O. sugillatus* and *O. variegatus* did not show dominance in the grassveld habitats but were dominant in the bushveld habitats. *O. sugillatus* occurred dominantly in the natural bushveld habitat during November 1996 and eudominantly in December 1996 and December 1997, March 1998 and April 1998 (Fig. 4.8.). *O. variegatus* were found eudominantly in this habitat during February, September and November 1997 (Fig. 4.8.). In the disturbed bushveld habitat *O. sugillatus* occurred dominantly during November 1996 and eudominantly in January 1998 and *O. variegatus* occurred dominantly during December 1996, eudominantly during February 1997, dominantly during November 1997 and eudominantly during December 1998 (Fig. 4.8.). Species dominating during only one month in the disturbed bushveld habitat were *Onthophagus sp. 1* during September 1996, *O. vinctus* during September 1997 and *Drepanocathus eximius* during April 1997 (Fig. 4.8.).

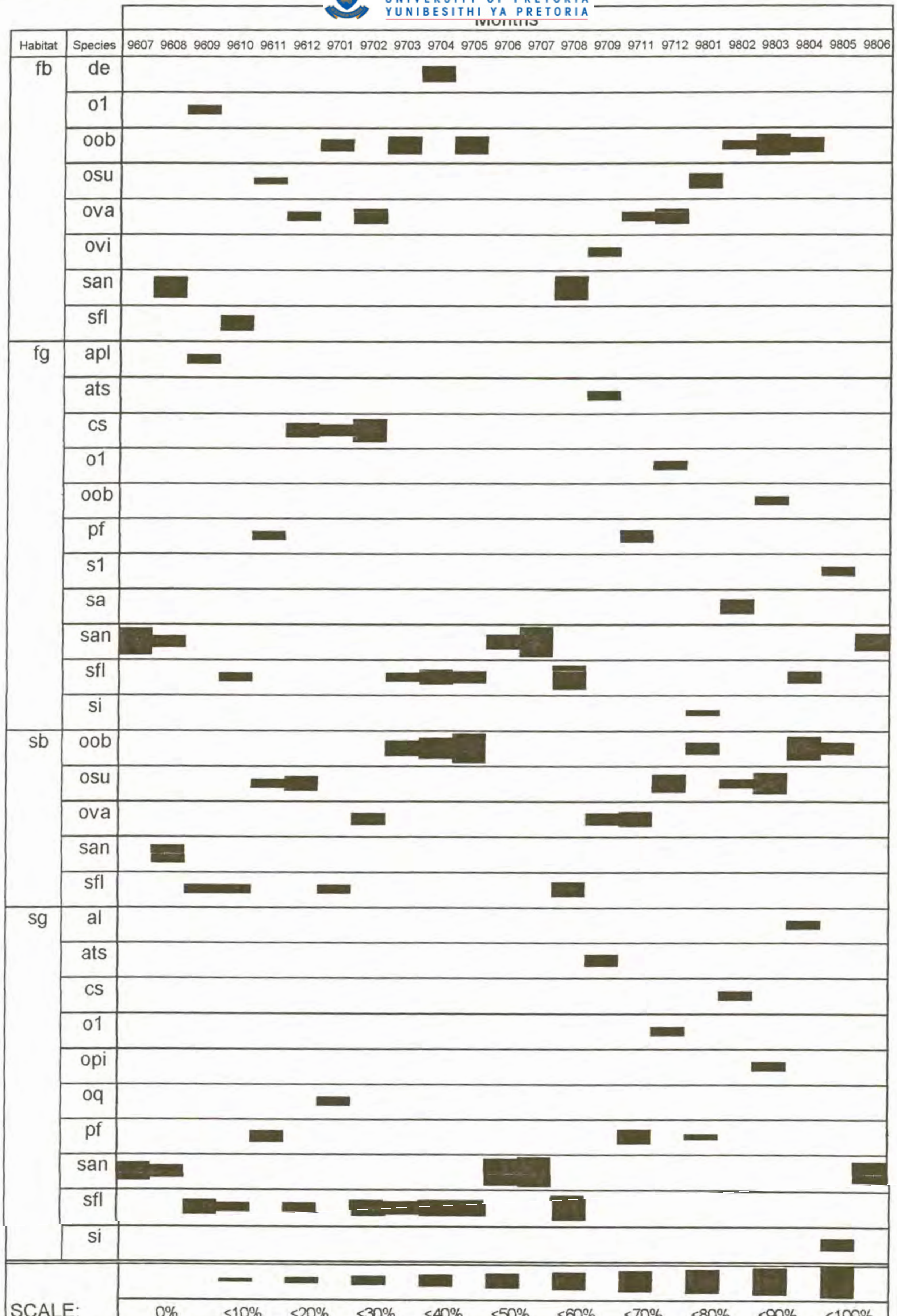
In terms of biomass fewer species dominated seasonally. Two species dominated in the grassveld habitats, viz. *P. femoralis* and *S. flavicornis.* In the natural grassveld habitat *P. femoralis* showed biomass dominance during most of the summer months, from October 1996 to February 1997 and from November 1997 to April 1998 (Fig. 4.9.). *S. flavicornis* showed biomass dominance during the colder drier months, July 1996 to September 1996, March 1997 to May 1997, and August 1997 and September 1997 (Fig 4.9.). *S.*

anderseni showed biomass dominance during the coldest months, June and July when the other two species were absent, while *S. inoportunis* showed biomass dominace only during May 1998 (Fig. 4.9.). In the disturbed grassveld habitat *P. femoralis* showed less frequent biomass dominance than in the natural grassveld habitat. This species showed dominance during October 1996, November 1996, November 1997, December 1997, January 1998 and March 1998 in this habitat (Fig. 4.9.). *S. flavicornis* showed more frequent biomass dominance in the disturbed habitat. This species was dominant during August 1996, September 1996, December 1997, February to May 1997, and August 1997, September 1997, April and May 1998 (Fig. 4.9.). *S. anderseni* showed biomass dominance during June and July and *S. ambiguus* during February in the disturbed grassveld habitat (Fig. 4.9.).

In the bushveld habitats *S. flavicornis* and *P. femoralis* showed less frequent biomass dominance than in the grassveld habitats. In the natural bushveld habitat *S. flavicornis* was dominant during August, September and December 1996 and August and September 1997. *P. femoralis* showed dominance during October, November 1996; January, February 1997 and November 1997 to January 1998 (Fig. 4.9.). The less frequent dominance of these two species enabled *O. obtusicornis* to show more frequent dominance, occurring from March to May during both years (Fig. 4.9.). *S. ambiguus* showed dominance during February 1998 (Fig. 4.9.). In the disturbed bushveld habitat *S. flavicornis* showed biomass dominance during September and October 1996 and *P. femoralis* during November 1996, January 1997 and from November 1997 to January 1998 (Fig. 4.9.). *S. anderseni* showed dominance during August 1996 and August and September 1997, while *O. obtusicornis* was dominant during December 1997, from March to May 1997 and from March to April 1998 (Fig. 4.9.). *O. gazella* occurred dominantly during February 1997 and *S. ambiguus* during February 1998 (Fig. 4.9.).

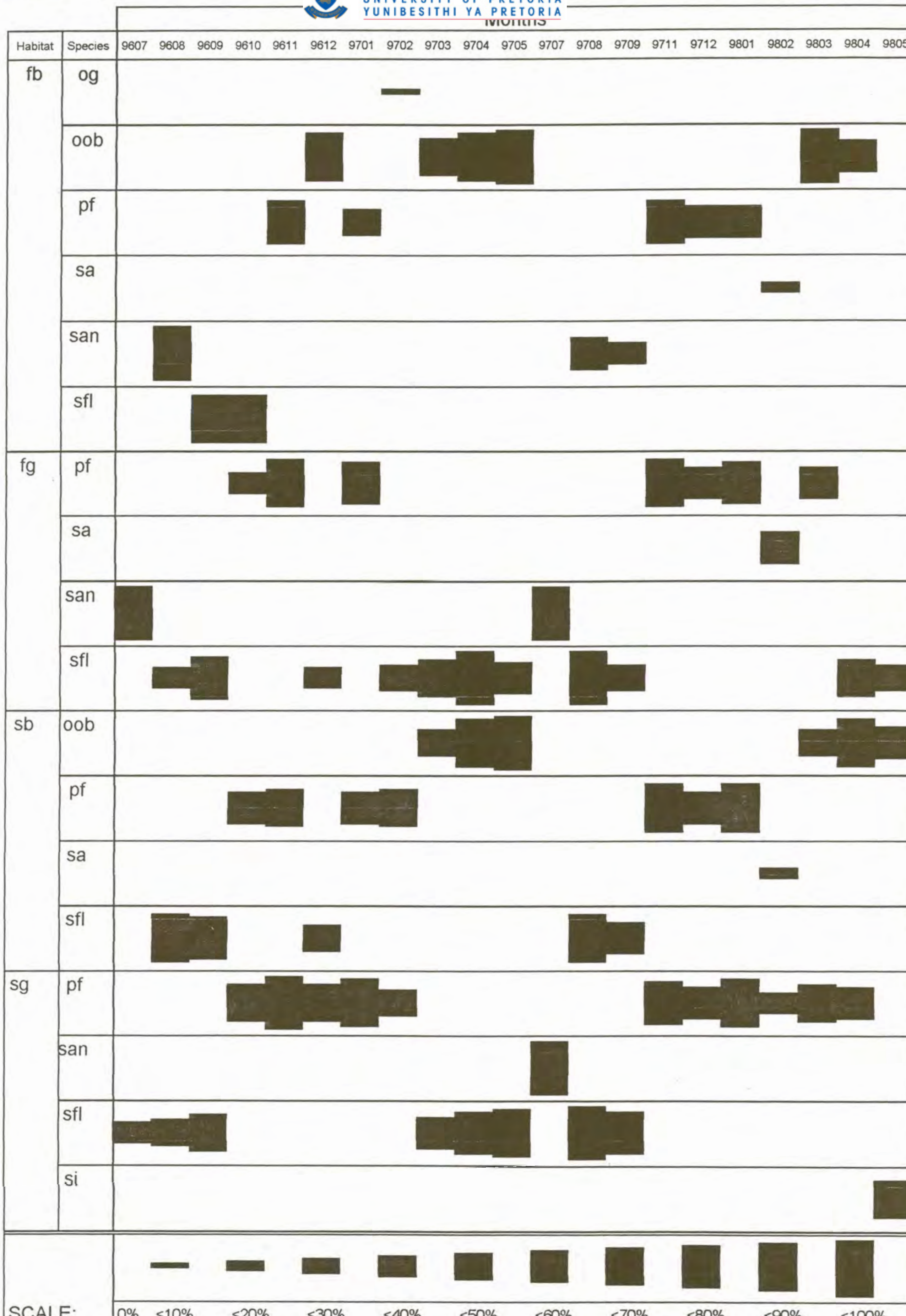
During the spring and summer months the larger, most effective competitor, *P. femoralis,* belonging to F.G. I, dominated the natural grassveld habitat in terms of biomass. This dung beetle showed less frequent biomass dominance in the disturbed grassveld and the bushveld habitats, enabling the smaller species to be more frequently dominant there. Because *P. femoralis* is a highly effective competitor that removes and buries large amounts of dung at a fast rate, it can be concluded that because of the frequent dominance of this species in the natural grassveld habitat during the spring and summer months dung degradation will also be more effective in this habitat during this time. In the other habitats where smaller less effective competitors dominate in terms of biomass, resulting in a lower overall biomass during the spring and summer months in these habitats, breaking down of dung will be less effective.

In order to understand the position of the seasonal niche of a single species it is necessary to compare it with the phenology of the other species (Wassmer, 1994). For such a comparison, total biomass of a species is a better means than numerical occurrence would be, because it reflects species differences in terms of resource utilisation. There was clear distinction in the dominance of different species during different months of the year. This dominance did not only differ between the seasons of the year but also between different habitats. According to Begon *et al.* (1995), in patchy ecosystems where some species are competitively superior to others, an initial coloniser of the patch cannot necessarily maintain its presence there. Dispersal between patches or growth of an individual within a patch, will bring about a reshuffle and species may be competitively excluded. This community can be called dominance-controlled. The community in the present study can also be seen as dominance-controlled. Certain species are better adapted to certain environmental conditions, resulting in exclusion of some species and enabling others to dominate when environmental conditions change. This will enable different dung beetle species belonging to different functional groups to co-occur in similar habitats. Sowig (1997) found season to be the most important factor associated with niche separation within each functional group. The dominance of species was not necessarily similar between natural and disturbed habitats indicating that environmental change affects the communities in the different habitats differently.



*For codes of species names see Chapter 2 - Table 2.4

Fig. 4.8. Percentage seasonal dominance in abundance of dung beetle species in four different habitats (fb-disturbed bushveld, fg-disturbed grassveld, sb-natural bushveld, sg-natural grassveld).



*For codes of species names see Chapter 2 - Table 2.4.

Fig. 4.9. Percentage seasonal dominance in biomass of dung beetle species in four different habitats (fb-disturbed bushveld, fg-disturbed grassveld, sb-natural bushveld, sg-natural grassveld).

4.4. CONCLUSION

According to Begon *et al.* (1995) a habitat can be constant (remain favourable or unfavourable indefinitely), predictably seasonal (regular alternation of favourable and unfavourable periods), unpredictable (favourable periods of variable duration are interspersed with equally variable, unfavourable periods), or it can be ephemeral (favourable period of predictably short duration followed by an unfavourable period of indefinite duration). The distribution of species throughout the year will depend on the type of habitat in which they occur. The study area is an unpredictable habitat with wet and dry seasons of varying length, and downpours alternating with extended periods of drought. As a result of seasonal fluctuation the dung beetle abundance, biomass, dominance, evenness and species richness were not uniform throughout the year. The successful decomposition of dung would depend on both the time of deposit and the habitat in which the dung is deposited. During the winter months activity was minimal. There was an increase in abundance, biomass, dominance and species richness during the summer rainy season from November 1996 to March 1997 and dung beetle activity was consistently higher in mid-summer in all the habitats, while there was a decrease in activity from August. Temperature seemed to be a key factor in the distribution of dung beetle assemblages, while rainfall was less important and R.H. had a negative effect on dung beetle activity. The dung beetles in this area seemed to be adapted to arid conditions and high temperatures. There were differences between the different habitats in seasonal abundance. Abundance across the whole seasonal spectrum was higher in the grassveld habitats and also higher in the natural habitats. Peaks in biomass were also higher in the natural grassveld habitat than in the disturbed grassveld habitat, indicating that throughout the year environmental conditions were more favorable in the natural habitat than in the disturbed habitat for the larger dung beetle species. Dung beetle species here are adapted to different environmental conditions resulting in different distribution patterns and enabling smaller less effective competitors to co-exist with larger superior competitors. The dung beetle community in the study area is dominance controlled with variation between dominance of species between different months of the year. The species here showed very high dominance, albeit often for only short periods. Since the habitat is unpredictable many different species can co-occur here, simply because certain species are better adapted to certain environmental conditions than others. Environmental changes throughout the year enable many different species to become dominant for short periods of the year. There was, however a difference in the seasonal dominance of species in different habitats. In the grassveld habitats, *S. flavicornis* was more frequently dominant and also more frequently dominant in the natural than disturbed habitat, while in the bushveld habitat *O. obtusicornis* was more frequently dominant. In terms of biomass *P. femoralis* dominated most frequently in the natural grassveld habitat. This species occurred less frequently in the disturbed grassveld habitat and in the bushveld habitats, enabling smaller species to dominate here in terms of biomass more frequently than in the natural grassveld habitat. Since *P. femoralis* is a large, highly effective competitor which removes large amounts of dung at a fast rate, it can be concluded that the most successful decomposition of dung will take place in the natural grassveld habitat in the summer months from October to February when this species is most abundant.