# Chapter 3

# EFFECT OF HABITAT TRANSFORMATION ON DUNG BEETLE ASSEMBLAGES

## 3.1. INTRODUCTION

Dung beetles play a vital role in any grazing ecosystem. Humans have greatly altered the plant composition of habitats through direct or indirect activities. The characteristics of the vegetational cover will influence a wide variety of ecological patterns and processes and the structure of the habitat in turn will influence the success of different groups of dung beetles differently. Mico *et al.* (1998) found that different local conditions give rise to different communities of dung beetles. Merrit & Anderson (1977) also found that the type of pasture ecosystem and the season in which the cow dung is dropped were most important in determining the diversity and abundance of insects colonising dung and the rate of pat degradation. Habitat selection of dung beetles takes place at two spatial scales, the single dropping and its immediate surroundings and the macrohabitat (Hanski & Cambefort, 1991a). Hanski & Koskela (1977) proposed that the macrohabitat dimension is stronger than the successional or seasonal dimensions. If there is a change along the habitat dimension in average temperature and moisture, there will be a change along the two other dimensions, but not necessarily vice versa. In the macrohabitat the distribution of dung beetles is influenced most strongly by soil type (Nealis, 1977; Davis, Doube & McLennan, 1988; Doube, 1990; Doube, 1991; Osberg *et al.*, 1993; Davis, 1996) and vegetation type (Howden & Nealis, 1975; Hanski & Koskela, 1977; Doube, 1983; Davis, 1994). Differing factors in the macrohabitat, like a change in vegetation, will influence the different factors in the microhabitat, the dung pat and also factors around the dung pat, such as breeding space in the soil. Factors like temperature, moisture content and consistency of the dung will be influenced by the macrohabitat. The microhabitat of dung beetles tends to be diverse and patchily but non-randomly distributed due to the social behaviour of the mammals (Lumaret & Iborra, 1996). The macrohabitat will also influence the behaviour and movement of mammals. For example, on a farm where the landscape is fragmented into different pastures there will be a concentration of large herbivores (in this case cattle) in a small area. This will not only result in a concentration of dung in an area, but also trampling of the dung and vegetative cover. According to Jameson (1989) cattle exert constant forces in a limited area, thus possibly degrading potential habitat for dung-burying Scarabaeinae. Grazing by cattle affects the height and density of vegetation and, hence, the relative humidity in the micro-environment. In a well-managed nature reserve, on the other hand, there is usually a relatively large area through which the large herbivores are able to move and consequently fewer concentrations of large mammals. This will result in a more random distribution of dung and less trampling of the dung and vegetative cover. All these factors will eventually influence the community structure of the dung beetles colonising the dung pat. There are many factors that influence the success of dung beetles in these habitats, but it is the type of cover that has to be considered when the ecological role of dung beetles in pasture ecosystems is investigated. Howden & Nealis (1975) considered the absence of a scarab fauna native to the new food and altered habitat as one of the many problems associated with the introduction of a livestock economy. The new food, though, would not necessarily influence the distributions of most dung beetle species, because most will use a wide variety of faecal matter (Gordon & Cartwright, 1974). The change in the type of vegetative cover as a result of grazing pressure might, however, influence the distribution of dung beetles. It is not necessarily a decrease in numbers of scarabs that poses a problem, but a change in community structure. Large dung beetle species, which remove the dung at a fast rate, play an important role in the fast decomposition of dung in an ecosystem. If the larger species decrease in numbers and the community of dung beetles changes in such a way that the smaller dung beetles, which remove dung slowly, become the dominant species, the rate of dung degradation will decrease and the ecosystem will be influenced negatively by an accumulation of dung. An understanding of the ecological consequences both at the species and community levels is necessary to understand the influence of habitat change brought about by farming and agricultural practices.

## 3.2. MATERIAL & METHODS

### Sampling procedure

Dung beetle sampling was done in four different localities within two different habitat types, a grassveld area and a bushveld area. In these two habitat types dung beetle assemblages in a natural habitat (SNR) and on farms (where habitats were disturbed by overgrazing) were compared. The farm Rietvlei represented a grassveld area and the farm Josina a bushveld area. Three sites, spaced 1 km apart, were chosen in each of the four localities. In each site three plots, spaced 50 m apart, were chosen. Each plot contained four pitfall traps, spaced 1 m apart. The beetles from these four traps were pooled and statistically treated as a single sample. To avoid pseudoreplication the sites on the farms and in the nature reserve were between 10 and 20 km apart. 1 l plastic pitfall traps were used for sampling. The traps were buried up to the rim and the bottom filled with salt water. Dung preference studies showed that dung beetles in all the habitats were most strongly attracted to cattle dung (Geyser, 1994). Cattle dung was therefore used as bait in all the localities to ensure that dung beetles were equally attracted to traps in all the localities and that dung type did not affect the differences in dung beetles caught between the different habitats. A container with 200 g of fresh cattle dung was used as bait. This was sufficient to attract both flying and walking dung beetles. Dung beetles attracted by the dung fell into the traps and were collected later. Fresh, uncolonized 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, covered tightly with lids to avoid desiccation and oxidation. After baiting the traps with fresh dung they were left for 24 hours after which the dung beetles in the traps were collected and preserved in 70% alcohol for later identification. Sampling was done every month for a period of 2 years (July 1996 to June 1998).

**Analysis of community structure**

Doube's (1990) classification was used to divide the dung beetles into functional groups according to the way in which the dung beetles use and disturb dung. Telecoprids roll and bury the dung away from the source, paracoprids tunnel beneath the dung to form brood and feeding chambers, endocoprids feed on dung within the pad, and kleptocoprids use dung buried by other dung beetles. F.G.s I and II include the large (I) and the small (II) telecoprids, F.G. III the fast-burying paracoprids, F.G. IV the large slow-burying paracoprids, F.G. V the small, slow-burying paracoprids, F.G.VI kleptocoprids and F.G.VII the endocoprids. The species richness, number of individuals and biomass of each functional group were determined for each habitat. The number and biomass of trapped individuals of each functional group were calculated as a percentage of the total dung beetle fauna collected in each habitat. Significant differences in abundance and biomass of functional groups between different habitats were determined with two way Analysis of Variance.

**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. Two major components of diversity are recognised, species richness 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 $D_{mg}$=(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 $H'=-\sum [p_i \ln p_i]$, 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. These indices were calculated for each month over the two-year period and the mean ± SE for the two years was determined from this. Significant differences in indices between habitats were determined with two way Analysis of Variance.

Rank/abundance plots determined the relationship between number of species and number of individuals. There are four species abundance models. When plotted on a rank/abundance graph the four models can be seen to represent a progression ranging from the geometric series where a few species are dominant with the remainder fairly uncommon, the log series and log normal distributions where species of intermediate abundance become more common and the broken stick model where species are equally abundant. These four models were applied to the dung beetle assemblages in the present study. According to Begon *et al.* (1995) rank-abundance diagrams, like indices of richness, diversity and equitability, should be viewed simply as abstractions of the highly complex structure of communities, which may be useful when making comparisons.

The degree of similarity in abundance and biomass in dung beetle assemblages between different habitat types was determined by using the Sorensen index modified by Bray & Curtis (1957). This index is calculated by $C_N=2jN/(aN+bN)$, where aN=the total number of individuals in site a, bN=the total number of individuals in site B and, jN=the sum of the lower of the two abundances recorded for species found in both sites. This index is designed to equal 1 in cases of complete similarity and 0 if the sites are dissimilar and have no species in common. The index was calculated for each month over the two-year period and the mean ± SE for the two years was determined from this.

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 (10 males 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. To determine significant linear relationships between biomass and mass classes and abundance and mass classes 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.

## 3.3. RESULTS & DISCUSSION

**Species richness, diversity and evenness in different habitats**

Species richness and Margalef indices measure the species richness component of diversity, the Berger-Parker index measures the dominance, while the Shannon Weaver index includes both richness and evenness. None of the diversity indices measuring the species richness component nor the dominance component showed significant differences among the four habitats, indicating that the species richness and the proportional importance of the most abundant species in the four different habitats were essentially similar. (Table 3.1). According to Magurran (1988) the proportional abundance of species is independent of species richness. Davis (1993), however, found that there is a fairly strong relationship between dominance and species richness. With increasing species richness and evenness there would be a decrease in dominance. In the present study there was no clear trend between species richness and dominance. It is important to note that diversity in terms of species is just one of many possible ways of describing communities and there are other important aspects when considering a community. Dufrêne & Legendre (1997) consider species diversity a questionable criterion when habitats with different productivity levels are compared, or when the number of rare species is large.

**Table 3.1: Species richness (S), Margalef diversity index ($D_{mg}$), Shannon diversity index (H), Shannon evenness index (E) and Berger-Parker dominance index (1/d) for dung beetle assemblages in four different habitats (S.G. –natural grassveld area in Sandveld Nature Reserve, Rietvlei – disturbed grassveld area, S.B. – natural bushveld area in Sandveld Nature Reserve and Josina – disturbed bushveld area)**

| Habitat | Mean S ± SE | Mean Dmg ± SE | Mean H ± SE | Mean E ± SE | Mean 1/d ± SE |
|---|---|---|---|---|---|
| **S.G.** | 13.09 ± 1.82 | 2.05 ± 0.23 | 1.55 ± 0.15 | 0.64 ± 0.06 | 2.68 ± 0.23 |
| **Rietvlei** | 12.39 ± 1.59 | 2.10 ± 0.22 | 1.48 ± 0.76 | 0.61 ± 0.06 | 2.69 ± 0.27 |
| **S.B** | 12.3 ± 2.06 | 1.95 ± 0.29 | 1.25 ± 0.19 | 0.51 ± 0.07 | 2.09 ± 0.28 |
| **Josina** | 11.96 ± 2.00 | 2.05 ± 0.29 | 1.31 ± 0.20 | 0.57 ± 0.07 | 2.13 ± 0.33 |
| **F** | 0.507 | 0.326 | 2.203 | 1.71 | 3.299 |
| **d.f.** | 3 | 3 | 3 | 3 | 3 |
| | $P>0.05$ | $P>0.05$ | $P>0.05$ | $P>0.05$ | $P>0.05$ |

**Rank-abundance in different habitats**

Changes in the structure of the assemblage and shifts in dominance are important factors to consider in a dung beetle assemblage. The dung beetle assemblages in all four habitats showed a log series pattern, which has a steep slope (Fig. 3.1). In communities where species show strong, sequential dominance, a steep slope will result, whereas those composed of species of similar competitiveness/resource use will be associated with a shallow slope (Tokeshi, 1993). There is a very high abundance of a few dominant species and a large number of 'rare' species, which are represented by few individuals. A log series pattern results if the intervals between the arrival of the species are random rather than regular (Magurran, 1988). This agrees with the situation where dung beetles colonise dung, which is a patchy microhabitat. The microhabitats colonised by dung beetle assemblages are of relatively small size, scattered spatial occurrence and short durational stability (Hanski, 1991). Because of the temporary nature of the resource which dung beetles colonise, the pattern of a few abundant species, some common species and many rare species seems to be a general pattern for them (Hanski & Koskela, 1977; Peck & Forsyth, 1982; Doube, 1983). Not only is the resource used by dung beetles temporary and patchy, but competition is also severe in African savannas on sandy soils in the rainy season (Hanski & Cambefort, 1991a) and this can also greatly influence the structure of the communities. Other field and laboratory studies also show that competition is important in this patchy and ephemeral microhabitat (Holter, 1979a; Ridsdill-Smith *et al.*, 1982, Peck & Forsyth, 1982). Schoener (1986), on the other hand, found that among invertebrates, physical environmental factors seem to shape the species assemblages more than biological relationships such as competition, predation, and parasitism.

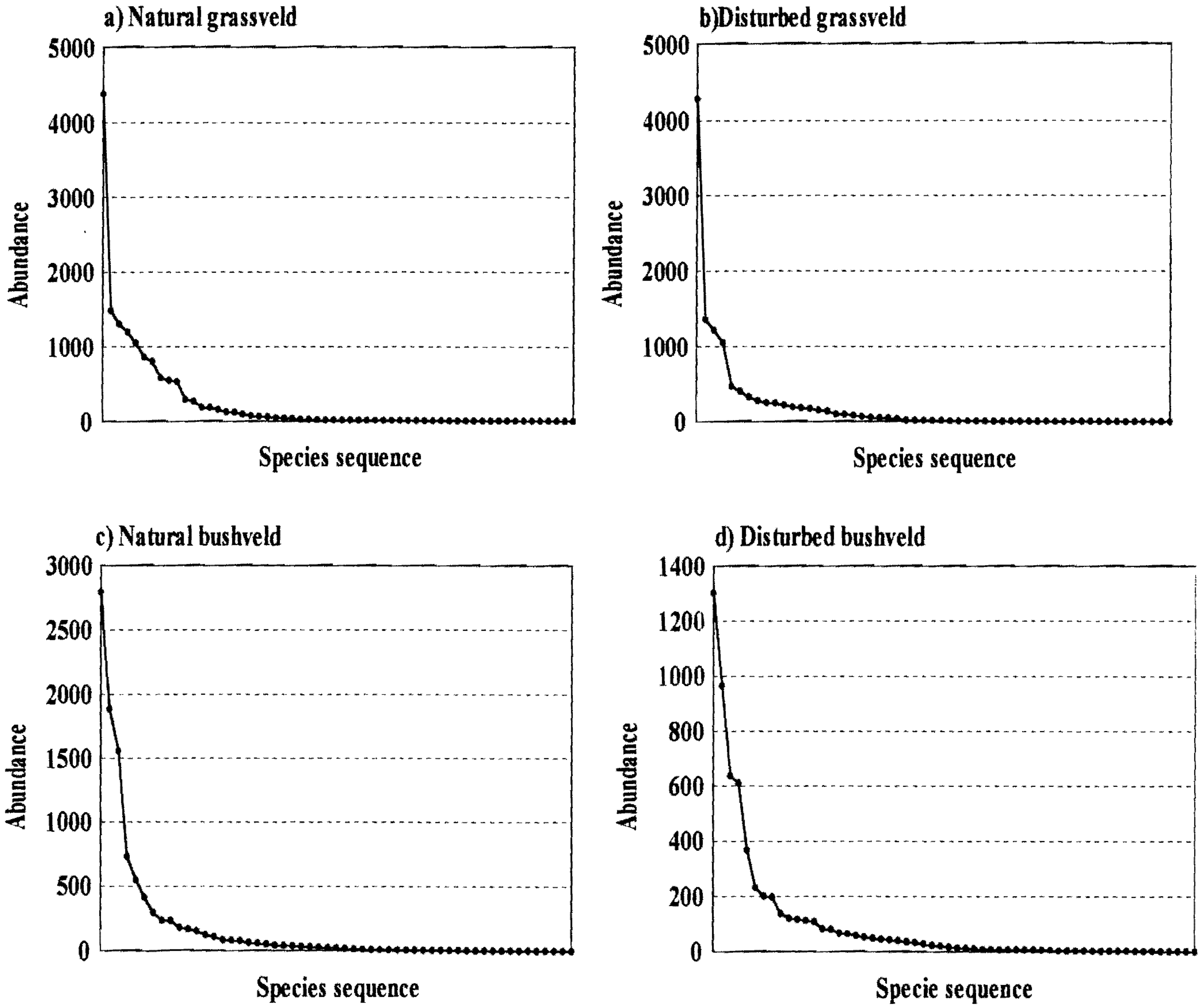


**Fig. 3.1: Rank species abundance plots for dung beetle assemblages in four different habitats: a) Sandveld Grassveld-natural grassveld habitat, b) Rietvlei-disturbed grassveld habitat, c) Sandveld Bushveld-natural bushveld habitat, d) Josina-disturbed bushveld habitat.**

Although the pattern of species abundance was similar in all the habitats, different species dominated in each habitat. *Scarabaeus flavicornis* was the dominant species in the natural grassveld, *Caccobius seminulum* in the disturbed grassveld habitat, *Onthophagus sugillatus* in the natural bushveld habitat and *Onthophagus variegatus* in the disturbed bushveld habitat (Table 3.2). The abundance, size and ecological role of the dominant species in different habitats are important factors to consider. Although the log-series patterns were similar in the different habitats, the dominant species in each habitat played a different ecological role. Davis (1994) found that the dominant species reflected the faunal differences between disturbed, west coast shrubland and shrubland on the Cape of Good Hope Peninsula and that vegetation type was the principal determinant of spatial distribution patterns.

A small number of species made up the majority of dung beetles sampled in the study area at Sandveld, with the 18 most abundant species in the area constituting between 83 and 95% of the total individuals collected (Table 3.2.). This is in agreement with Doube (1983) who found that the 15 and 25 most abundant species respectively constituted 93% and 97% of all the individuals trapped in the Hluhluwe Game Reserve and Doube (1987) found that the 20 most abundant species collected at Hluhluwe Game Reserve over a period of five years (1980-1986) made up between 76% and 94% of all individuals trapped and the rank of most species varied widely between the years. In the present study there is a greater variation in species rank between the two years in the pasture habitats than in the natural habitats (Table 3.2). According to Doube (1987) a wide variation in species rank over a time indicates a non-equilibrium system. It must, however, be remembered that no natural system is in perfect equilibrium and that changes take place all the time, in all sorts of directions and at all sorts of scales, catastrophically, gradually, and unpredictably (Stott, 1998). The important thing therefore to consider here is not whether the assemblage is stable, but whether the change in species rank is moving towards an assemblage of dung beetles which is more effective or less effective in fulfilling their ecological role in the environment.

In the natural grassveld habitat the species which ranked first in abundance during both years was *S. flavicornis* (Table 3.2), which is a highly effective competitor for dung and removes dung quickly from the environment (Table 3.2). *P. femoralis*, which is also highly effective at removing dung from the environment because of its large size and the speed at which it can remove dung from the pat, also ranked high in abundance during both years in the natural grassveld area (Table 3.2). The greatest variation in species rank in the natural grassveld habitat also seemed to occur in the smaller species, which are less effective competitors. *C. seminulum* ranked second during the first year, but only eighth during the second year, while *A. (Pleuraphodius) teter* ranked 22$^{nd}$ during the first year and third during the second (Table 3.2). *C. seminulum* is a kleptocoprid which uses dung buried by other dung beetles, while *A. (Pleuraphodius) teter* is an endocoprid which feeds and breeds within the pat. Both these species are small and neither contributes much to dung degradation. *C. seminulum* was dominant in the disturbed grassveld habitat, ranking first during the first year and second during the second year. *S. flavicornis* was also abundant in the disturbed grassveld habitat. Although this species ranked fourth during the first year, it ranked first during the second year. *C. seminulum*, however, constituted a much larger percentage of the total assemblage during the first year than *S. flavicornis* during the second year (Table 3.2.). There was no clear pattern or consistency in species rank in these systems. This might be an indication of a system which fluctuates widely between dominant species. Environmental factors fluctuate widely favouring the success of different dung beetle species at different times. It is important to determine the ecological role of dung beetles being favoured by these fluctuations in a certain habitat. The dung beetle assemblage in the natural grassveld habitat was consistently dominated by *S. flavicornis*, while the dominance in the disturbed grassveld habitat varied between *C. seminulum* and *S. flavicornis*, indicating a less effective assemblage in the disturbed habitat. The bushveld habitats were dominated by totally different species. In both the natural and disturbed bushveld habitats *O. obtusicornis* ranked first during the first year, while *O. sugillatus* ranked first in the natural habitat and *O. variegatus* first in the disturbed habitat during the second year. All these species are slow-burying paracoprids, which are less effective competitors for dung than the telecoprids which dominate the dung beetle assemblage in the grassveld habitats. The assemblages in the bushveld habitats can therefore be considered less effective than the assemblages in the grassveld habitats.

**Table 3.2: Rank in order of abundance of the 18 most abundant species collected in the four different habitats (Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat) over a period of two years (July 1996 - June 1998).**

| | Sandveld Grassveld | | Rietvlei | | Sandveld Bushveld | | Josina | |
|---|---|---|---|---|---|---|---|---|
| | 1996/7 | 1997/8 | 1996/97 | 1996/7 | 1996/7 | 1997/8 | 1996/7 | 1997/8 |
| *Pachylomerus femoralis* | 4 | 2 | 6 | 4 | 10 | 11 | 15 | 10 |
| *Scarabaeus flavicornis* | 1 | 1 | 4 | 1 | 4 | 15 | 3 | 7 |
| *Scarabaeus inoportunus* | 9 | 6 | 13 | 5 | 33 | - | 44 | - |
| *Scarabaeus anderseni* | 10 | 14 | 12 | 7 | 16 | 16 | - | 16 |
| *Neosisyphus ruber* | 24 | 36 | 5 | 21 | 46 | - | 34 | 31 |
| *Metacatharsius sp. 1* | 5 | 7 | 8 | 16 | 8 | 7 | 11 | 11 |
| *Onthophagus obtusicornis* | 12 | 9 | 19 | 8 | 1 | 3 | 1 | 4 |
| *Onthophagus quadraliceps* | 3 | 10 | 2 | 12 | 11 | 10 | 22 | 5 |
| *Onthophagus aeruginosus* | - | 20 | - | - | 13 | 8 | 8 | 8 |
| *Onthophagus vinctus* | 32 | 30 | 33 | - | 15 | 12 | 16 | 9 |
| *Onthophagus pilosus* | 19 | 21 | - | - | 7 | 9 | 21 | 19 |
| *Onthophagus sugillatus* | 14 | 16 | 30 | - | 2 | 1 | 5 | 2 |
| *Onthophagus variegatus* | 8 | 11 | 15 | 9 | 3 | 2 | 2 | 1 |
| *Onthophagus sp. 1* | 6 | 4 | 3 | 3 | 6 | 5 | 7 | 6 |
| *Onthophagus sp. 4* | 7 | 5 | 7 | 6 | 12 | 18 | 10 | 18 |
| *Caccobius seminulum* | 2 | 8 | 1 | 2 | 5 | 4 | 4 | 3 |
| *Drepanocanthus (Pseudoxyomus) eximius.* | - | - | - | - | 21 | - | 6 | - |
| *Aphodius (Pleuraphodius) teter (sensu lato)* | 22 | 3 | 11 | 10 | 27 | 6 | 30 | 14 |
| **% of total numbers** | 94.05 | 90.64 | 91.62 | 84.34 | 90.18 | 95.42 | 83.9 | 90.89 |
| **Total numbers** | 9287 | 5418 | 8866 | 2791 | 5857 | 4408 | 2921 | 3064 |
| **Total no. of species** | 47 | 43 | 45 | 36 | 48 | 39 | 49 | 42 |
| **% of most abundant species** | 33.86 | 22.78 | 45.17 | 15.51 | 23.95 | 36.91 | 20.71 | 06 |

## Analysis of assemblage structure

The functional group classification provides a convenient basis for summarising the structure of diverse assemblages of dung beetles in a way that reflects its ecological role in a habitat. The use of numerical abundance and biomass increases the sensitivity of this analysis for pattern recognition (Doube, 1990). Doube (1991) found that while the relative abundance of species change across vegetational boundaries the relative abundance of the functional groups frequently remains more constant. In the present study the functional group structure of the dung beetle assemblages in terms of biomass did not differ significantly between the natural and disturbed habitats ($F=0.048$; $P>0.05$), but it was significantly different between the grassveld and bushveld habitats ($F=14.85$;

P<0.05). In the natural grassveld habitat F.G. I made up 35% and F.G. II 57% of the total biomass in the assemblage, while in the disturbed grassveld habitat F.G. I made up 27% and F.G. II 61% of the total biomass (Fig. 3.2). In terms of biomass these two functional groups were therefore dominant in both the natural and disturbed grassveld habitats. The structures of the dung beetle assemblages in terms of biomass in the natural and disturbed bushveld habitats were also similar, but these habitats differed from the grassveld habitats in that F.G. I and F.G. II were less dominant than in the grassveld habitats (F=8.622, P<0.05; F=8.718, P<0.05), while F.G. IV was more dominant in these habitats than the grassveld habitats (F=2.05, P<0.05) (Fig. 3.2). F.G. I made up 23%, F.G. II 28% and F.G. IV 25 % of the total biomass in the natural bushveld habitat, while F.G. I made up 20%, F.G. II 32% and F.G. IV 17% of the total biomass in the disturbed bushveld habitat (Fig. 3.2).

In terms of individuals the structure of the dung beetle assemblages differed significantly between the natural and disturbed grassveld habitats (F=1.33, P<0.05) and also between the grassveld and bushveld habitats (F=2.05, P<0.05). In the natural grassveld habitat F.G. II was dominant (F=4.64, P<0.05) making up 35% of the total number of individuals in the assemblage, while F.G. VI (F=18.02, P<0.05) was dominant in the disturbed grassveld habitat, making up 36% of the total number of individuals in the assemblage (Fig. 3.3). In the bushveld habitats F.G. V (F=8.16, P<0.05) was dominant, making up between 40 and 48% of the total number of individuals in the assemblage (Fig. 3.3).

There is a clear difference between the different functional groups in their ability to compete for dung. The best competitors are the large telocoprids (F.G. I) and the fast-burying paracoprids (F.G. III), whilst the small telocoprids (F.G. II) are also good competitors because they remove the dung soon after arrival at the pat (Doube, 1991). Compared to these groups the paracoprids (F.G. IV and V) are subordinate and the endocoprids (F.G. VI) are especially likely to have their breeding activities disrupted by members of the other functional groups, while kleptocoprids (F.G. VI) use the dung buried by other groups (Doube, 1991). The natural grassveld habitat in the present study is dominated by larger dung beetle species, which buries dung at a fast rate, while the bushveld habitats are dominated by smaller species, which buries dung at a slower rate. The disturbed grassveld habitat is dominated by kleptocoprids that contribute nothing to the removal of dung.

In terms of species richness, the larger dung beetles of F.G. I, F.G. II and F.G. III made up a smaller percentage of the assemblage than the smaller dung beetles of F.G. IV in all four habitats (Fig 3.4). It seems that in these assemblages the larger species have lower species richness and the smaller species higher species richness. This might be explained by the fact that larger species will use more of the resource than smaller species, resulting in fewer large species utilising the same resource. This is in agreement with Hanski & Cambefort (1991b) who predicted lowest species richness in telocoprids and large paracoprids, and highest species richness in endocoprids and small paracoprids. In telocoprids a few species strongly dominate local communities, while the distribution of species abundance is more even in the paracoprids (Hanski & Cambefort, 1991b).

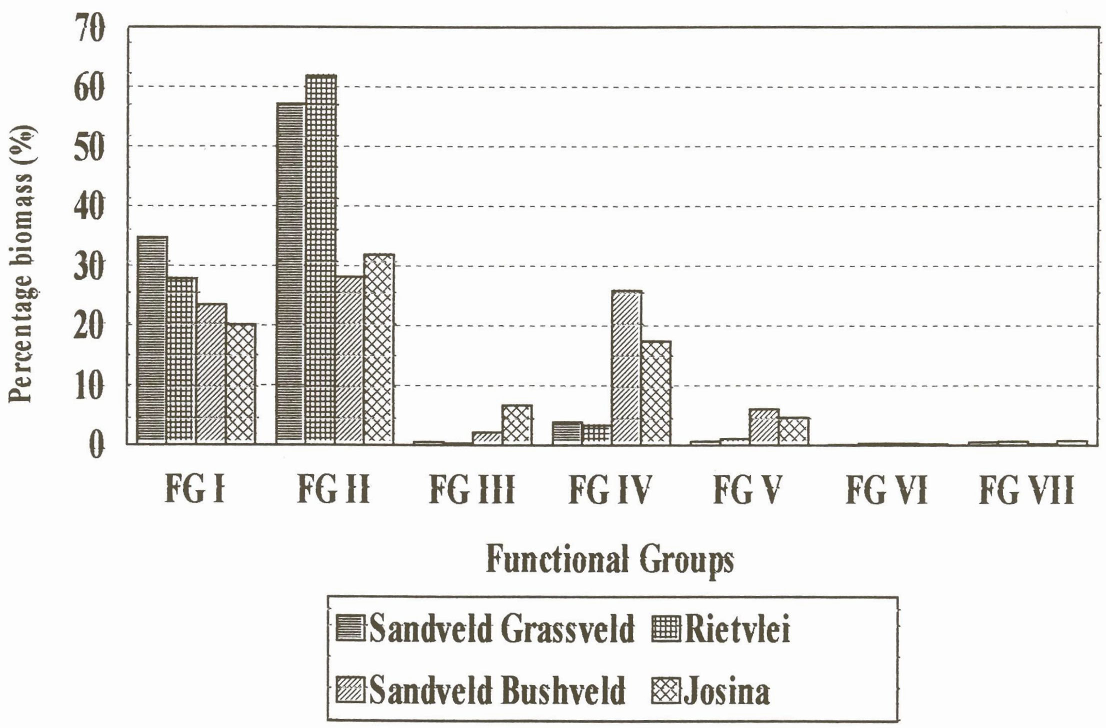


**Fig. 3.2: Functional group classification, using the biomass in each functional group in each of the four habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.**

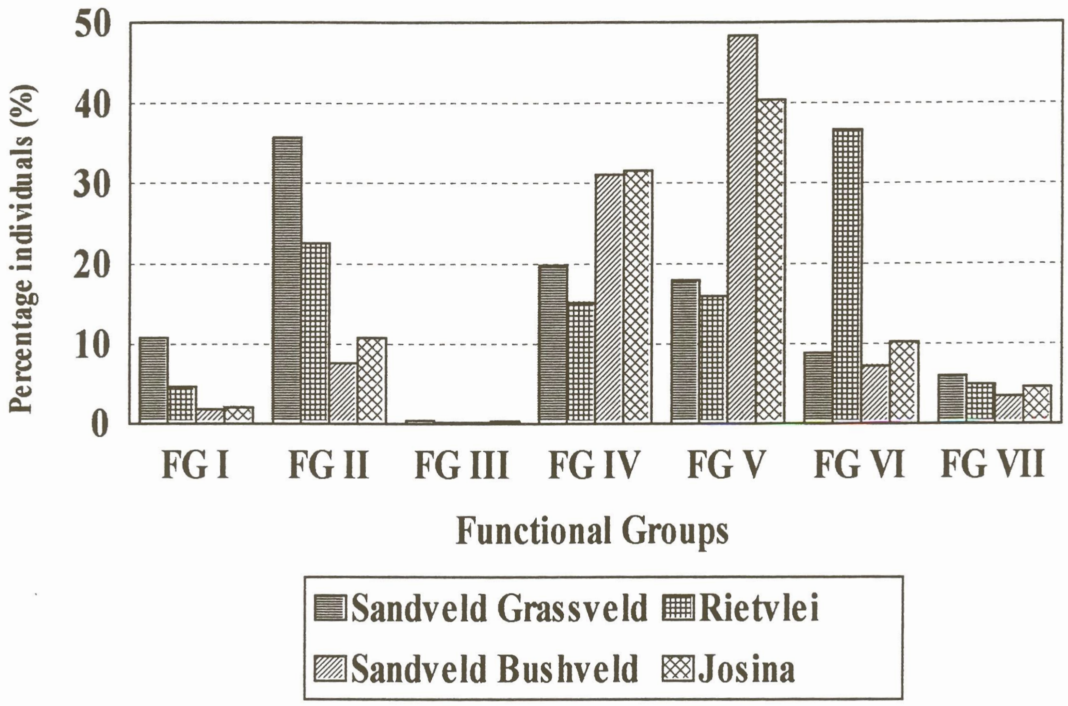


**Fig. 3.3: Functional group classification, using the number of individuals in each functional group in each of the four habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.**

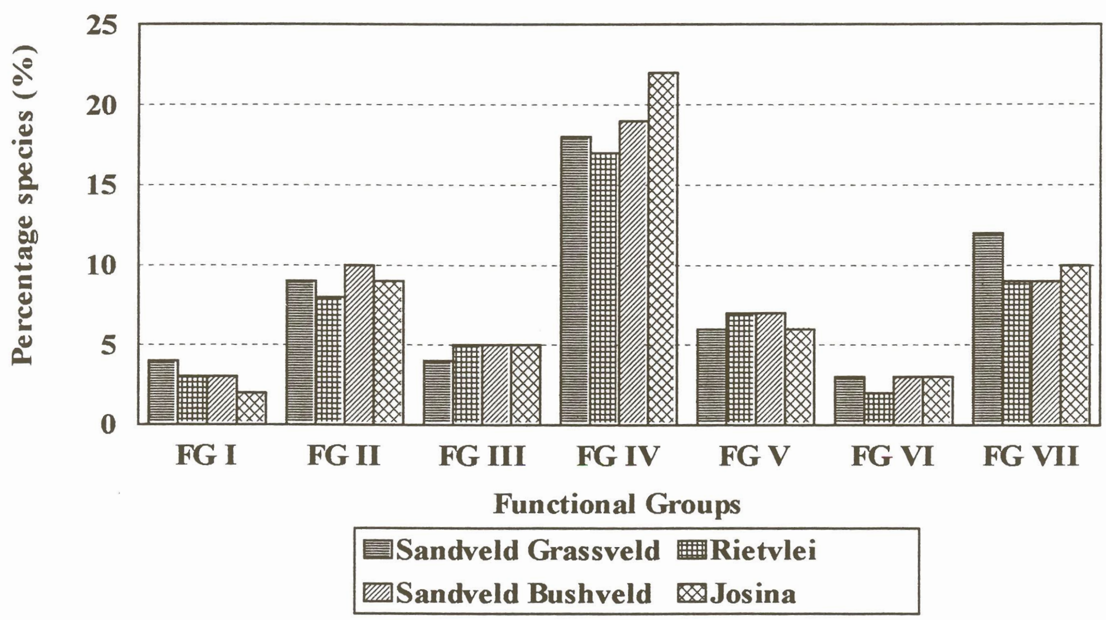


**Fig. 3.4: Functional group classification, using the number of species in each functional group in each of the four habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.**

**Distribution of dung beetle species in four different habitats**

Seventy-five species belonging to 26 genera were captured in the study area during the study period. In a savanna ecosystem dung beetles show greatly diversified activity in different habitat types resulting in and irregular distribution of dung beetles in space. The habitat did not only influence the functional group structure, but functional groups also showed preferences for certain habitats. There was uneven distribution of functional groups in the different habitats. Dung beetles belonging to F.G. I and II were more abundant in the open grassveld habitat (F.G. I - $F=10.85$, $P<0.05$; F.G. II - $F=7.15$, $P<0.05$) and dung beetles in these groups were also more abundant in the natural habitat than in the disturbed habitat (F.G. I - $F=10.93$, $P<0.05$; F.G. II - $F=3.29$, $P<0.05$) (Fig. 3.5). Ones in F.G. IV did not show distinct preferences for either open grassveld or bushveld habitat ($F=0.038$, $P>0.05$), but were, however, more abundant in both the natural habitats ($F=6.46$, $P<0.05$; $F=1.7$, $P<0.05$) (Fig. 3.5). Species belonging to F.G. V were more abundant in the bushveld habitats than in the grassveld habitats ($F=9.05$, $P<0.05$) and also more abundant in the natural habitat ($F=7.00$, $P<0.05$) (Fig. 3.5). F.G. VI species were most abundant in the disturbed grassveld habitat ($F=3.36$, $P<0.05$) (Fig. 3.5).

Adult searching success might explain the abundance of species belonging to F.G. I and II in the natural grassveld habitat. Generation success is determined by the success of the adult in finding the resource and the energy used (Nealis, 1977). Food-search by dung beetles is usually carried out on the wing (Halffter & Matthews, 1966) and tree cover in the bushveld area can affect the searching and movement of larger species significantly. Vegetation cover can also affect the rolling of the dung ball. According to Halffter & Matthews (1966) the evolution of ball rolling behaviour coincides with the expansion of dung beetles from forests into grassland. The lower numbers in F.G. I and II in the disturbed grassveld habitat might be explained by an abundance of woody shrubs as a result of overgrazing (Chapter 2, Table 2.1). These shrubs may impede the searching and rolling success of the adults.

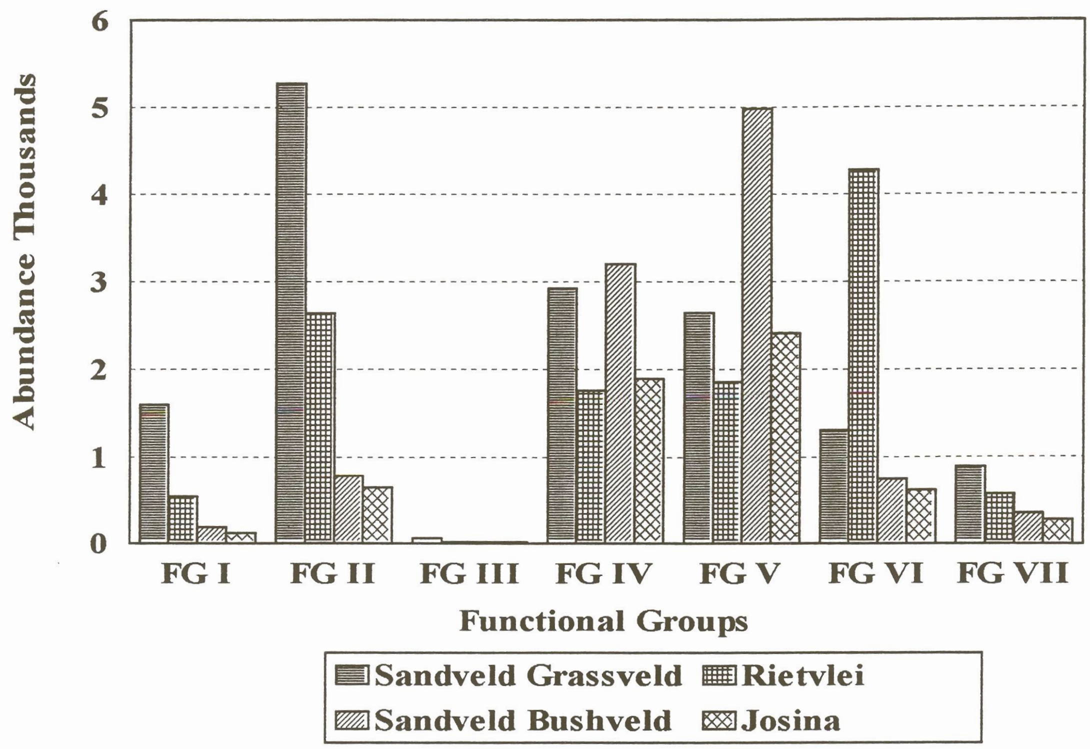


**Fig. 3.5: Distribution of different functional groups in four different habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.**

Where 70-100% of individuals of a species were trapped in either the open grassveld or bushveld habitat this species was considered to be a habitat specialist (Table 3.3), and as such more successful in a specific habitat than the other habitats. Species with less than 20 individuals were not considered in the present study. Although species showed a degree of habitat preference, there were no sharp boundaries between communities occurring in the different habitats and the communities graded into each other. According to Begon *et al.* (1995) community boundaries do not exist.

In Spain Galante, *et al.* (1991) found that in most cases, the same species were found in wooded and open habitats but the number of specimens captured differed so that there is a clear separation between the communities in wooded areas and in open pastureland. In the present study the majority of dung beetles were collected in an open grassveld habitat and in general they were more abundant in the natural than disturbed habitats. In France

Lumaret & Kirk (1987) also found that the coprophagous fauna was concentrated in areas of open pastureland and in South Africa Giller & Doube (1994) found that 73% of all individuals trapped were concentrated in a grassveld area on sandy soil. Comparison of the different species in the functional groups showed that there were preferences for either grassveld or bushveld habitats and also for natural or disturbed habitats. In F.G. I *Pachylomerus femoralis, P. opaca* and *Drepanopodus costatus* were open grassveld specialists (Table 3.3). Of these species *P. femoralis* (65.87%) and *P. opaca* (80.17%) occurred more abundantly in the natural habitat, while *D. costatus* (76%) occurred more abundantly in the disturbed habitat (Table 3.3). In F.G. II *Scarabaeus flavicornis, S. inoportunus, S. anderseni, Scarabaeus sp. 1, Neosisyphus ruber* and *Allogymnopleurus thalassinus* were open grassveld specialists, while *Gymnopleurus aenescens* was a bushveld specialist occurring more abundantly in a disturbed habitat (Table 3.3). *S. flavicornis* (65.86%) and *S. inoportunus* (60.9%) were more abundant in the natural grassveld habitat than in the pasture habitat, while *N. ruber* (93%) and *A. thalassinus* (82%) were much more abundant in the disturbed habitat than in the natural habitat. In F.G. III *Copris inhalatus* (88.46%) and *Catharsius melancholicus* (66.04%) were grassveld specialists occurring more abundantly in the natural habitat than in the disturbed habitat (Table 3.3). The largest number of species occurring in the study area belonged to F.G. IV because of the abundance of species in the genus *Onthophagus*. Members of this genus seemed to be more evenly distributed between the different habitats. *Metacatharsius laticollis* and *Metacatharsius. sp. 1* were open grassveld specialists occurring more abundantly in the natural grassveld habitat (Table 3.3). *Onthophagus quadraliceps* was a grassveld specialist equally abundant in the natural and disturbed habitats (Table 3.3). *Metacathrsius sp. 3* and *O. pilosus* were bushveld specialists occurring more abundantly in the natural habitat, while *O. gazella* (F) was a bushveld specialist occurring more abundantly in the disturbed habitat (Table 3.3). *O. fimetarius, O. aeruginosus* and *O. obtusicornis* were bushveld specialists equally abundant in both the natural and disturbed habitats (Table 3.3). Species belonging to F.G. V were predominantly bushveld specialists. *O. vinctus* and *O. variegatus* were bushveld specialists occurring evenly in both natural and disturbed habitats, while *Onthophagus sp. 18* (66%) occurred predominantly in the disturbed bushveld habitat and *O. sugillatus*

(77%) occurred predominantly in the natural bushveld habitat (Table 3.3). *Onthophagus sp. 1* occurred evenly in the natural and disturbed grassveld habitat, while *Onthophagus sp. 4* occurred predominantly in the natural grassveld habitat. *Caccobius seminulum*, belonging to F.G. VI occurred in all the habitats, but by far more abundantly in the disturbed grassveld habitat (62%) (Table 3.3). In F.G. VII *Aphodius (Bodilus) laterosetosus, A. (Pleuraphodius) teter (sensu lato)* and *A. (Plagiogonus) separatus* were most abundant in the natural grassveld habitat, while *A. (Labarus) pseudolividus* (85%) was most abundant in the disturbed grassveld habitat (Table 3.3). *Drepanocanthus (Pseudoxyomus) eximius* was a bushveld specialist occurring more abundantly in the disturbed habitat (Table 3.3).

Dung beetles in this area not only showed preferences for grassveld or bushveld habitats, but they also showed preferences for natural or disturbed habitats. The majority of dung beetle species occurred most abundantly in the natural grassveld habitat, but a few species occurred more abundantly in the bushveld habitat and there were also a small number of species that occurred predominantly in the disturbed areas. Of the 75 species 21 occurred predominantly in the grassveld area of which eleven were more abundant in the natural habitat, six more abundant in the disturbed habitat and four equally abundant in the natural and disturbed habitats (Table 3.3). Fourteen species occurred predominantly in the bushveld habitats of which three were more abundant in the natural habitat, six more abundant in the disturbed habitat and five equally abundant in the natural and disturbed habitats. The rest of the species either occurred in very small numbers and are not considered here or they were equally abundant in all the habitats.

**Table 3.3: Numbers of individuals and percentages of total dung beetle captures in four different habitats: S.G.-natural grassveld habitat, Rietvlei-pasture grassveld habitat, S.B.-natural bushveld habitat, Josina-pasture bushveld habitat.**

| Species | S.G. | | Rietvlei | | S.B. | | Josina | | Mean Dry mass (g) |
|---|---|---|---|---|---|---|---|---|---|
| | No. ind. | % | No. ind. | % | No. ind. | % | No. ind. | % | (n=20) |
| **Functional Group I** | | | | | | | | | |
| *Pachylomerus femoralis* | 1482 | 65.9 | 472 | 21 | 180 | 8 | 116 | 5.2 | 1.49 |
| *Pachylomerus opaca* | 93 | 80.2 | 20 | 17 | 3 | 2.6 | - | 0 | 0.635 |
| *Scarabaeus goryi* | 4 | 44.4 | - | 0 | 1 | 11 | 4 | 44 | 1.351 |
| *Drepanopodus costatus* | 16 | 24.2 | 50 | 76 | - | 0 | - | 0 | 0.132 |
| **Functional Group II** | | | | | | | | | |
| *Scarabaeus flavicornis* | 4379 | 65.9 | 1355 | 20 | 548 | 8.2 | 367 | 5.5 | 0.158 |
| *Scarabaeus inoportunus* | 528 | 60.9 | 329 | 38 | 7 | 0.8 | 3 | 0.3 | 0.158 |
| *Scarabaeus ambiguus* | 6 | 1.64 | 174 | 48 | 78 | 21 | 108 | 30 | 0.207 |
| *Scarabaeus bohemani* | 11 | 28.9 | 14 | 37 | - | 0 | 13 | 34 | 0.066 |
| *Scarabaeus anderseni* | 270 | 40.6 | 250 | 38 | 81 | 12 | 64 | 9.6 | 0.0289 |
| *Scarabaeus sp. 1* | 64 | 36.8 | 97 | 56 | 6 | 3.4 | 7 | 4 | 0.066 |
| *Neosisyphus ruber* | 13 | 4.32 | 279 | 93 | 1 | 0.3 | 8 | 2.7 | 0.019 |
| *Sisyphus macroruber* | - | 0 | - | 0 | 1 | 10 | - | 0 | 0.0188 |
| *Allogymnopleurus thalassinus* | 6 | 3.53 | 139 | 82 | 14 | 8.2 | 11 | 6.5 | 0.061 |
| *Gymnopleurus aenescens* | 3 | 2.78 | - | 0 | 39 | 36 | 66 | 61 | 0.023 |
| *Gymnopleurus sp. 4* | - | 0 | - | 0 | 5 | 10 | - | 0 | 0.025 |
| **Functional Group III** | | | | | | | | | |
| *Heliocopris atropos* | - | 0 | - | 0 | 1 | 10 | - | 0 | 0.61 |
| *Copris cassius* | 2 | 22.2 | 4 | 44 | 2 | 22 | 1 | 11 | 0.069 |
| *Copris inhalatus* | 23 | 88.5 | 2 | 7.7 | | 0 | 1 | 3.8 | 0.018 |
| *Catharsius melancholicus* | 35 | 66 | 3 | 5.7 | 8 | 15 | 7 | 13 | 0.59 |
| *Catharsius calaharicus* | - | 0 | 1 | 11 | 2 | 22 | 6 | 67 | 0.588 |
| *Catharsius tricornutus* | 3 | 21.4 | 3 | 21 | 5 | 36 | 3 | 21 | 0.686 |
| **Functional Group IV** | | | | | | | | | |
| *Metacatharsius laticollis* | 59 | 46.8 | 16 | 13 | 34 | 27 | 17 | 13 | 0.08 |
| *Metacatharsius latifrons* | - | 0 | 9 | 82 | 1 | 9.1 | 1 | 9.1 | 0.07 |
| *Metacatharsius exiguus* | 13 | 39.4 | 8 | 24 | 6 | 18 | 6 | 18 | 0.07 |
| *Metacatharsius sp. 1* | 800 | 57 | 196 | 14 | 296 | 21 | 112 | 8 | 0.028 |
| *Metacatharsius sp. 2* | 43 | 27 | 15 | 9.4 | 65 | 41 | 36 | 23 | 0.014 |
| *Metacatharsius sp. 3* | 11 | 11.7 | 2 | 2.1 | 60 | 64 | 21 | 22 | 0.004 |
| *Onitis alexis* | - | 0 | - | 0 | - | 0 | 2 | 10 | 0.46 |
| *Phalops wittei* | 6 | 17.1 | 19 | 54 | 3 | 8.6 | 7 | 20 | 0.035 |
| *Phalops flavocinctus* | - | 0 | - | 0 | 3 | 9.7 | 28 | 90 | 0.034 |
| *Euoniticellus intermedius* | 3 | 4.11 | 37 | 51 | 19 | 26 | 14 | 19 | 0.029 |
| *Euoniticellus africanus* | - | 0 | 8 | 10 | - | 0 | - | 0 | 0.04 |
| *Chironitis sp.* | - | 0 | 3 | 50 | - | 0 | 3 | 50 | 0.072 |
| *Liatongus millitaris* | - | 0 | - | 0 | - | 0 | 3 | 10 | 0.02 |
| *Hyalonthophagus alcyon* | - | 0 | 6 | 10 | - | 0 | - | 0 | 0.021 |
| *Onthophagus flavimargo* | 184 | 42.7 | 100 | 23 | 124 | 29 | 23 | 5.3 | 0.009 |
| *Onthophagus fimetarius* | 4 | 5.71 | - | 0 | 32 | 46 | 34 | 49 | 0.01 |
| *Onthophagus leucopygus* | 122 | 46.7 | 58 | 22 | 41 | 16 | 40 | 15 | 0.009 |
| *Onthophagus pilosus* | 42 | 13.2 | - | 0 | 233 | 73 | 43 | 14 | 0.011 |
| *Onthophagus gazella* | 3 | 3.53 | - | 0 | 24 | 28 | 58 | 68 | 0.027 |
| *Onthophagus xanthopterus* | 119 | 39.3 | 51 | 17 | 53 | 17 | 80 | 26 | 0.01 |
| *Onthophagus quadraliceps* | 1192 | 46 | 1048 | 40 | 153 | 5.9 | 196 | 7.6 | 0.014 |

**Table 3.3: continued**

| Species | S&G No. ind. | S&G % | Rietvlei No. ind. | Rietvlei % | S&B No. ind. | S&B % | Josina No. ind. | Josina % | Mean Dry mass (g) (n=20) |
|---|---|---|---|---|---|---|---|---|---|
| **Functional Group IV** | | | | | | | | | |
| *Onthophagus carbonarius* | 2 | 100 | - | 0 | - | 0 | - | 0 | 0.022 |
| **Functional Group V** | | | | | | | | | |
| *Onthophagus vinctus* | 9 | 3.73 | 4 | 1.7 | 108 | 45 | 120 | 50 | 0.006 |
| *Onthophagus sp. 18* | - | 0 | - | 0 | 23 | 34 | 45 | 66 | 0.005 |
| *Onthophagus sugillatus* | 186 | 5.13 | 5 | 0.1 | 2795 | 77 | 637 | 18 | 0.003 |
| *Onthophagus variegatus* | 548 | 15.1 | 220 | 6.1 | 1557 | 43 | 1302 | 36 | 0.003 |
| *Onthophagus sp. 1* | 1046 | 36 | 1211 | 42 | 414 | 14 | 231 | 8 | 0.005 |
| *Onthophagus sp. 2* | - | 0 | - | 0 | 3 | 10 | - | 0 | 0.0018 |
| *Onthophagus sp. 4* | 858 | 60 | 406 | 28 | 84 | 5.9 | 82 | 5.7 | 0.002 |
| *Epirinus gratus* | 3 | 42.9 | 4 | 57 | - | 0 | - | 0 | 0.009 |
| *Drepanocerus putrizii* | - | 0 | 4 | 10 | - | 0 | - | 0 | 0.004 |
| **Functional Group VI** | | | | | | | | | |
| *Caccobius seminulum* | 1302 | 18.8 | 4278 | 62 | 731 | 11 | 611 | 8.8 | 0.001 |
| *Caccobius ferruginus* | 1 | 20 | 1 | 20 | 2 | 40 | 1 | 20 | 0.004 |
| *Pedaria sp. 4* | 5 | 33.3 | - | 0 | 9 | 60 | 1 | 6.7 | 0.006 |
| **Functional Group VII** | | | | | | | | | |
| *Oniticellus planatus* | 4 | 44.4 | 5 | 56 | - | 0 | - | 0 | 0.029 |
| *Rhysemus africanus* | 2 | 25 | 6 | 75 | - | 0 | - | 0 | 0.0007 |
| *Drepanocanthus eximius* | - | 0 | - | 0 | 30 | 18 | 138 | 82 | 0.002 |
| *Drapanocanthus rubescens* | 10 | 5.29 | 84 | 44 | 42 | 22 | 53 | 28 | 0.001 |
| *Aphodius periculosus* | - | 0 | 3 | 75 | 1 | 25 | - | 0 | 0.002 |
| *Aphodius calcaratus* | 12 | 52.2 | - | 0 | 9 | 39 | 2 | 8.7 | 0.002 |
| *Aphodius vestitus* | 10 | 40 | 1 | 4 | 10 | 40 | 4 | 16 | 0.002 |
| *Aphodius dubiosus* | 14 | 77.8 | - | 0 | - | 0 | 4 | 22 | 0.003 |
| *Aphodius nigrita* | 1 | 20 | - | 0 | - | 0 | 4 | 80 | 0.002 |
| *Aphodius laterosetosus* | 158 | 64.2 | 68 | 28 | 13 | 5.3 | 7 | 2.8 | 0.002 |
| *Aphodius dorsalis* | 6 | 24 | 5 | 20 | 7 | 28 | 7 | 28 | 0.0007 |
| *Aphodius pseudolividus* | 13 | 7.39 | 150 | 85 | 5 | 2.8 | 8 | 4.5 | 0.002 |
| *Aphodius teter* | 582 | 52.3 | 247 | 22 | 235 | 21 | 48 | 4.3 | 0.0006 |
| *Aphodius separatus* | 72 | 100 | - | 0 | - | 0 | - | 0 | 0.001 |

Doube (1983) considers habitat preferences to be influenced by different light intensities in bushveld and grassveld habitats. In Hluhluwe Game Reserve (South Africa) he found that 26 species were significantly more abundant in bushveld than in grassveld, eight species were significantly more abundant in grassveld than in bushveld, and 16 species were equally abundant in both habitats. According to Nealis (1977) habitat associations can be considered diagnostic characteristics of species. The communities in the different habitats will not only differ in their specific components, but also in their rates of dung disposal. Size plays a very important role where it comes to the efficient removal of dung. According to Halffter & Matthews (1966) there is a correlation between the length of an adult and the size of the food ball. *P. femoralis* and *S. flavicornis*, with a dry mass of 1.49g and 0.158g respectively were the most dominant species occurring predominantly in the grassveld habitat. They were more abundant in the natural habitat (Table 3.3, 1482 and 4379 individuals collected respectively) than the pasture habitat (Table 3.3, 472 and 1355 individuals collected respectively). *P. femoralis* and *S. flavicornis* are highly effective competitors for dung. They arrive early at the dung pats (within 5-10 minutes after deposition) and remove the dung rapidly. According to Doube (1990) most telocoprids makes dung balls 5-20 times their own live mass. The dung beetles belonging to F.G. II occurring more abundantly in the pasture habitat, *N. ruber* and *A. thalassinus*, are less effective competitors. They arrive later at the dung (between 1 and 2 days) than *P. femoralis* and *S. flavicornis* and they remain feeding at the dung pat for a longer time before rolling a ball. Because *P. femoralis* and *S. flavicornis* were less abundant in the disturbed habitat, *N. ruber* and *A. thalassinus* had a better chance to colonise the dung than in the natural habitat where the dung was removed very rapidly. *Caccobius seminulum* (F.G. VI) was very abundant in the disturbed grassveld habitat (Table 3.3, 4278 individuals collected) and less abundant in the natural grassveld habitat (Table 3.3, 1302 individuals collected). It is a small species (0.003g), which uses the dung mass buried by other dung beetles. They, therefore, contribute very little to the removal of dung.

Galante *et al.* (1991) and Galante *et al* (1993) found that in the dung beetle populations of a Mediterranean holm-oak habitat the smaller species seemed to prefer the open pasture. Contrary to this the larger dung beetles at Sandveld and neighbouring farms seemed to prefer an open grassveld habitat, while the smaller species were more abundant in the bushveld habitats. The smaller species *O. sugillatus, O. obtusicornis* and *O. variegatus,* belonging to F.G. V were more abundant in the bushveld habitats. They have a dry weight of 0.003g, 0.018g and 0.003g respectively and make superficial nests in shallow concavities excavated immediately beneath the pad or in shallow tunnels. Galante *et al.* (1995) found that dung pats dry quickly in open habitats so they must be used quickly if they are to be used by dung beetles. In the wooded areas, on the other hand, dung pats dry slowly under trees as a consequence of lower temperatures. Nealis (1977) also considers temperature to play an important role in those species favouring shaded sites. The dung pats in the bushveld area will therefore provide a habitat for a longer period which will allow the smaller dung beetles of F.G. V to feed and breed under the dung pat. Although the larger species occurred more abundantly in both the grassveld habitats, they were far more abundant in the natural than in the disturbed habitat. On the basis of abundance of certain key species and their size, the community of dung beetles in the natural grassveld habitat seems to be much more successful at removing dung than in the disturbed grassveld habitat and the bushveld habitats.

**Total biomass and number of individuals in different habitats**

Analysis of similarity indicated differences in both abundance and biomass in dung beetle assemblages between the different habitats (Table 3.4). The largest difference was between the natural grassveld and natural bushveld habitat and there was a larger difference in biomass than abundance of dung beetle assemblages in the different habitats (Table 3.4).

**Table 3.4: Similarity in abundance and biomass between different habitats (Sandveld Grassveld –natural grassveld area in Sandveld Nature Reserve, Rietvlei – disturbed grassveld area, Sandveld Bushveld – natural bushveld area in Sandveld Nature Reserve and Josina –disturbed bushveld area).**

| Habitats | Mean similarity in abundance ± SE | Mean similarity in biomass ± SE |
|---|---|---|
| Sandveld Grassveld vs Rietvlei | 0.635 ± 0.04 | 0.530 ± 0.05 |
| Sandveld Grassveld vs Sandveld Bushveld | 0.486 ± 0.07 | 0.296 ± 0.05 |
| Sandveld Bushveld vs Josina | 0.664 ± 0.04 | 0.620 ± 0.04 |
| Rietvlei vs Josina | 0.596 ± 0.07 | 0.43 ± 0.06 |

*** Index equals 1 in cases of complete similarity and 0 when habitats are dissimilar and have no species in common.**

There were non-significant differences in numbers of individuals in dung beetle assemblages in the different habitats ($F=1.508$; $P>0.05$). The number of individuals was higher in the grassveld habitats than the bushveld habitats and higher in the natural habitats than in the pasture habitats (Fig. 3.6). There were significant differences in dung beetle biomass between the four different habitats. The average biomass of the dung beetle assemblages over two years was higher in the natural grassveld area than the disturbed grassveld area ($F=8.588$, $P<0.05$) (Fig. 3.6) and the biomass was also higher in the grassveld habitats than the bushveld habitats ($F=9.196$, $P<0.05$) (Fig. 3.6). If we consider the role of dung beetles in their respective habitats the most important factor is the disposal of dung. The total number of beetles in each habitat would be one measure of dung disposal but disregards the fact that species differ in size and hence resource use per individual (Nealis, 1977). According to Magurran (1988) biomass is a more direct measure of resource use than number of individuals. Lumaret *et. al.* (1992) and Peck & Forsyth (1982) also consider results expressed in biomass to give better information from an ecological point of view than that expressed in numbers. The difference in biomass and abundance between the bushveld and grassveld habitats might be a result of different sub-surface soil temperatures because of differences in shade. Davis (1996) found that the biomass and abundance of Scarabaeidae were much greater in open woodland than in other vegetation types where there were significantly lower maximum annual, sub-surface, soil temperatures. These results are also in agreement with Galante *et. al.* (1995) who found the highest biomass in open pastureland. In the present study abundance and biomass was also higher in both natural habitats compared to the disturbed habitats on farms. At Los Tuxtlas, Mexico, Estrada *et al.* (1998) also found that natural forest fragments were richest in dung beetle abundance with man-made pastures being the poorest habitats. In the present study the different natural and disturbed habitats differed in the type and availability of the resource. In the disturbed habitats the resource was cattle dung, while the dung of wild large herbivores was the main resource in the natural habitats. The pattern in biomass and total abundance did, however, not reflect the variation in resource availability, because dung was consistently more abundant in disturbed habitats. There must therefore be another factor, which affects the abundance of dung beetles in the different habitats. In the disturbed habitats the vegetational ground cover has been affected by trampling and overgrazing resulting in differences in vegetational cover between natural and disturbed habitats (Chapter 2, Table 2.1). The differences in biomass and total abundance of dung beetles in different disturbed and natural habitats in the present study is possibly a result of differences in vegetation caused by farming practices.

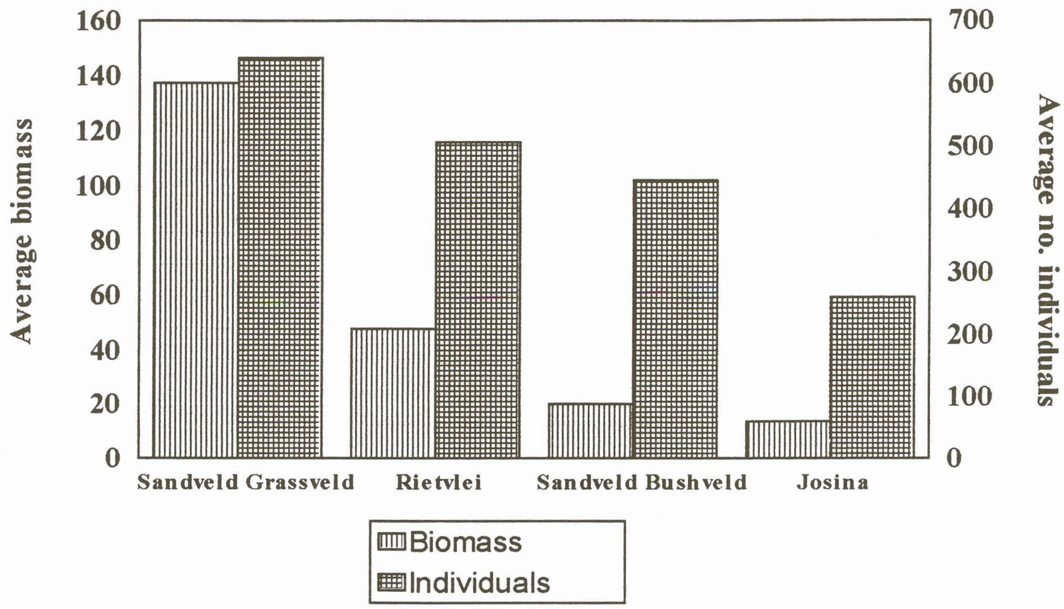


**Fig. 3.6: Biomass and number of individuals based on two years average (July 1996-June 1998) in four different habitats: S.G.-natural grassveld habitat in S.N.R., Rietvlei-disturbed grassveld habitat, S.B.-natural bushveld habitat in S.N.R., Josina-disturbed bushveld habitat.**

The dung beetles ranged in dry mass from 0.0006g ± 0.0002 to 1.49g ± 0.27 (Chapter 2, Table 2.4). There was a strong positive correlation between mass classes and the biomass in all four habitats (S.G.-r=0.896; Rietvlei-r=0.931; S.B-r=0.889; Josina-r=0.920). The larger the species the more dominant in biomass they tended to be (Fig 3.7). This is in agreement with Cambefort (1991) who also found a positive correlation between individual fresh weight and the average biomass of the species across six sites. This can in part be explained by the large body size, but can also be explained by the soil type. In the study area all four habitats are characterised by deep sandy soil (Chapter 2; 2.2). Nealis (1977) found that sand-based habitats had the highest Scarabaeidae biomass and Davis (1996) found that the soil tunnelling and dung-burying Scarabaeidae dominated the community in terms of biomass because of the large body size of many species. He ascribes the greater biomass of the assemblage on the sand to the softer consistency of this soil type with a greater softness of sand facilitating deeper burial of dung by larger tunneling and rolling beetles and thus provides more breeding space. The smaller species breed and feed inside the dung pat or make shallow tunnels under the dung pat. The soil type therefore does not affect them.

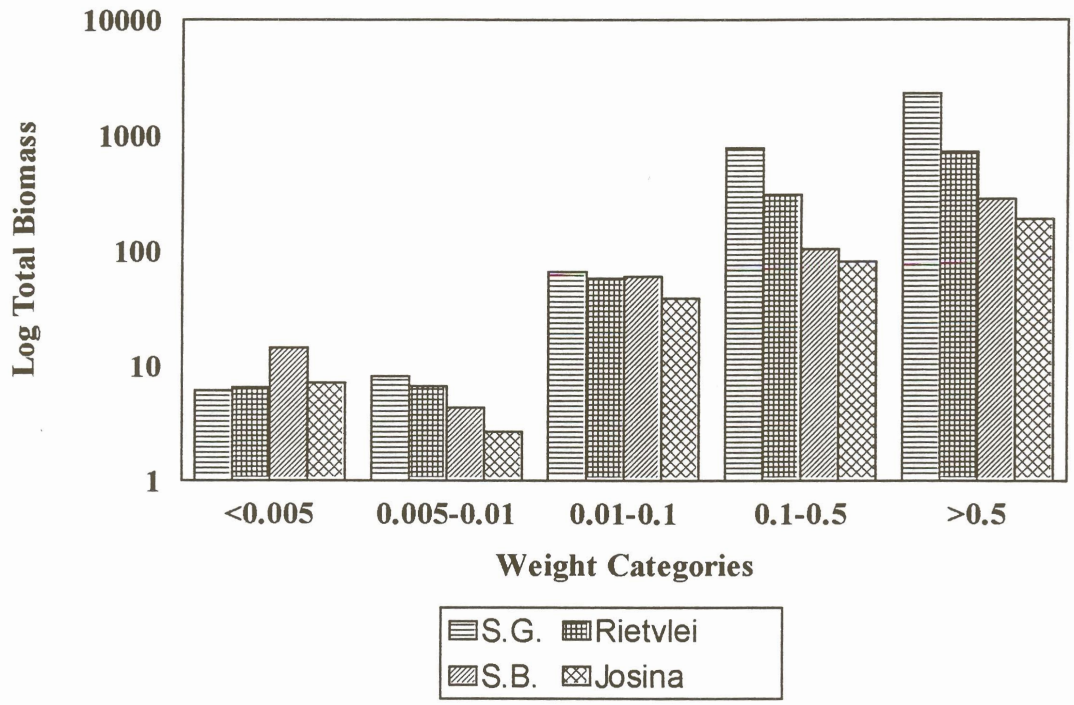


**Fig 3.7: Distribution of dung beetle biomass according to size in four different habitats: S.G.-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, S.B.-natural bushveld habitat, Josina-disturbed bushveld habitat.**

In the smaller mass classes (<0.005; 0.005-0.01; 0.01-0.1) there was very little difference in biomass between the four different habitats ($F=1.081$; $P>0.05$), but in the higher mass classes (0.1-0.5 and >0.5) there was a difference ($F=9.023$, $P<0.05$) (Fig. 3.7). The biomass in the higher mass classes was higher in the grassveld habitats than in the bushveld habitats and also higher in the natural habitats than in the disturbed habitats. It seems, therefore, that the larger dung beetle species, which are dominant in biomass are more severely affected by a change in habitat from grassveld to bushveld and from natural habitat to disturbed habitat than the smaller species. Davis (1994) found that the dominant species reflected the faunal differences between disturbed, west coast shrubland and shrubland on the Cape of Good Hope Peninsula and vegetation type was the principal determinant of spatial distribution patterns.

The numerical dominance of certain guilds was not necessarily correlated with dominance in biomass. There was a negative correlation between the mass class and the abundance of the species in the bushveld habitats and the disturbed grassveld habitat (S.B.-r=-0.624; Josina-r=-0.647; Rietvlei-r=-0.623), while there was no linear correlation between the mass class and the abundance of species in the natural grassveld habitat (S.G.-r=-0.131). Cambefort (1991) found that, on average, the smaller species are more abundant and Peck & Forsyth (1982) also found that the most numerically abundant species tend to be small or medium in size, averaging about 10mm or less in body length. In the present study this is true for dung beetle assemblages in all the habitats except the natural grassveld habitat. In the bushveld habitats and disturbed grassveld habitat the smallest mass class (<0.005) were most abundant, while in the natural grassveld, however, the higher mass class (0.1-0.5) were more abundant (Fig. 3.8).

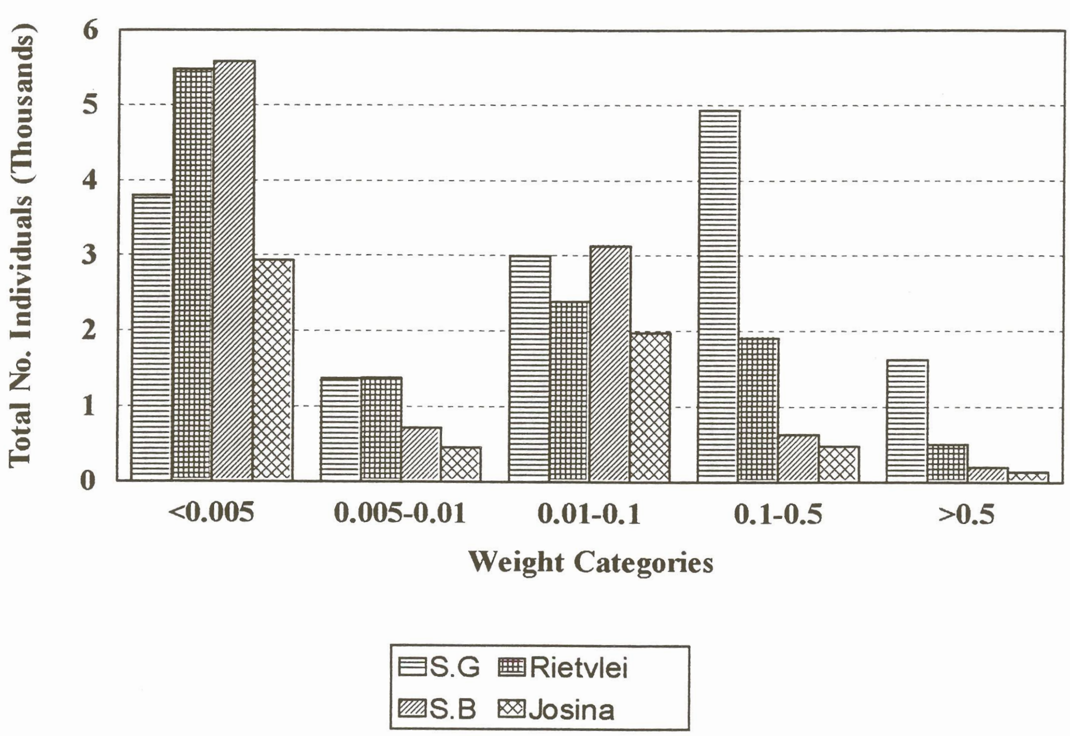


**Fig 3.8: Distribution of dung beetle individuals according to size in four different habitats: S.G.-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, S.B.-natural bushveld habitat, Josina-disturbed bushveld habitat.**

The size of beetles seems to be an important factor in the determination of the guild structure. Large size can be of advantage in the dung environment, improving the capacity to borrow into the dung and compete more effectively for dung. Hanski & Cambefort (1991b) came to the conclusion that in paracoprids, the use of space in the soil below the dung pat must depend on the size of the beetle and that size is also important in telocoprids because of interference competition. Smaller size, on the other hand, probably permits the utilisation of a greater range of microhabitats and food resources. The assemblage in the natural grassveld habitat is dominated by larger specialist species while in the bushveld habitats and disturbed grassveld habitat the assemblages seemed to be dominated by smaller generalist species. There must be a limiting factor influencing the larger dung beetle species in the disturbed and bushveld habitats, while the smaller species seems unaffected by this change. The soil type is similar in the different habitats and dung is more abundant in the disturbed habitats where the abundance and biomass of large dung beetles are lower. Neither the soil nor the resource, therefore, can explain the difference in the abundance and biomass of large dung beetles in the different habitats. Menendez & Gutierrez (1996) found that total abundance of dung beetles varied with vegetation type. Tree cover may explain the differences in the grassveld and bushveld habitats, as it can affect the searching and movement capabilities of the larger species in the bushveld area significantly. Trampling and overgrazing by cattle on the farms changes the ecological status of the vegetation, the basal cover and the relative veld condition (Chapter 2, Table 2.1). This might influence the larger dung beetle species more severely than the smaller species, causing competitive exclusion in the disturbed habitats and making the natural habitats more favourable for co-existence of larger species. Since larger dung beetle species belonging to F.G. I and II remove larger amounts of dung at a faster rate (Doube, 1990), this will have consequences for the effective degradation of dung on the farms where the larger dung beetles are less abundant. Doube (1991) ascribed the complete dung dispersal on sandy soils in the Hluluwe region (South Africa) to the dominance on sands of large beetles (>1.024 mg dry wt), which bury large amounts of dung in a short time. In northern Italy, Borghesio *et al.* (1999) found that the transfer of dung to soil determined an increase of above ground primary production and also showed that dung transferred into the soil by the coprophilous organisms can influence the growth of a natural plant community. They also found that one third of dung burial was attributed to paracoprid dung beetles A higher abundance of large dung beetle species in the natural grassveld habitat can, therefore, possibly also result in better plant cover in the natural habitat than on the farm.

## 3.4. CONCLUSION

There was no difference in species richness or dominance between the dung beetle assemblages in the four different habitats. This does not, however, mean that the dung beetle assemblages in the different habitats were similar. It is important to note that diversity in terms of species are just one of many possible ways of describing communities and there are other aspects just as important when considering a community. There are several aspects to be considered in the present study. The dung beetle assemblages in the four habitats followed a log-series pattern, with a few dominant species and a large number of rare species. The grassveld habitats were dominated by larger dung beetles belonging to F.G. I and II, while in the bushveld habitats the smaller dung beetles belonging to F.G. IV and V were more dominant. There was definite habitat preferences with the larger dung beetles belonging to F.G. I, II and III preferring the grassveld habitats and being more abundant in the natural than the disturbed habitats. The smaller dung beetles belonging to F.G. V preferred the bushveld habitats. It seems that the better competitors, which are the larger dung beetles, occurred more abundantly in the grassveld habitats and also more abundantly in the natural grassveld habitat than in the disturbed habitat. Size seems to be a very important factor in a dung beetle assemblage. It is important to consider the size and the competitive ability of the dominant species in a habitat. A change in habitat from natural to disturbed seems to affect the larger better competitors most severely. It is, therefore this group of dung beetles that must be considered when the influence of a change in the habitat on a dung beetle assemblage is to be determined. It seems that a change in vegetational ground cover caused by overgrazing and trampling has a greater affect on the larger more effective competitors in the assemblage, while the smaller less effective competitors do not seem to be affected by this change. This will have consequences for the degradation of dung and subsequently the success of the whole grazing ecosystem.