THE EFFECT OF HABITAT CHANGE ON THE STRUCTURE OF DUNG BEETLE ASSEMBLAGES IN THE NORTH-EASTERN FREE STATE: A COMPARISON OF CONSERVED AND FARMED LAND

by

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SUMMARY

The effect of habitat transformation on dung beetle assemblages in the north-western eastern Free State was investigated by comparing the fauna of a nature reserve (Sandveld Nature Reserve (SNR) (27°37'S;25°46'E)) with that on neighbouring farms. Dung beetle sampling was done in four different localities within two different habitat types, a grassveld area and a bushveld (savanna) area. In these two habitat types dung beetle assemblages in SNR and on farms were compared. The grassveld habitats were dominated by larger dung beetles belonging to FG I and II, while in the bushveld habitats smaller dung beetles belonging to FG IV and V were dominant. None of the indices measuring species richness nor dominance showed significant differences between the four habitats. This does not, however, imply that the dung beetles were similarly affected by the different habitats, because the biomass of dung beetles was higher in the grassveld than the bushveld habitats and also higher in the natural habitats. A change in vegetational ground cover caused by overgrazing and trampling has a greater effect on the larger, more effective competitors in the assemblage, while the smaller less effective competitors do not seem to be affected by this change. Continued adverse environmental disturbances caused by farming activities such as overgrazing have placed stress on dung beetle assemblages on farms. These disturbances have influenced the dung beetle assemblages on farms in such a way that their ecological role in the grazing ecosystem has been affected. A simple model was constructed to describe the most important factors influencing dung beetle assemblages and the key variables responsible for changes in the assemblages were determined. The focus of this study was on the dung beetle assemblages in a particular habitat and their ecological role in an ecosystem. The important shared parameters in this system were human impact, season and habitat as external factors and succession, diel activity, aggregation and dung preferences in dung beetle assemblages as internal factors. Two key variables could be extracted, *ie.* influence of habitat and the size of the dominant species in this habitat. These two key variables represent the essentials of the system and by looking at them predictions can be made as to which direction the dung beetle assemblage in a habitat will move. This will then enable us to make predictions about the condition of the habitat.

Key words: Dung beetle assemblages; grazing ecosystem; overgrazing; habitat transformation; seasonal variation; diel flight activity; succession; dung preferences; aggregation; ecological role; dominant species; size index.

OPSOMMING

Die invloed van habitat transformasie op miskruier gemeenskappe in die noord-wes oos Vrystaat is ondersoek deur fauna in 'n natuurreservaat (Sanveld Natuurreservaat (SNR) (27°37'S;25°46'E)) te vergelyk met dié op aangrensende plase. Opnames van miskruier gemeenskappe is in vier lokaliteite binne twee habitat tipes gedoen, 'n grasveld habitat en 'n bosveld habitat. Binne hierdie habitat tipes is miskruiers in die natuurreservaat vergelyk met dié op die plase. In die grasveld habitatte was groter miskruiers wat aan FGI en II behoort dominant, terwyl kleiner miskruiers (FG IV en V) in die bosveld habitatte dominant was. Indekse wat spesies rykheid of dominansie meet het geen betekenisvolle veskille tussen die habitatte getoon nie. 'n Hoër biomassa van miskruiers in die natuurlike grasveld as in die bosveld en op die plase het egter daarop gedui dat miskruiers in die verskillende habitatte verskillend beïnvloed word. 'n Verandering in plantbedekking as gevolg van oorbeweiding en vertrapping het 'n groter invloed op die groter, meer effektiewe kompeteerders, terwyl dit blyk asof die kleiner miskruiers nie deur hierdie verandering beïnvloed word nie. Aanhoudende versteuring van die habitat, a.g.v. verkeerde boerderypraktyke soos oorbeweiding het 'n negatiewe invlod op miskruier gemeenskappe op plase. Hierdie miskruier gemeenskappe word tot so mate beïnvloed dat hulle ekologiese rol in die omgewing benadeel word. 'n Eenvoudige model is opgestel om die belangrikste faktore wat miskruier gemeenskappe beïnvloed te beskryf en die kern veranderlikes verantwoordelik vir veranderinge in die gemeenskappe is bepaal. Die fokus van die studie was miskruier gemeenskappe in 'n spesifieke habitat en hul ekologiese rol in 'n ekosisteem. Die veranderlikes in hierdie sisteem was menslike impak, seisoen en habitat as eksterne faktore en suksessie, daaglikse fliegaktiwiteit, aggregasie en misvoorkeure as interne faktore. Die kern veranderlikes was invloed van habitat en grootte van die dominante spesies in die habitat. Hierdie veranderlikes verteenwoordig die kern van die sisteem en deur daarna te kyk kan voorspellings gemaak word oor die toestand van die habitat.

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Chapter 1
INTRODUCTION

1.1. Influence of farming and agricultural practices on grassland ecosystems in southern Africa.

Natural grasslands occur where rainfall is intermediate between that of deserts and forests. Large grassland areas occupy the interior of the north American and Eurasian continents and extensive natural grasslands are also located in southern South America, central and southern Africa, and Australia (Odum, 1993). Large herbivores, mostly mammals, are a characteristic feature of grasslands (Odum, 1993). In the past a great diversity of wild herbivore populations used to dominate the South African landscape and the grazers and browsers occurring here maintained a balance in the variety of herbs and woody plants (Downing, 1978). According to Owen-Smith (1989) African savannas have an evolutionary history of high levels of grazing and browsing ungulate herbivory, capable of significantly modifying vegetation structure and composition. During the latter part of the 19th century the wild herbivore populations were replaced as dominants by cattle and sheep. Odum (1993) states that, because grasslands are adapted to heavy energy flow along the grazing food chain, the switch from native grazers to domestic grazers is ecologically sound, but that humans, however, have had a history of misuse of grassland resources by allowing overgrazing and overploughing. The carrying capacity (in biomass kg/ha) of a grassland ecosystem is much higher for wild ungulates (52,5-80,00) than for cattle, sheep and goats (40,7-53,5) (Opperman, 1980). The grassland ecosystems in South Africa can therefore support fewer cattle, sheep and goats than wild herbivores, yet more of these animals are kept in smaller areas than wild herbivores resulting in degradation of the veld. The ratio of domestic grazers to browsers is also higher than for indigenous grazers and browsers and this results in encroachment of woody plants (Trollope, 1975). Teague & Smit (1992) also found that the replacement of grazing herbivores by domestic livestock, mainly cattle, has placed a great deal of pressure on grazing resources and is one of the main reasons for large increases in woody biomass. Preferred grasses are also reduced by cattle and sheep and continuous grazing and overstocking can ultimately reduce even unpalatable grasses to such an extent that inferior forbs become common (Downing, 1978). According to Opperman (1980) the problem with grazing ecosystems in South Africa is that in many cases they are artificial and have to stabilise on different levels needing high energy inputs for maximum productivity. The recycling of minerals has decreased drastically due to total utilisation practices by farmers and mineral supplementation costs farmers millions annually (Opperman, 1980). Due to wrong management practices microclimatic conditions have changed resulting in slow recovery of veld (Opperman, 1980). Danckwerts & Stuart-Hill (1988) attribute the slower rate of recovery on grazed than on ungrazed veld to the effect grazing has on seedling establishment and tuft regeneration from a limited number of secondary tillers. The botanical diversity of old grasslands is also often reduced by replacing the lands with grass leys or by treating them with selective herbicides and fertilizers, resulting in a habitat that does not contain some of the basic requirements essential for many species (Goudie, 1990). Grazing also damages soil structure through trampling and compaction. Heavily grazed lands have a lower infiltration capacity than ungrazed lands and the removal of vegetation cover and associated litter also changes infiltration capacity (Goudie, 1990). According to Skinner (1981) semi-arid grassveld is particularly susceptible to drought. Opperman (1980) states that 64% of South Africa's natural grazing receives less than 500mm rain per year and is therefore susceptible to drought. Replacement of wild herbivores with cattle, goats and sheep therefore places further stress on an already stressed ecosystem. According to Eckholm (1985) 12 million hectares world-wide deteriorate each year to a point where they are agriculturally worthless, 40 percent are rainfed croplands that lose topsoil and nutrient stocks and the rest are rangelands, which, through over-grazing, suffer erosion and a shift in vegetation from nutritious grasses to weeds. This results in many grasslands becoming human-made deserts, thus stressing the importance of ecological indicators in the early detection of overgrazing. Were these lands to continue to support agriculture, their output could be worth at least $20 billion a year (Eckholm, 1985).

Insects are severely influenced by the misuse of land. According to Samways (1994) several thousands of species extinctions can be expected world-wide by the year 2000 as a result of habitat loss and modification A disturbance can be seen as an event which disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment (White & Pickett, 1985). Reduction in species and genetic diversity resulting from human activities will influence the future adaptability of species in both natural ecosystems and agroecosystems (Odum, 1983). Fences do not limit insects, but they are limited by the habitat. Insects are able to adapt to small environmental changes, but it is the major disturbances such as ploughing, heavy grazing, fertilising plots and recreational pressure that contribute to declining population levels and eventual loss of the local insect populations (Fry & Lonsdale, 1991). Insects can survive in the most intensively farmed landscapes and a major aim of conservationists is to enhance, perpetuate and improve this survival (Collins & Thomas, 1990).

1.2. The dung beetle assemblage

Dung beetles are essential for the correct functioning of any grazing ecosystem. Dung serves as food for adult dung beetles and their immature stages. The two main types of food resource used by dung beetles are large herbivore dung and omnivore dung (Hanski & Cambefort, 1991a), while relatively few dung beetles are attracted to carnivore dung (Hanski, 1987a). Some species feed within the dung mass, while others feed on buried dung. Three distinct groups of dung beetles are recognised according to their habits of food manipulation. Telecoprids form dung into balls and remove the ball from the dung pat, paracoprids bury the dung underneath the dung pat and endocoprids feed on the dung and complete their life-cycle inside the dung pat. The size and dung burial behaviour of dung beetles are important determinants of their capacity to compete for dung and Doube (1990) used these determinants to further divide groups of species with similar habits into separate functional groups. The large telocoprid dung beetles represent FG I, the small telocoprid dung beetles FG II, the fast burying paracoprid dung beetles FG III, the large slow burying paracoprid dung beetles FG IV, the small slow burying paracoprid dung beetles FG V, the kleptocoprid dung beetles FG VI and the endocoprid dung beetles are represented by FG VII.

There are three basic “niche dimensions” for dung beetles, namely space, food and time (Christiansen & Fenchel, 1977). Giller & Doube (1994) found that different dung beetle species differ in their behavioural responses to environmental conditions. Some species show a high degree of habitat specificity, while others are much more widespread. Certain dung beetle species will quickly adapt to a new environment and become dominant, while those with low dispersal ability and adaptability will not be able to survive in a changing environment. Species may be represented in small local populations, but be well distributed on a local scale, because their environmental tolerance allows them to colonise all the dung pats in a particular area despite environmental differences. Species found with greatest frequency in dung pats are those with a greater ecological capacity, not those with the highest abundance (Lobo, 1993). According to Hanski & Cambefort (1991a) the large African tunneling beetles have low rates of dispersal compared to the many smaller species. This may result in communities where the large tunneling beetles are excluded in changed environments, while smaller paracoprids and endocoprids become dominant because of better dispersal abilities. Competition for dung appears to play a major role in structuring communities dominated by FG I and FG II (Giller & Doube, 1989). Competition is, however, not a limiting factor in other communities where dung is not limiting and FG V and FG VI are major elements. As the community structure changes with a changing environment the ability of the dung beetle community to remove dung efficiently will also change. According to Doube (1990) the potential of dung beetles to remove dung varies markedly between functional groups.

Succession in coprophages is a typical example of heterotropic succession (Koskela & Hanski, 1977). The energy sources available to the animals are largest at the beginning and decrease continually. Flight activity of dung beetles begins at different times depending on the species. This results in a succession pattern of species colonising the dung depending on the time the dung is deposited and also on the habitat in which the dung is dropped

(Fincher *et al.*, 1971). Environmental changes seem to play an important role in the succession of dung beetles. Valiela (1974) found that during succession, neither food limitation nor predation appeared to be limiting to dung beetles, but that local alterations in the environment and in the dung itself, however, may influence the succession in a dung pat. According to Koskela & Hanski (1977) the variation in the early successional stages among dung beetles is mainly due to macrohabitat differences.

The quality of dung might also have a significant influence on dung beetle assemblages. Edwards (1991) found that dung quality can produce a 100-fold change in the reproductive rate of dung beetles. This indicates that it is potentially a major variable in the population dynamics of species. With the changes in the environment caused by farming it was important for dung beetles to adapt to a new dung type. In many areas of Africa, many herds of game animals have been exterminated by man, but many species of dung beetles are still abundant because they have adapted to the dung of introduced animals (Bornemissza, 1960).

1.3. Influence of habitat on dung beetle assemblages

In South Africa there are 780 species of dung beetles plus approximately 60 species of dung dwelling Aphodiinae (Doube, 1991) currently known. There is considerable specialisation, particularly amongst African dung beetles, along a variety of environmental niche axes (Hanski & Cambefort, 1991a). There are several factors influencing the presence or absence of dung beetle species in an area. Of all the factors the habitat structure seems to be the most important. According to Mohr (1943) the environment in which dung is dropped has a profound effect on the composition of its dung fauna. More specifically, it would seem that vegetational ground cover and soil type have the most important effect on habitat preference of dung beetles (Hallfter & Matthews, 1966; Fincher *et al.*, 1970; Howden & Nealis, 1975; Hanski & Koskela, 1977; Nealis, 1977; Doube, 1983; Janzen, 1983; Davis *et al.*, 1988). Davis *et al.* (1988) found that 32 of the 46 species and species complexes he studied showed significant associations with either vegetative cover, soil type or both. In this context, Doube (1991) found that the relative abundance of species changed across vegetational boundaries, where, in Mkuzi Game Reserve, many species showed a preference for either grassveld or bushveld. Here there was no important variation in habitat parameters other than vegetation cover. Thus overall, the habitat affects the microclimatic conditions of the dung, which in turn influences the dung beetle community colonising the dung. Jameson (1989) compared diversity of coprophagous Scarabaeidae in grazed and ungrazed Sandhills Prairie in Western Nebraska. She found that key elements of microclimate (wind, sun, soil, plant cover, humidity and precipitation) influenced the quality, availability and malleability of the dung as a nutritional resource for dung-feeding scarabs. Doube (1983) found that some species are characterised by preferences for habitat of particular light intensities. Natural dispersal of these species will occur through connecting corridors of bushveld. This may pose problems for dispersal. Changes in the environment might have an influence on certain species. The biomass of large telocoprids is greater in regions of grassveld within a bush-grass mosaic than in areas of extensive grassveld, which may be related to the dung and microhabitat requirements of breeding beetles. *Kheper nigroaeneus* uses many types of dung, which it buries in soft soil. This species is abundant in Mkuzi Game Reserve, but scarce in the surrounding pastoral regions, irrespective of soil type (Doube, 1991).

The environmental change created by man in his destruction of grasslands also affects the dung beetles through changes in the species and numbers of food-producing vertebrate animals (Fincher, *et al.*, 1970). It is thus clear from observations by several authors that habitat seems to be one of the most important factors influencing the structuring in dung beetle assemblages. It can therefore be assumed that the influence of man by changing the habitat through farming and agriculture will also have an important influence on dung beetle assemblages.

1.4. Importance of dung beetles in a grazing ecosystem

Dung beetles evolved together with large grazers and browsers, exploiting an important niche within the grasslands. An indispensable condition for the correct functioning of all pasture ecosystems is that the dung be rapidly utilised and transformed (Galante *et. al.*, 1991). Dung beetles play a very important role in grazing ecosystems. They form a part of a lengthy food-chain which starts with the assimilation of energy from the sun in plants used by grazing animals. The viability of every pasture ecosystem is based on the normal functioning of its nutrient cycle. Different components, including the grazing animal, play a role to keep the system running productively (Bornemissza, 1960). The malfunction or disappearance of any of the components in the grazing ecosystem or the invasion of external elements in the system could lead to serious repercussions. A sign of a grazing ecosystem functioning improperly is accumulation of dung. This happens in the absence of a viable dung beetle population or when the existing dung beetle population cannot cope with the large amounts of dung. According to Waterhouse (1974) dung deposited on the soil can eventually cause serious damage because it deteriorates the pastureland by preventing plant growth. It also causes the loss of nitrogen by, which then cannot be incorporated into the soil and other nutrients are tied up in the deposits for several months or years and are unavailable for plant growth (Fincher, 1981). The substantial amounts of nutrients that are contained in cattle dung can potentially be recycled back to the soil in an available form. Fincher (1981) states that the accumulation of dung in a pasture takes many hectares of pasture out of production by smothering the herbage under each deposit and by creating areas of rank growth around each deposit that is not normally grazed by cattle. According to Bornemissza (1960) undegraded cattle dung from five cows would decrease the effective area of pasture by one acre over a period of a year. Jones & Ratcliff (1983) found that dung pats were a source of patchiness in pastures and that the proportion of a pasture where grazing is reduced due to deposition of dung pats is much greater than the area of pasture physically covered by dung pats. Furthermore, reduced grazing on areas affected by dung increases grazing pressure on the remaining area. Shifting patterns of grazing pressure, following the deposition of dung pats, have the potential to affect botanical composition on the micro scale and, consequently, at the paddock level (Jones & Ratcliff, 1983). There is an impression that this problem can be overcome successfully under conditions of intensive grassland management, *i.e.* where high rates of fertiliser N are applied and the rate of stocking is high, but Castle & MacDaid (1972) found that the level of fertiliser N applied to the grazing sward had no direct effect on the rate of breakdown of dung. This problem can, however, be solved when there is a dung beetle assemblage able to successfully break down the dung. According to Gillard (1967) 80% of the nitrogen content is lost when cattle dung remains on the surface until it is dry, but when adequate numbers of dung beetles are present and bury the dung the nitrogen loss is reduced to 5-15%. According to Jenkinson (1988) soil microbial biomass plays a key role in nutrient transformations in soil and largely controls the rate at which C, N and other nutrients cycle through the agricultural ecosystem. Addition of mineral nutrients alone may not have marked effects on soil microbial biomass, whereas incorporation of mobile organic materials from dung may cause changes by providing readily-available energy sources and substrates for metabolism (Lovell & Jarvis, 1996). Lovell & Jarvis (1996) found that complete mixing of finely-chopped dung with soil had a major impact on both the size and activity of the soil microbial biomass, whereas the slow breakdown and release of nutrients from dung pats did not. By breaking down the dung, dung beetles therefore play a key role in increased size and activity of soil microbial biomass and ultimately in the increased rate of C, N and other nutrient cycling.

In addition to playing a key role in nutrient cycling dung beetles also act as biological control agents for nematode parasites of cattle and sheep (Miller, 1961; Fincher, 1973; Bergstrom *et al.*, 1976; Gormally, 1993) and dung breeding flies (Hughes *et al.*, 1978; Moon *et al.*, 1980; Ridsdill-Smith, 1981; Fay & Doube, 1983; Walker & Doube, 1984; Ridsdill-Smith & Hayles, 1987; Doube *et al.*, 1988; Fay *et al.*, 1990; Kirk, 1992; Peitzmeier *et al.*, 1992; Davis, 1994). Communities rich in dung beetles that are able to degrade cattle dung efficiently are therefore of great economic importance.

1.5. Research plan and hypothesis

In view of the important role that dung beetles play in grazing ecosystems the main aim of this study was to determine whether disturbance in a habitat caused by human activities, such as farming, has an effect on the dung beetle assemblages in these habitats. Behavioural factors such as succession, diel flight activity, aggregation and dung preferences influence the success of certain dung beetle species in an assemblage. Seasonal affects are also important to the behaviour of dung beetle species. All these factors were taken into account in the different natural and disturbed habitats.

The following hypotheses were tested:

i) Will natural veld support a different assemblage of dung beetles to disturbed farms? The changes in habitat caused by farming will possibly have an effect on the dung beetle assemblage. Domestic cattle exert constant forces in a limited area, thus possibly degrading potential habitat for dung burying beetles.

ii) Will there be a difference in the assemblage of dung beetles between different habitats in natural veld (grassveld and bushveld)? Different species are adapted to different environments resulting in some species being more successful in certain habitats than others, consequently affecting the community structure.

iii) Will decomposition of dung differ in the different habitats? The most important factor influencing the decomposition of dung is probably the dung insects colonising it and disturbing it by their feeding activity. The influence which disturbance of a habitat has on dung beetle assemblages will therefore also affect the decomposition of dung in this habitat.

iv) Will some habitats be more easily disturbed than others?

This study will enable us to identify certain key factors influencing dung beetle assemblages. Changes in a dung beetle community, which may act as an early indication of habitat degradation, might also be identified. This will enable us to make predictions and recommendations on veld management.

Chapter 2
STUDY AREA

2.1 INTRODUCTION

This study was carried out in Sandveld Nature Reserve (SNR) ($27^0$37'S; $25^0$46'E) situated in the north-western eastern Free State and on two neighbouring farms Josina and Rietvlei. The study area lies between Hoopstad and Bloemhof on the banks of the Bloemhof dam. The area is situated in the eastern variance of the Kalahari Thornveld (Acocks, 1988). SNR covers an area of 15283 ha. It was proclaimed a nature reserve on 9 May 1980. Before its proclamation as nature reserve the area was fragmented into different farms where maize was the main crop cultivated. The Bloemhof dam within the nature reserve covers 25 000 ha when full. Building of the dam, which is situated in the confluence of the Vaal River and the Vet Rivers, commenced in 1965 and was completed in 1970 (Potgieter, 1975). The study took place in four areas, a grassveld area in the nature reserve; a grassveld area on the farm Rietvlei; a bushveld area in the nature reserve and a bushveld area on the farm Josina. The grassveld area lies in the north-east of the nature reserve and covers an area of 4010 ha. The farm Rietvlei borders this grassveld area. It covers an area of 4500 ha of which 3800 ha consists of grazing fenced off into different pastures and 700 ha consist of maize fields. The bushveld area in this study, 4947ha in extent, lies on the south-eastern side of the nature reserve. The farm Josina borders on this bushveld area. This farm covers an area of 538 ha and consists of 147 *Acacia erioloba*-bushveld, 48 ha cleared *A. erioloba*-grassveld, 110 ha maize fields, 50 ha artificial pastures, 26 ha *A. erioloba* and *A. karoo*-grassveld, 70 ha *A. karoo*-grassveld and 89 ha abandoned fields.

The study area is a typical savanna ecosystem, which is characterised by high daytime temperatures, distinct wet and dry seasons of varying length, with downpours alternating with extended periods of drought. This is a system also characterised by the dominance of grass. In most places, however, savannas also support a scattering of trees and certain other woody plants that can withstand the long dry seasons. Although all savanna ecosystems are by definition similar, functionally each situation is unique. There are differences in physical determinants and these in turn influence the biological interactions that are based on these determinants. Individual specie's properties are unique to each spatial and temporal situation (Teague & Smit, 1992). The problem in South Africa today is that the grazing ecosystems are, in many cases, artificial. As early as 1835 farmers, looking for better grazing for their cattle, settled in the area between the Vaal- and the Vet River (the area between Hoopstad and Bloemhof today) (Potgieter, 1975). In 1880 there were already 77000 cattle, 583 000 Merino sheep, 18 000 Afrikaner sheep and 13 000 horses in this area (Jacobs, 1952 in Viljoen 1979). As a result of this a great deal of pressure has been placed on grazing resources in the area, and this is one of the main reasons for large increases in woody biomass. Teague (1992) states that the arid/eutrophic savannas are characterised by high levels of grazing and browsing herbivory, which results in relatively low plant biomass. According to Opperman (1980) the biotic diversity of both the producers and consumers, as well as the circulation of minerals also declined radically due to farming practices in South Africa. The result of these farming practices is a drastic change in the abiotic environment, which affects microclimatic conditions. This in turn affects the organisms occurring in the ecosystem. Farming practices therefore resulted, to a large extent, in artificial grazing ecosystems in South Africa today. In order to understand the interactions in the study area it is important to look at both the abiotic and biotic components in the system.

2.2. ABIOTIC FACTORS

Topography

The study area lies between 1228 and 1271 m above sea level (Viljoen, 1979). It is a flat plane, which gradually slopes down towards the dam. An approximately 1km long stabilised sand dune occurs in the northern part.

Climate

The climate of an area can be seen as the interaction of different climatic factors. To get an idea of the climate of the study area different climatic aspects will be discussed. Data for the area Was were obtained from the weather station at Bloemhof. Ten year's data were available for the rainfall and temperature and five year's data for the relative humidity.

Rainfall

The study area is characterised by semi-arid conditions with moisture shortages in both the wet and the dry season and is subject to low rainfall and often long drought periods. The average rainfall in the study area from 1988 to 1997 was 509.4mm. The lowest rainfall during the ten-year period was 230mm in 1994 (Fig. 2.1). In 1992 274.1mm fell (Fig.2.1), also much lower than the 10-year average. The highest rainfall during the ten-year period was 772mm in 1988 and 616.25mm in 1996, which is above the 10-year average (Fig 2.1). In this area, wet years are alternated with dry years (Fig 2.1). According to Opperman (1980), every 2-4 years, 31% of South Africa's rainfall is 20% or more lower than average. Consequently, it appears that drought is a normal phenomenon in the study area.

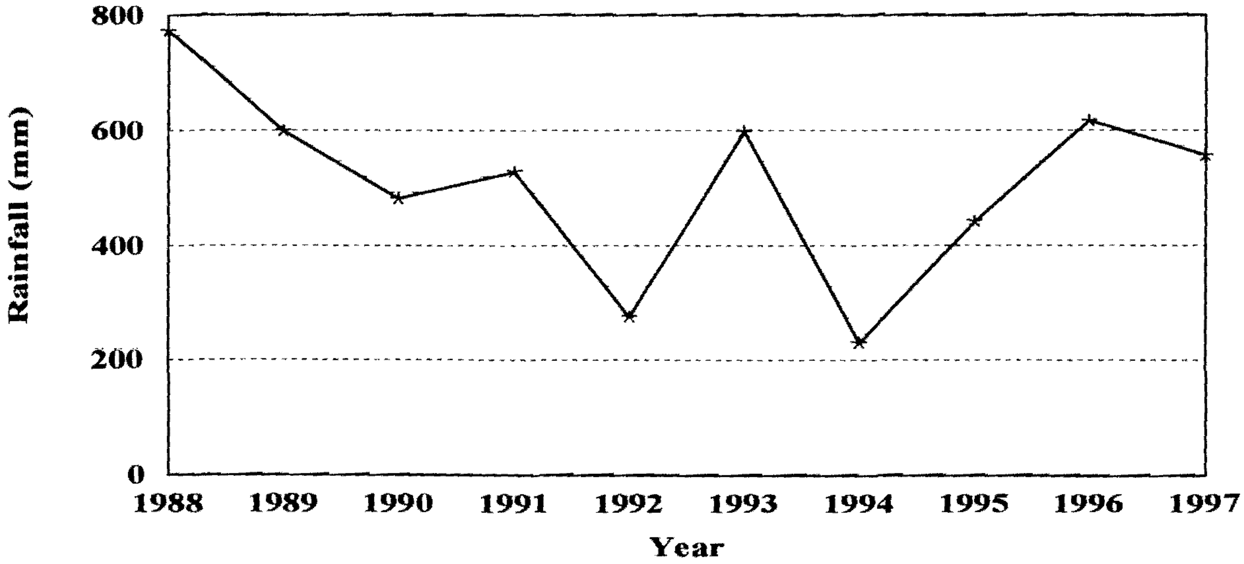


Fig. 2.1: Average yearly rainfall at SNR and neighbouring farms between 1988 and 1997.

The highest rainfall in the study area occurred from January to April. It decreased from May, with May, June, July, August and September as the driest months (Fig 2.2). The highest average monthly rainfall between 1988 and 1997 was 90.2mm during February and the lowest was 3.6mm during June (Fig. 2.2.). Rain in the area usually occurs as isolated showers and thunderstorms.

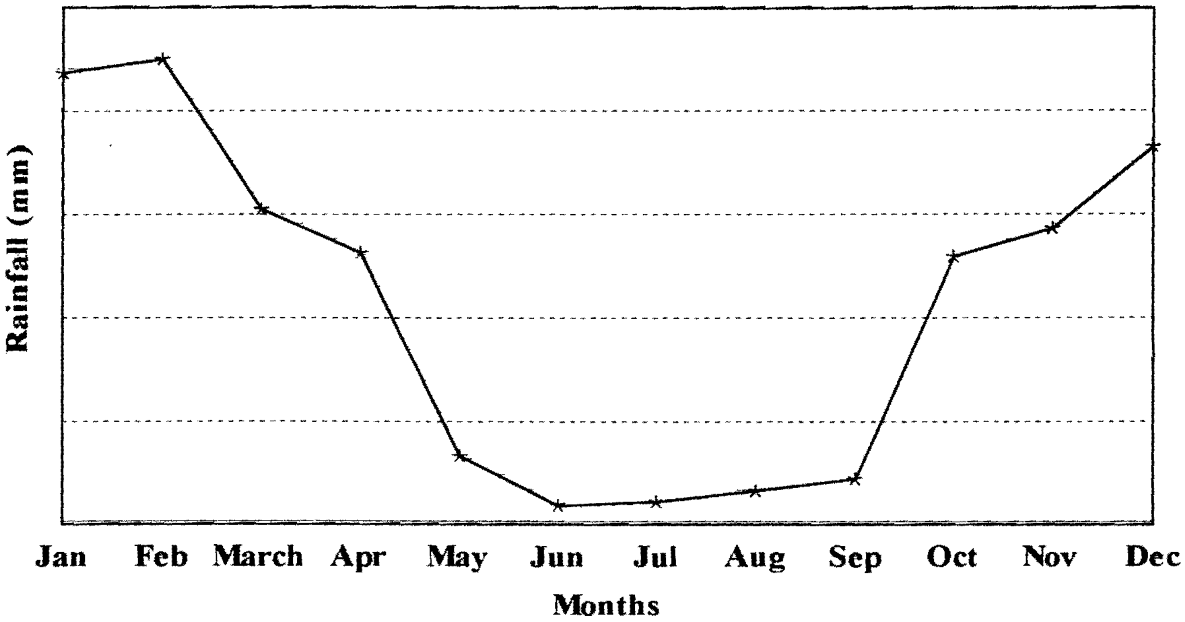


Fig. 2.2: Average monthly rainfall at SNR and neighbouring farms between 1988 and 1997.

Temperature

The study area is characterised by very hot summers and very cold winters. The average maximum temperature in this area, from 1988 to 1997, was 26.8°C. The average minimum temperature during the period was 9.7°C, while the average daily temperature was 18.25°C. The days are usually very hot throughout the year, while the nights are cold. The mean daily shift in temperature was 17.1°C. The highest shift in daily temperatures occurred during the winter months from June to September where the mean daily temperature shift was 18.1°C, 18.4°C, 18.7 °C and 19°C for June, July, August and September respectively (Fig. 2.3).

The hottest time of the year was between November and February. The average maximum temperatures for these months were 31.7°C, 32.6°C, 33.2°C and 31.3°C for November, December, January and February respectively (Fig. 2.4). The average minimum temperatures for these months were 13.9°C, 15.7°C, 17.6°C and 16.1°C respectively (Fig. 2.4). The highest daily maximum temperature recorded during the ten-year period was 40,4°C on 10 December 1997. The highest average monthly maximum temperature ever recorded in this area was 40°C during November 1904 (Viljoen, 1979).

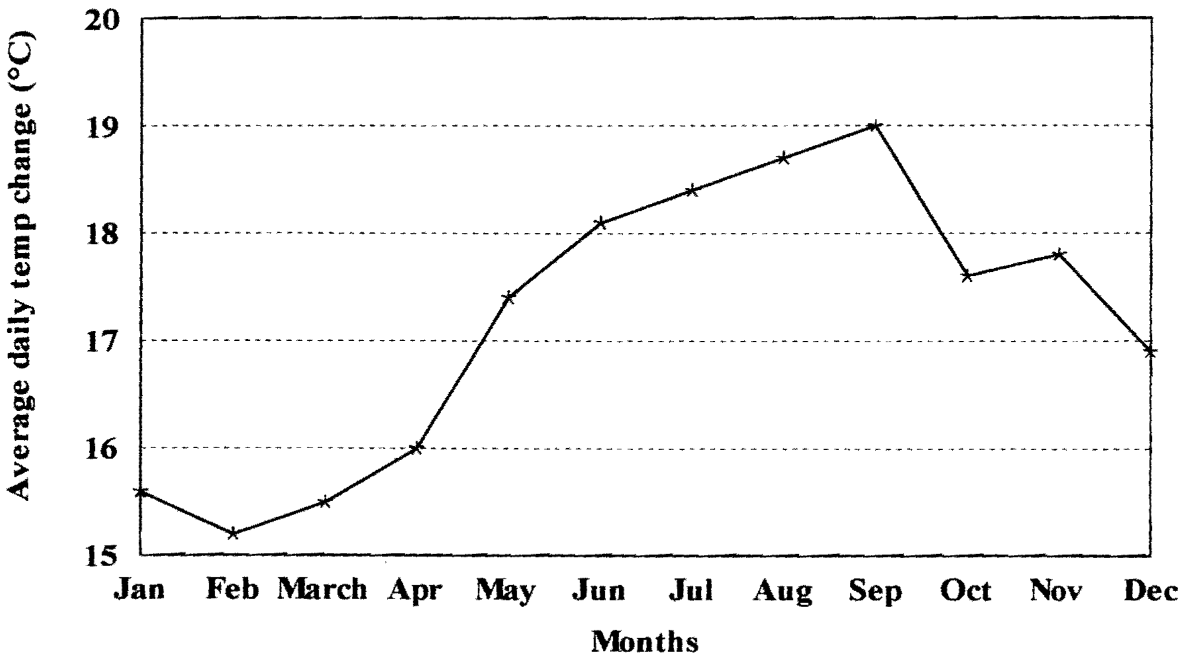


Fig. 2.3: Average daily temperature shift at SNR and neighbouring farms between 1988 and 1997.

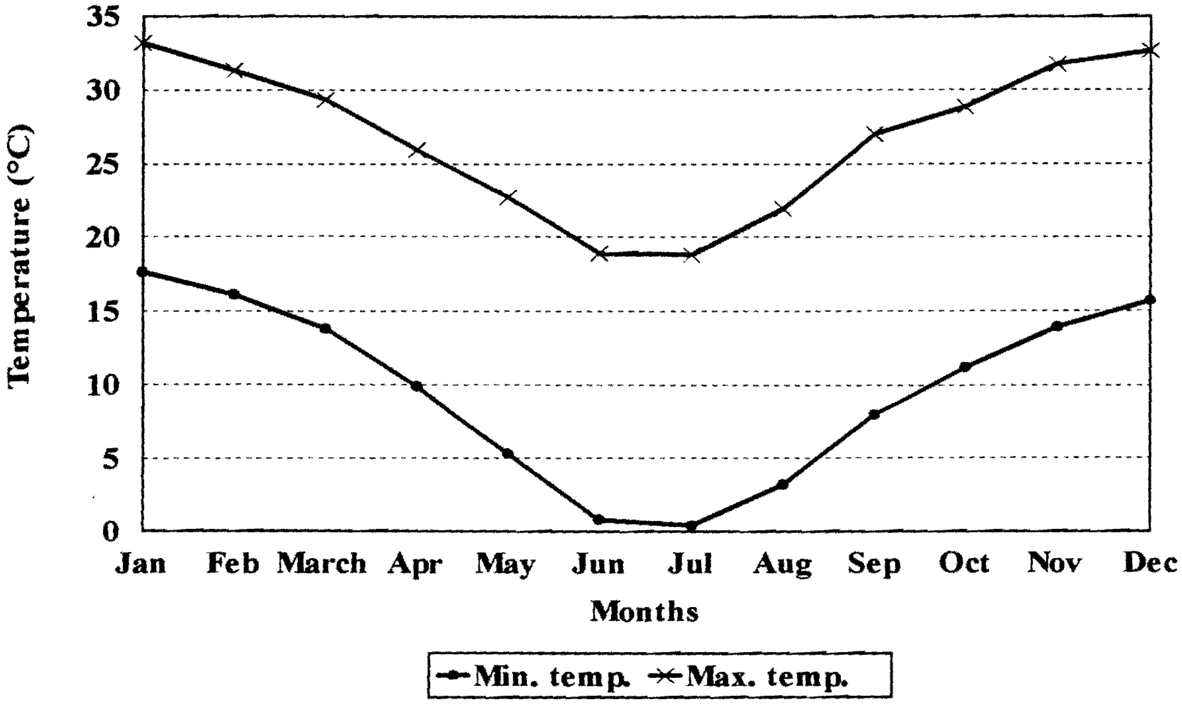


Fig. 2.4: Average monthly minimum and maximum temperature at SNR and neighbouring farms between 1988 and 1997.

The coldest time of the year is during June and July. The average maximum temperatures were 18.9°C and 18.8°C for June and July respectively, while the average minimum temperatures were 0.8°C and 0.4°C (Fig. 2.4.). The lowest daily minimum temperature recorded during the ten-year period was –8°C on 12 July 1994 and 19 July 1995. The lowest average monthly temperature ever recorded at the study area was -11.1°C during June 1920 (Viljoen, 1979).

Relative Humidity (RH)

RH is a percentage-indication of the moisture saturation in the atmosphere, regardless of the temperature. The lowest minimum RH in the study area during a five-year period from 1993 to 1997 was 11% in September 1994, while the highest maximum RH was 98% during March 1997. Average monthly minimum and maximum RH was lowest from August to November, while it was highest from March to May (Fig.2.5). The relatively low humidity in this area may result in a high evaporation and transpiration rate and is therefore of great ecological importance for the biotic components in this area.

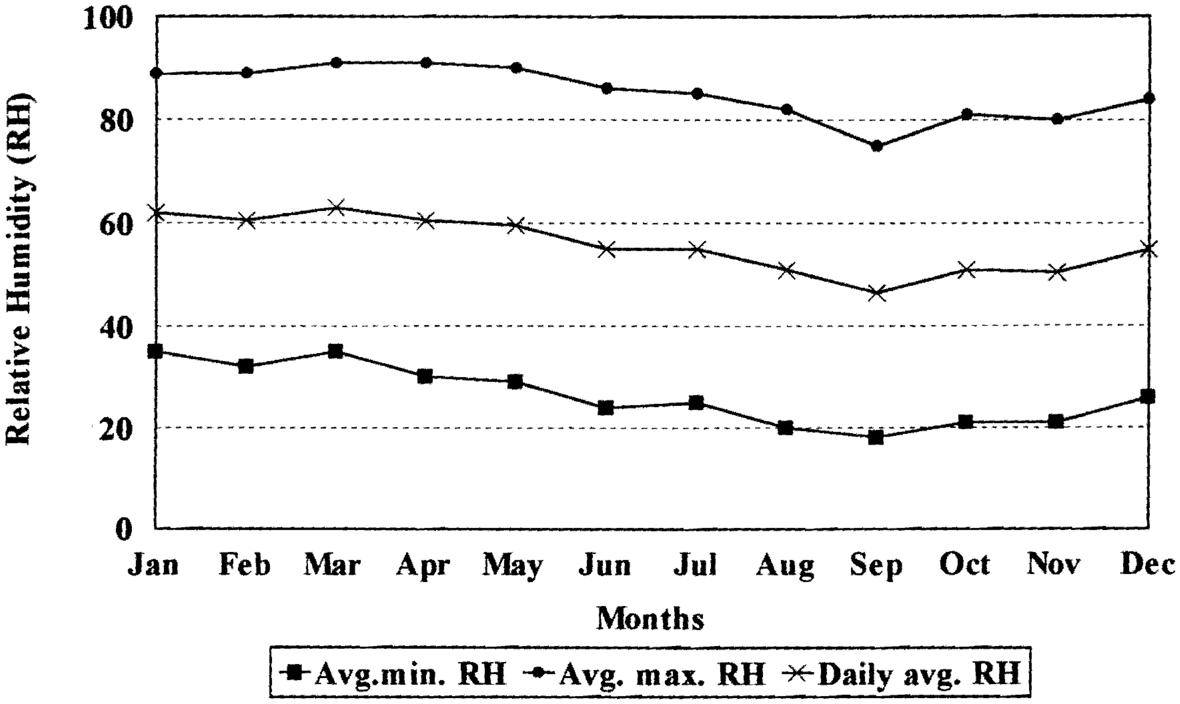


Fig. 2.5: Average monthly minimum, maximum and daily Relative Humidity at SNR and neighbouring farms between 1993 and 1997.

Soil

On the basis of colour, texture, chemical composition, plants growing in the soil and other distinctive characteristics, the soil at Sandveld can be divided into various groups.

The soil in the grassveld area at Sandveld and on the farm Rietvlei consists mainly of yellow/brown sandy soil. It consists of 0.85% silt; 3.9% clay; 21.5% fine sand; 68.1% medium sand and 5.2% coarse sand (Viljoen, 1979). With the exception of yellow sandy soil this is the most barren in the study area (Viljoen, 1979). Yellow sandy soil occurs in the stabilised sand dune. It contains the least nutrients and has the coarsest structure of all the soil types in the study area. It consists of 0.2% clay; 24.2% fine sand; 69.6% medium sand and 4.3% coarse sand (Viljoen, 1979).

The soil in the bushveld area at Sandveld and on the farm Josina consists of a combination of brown sandy soil and organic soil. The brown sandy soil differs in colour from the yellow sandy soil and is also richer in nutrients and has a finer texture. It consists of 0.85% silt; 6.4% clay; 44% fine sand; 43.7% medium sand and 4.2% coarse sand (Viljoen, 1979). The organic soil is characteristic of areas where scatterings of trees occur in the grassveld areas and is confined to areas under trees or bushes. This soil type occurs as a mosaic in the brown sandy soil and has a high nutrient value. It consists of 1.60% silt; 8.0% clay; 31.2% fine sand; 52.5% medium sand and 3.8% coarse sand (Viljoen, 1979).

2.3. BIOTIC FACTORS

Vegetation

According to Fourie and du Toit (1983) low growth potential is usually the first indicator of deterioration of the veld and poor ground cover is usually a symptom of advanced deterioration. The plant species composition shows the relative abundance and interactions of plant species in the cover and gives and idea of where the plant community occurs in succession. The plant species composition for the four different habitats concerned in the study area was determined with a 100 point survey at different sites. Strikes on living basal area were recorded and, in the absence of a strike, nearest plant data was recorded. The ecological classification, successional classification and basal cover were determined from this information. The grass species in the study area can be divided into four groups:

i) Decreasers: species which are typically found in veld in good condition, and which decrease in abundance with under- and over-utilization.

ii) Increaser 2A: species which increase when the veld is moderately overgrazed or selectively moderately grazed.

iii) Increaser 2B: species which increase when veld is heavily overgrazed or selectively heavily grazed.

iv) Increaser 2C: species which increase when the veld is excessively overgrazed.

The grassveld area of SNR used to be cultivated fields. The grass component is relatively uniform in this area. The most abundant grass species occurring in the grassveld area at SNR are *Eragrostis lehmanniana* (11.78%), *Eragrostis trichophora* (7.78%), *Setaria sphacelata* (6.44%) and *Cynodon dactylon* (6.22%) (Table 2.1). The relatively high occurrence of shrubs (39.44%), *Eragrostis lehmanniana* (11.78%) and *E. trichophora* (7.78%), which are sub-climax species, and the low percentage of climax (decreaser) species are indications that the veld in this area is in subclimax (Fig. 2.6). The plant community in this area is dominated by species belonging to Increaser 2B (40.66%; Table 2.1), which increases when veld is heavily overgrazed. Species belonging to the other groups, however, also make up a fairly large percentage of the plant community, indicating that, although the veld is not in a perfect condition, the level of overgrazing is still manageable (Table 2.1).

The most abundant species at Rietvlei are *Cynodon dactylon* (67.67%), *Eragrostis lehmanniana* Nees and *Aristida mollissima* (5.67%) (Table 2.1.). The very high occurrence of *Cynodon dactylon* (67.67%), which is a pioneer species, and the low occurrence of climax and sub-climax species are indications that the veld at Rietvlei is in a pioneer stage (Fig. 2.6). The very high percentage of 2C increaser species and the low percentage of decreaser species are indications that the veld is excessively overgrazed.

In the bushveld area at SNR *Acacia erioloba* is the dominant tree species with *Acacia karoo, Rhus lancea, Rhus pyroides, Grewia flava, Ziziphus mucronata, Diospyros lycioides, Boscia albitrunca* and *Ehretia rigida* also occurring here. The most abundant grass species in the bushveld area at Sandveld are *Eragrostis trichophora* (19.25%), *Eragrostis lehmanniana* (12.5%), *Cynodon dactylon* (10.25%) *Schmidtia pappophoroides* (7.25%) and *Brachiaria nigropedata* (4.75%) (Table 2.1). The high occurrence of shrubs (23.75%), *Eragrostis lehmannian* (12.5%) and *E. trichophora* (19.25%), which are sub-climax species and the low occurrence of climax (decreasers) and pioneer species are indications that the veld is in subclimax (Fig. 2.6). There is not high dominance of either of the three groups Increaser 2A, Increaser 2B or Increaser 2C (Table 2.1), indicating that the degree of overgrazing is manageable.

The most abundant grass species on the farm Josina are *Schmidtia pappophoroides* (14%), *Eragrostis lehmanniana* (17.5%), *Eragrostis trichophora* (30%), *Stipagrostis uniplumis* (4.25%) and *Tragus koelerioides* (3.75%) (Table 2.1). The high occurrence of *Eragrostis lehmanniana* (17.5%) and *Eragrostis trichophora* (30%), and the relatively low occurrence of climax and pioneer species are indications that the veld is in subclimax (Fig. 2.6). The plant community is dominated by species belonging to the group increaser 2A (Table 2.1) indicting the veld is moderately overgrazed.

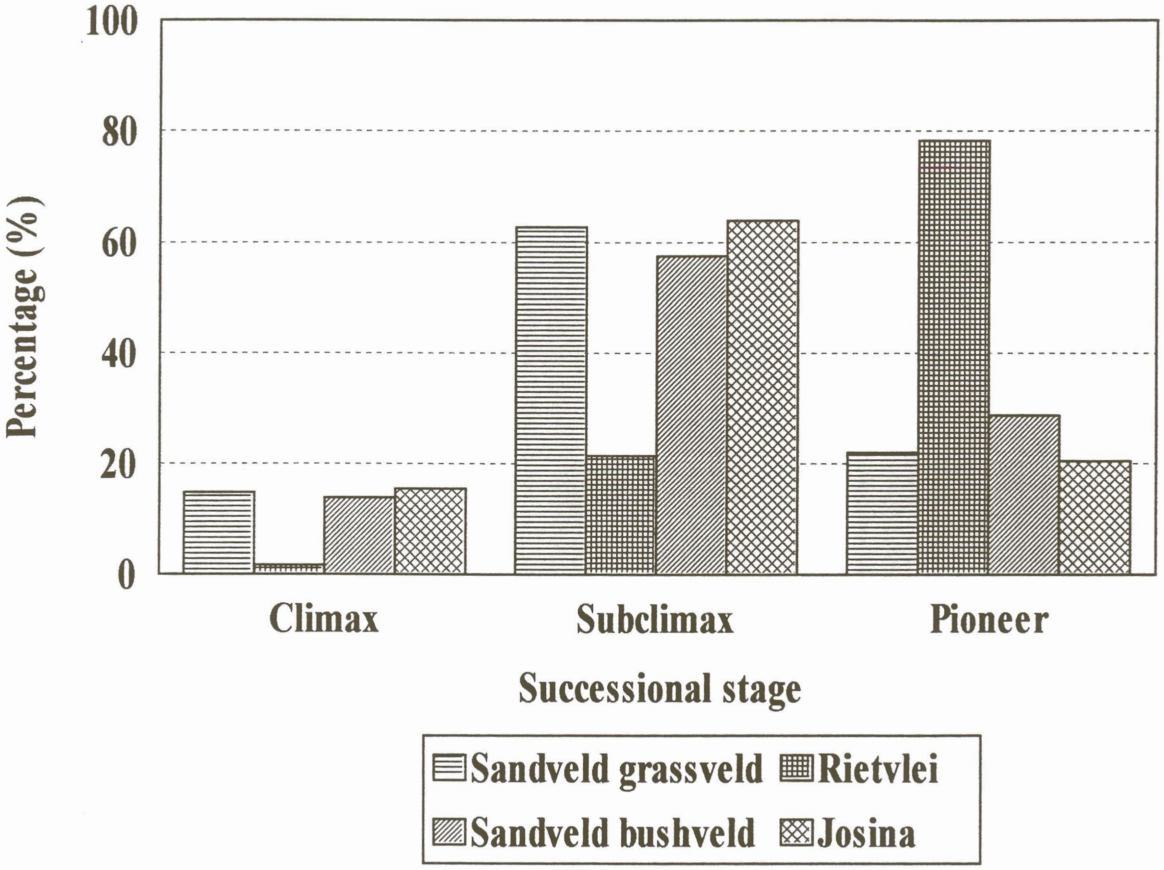


Fig. 2.6: Successional stages of the veld in the four different habitats (Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.)

Table 2.1: Percentage species composition, ecological classification, successional classification, basal cover and relative veld condition of the four different habitats (Sandveld Grassveld-natural grassveld habitat in Sandveld Nature Reserve, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat in Sandveld Nature Reserve, Josina-disturbed bushveld habitat.)

Species	**Sandveld Grassveld**	**Rietvlei (Grassveld)**	**Sandveld Bushveld**	**Josina (Bushveld)**
Decreaser	**%**	**%**	**%**	**%**
Antephora pubescens	3.33		0.5	
Brachiaria nigropedata			4.75	1
Digitaria argyrograpta	0.56			
Digitaria eriantha	0.56	0.17		
Eragrostis capensis			0.25	
Panicum coloratum	2.22			
Panicum kalaharense	0.22	0.17		
Panicum stapfianum	0.44	0.17		
Schmidtia pappophoroides	0.33		7.25	14
Setaria sphacelata	6.44	1.17	0.75	
Sporobolus fimbriatus	0.11		0.25	
Themeda triandra	0.56			0.5
Increaser 2a				
Eragrostis lehmanniana	11.78	8.33	12.5	17.5
Eragrostis trichophora	7.78	1.33	19.25	30
Stipagrostis uniplumis	2.56	2.83	0.5	4.25
Increaser 2B				
Chloris virgata			0.25	
Cynodon hirsutus	0.22			
Elionurus muticus	0.11	0.33		
Eragrostis biflora			0.25	
Eragrostis pallens	0.67	0.17		
Eragrostis gummiflua		0.17		
Urochloa panicoides	0.22		1	
Schrubs	8.3	39.44	23.75	12.25
Increaser 2C				
Aristida mollissima	1.44	5.67		
Aristida meridionalis	0.89	0.17		
Aristida congesta.	0.56	1.17	2	0.5
Aristida junciformis		0.17		
Aristida stipitata	0.33	0.5	2.25	1.75
Cynodon dactylon	6.22	67.67	10.25	14
Microchloa caffra	0.11			
Pogonarthria squarrosa	2.11	2.3		0.5
Setaria sp.	0.11			
Tragus koelerioides	0.67	0.17	0.5	3.75
Urelytrum agropyroides	0.11	0.5		
Grass seedlings	9.44		13.75	
Ecological classification				
Decreasers	14.77	1.68	13.75	15.5
Increasers 2a	22.12	12.49	32.25	51.75
Increasers 2B	40.66	8.97	25.25	12.25
Increasers 2C	21.99	78.32	28.75	20.5
Sucessional classification				
Climax	14.77	1.68	13.75	15.5
Subclimax	62.78	21.46	57.5	64
Pioneer	21.99	78.32	28.75	20.5
Basal cover	3.71	1	3.22	2.25
Relative veld condition	64.3	42.8	59.1	55.06

According to Nel (1991) the condition of the veld is primarily related to its ecological status (such as succession stage, species composition and cover density). Van Oudtshoorn (1991) also states that there is a definite correlation between the grazing value of an area and the stage of succession of the veld. Grass in a pioneer stage has a short growth cycle and is dependent on seed-production for survival. Very little energy for leaf production is available, resulting in low leafmass production and low grazing value. Climax- and subclimax-species are perennial and dependent on leaf production for survival. This survival mechanism results in a higher grazing value. Climax- and subclimax communities also prevent soil erosion and ensure the best utilization of soil moisture. Climax vegetation is therefore, from a conservation point of view, the ideal condition (Nel, 1991). The veld in the grassveld and bushveld area at Sandveld and at Josina is in a subclimax stage, and therefore in a satisfactory condition, while the veld at Rietvlei is in a pioneer stage and therefore in a less satisfactory condition (Fig. 2.6). Pioneer species should not make out more than 3% of the total botanical composition (H. du Toit, unpublished) and at Rietvlei the pioneer species make up 78.32% of the botanical composition (Fig. 2.6.).

According to Fourie et. al. (1984 in Snyman & Fouche, 1993) basal cover in arid areas is a better indicator of veld condition than plant composition. A percentage value is an indication of the percentage of ground covered by living plants. A basal cover of 10%-14% is excellent, 8%-9% good, 6%-7% relatively good and < 6% bad (H. du Toit, unpublished). Veld in good condition responds better to good rain than veld in bad condition and this results in low plant production in veld in a poor condition (Snyman & Fouche, 1993). Water flows away and pseudo-drought occurs despite good rain. The climax grass is replaced by hardier grass species, which are better able to survive drought (Snyman & Fouche, 1993). The farm Rietvlei has the lowest basal cover of only 1%. The farm Josina has a higher basal cover of 2.25%, while the highest basal cover can be found in the grassveld area (3.71%) and the bushveld area (3.22%) at Sandveld (Table 2.1). The basal cover here is an indication that the veld in all these areas is vulnerable to over-exploitation.

Relative veld condition describes the state of health of a specific part of the veld. Fourie & du Toit (1983) found that veld is in an optimal condition when 60% to 80% consists of group A species, 10% to 30% group B species, 10% to 20% group C species and 1% to 5% group D species. A reference point as suggested by Fourie & du Toit was used to measure the veld condition as follows: a plant composition of 70%, 25%, 3% and 2% for groups A, B, C and D respectively. The grassveld area at SNR has the best veld condition of 64%, followed by the bushveld area at SNR (59.1%) and Josina (55.06%) (Table 2.1). The farm Rietvlei has the lowest percentage veld condition of all four habitats (42.8%) (Table 2.1).

It can be concluded from the data in Table 2.1 and Fig. 2.6. that the veld in the grassveld area and bushveld area in SNR is in a better condition than the veld on the neighbouring farms. The veld at Josina is also in a better condition than the veld at Rietvlei.

Large Herbivores

Large herds of antelope occurred in the Hoopstad district before the settlement of farmers. According to Harris (1841 in Viljoen 1979) large herds of *Antidorcas marsupialis* (springbuck) and *Damliscus dorcal phillipsi* (blesbuck) occurred abundantly in this area. Although blesbuck does not occur in the area today springbuck were reintroduced after the proclamation of Sandveld as a nature reserve. Various other species of large antelope were also introduced and today a large variety of antelope, which settled successfully, occur here.

Large herbivores occurring in the grassveld area of SNR are *Antidorcas marsupialis* (springbuck), *Aepyceros melampus* (impala), *Alcelaphus buselaphus* (red hartebeest), *Oryx gazella* (gemsbuck), *Taurotragus oryx* (eland), *Connochaetes gnou* (black wildebeest) and *Equus burchelli* (zebra). Game counts were done from October 1997 to May 1998 and the average abundance per month for each species was taken as an indication of abundance of these species. Black wildebeest occurred most abundantly

(258), followed by gemsbuck (159), zebra (147) and red hartebeest (128) (Table 2.2.). The largest concentration of large herbivores in this area occurred during November. Their numbers in this area decreased from December to February and increased again during March (Table 2.2). This is probably due to the fact that most of the large herbivores favour the trees on other parts of the reserve during the hotter time of the year.

A greater diversity of large herbivores occurs in the bushveld area of Sandveld than in the grassveld area. Large herbivores occurring here are *Antidorcas marsupialis (*springbuck), *Aepyceros melampus* (impala), *Alcelaphus buselaphus* (red hartebeest), *Oryx gazella (*gemsbuck), *Hippotragus equinus (*roan), *Hippotragus niger* (sable), *Giraffa camelopardalis* (giraffe), *Tragelaphus strepsiceros* (kudu), *Taurotragus oryx* (eland), *Connochaetes taurinus* (blue wildebeest), *Syncerus caffer* (buffalo), *Equus burchelli* (zebra) and *Ceratotherium simum* (white rhinoceros). Game counts were done from August 1997 to May 1998 and the average abundance per month for each species was taken as an indication of abundance of these species. Springbuck occurred most abundantly in this area (836), followed by gemsbuck (346), blue wildebeest (262) and red hartebeest (216) (Table 2.3).

The farm Rietvlei is fenced off into pastures. The only large herbivores occurring on this farm are cattle. Each pasture of 5 ha is grazed by ±20 head of cattle per year.

The farm Josina is in the process of being turned into a game farm. The result is a combination of wild herbivores and domesticated herbivores occurring together in the same area. Currently 40 sheep, 80 head of cattle, 60 Springbuck and 40 Eland occur on the farm. The farm is not fenced off into different camps and the animals are free to move across the whole area.

Table 2.2: Distribution of large herbivores in the grassveld area of SNR based on game counts from October 1997 to May 1998.

Month	Ruminants						Non-ruminants	
	Antidorcas marsupialis (Springbuck)	*Aepyceros melampus* (Impala)	*Alcelaphus buselaphus* (Red Hartebeest)	*Oryx gazella* (Gemsbuck)	*Taurotragus oryx* (Eland)	*Connochaetes gnou* (Black wildebeest)	*Equus burchelli* (Zebra)	**Total**
1997								
October		8	7	29	9	29	21	**103**
November			37	35	32	77	23	**204**
December	18		31			7	61	**117**
1998								
February			15	12	10	37		**74**
March	7	12	22	47	9	44		**141**
May			16	36		64	42	**158**
Total	**25**	**20**	**128**	**159**	**60**	**258**	**147**	

Table 2.3: Distribution of large herbivores in the bushveld area of SNR based on game counts from August 1997 to May 1998.

Month	Ruminants											Non-ruminants		
	Antidorcas marsupialis (Springbuck)	*Aepyceros melampus* (Impala)	*Alcelaphus buselaphus* (Red Hartebeest)	*Oryx gazella* (Gemsbuck)	*Hippotragus equinus* (Roan)	*Hippotragus niger* (Sable)	*Giraffa camelopardalis* (Giraffe)	*Tragelaphus strepsiceros* (Kudu)	*Taurotragus oryx* (Eland)	*Connochaetes taurinus* (Blue wildebeest)	*Syncerus caffer* (Buffalo)	*Equus burchelli* (Zebra)	*Ceratotherium simum* (White rhinocerous)	Tot.
1997														
Aug	40		2	52		15				36		7	3	**155**
Sept	85	7	18	35		6		6	5	16	2	14	4	**198**
Oct	33	2	9	23		5	4	2	1	15	2	3	2	**101**
Nov	106		23	38	2	5	11	2	3	19	1	3	1	**214**
Dec	170	4	47	21	1		3			45				**291**
1998														
Febr	47	2	13	21	2	9	2			23		2	8	**129**
March	135	16	36	38	1	5	7	2		34		2	2	**278**
Apr	130	18	33	52	1	6	3	1	2	39		13	1	**299**
May	90	15	35	66		8	2	4	2	35		6	2	**265**
Total	**836**	**64**	**216**	**346**	**7**	**59**	**32**	**17**	**13**	**262**	**5**	**50**	**23**	

Dung beetles

All the above mentioned factors will probably influence the distribution of dung beetle assemblages in the area significantly. There is a diverse dung beetle fauna at SNR and the neighbouring farms. Eighty-three species belonging to 26 genera were collected in the area from July 1996 to June 1998 (Table 2.4). All the functional groups proposed by Doube (1990) (F.G. I – F.G. VII) are represented here and sizes range from 0.0006 ± 0.0002g dry mass to 1.49 ± 0.27g dry mass (Table 2.4).

Table 2.4: Dung beetle species occurring at Sandveld Nature Reserve and neighbouring farms

Abbreviation	Name	Functional Group	Mean Dry Mass (g) ± SD (n=20)
at	*Allogymnopleurus thalassinus*	II	0.061 ± 0.51
ap	*Aphodius (Aganocrossus) periculosus*	VII	0.002 ± 0.0005
av	*Aphodius (Aganocrossus) vestitus*	VII	0.002 ± 0.0007
al	*Aphodius (Bodilus) laterosetosus*	VII	0.002 ± 0.003
apl	*Aphodius (Labarus) pseudolividus*	VII	0.002 ± 0.0005
ad	*Aphodius (Mesontoplatys) dorsalis*	VII	0.0007 ± 0.012
an	*Aphodius (Nialaphodius) nigrita*	VII	0.002 ± 0.004
adu	*Aphodius (Pharaphodius) dubiosus*	VII	0.003 ± 0.0005
ai	*Aphodius (Pharaphodius) impurus*	VII	0.003 ± 0.0007
as	*Aphodius (Plagiogonus) separatus*	VII	0.001 ± 0.0005
ats	*Aphodius (Pleuraphodius) teter sensu lato*	VII	0.0006 ± 0.0002
ac	*Aphodius (Trichaphodioides) calcaratus*	VII	0.002 ± 0.0004
acs	*Aphodius consimilis*	VII	0.002 ± 0.0007
cf	*Caccobius ferruginus*	VI	0.004 ± 0.003
cs	*Caccobius seminulum*	VI	0.001 ± 0.003
cc	*Catharsius calaharicus*	III	0.588 ± 0.02
cm	*Catharsius melancholicus*	III	0.59 ± 0.03
ct	*Catharsius tricornutus*	III	0.686 ± 0.001
ch	*Chironitis sp*	IV	0.072 ± 0.001
cts	*Colobopterus (Teuchestes) sorex*	VII	0.031 ± 0.0002
ccs	*Copris cassius*	III	0.069 ± 0.002
ce	*Copris elphenor*	III	0.52 ± 0.0003
ci	*Copris inhalatus*	III	0.018 ± 0.04
de	*Depanocanthus (Pseudoxyomus) eximius*	VII	0.002 ± 0.0005
dr	*Drepanocanthus (Pseudoxyomus) rubescens*	VII	0.001 ± 0.0003
dp	*Drepanocerus putrizii*	V	0.004 ± 0.0005
dc	*Drepanopodus costatus*	I	0.132 ± 0.003
eg	*Epirinus gratus*	V	0.009 ± 0.001
ea	*Euoniticellus africanus*	IV	0.04 ± 0.002
ei	*Euoniticellus intermedius*	IV	0.029 ± 0.007
ga	*Gymnopleurus aenescens*	II	0.023 ± 0.01
g4	*Gymnopleurus sp. 4*	II	0.025 ± 0.03
ha	*Heliocopris atropos*	III	0.61 ± 0.06
hya	*Hyalonthophagus alcyon*	IV	0.021 ± 0.04
lm	*Liatongus millitaris*	IV	0.02 ± 0.006

Table 2.4 Continued: Dung beetle species occurring at Sandveld Nature Reserve and neighbouring farms

Abbreviation	Name	Functional Group	Mean Dry Mass (g) ± SD (n=20)
me	*Metacatharsius exiguus*	IV	0.07 ± 0.05
ml	*Metacatharsius laticollis*	IV	0.08 ± 0.02
m3	*Metacatharsius sp. 3*	V	0.004 ± 0.0005
nr	*Neosisyphus ruber*	II	0.019 ± 0.002
op	*Oniticellus planatus*	VII	0.029 ± 0.03
oax	*Onitis alexis*	IV	0.46 ± 0.004
oay	*Onitis aygulus*	IV	0.51 ± 0.01
ocf	*Onitis caffer*	IV	0.45 ± 0.02
ocu	*Onitis confusus*	IV	0.49 ± 0.009
oun	*Onitis uncinatus*	IV	0.43 ± 0.0004
oae	*Onthophagus aeruginosus*	IV	0.01 ± 0.002
ocb	*Onthophagus carbonarius*	IV	0.022 ± 0.004
oeb	*Onthophagus ebenus*	IV	0.023 ± 0.003
ofi	*Onthophagus fimetarius*	IV	0.01 ± 0.0009
of	*Onthophagus flavimargo*	IV	0.009 ± 0.06
og	*Onthophagus gazella*	IV	0.027 ± 0.002
ol	*Onthophagus leucopygus*	IV	0.009 ± 0.03
oob	*Onthophagus obtusicornis*	IV	0.018 ± 0.004
opi	*Onthophagus pilosus*	IV	0.011 ± 0.006
opu	*Onthophagus pugionatus*	IV	0.013 ± 0.09
oq	*Onthophagus quadraliceps*	IV	0.014 ± 0.005
osu	*Onthophagus sugillatus*	V	0.003 ± 0.0008
ova	*Onthophagus variegatus*	V	0.003 ± 0.0006
ovi	*Onthophagus vinctus*	V	0.006 ± 0.0004
o1	*Onthophagus sp. 1*	V	0.005 ± 0.001
o2	*Onthophagus sp. 2*	V	0.0018 ± 0.0009
o4	*Onthophagus sp. 4*	V	0.002 ± 0.0005
o16	*Onthophagus sp. 16*	V	0.006 ± 0.0004
o18	*Onthophagus sp. 18*	V	0.005 ± 0.001
ox	*Onthophagus xanthopterus*	IV	0.01 ± 0.009
pf	*Pachylomerus femoralis*	I	1.49 ± 0.27
po	*Pachylomerus opaca*	I	0.635 ± 0.24
p4	*Pedaria sp. 4*	VI	0.006 ± 0.026
pfl	*Phalops flavocinctus*	IV	0.034 ± 0.009
pw	*Phalops wittei*	IV	0.035 ± 0.014
ra	*Rhysemus africanus*	VII	0.0007 ± 0.003
sa	*Scarabaeus ambiguus*	II	0.207 ± 0.026
san	*Scarabaeus anderseni*	II	0.0289 ± 0.23
sb	*Scarabaeus bohemani*	II	0.066 ± 0.09
sf	*Scarabaeus flavicornis*	II	0.158 ± 0.31
sg	*Scarabaeus goryi*	I	1.351 ± 0.19
si	*Scarabaeus inoportunus*	II	0.158 ± 0.002
s1	*Scarabaeus sp. 1*	II	0.066 ± 0.01
sm	*Sisyphus macroruber*	II	0.0188 ± 0.001

Voucher specimens of all material studied are stored in the Department of Zoology and Entomology, U.F.S., Bloemfontein, South Africa.

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 $D_{mg}=(S-1)/\ln N$, 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 $H'=-\Sigma [p_i \ln p_i]$, where p_i is the proportional abundance of the i'th species=(n_i/N). Shannon evenness is calculated using the formula $E=H'/\ln S$. 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.

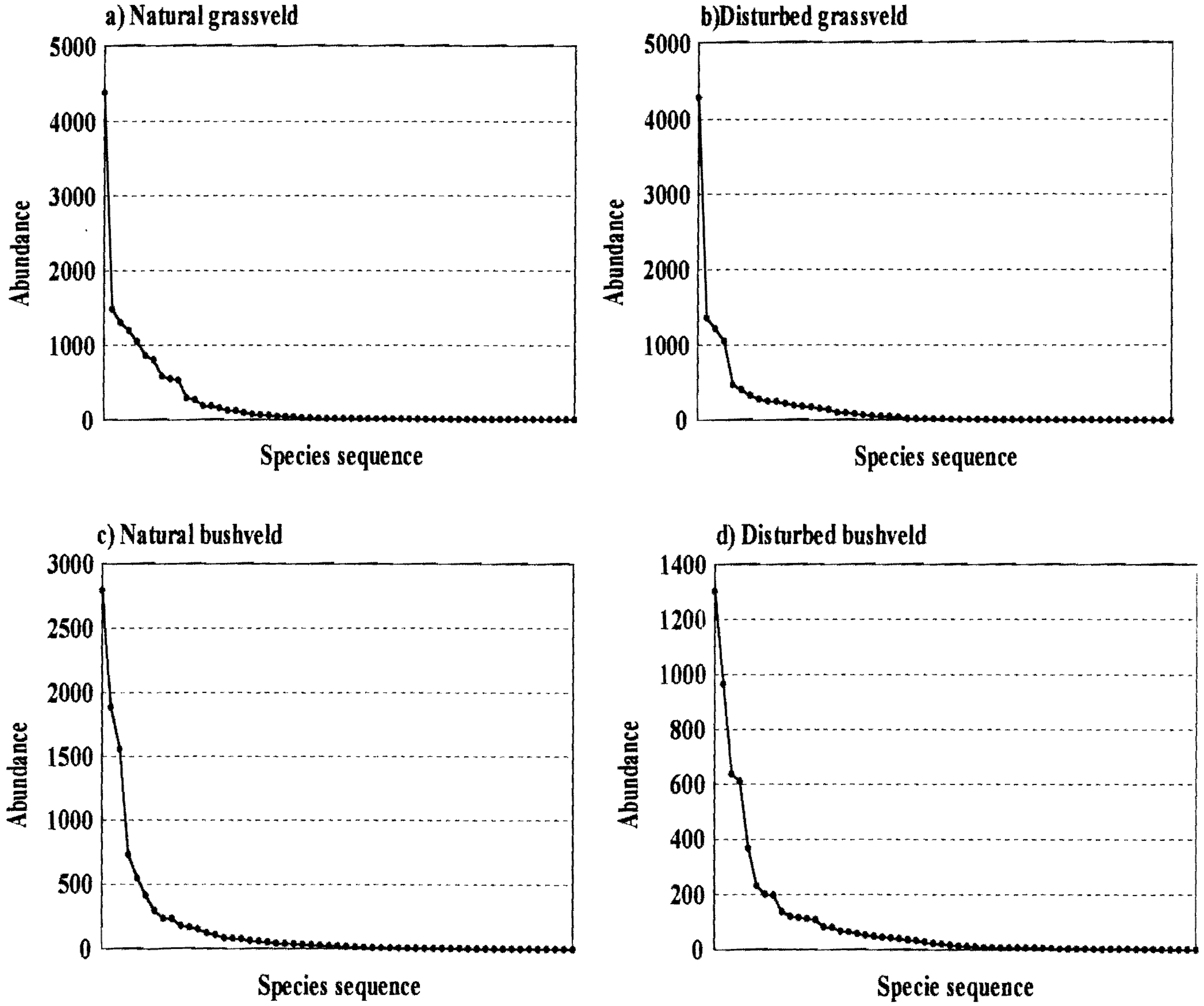


Fig. 3.1: Rank species abundance plots for dung beetle assemblages in four different habitats: a) Sandveld Grassveld-natural grassveld habitat, b) Rietvlei-disturbed grassveld habitat, c) Sandveld Bushveld-natural bushveld habitat, d) Josina-disturbed bushveld habitat.

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 22nd 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 flavicomis	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 obtusicomis	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).

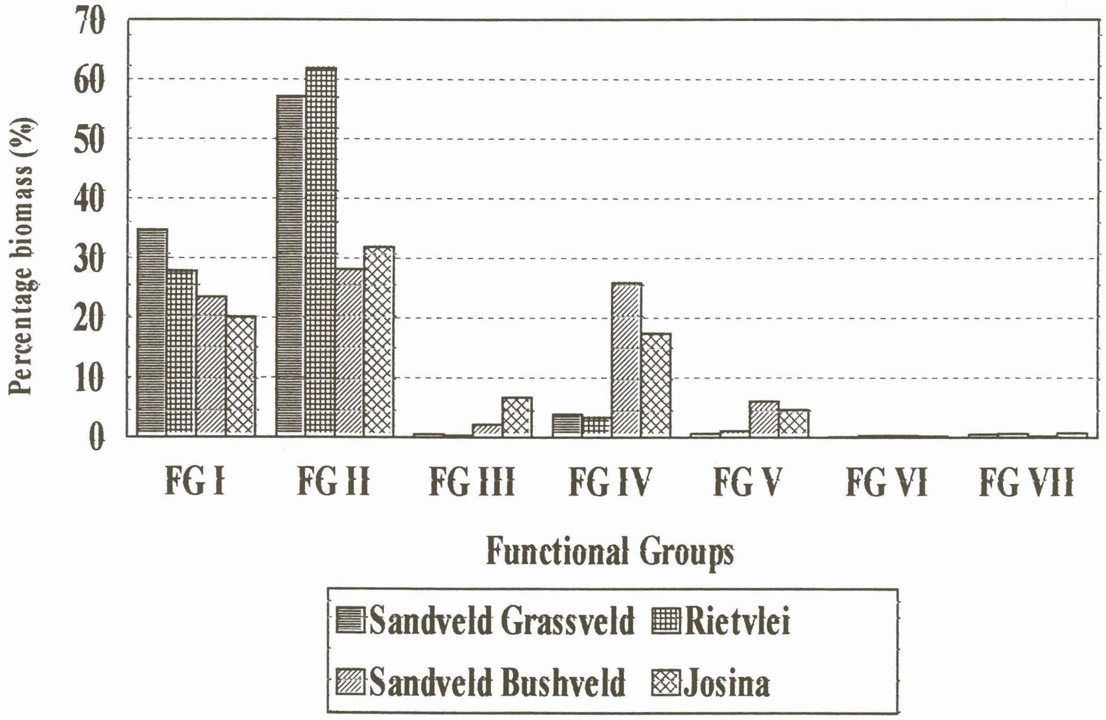


Fig. 3.2: Functional group classification, using the biomass in each functional group in each of the four habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.

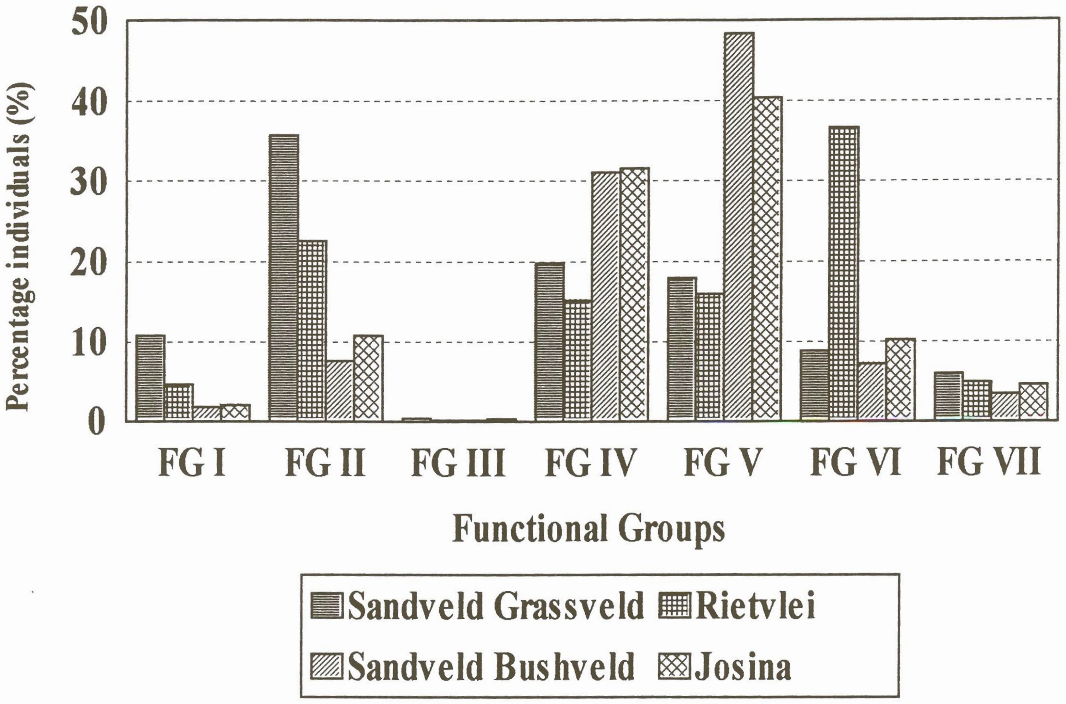


Fig. 3.3: **Functional group classification, using the number of individuals in each functional group in each of the four habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.**

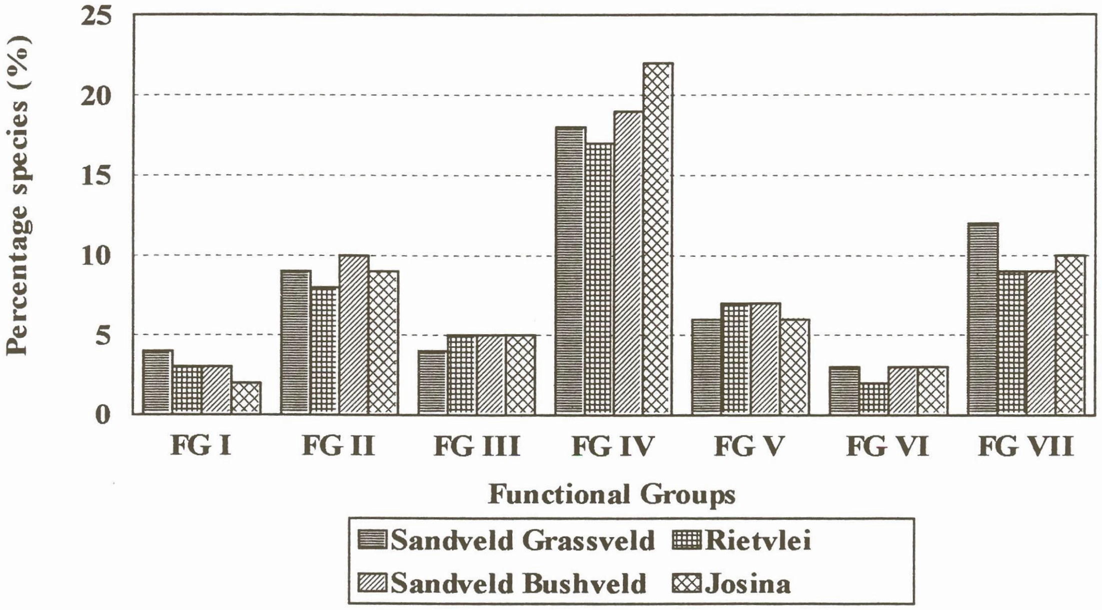


Fig. 3.4: **Functional group classification, using the number of species in each functional group in each of the four habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.**

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.

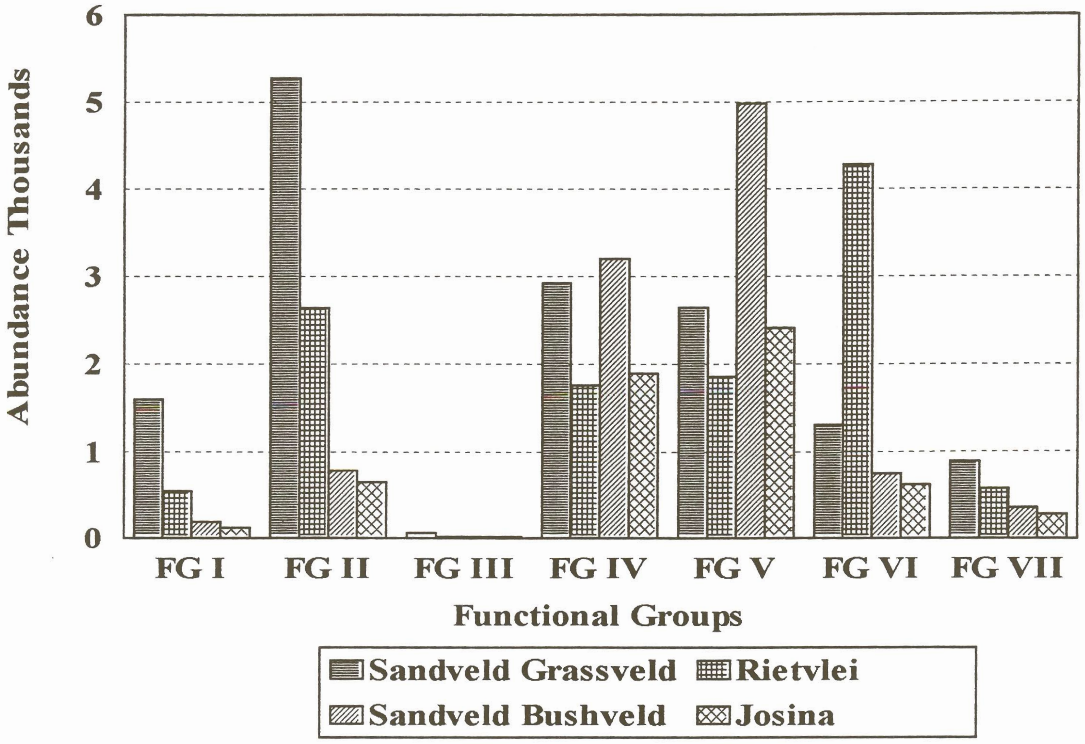


Fig. 3.5: Distribution of different functional groups in four different habitats: Sandveld Grassveld-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, Sandveld Bushveld-natural bushveld habitat, Josina-disturbed bushveld habitat.

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.	%	Rietvlei No. ind.	%	S&B No. ind.	%	Josina No. ind.	%	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.

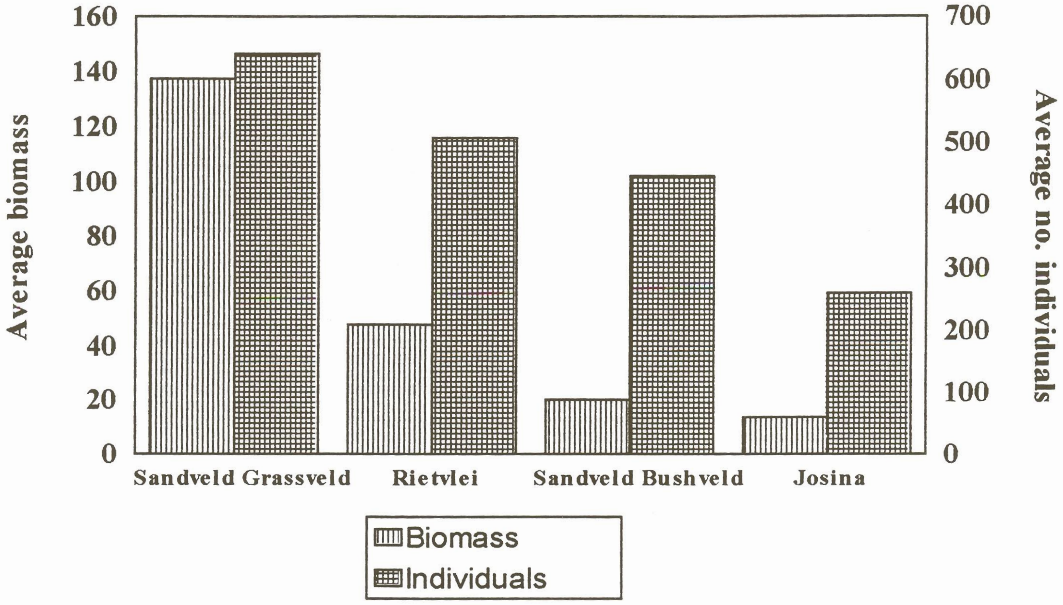


Fig. 3.6: Biomass and number of individuals based on two years average (July 1996-June 1998) in four different habitats: S.G.-natural grassveld habitat in S.N.R., Rietvlei-disturbed grassveld habitat, S.B.-natural bushveld habitat in S.N.R., Josina-disturbed bushveld habitat.

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.

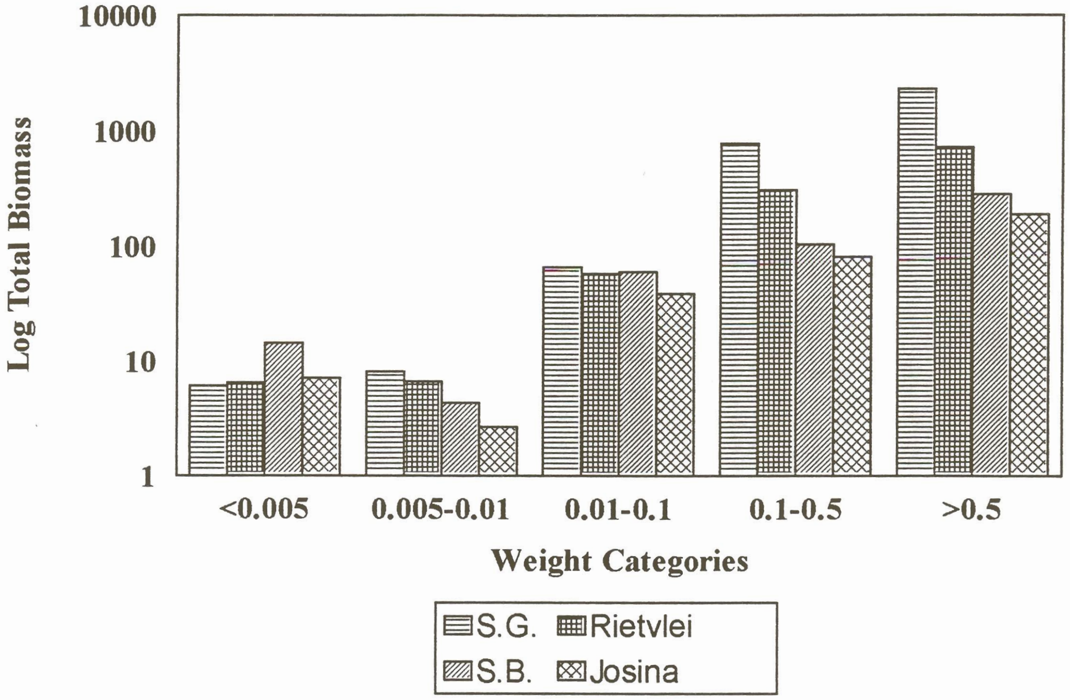


Fig 3.7: Distribution of dung beetle biomass according to size in four different habitats: S.G.-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, S.B.-natural bushveld habitat, Josina-disturbed bushveld habitat.

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).

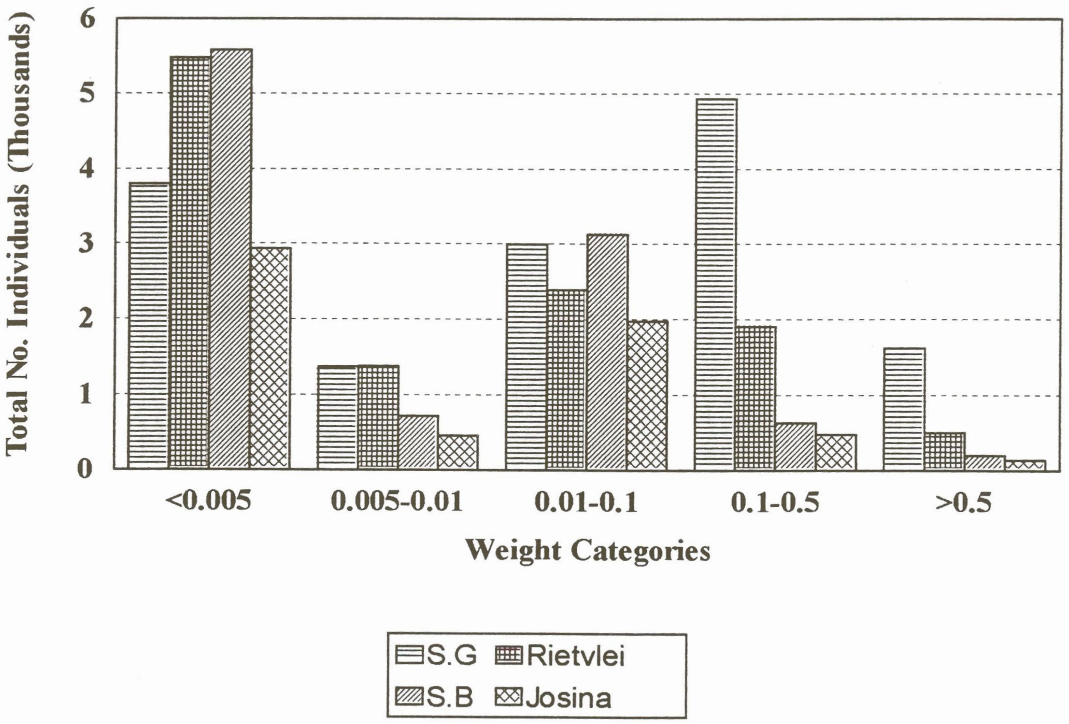


Fig 3.8: Distribution of dung beetle individuals according to size in four different habitats: S.G.-natural grassveld habitat, Rietvlei-disturbed grassveld habitat, S.B.-natural bushveld habitat, Josina-disturbed bushveld habitat.

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.

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. 11 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 $Dmg=(S-1)/\ln N$, 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 $E=H'/\ln S$.

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.)

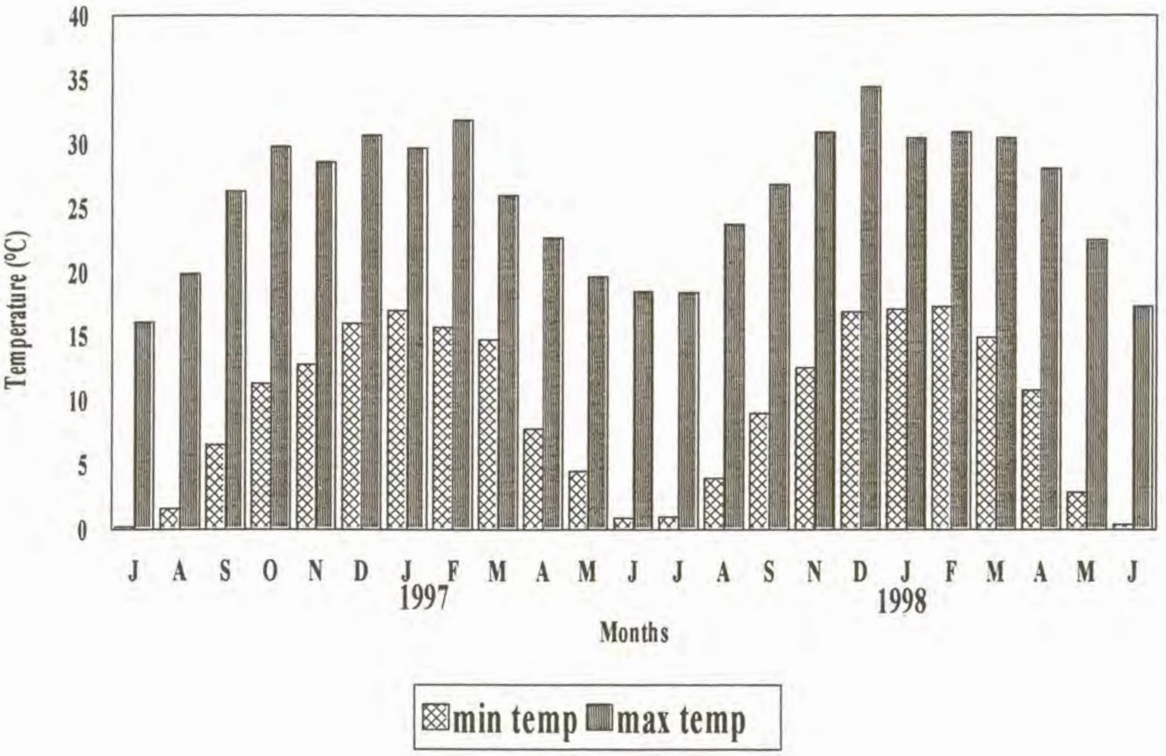


Fig. 4.1. Average monthly minimum and maximum temperatures at Sandveld Nature Reserve (July 1996 - June 1998)

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.).

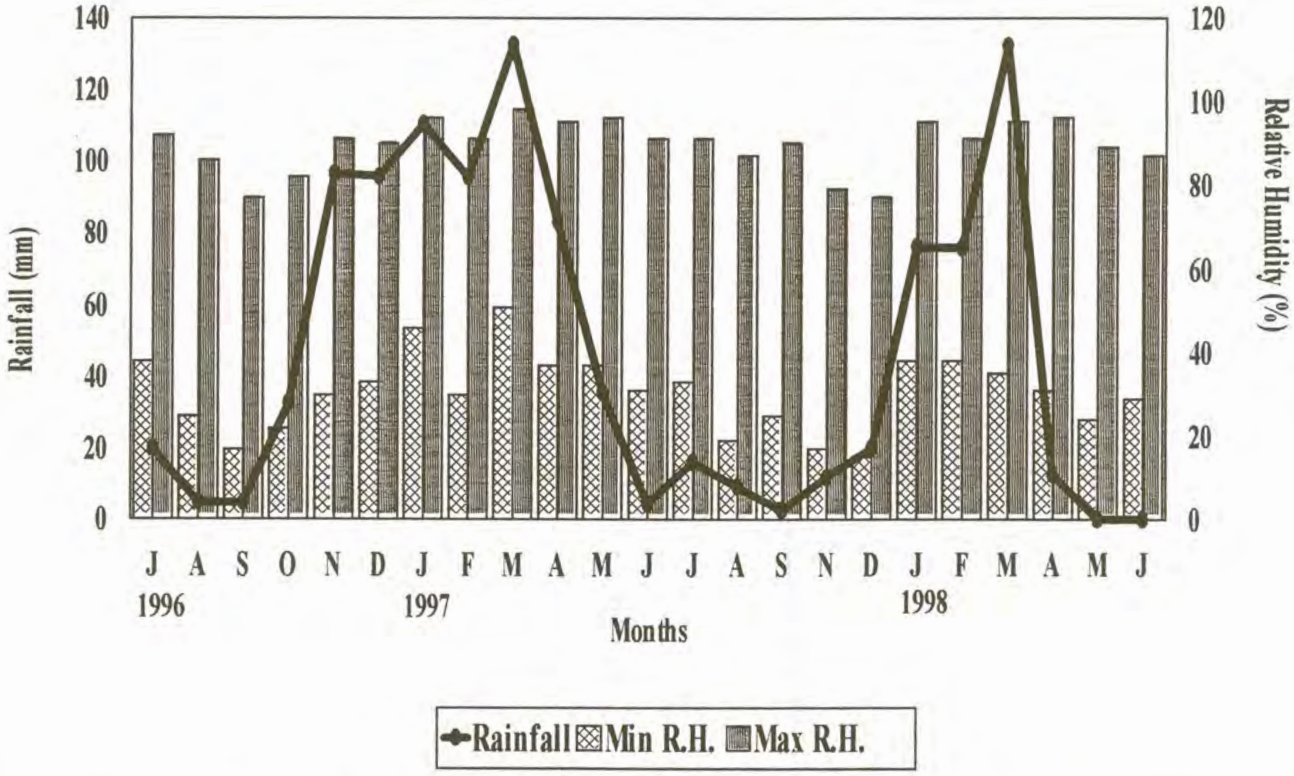


Fig. 4.2. Average monthly minimum and maximum relative humidity and average monthly rainfall at Sandveld Nature Reserve (July 1996 - June 1998).

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.

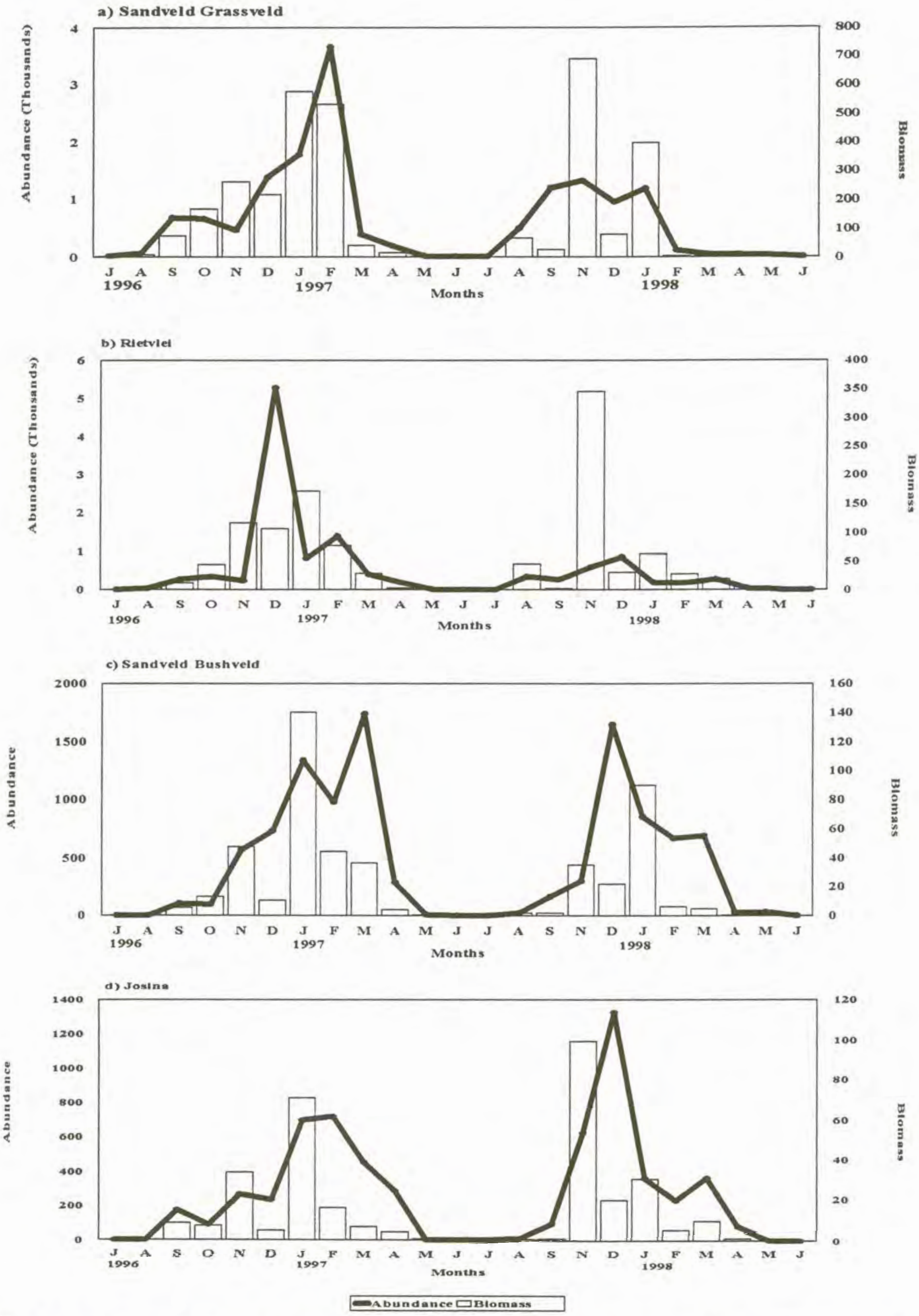


Fig. 4.3: Seasonal abundance and biomass in dung beetle assemblages over a period of two years (July 1996 - June 1998) in four different habitats.

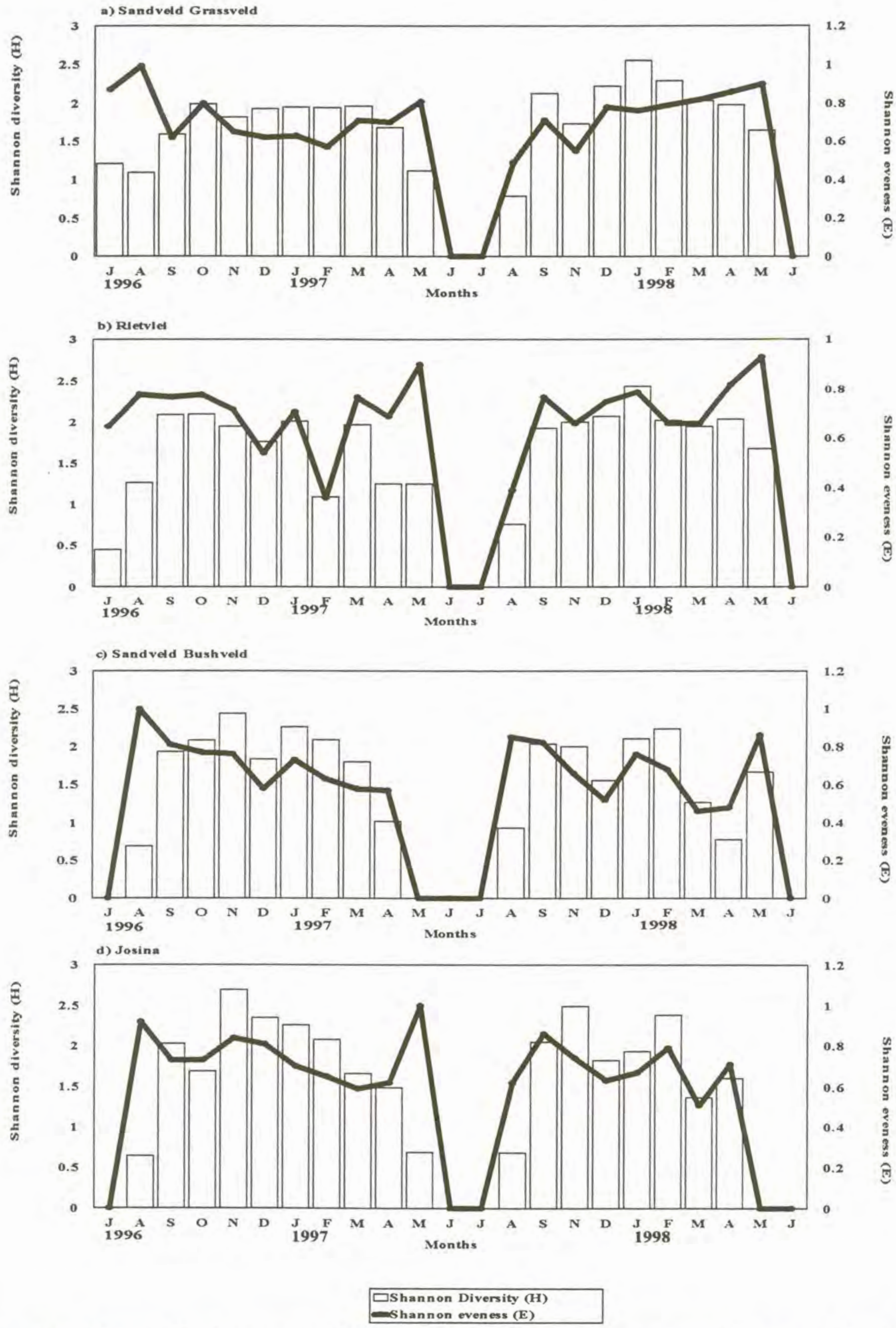


Fig. 4.4: Seasonal change in Shannon diversity and evenness for dung beetle assemblages in four different habitats.

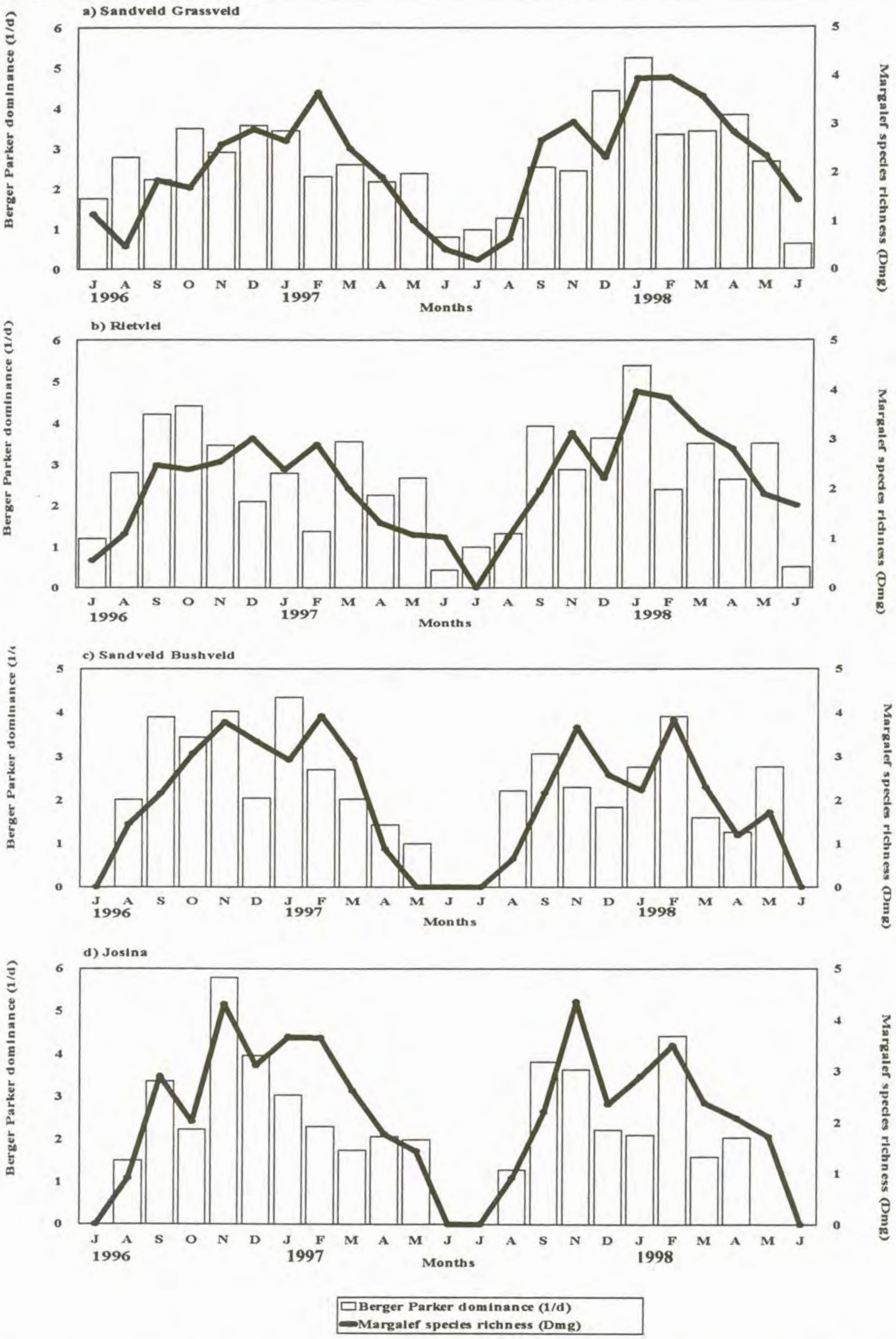


Fig. 4.5: Seasonal change in Berger Parker dominance and Margalef species richness for dung beetle assemblages in four different habitats.

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.

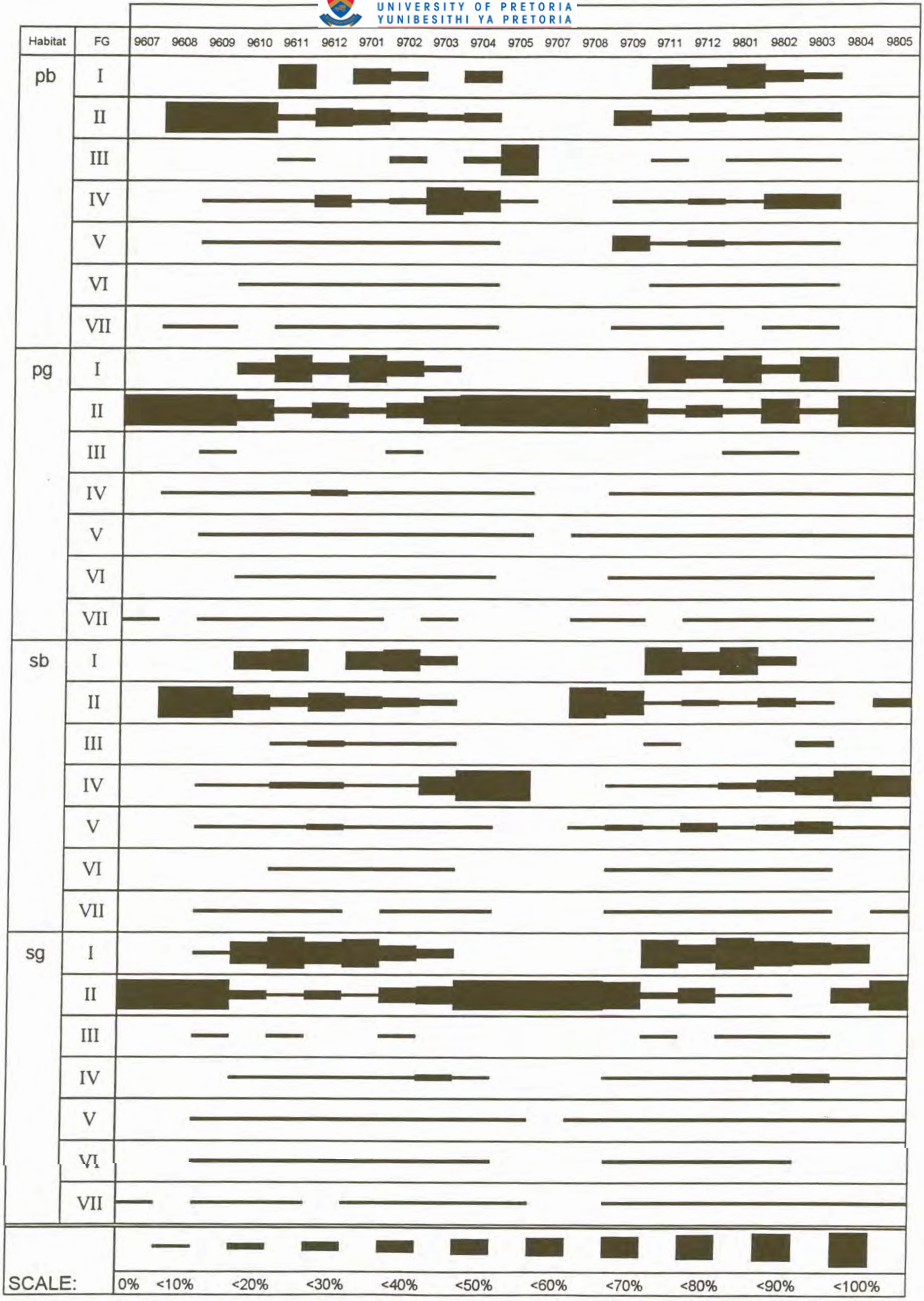


Fig. 4.6. Seasonal change in functional group (F.G.) structure, in terms of biomass, in dung beetle assemblages in different habitats (pb - disturbed bushveld, pg - disturbed grassveld, sb - natural bushveld, sg - natural grassveld)

Seasonal distribution of individual species

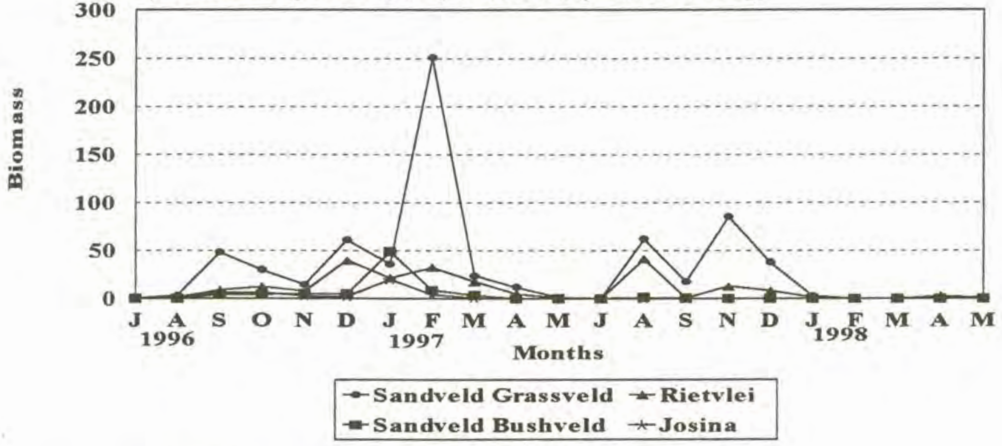
The most common dung beetle species in the whole study area throughout the study period was *Scarabaeus flavicornis, Pachylomerus femoralis, Onthophagus obtusicornis, Onthophagus sugillatus, Onthophagus variegatus* and *Caccobius seminulum.* The abundance of these species ranged between 1500 and 4500 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.).

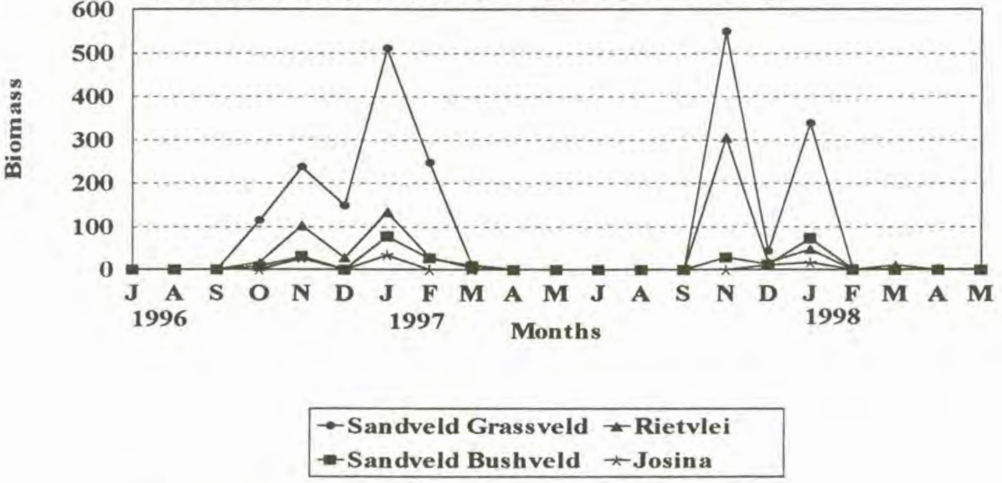
Although species in the natural and disturbed habitats showed similar seasonal patterns, all the species that occurred dominantly in either the bushveld or grassveld habitats were consistently more abundant in the natural than the disturbed habitats (Fig. 4.7.). This might be an indication that the microclimatic 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.

a) Scarbaeus flavicornis (individual dry mass: 0.158g)



b) Pachylomerus femoralis (individual dry mass: 1.49g)



c) Onthophagus obtusicornis (individual dry mass: 0.018g)

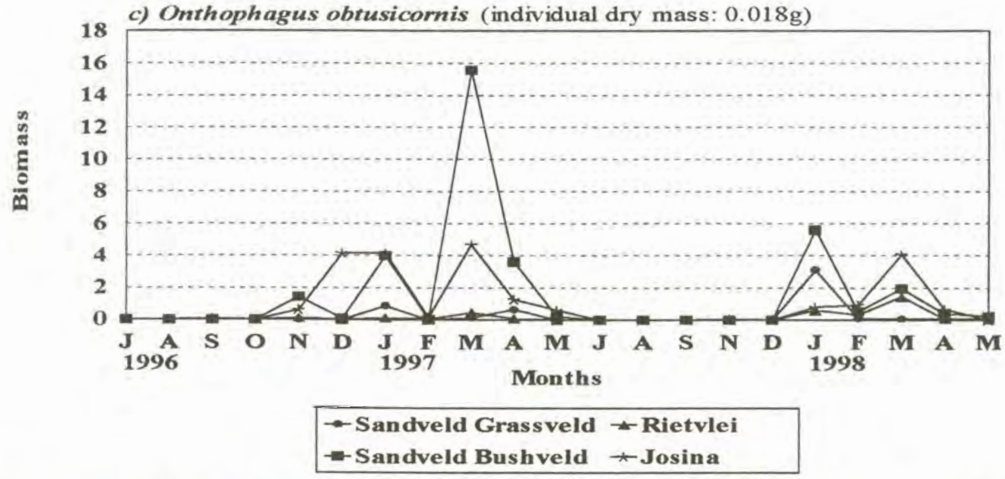
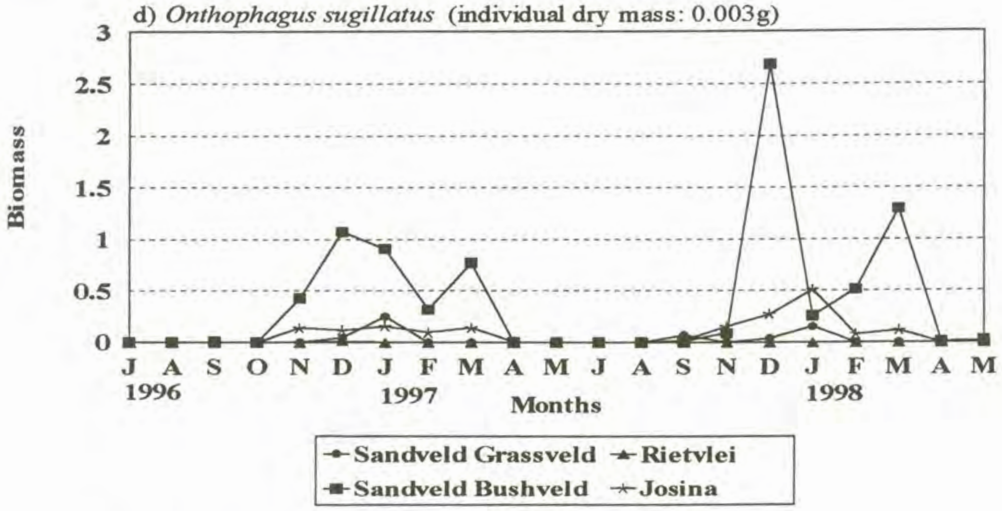
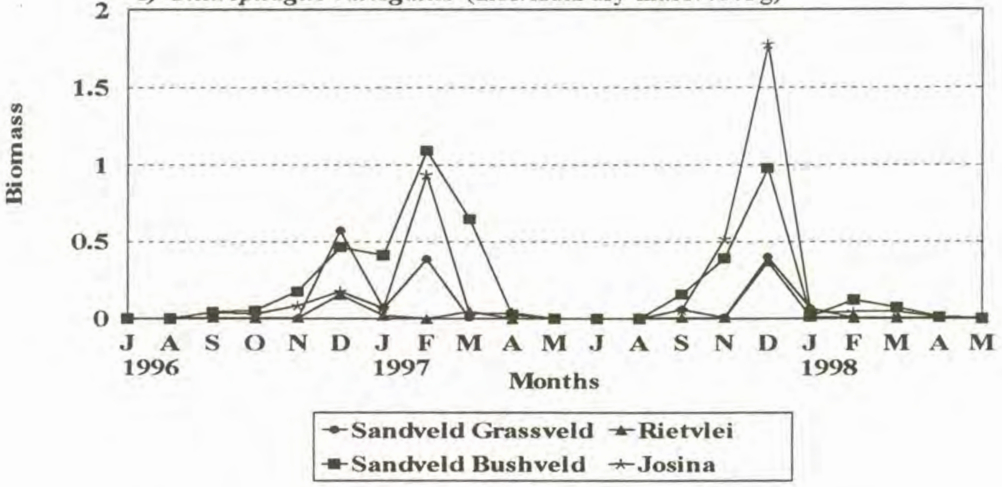


Fig. 4.7: Seasonal distribution of dominant dung beetle species from July 1996 to June 1998 at S.N.R. and neighbouring farms: a) *Scarabaeus flavicornis,* b) *Pachylomerus femoralis,* c) *Onthophagus obtusicornis*

d) *Onthophagus sugillatus* (individual dry mass: 0.003g)



e) ***Onthophagus variegatus*** (individual dry mass: .003g)



f) ***Caccobius seminulum*** (individual dry mass: 0.001g)

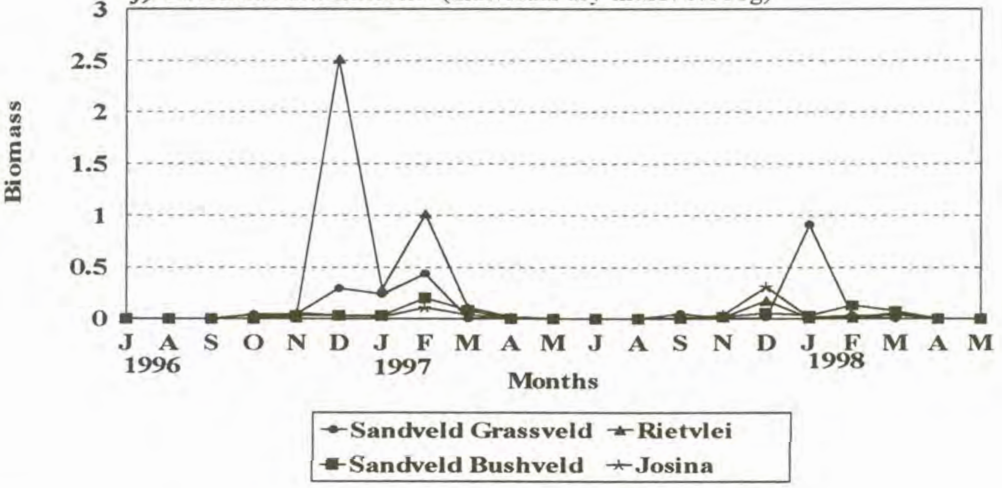


Fig. 4.7. (continued): Seasonal distribution of dominant dung beetle species from July 1996 to June 1998 at S.N.R. and neighbouring farms: d) *Onthophagus sugillatus,* e) *Onthophagus variegatus,* f) *Caccobius seminulum*

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.).

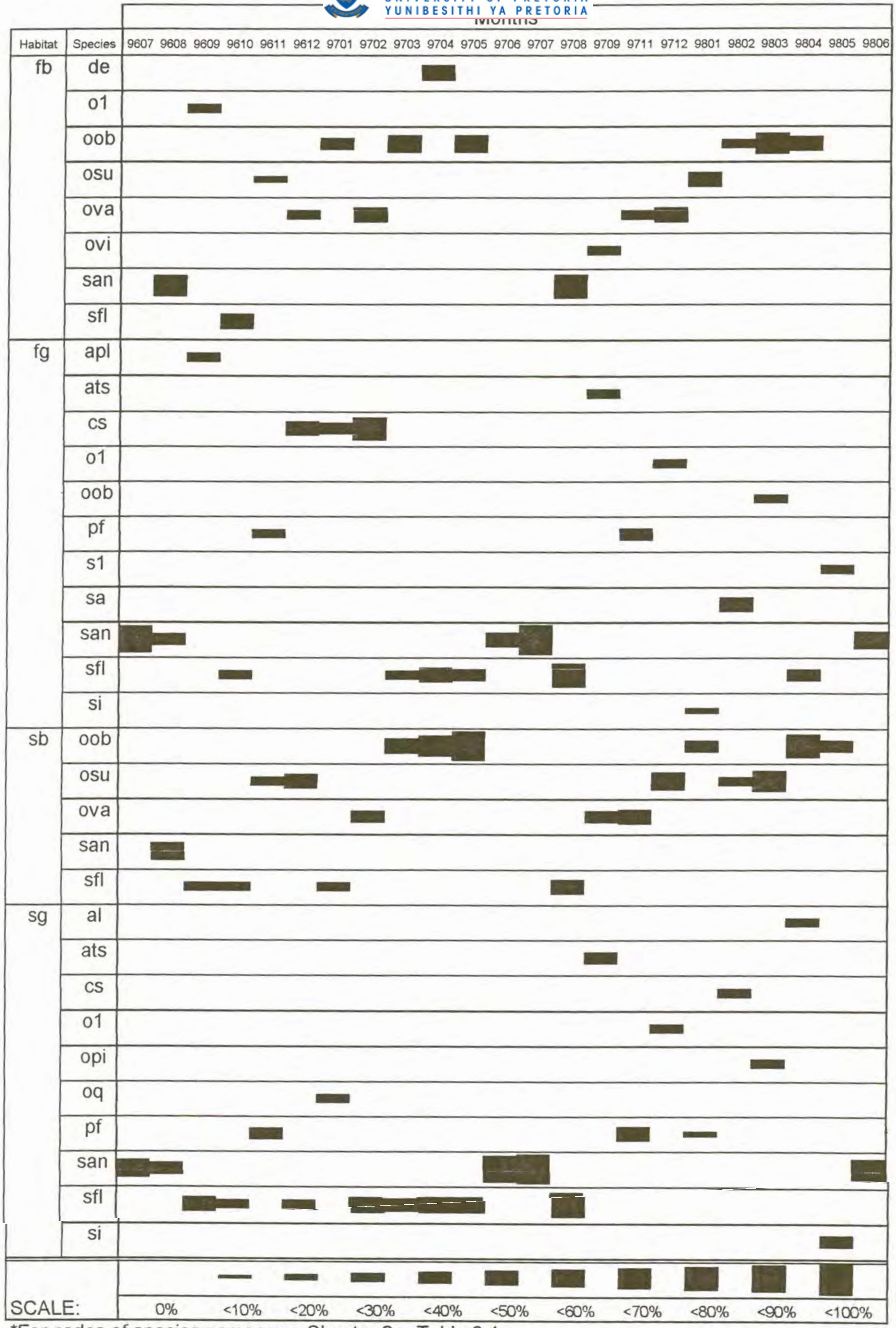
In terms of biomass fewer species dominated seasonally. Two species dominated in the grassveld habitats, viz. *P. femoralis* and *S. flavicornis.* In the natural grassveld habitat *P. femoralis* showed biomass dominance during most of the summer months, from October 1996 to February 1997 and from November 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.).

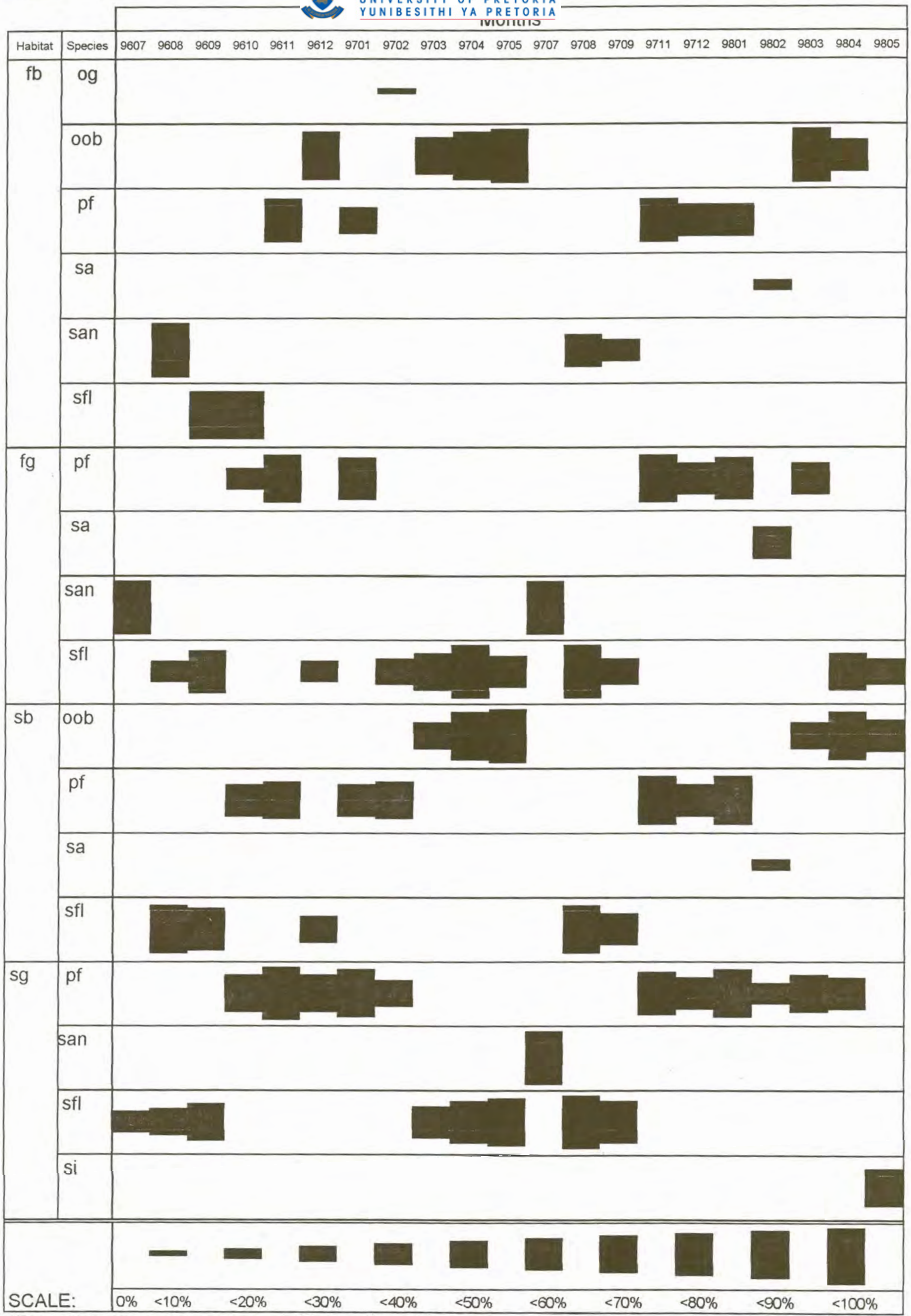
During the spring and summer months the larger, most effective competitor, *P. femoralis,* belonging to F.G. I, dominated the natural grassveld habitat in terms of biomass. This dung beetle showed less frequent biomass dominance in the disturbed grassveld and the bushveld habitats, enabling the smaller 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.

Chapter 5

PATTERNS OF DIEL FLIGHT ACTIVITY IN DUNG-INHABITING BEETLES IN DIFFERENT HABITATS DURING THREE DIFFERENT SEASONS

5.1. INTRODUCTION

Dung is a typical example of a temporarily and spatially unstable microhabitat. Short durational stability selects for quick colonisation and resource use. Dung is, however, generally distributed in small patches, which appears at regular intervals in the environment (Hanski, 1980a). The time of the day the dung beetles colonise the dung is an important aspect of dung beetle ecology and distribution. There are several ecological, behavioural and physiological traits for improved competitive ability in a dung microhabitat. According to Galante *et al.* (1991, 1995) dung beetles show greatly diversified activity in space resulting in an irregular distribution of dung beetle biomass in both space and time. Depending on the species, flight activity of dung beetles begins at different times during the day, resulting in a rapid succession of dung beetles in the dung, which ultimately leads to the disappearance of the dung microhabitat. The beginning of this succession is dependent on the time the dung is dropped and the habitat in which it is dropped. Adaptations such as rapid development, high production/assimilation efficiency and good flight ability is necessary for the survival of insects colonising this temporary habitat (Koskela, 1979). There are also ecological adaptations in dung beetles, which differ in different species and may facilitate coexistence of species in the microhabitat. These are differences in the type of dung used, and how it is used, diel activity, seasonality and habitat selection at small and large spatial scales (Hanski & Cambefort, 1991a). According to Caveney *et al.* (1995) intense competition for limited resources has contributed to the evolution of flight behaviour where each dung beetle species flies for a limited and often different period of the day. Differences in diel activity patterns may decrease spatial covariance and thus decrease competition in some cases (Otronen & Hanski, 1983). In certain parts of Sandveld Nature Reserve, during summer, the competition for dung is so intense that a dung pat seldom lasts more than 24 hours. According to Hanski (1990) diel activity becomes an important factor whenever the habitat patches last for less than 24 hours. If exclusion of competitors from the resource is not possible, or economical, a female may then attempt to give as early a start to her offspring as possible. Depending on the species, dung beetle flight activity can be diurnal, crepuscular or nocturnal and all species of dung beetle show some variation in diel activity throughout the day. Some diurnal species fly throughout the day and some nocturnal species throughout the night, but others have restricted flight periods lasting only for a few hours (Doube, 1991). Caveney *et al.* (1995) found that crepuscular activity occurs when the number of active dung beetles increases with a drop in light intensity at dusk or an increase in light intensity at dawn, while nocturnal flight activity occurs at near-constant low light intensities. The diel flight of dung beetles may be regulated by many different factors, which include abiotic factors (temperature, humidity, wind, light) or biotic factors (predation, competition), and the releasing factor may be formed by a combination of these factors. Houston & McIntyre (1985) consider ambient light intensity to be the dominant factor influencing flight activity, while Caveney *et al.* (1995) found that the flight activity may also be triggered by other factors such as temperature, starvation, local topography and wind. According to Koskela (1979) there are two components in the evolution of dispersal flight between resource patches. Firstly there is a trend towards maximisation of the benefit/cost ratio within the species, where benefit is derived from the utilisation of suitable patches, and cost refers to dispersal flight. Secondly, the evolution within a species will also be constrained by abiotic and biotic factors and the flight activity pattern of dung beetles may be seen as the net result of this interaction. According to Landin (1961) the releasing factor for flight in dung beetles may be formed by a combination of temperature, air humidity, and light. The difference in abiotic factors in different habitats will influence the population of dung beetles occurring in the habitat and this in turn will influence the competition and predation. The differences in abiotic and biotic factors in different habitats will therefore also influence the diel flight of dung beetles occurring in different habitats. The flexibility in the timing of the diel flight activity is an important adaptation in dung beetles allowing them to survive in many different habitats. As dung beetles depend on olfactory orientation, the structure of the macrohabitat may also affect their ability to find the dung (Koskela & Hanski, 1977). In this respect exposed habitats may be more favourable to dung beetles than habitats with dense vegetation. The question addressed is whether differences exist in diel flight activity of dung beetle assemblages, not only in bushveld and grassveld habitats, but also between natural habitats and disturbed habitats on farms.

5.2. MATERIAL & METHODS

Sampling for this study was done on three separate occasions in the four different habitats (natural bushveld habitat in SNR, disturbed bushveld habitat on the farm Josina, natural grassveld habitat in SNR and disturbed grassveld habitat on the farm Rietvlei), during three seasons, autumn (April 1997), spring (September 1997) and summer (December 1997). 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. One litre plastic pitfall traps, baited with 200g of fresh cattle dung were used for trapping dung beetles. In each habitat there were three plots, spaced 50 metres apart, containing four traps each. The traps were buried up to the rim and the bottom filled with salt water. Both flying and walking dung beetles could be caught in these traps. Dung beetles attracted by the dung fell into the traps and could be collected later. In each habitat the traps with fresh bait were put out at 8:00 in the morning. Sampling started at 9:00 and dung beetles were collected from the traps every hour until the next morning at 8:00. Between 18:00 and 19:00 the traps were baited with fresh dung so that the dung would have similar attraction for nocturnal dung beetles as for diurnal dung beetles. The activity of dung beetles occurring at different times during the day and night could be monitored effectively this way. A data logger was used to record temperature and relative air humidity at ground level, every hour of the day and night. The classification proposed by Doube (1990) was used to divide the dung beetles into seven functional groups according to the way in which the dung beetles use and disturb dung (Chapter 3, section 3.2.).

5.3. RESULTS & DISCUSSION

Community flight activity pattern in terms of species, individuals and biomass

According to Landin (1961) the releasing factor of activity of dung beetles may be formed by a combination of temperature, air humidity, and light. In the present study the daily temperature during autumn (April) varied between 7°C and 34°C (Fig. 5.1. a). The temperature during the day was relatively high, with the highest temperature between 14:00 and 16:00. There was a decrease in temperature after sunset between 18:00 and 19:00, with the lowest temperature between 01:00 and 03:00 in the morning (Fig. 5.1. a). After sunrise, between 06:00 and 07:00, there was a gradual increase in temperature. The relative humidity (R.H.) was high at night and early in the morning with the highest R.H. between 06:00 and 07:00 in the morning (Fig. 5.1. b). It decreased gradually throughout the day with the lowest R.H. between 14:00 and 17:00 in the afternoon (Fig. 5.1. b). The R.H. in the bushveld habitats did not drop as low as that in the grassveld habitats. The lowest R.H. in the grassveld habitats was 13% in the natural and 14% in the disturbed habitat, while the lowest R.H. in the bushveld habitats was 28% in the natural and 38% in the disturbed habitat (Fig.5.1. b). The activity patterns of dung beetle assemblages during the day were influenced by differences in temperature and R.H. throughout the day with dung beetle assemblages showing different activity patterns in the different habitats. Activity in the natural grassveld habitat began after 09:00 and ceased after 00:00, with peaks in number of species and individuals at 10:00, 14:00 and 19:00 (Fig. 5.1. c, d). Peaks in biomass occurred at 10:00 and 17:00 (Fig. 5.1. e). In the disturbed grassveld habitat flight started at the same time in the disturbed grassveld habitat but it ended much earlier than in the natural habitat at 16:00 (Fig. 5.1.). Peaks in species, individuals and biomass were also lower in this habitat. Peaks in number of species occurred at 12:00 and 14:00, number of individuals at 10:00 and 14:00 and biomass at 10:00 (Fig. 5.1). Flight in the bushveld habitats started later than in the grassveld habitats, after 10:00, but continued through most of the night, except for the period between 03:00 and 05:00 in the morning. In the natural bushveld habitat there was a peak in number of species between 15:00 and 17:00, at 19:00 and again at 06:00 (Fig. 5.1. c). A very high peak in number of individuals occurred at 12:00 and a smaller one at 14:00, while very high peaks in biomass occurred between 16:00 and 17:00, 19:00 and 20:00 and 06:00 and 07:00 (Fig. 5.1. d, e). In the disturbed bushveld habitat there were peaks in numbers of species at 12:00, 18:00 and 20:00 (Fig. 5.1 c). Peaks in number of individuals occurred at 12:00, 18:00 and 20:00 and peaks in biomass at 11:00 (Fig. 5.1 d, e).

During spring (September) temperatures in the natural grassveld habitat varied between 3°C and 35°C, in the disturbed grassveld habitat between 5°C and 38°C, in the natural bushveld habitat between 5 °C and 33°C and in the disturbed bushveld habitat between 5°C and 30°C (Fig 5.2. a). The highest temperatures were experienced between 12:00 and 14:00 and the lowest temperatures between 03:00 and 06:00. The highest R.H. was experienced between 4:00 and 6:00 in the morning and the lowest between 12:00 and 17:00 (Fig. 5.2. b). The R.H. dropped to a low of 7% in the grassveld habitats, while the lowest R.H. in the bushveld habitats was 12% (Fig. 5.2. b). In the natural grassveld habitat activity started at the same time of day as in autumn, but dung beetles were active for longer, i.e. up until 03:00 (Fig. 5.2). The number of species stayed relatively constant throughout the day, except for a sudden drop at 13:00 (Fig. 5.2. c). There was a peak in species richness and individuals at 19:00 (Fig. 5.2. c, d) and peak in biomass between 19:00 and 21:00 (Fig. 5.2. e). In the disturbed grassveld habitat activity started later, after 10:00 and dung beetles were active until 02:00 (Fig. 5.2.). Species richness was lower in the disturbed habitat, but the peak in species richness and individuals was at the same time as in the natural habitat (Fig. 5.2. c, d). The peak in biomass was earlier, at 17:00 (Fig. 5.2. e). Activity in the natural bushveld habitat started after 10:00 and ceased at

02:00 (Fig. 5.2). There was a peak in species richness at 11:00, 17:00 and between 19:00 and 20:00 (Fig. 5.2. c). A peak in number of individuals occurred between 19:00 and 20:00 (Fig 5.2. d) and in biomass at 20:00 (Fig. 5.2. e). There was a shorter period of activity in the disturbed habitat. Activity started after 11:00 and ended at 19:00 (Fig. 5.2.). There was a peak in species richness at 13:00 and between 17:00 and 18:00 (Fig. 5.2. c). A peak in number of individuals occurred at 17:00 and a peak in biomass at 13:00 and 16:00 (Fig. 5.2. d, e).

Very high temperatures were experienced during summer (December). The highest temperature in the natural grassveld area was 46°C, in the disturbed grassveld area 55°C, in the natural bushveld area 54°C and in the disturbed bushveld area 39°C (Fig. 5.3 a). The lowest temperature in the natural grassveld area was 18°C, in the disturbed grassveld area 20°C, in the natural bushveld area 20°C and in the disturbed bushveld area 18°C (Fig. 5.3. a). The temperature was highest between 12:00 and 17:00 and lowest between 00:00 and 06:00 (Fig. 5.3. a). The lowest R.H. was 12% in the natural grassveld habitat, 7% in the disturbed grassveld habitat, 5% in the natural bushveld habitat and 7% in the disturbed bushveld habitat (Fig. 5.3. a). The highest R.H. was 75% in the natural grassveld habitat, 55% in the disturbed grassveld habitat, 68% in the natural bushveld habitat and 66% in the disturbed bushveld habitat (Fig. 5.3. b). The lowest R.H. was experienced from 13:00 to 17:00 and the highest from 02:00 to 07:00 (Fig. 5.3. b). In the natural grassveld habitat dung beetles were active throughout the day and night, except for the period between 12:00 and 15:00 when the temperature was highest (Fig. 5.3.). The highest peak in species richness was between 20:00 and 22:00, with smaller peaks between 09:00 and 10:00, at 16:00 and at 18:00 (Fig.5.3 c). There was a very pronounced peak in number of individuals at 20:00 (Fig. 5.3. d). Peaks in biomass occurred early in the morning from 08:00 to 09:00, at 18:00 and smaller peaks occurred at 16:00 and from 20:00 to 21:00 (Fig. 5.3. e). In the disturbed grassveld habitat the dung beetles showed the same activity pattern and were active throughout the day and night except for the period between 13:00 and 16:00 when the temperatures were high (Fig. 5.3). There was a peak in species richness between 20:00 and 21:00, and smaller peaks between 10:00 and

11:00 and 17:00 and 18:00 (Fig. 5.3. c). There was a peak in number of individuals at 20:00 and a smaller peak at 10:00 (Fig. 5.3. d). The morning peak in biomass occurred later (at 10:00) in the disturbed habitat than in the natural habitat and the afternoon peak occurred earlier (at 17:00) (Fig. 5.3. e). In the natural bushveld habitats dung beetles were active throughout the day and night except for a period between 12:00 and 16:00 and between 02:00 and 05:00 (Fig. 5.3). There was a peak in species richness between 20:00 and 21:00 (Fig. 5.3. c). There was a peak both in number of individuals and biomass at 09:00 and again between 18:00 and 20:00 (Fig. 5.3. d, e). In the disturbed bushveld habitat dung beetles were active throughout the day and night except for a period from 02:00 to 05:00 in the morning (Fig. 5.3.) There were peaks in species richness at 10:00 and again at 20:00 (Fig. 5.3. c) and a peak in number of individuals at 20:00, with and a smaller peak between 09:00 and 10:00 (Fig. 5.3. d). The highest peak in biomass was between 09:00 and 10:00 and there was a smaller peak in biomass at 20:00 (Fig. 5.3. e).

The activity periods for dung beetle assemblages were shorter during autumn and spring and also seemed to be shorter in the disturbed habitats than in the natural habitats. In the disturbed habitats overgrazing has influenced the vegetational ground cover, which probably caused the dung beetles to be more severely influenced by extreme environmental conditions during the day, resulting in shorter activity periods in these habitats. During spring and autumn activity started later in the mornings and ended earlier in the evenings than during summer. Fincher, *et al.* (1971) also found that flight activity for dung beetles in southern Georgia (U.S.A.) began earlier in the mornings and ceased later in the afternoons as the number of daylight hours increased, while Koskela (1979) found that flight activity for dung beetles in southern Finland was longest in summer and shorter in spring and autumn. He also found that flight began earlier in summer and ceased later. Species richness, individuals and biomass showed a bimodal distribution with activity peaks early in the morning and late afternoon. The peaks in number of species, individuals and biomass in the present study also occurred later in the morning and earlier in the afternoon during autumn and spring. During summer activity peaks occurred earlier in the mornings and in the evenings. Koskela (1979) concluded that the onset of flight activity in the morning is determined by temperature and the cessation of flight in the evening by a combination of temperature, light intensity and air humidity. In the present study the activity peaks in the morning were later in spring and autumn because there was a later rise in temperature, while in summer the temperature was higher early in the morning. Activity peaks in the afternoon were earlier during spring and autumn because sunset was earlier and the dung beetles were probably influenced by an earlier decrease in light intensity than in summer. The species richness in all four habitats and during the three different seasons seemed to be highest during and just after sunset. According to Caveney, *et al.* (1995) dung beetles are crepuscular when activity increases with a drop in light intensity at dusk or increase in light intensity at dawn. Most species in the present study therefore seems to be crepuscular, predominantly active during late afternoon and early evening hours. There was also an increase in individuals and biomass during this time. Galante, *et al* (1995) also found that, in Spain, the most important daily period is the evening-crepuscular period and Fincher, *et al.* (1971) found that, in southern Georgia, flight activity increased during the late afternoon and early evening hours. The flight activity of dung beetles may also be influenced by the behaviour of the mammals. According to Gill (1991) dawn and dusk are the two periods when the defecation rate of mammals might be expected to peak due to a change in activity in both diurnal and nocturnal species. The activity pattern of many dung beetles seems to be geared to these periods. During summer there was no activity between 12:00 and 17:00. This period of inactivity coincided with very high temperatures and low R.H. and because of this most dung beetles were therefore restricted to early morning and early evening. Because of higher temperatures dung beetle activity could, however, continue throughout the night. During spring and autumn the daytime temperatures were lower and activity continued through most of the day, but ceased at night because of lower temperatures. In summer there was therefore a roughly bimodal distribution with high peaks early in the morning and early evening, while during spring and autumn there was a more even distribution of activity peaks throughout the day.

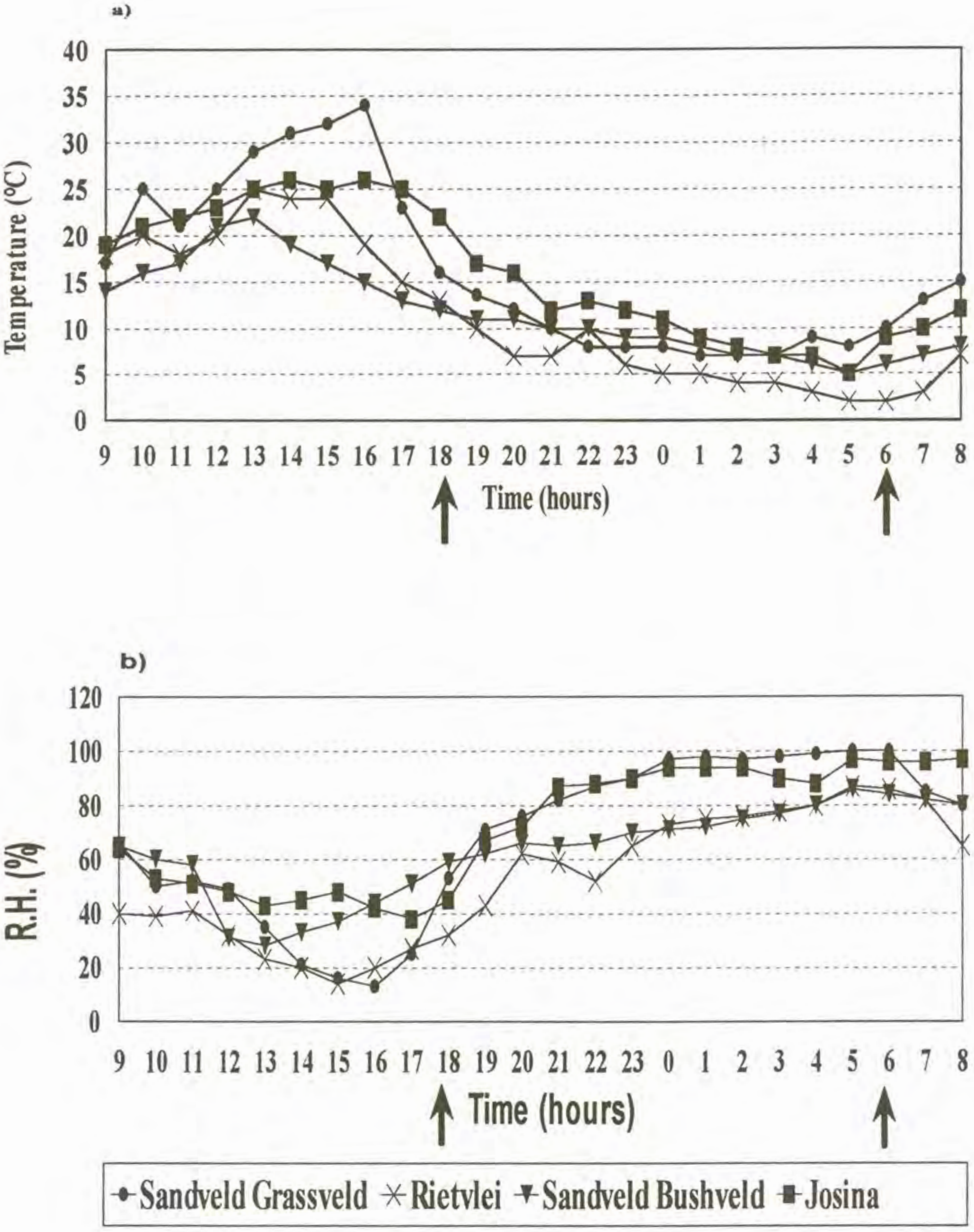


Fig. 5.1: Changes in ground temperature (°C) (a) and relative air humidity (%) (b) over a 24-hour period during autumn (April 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

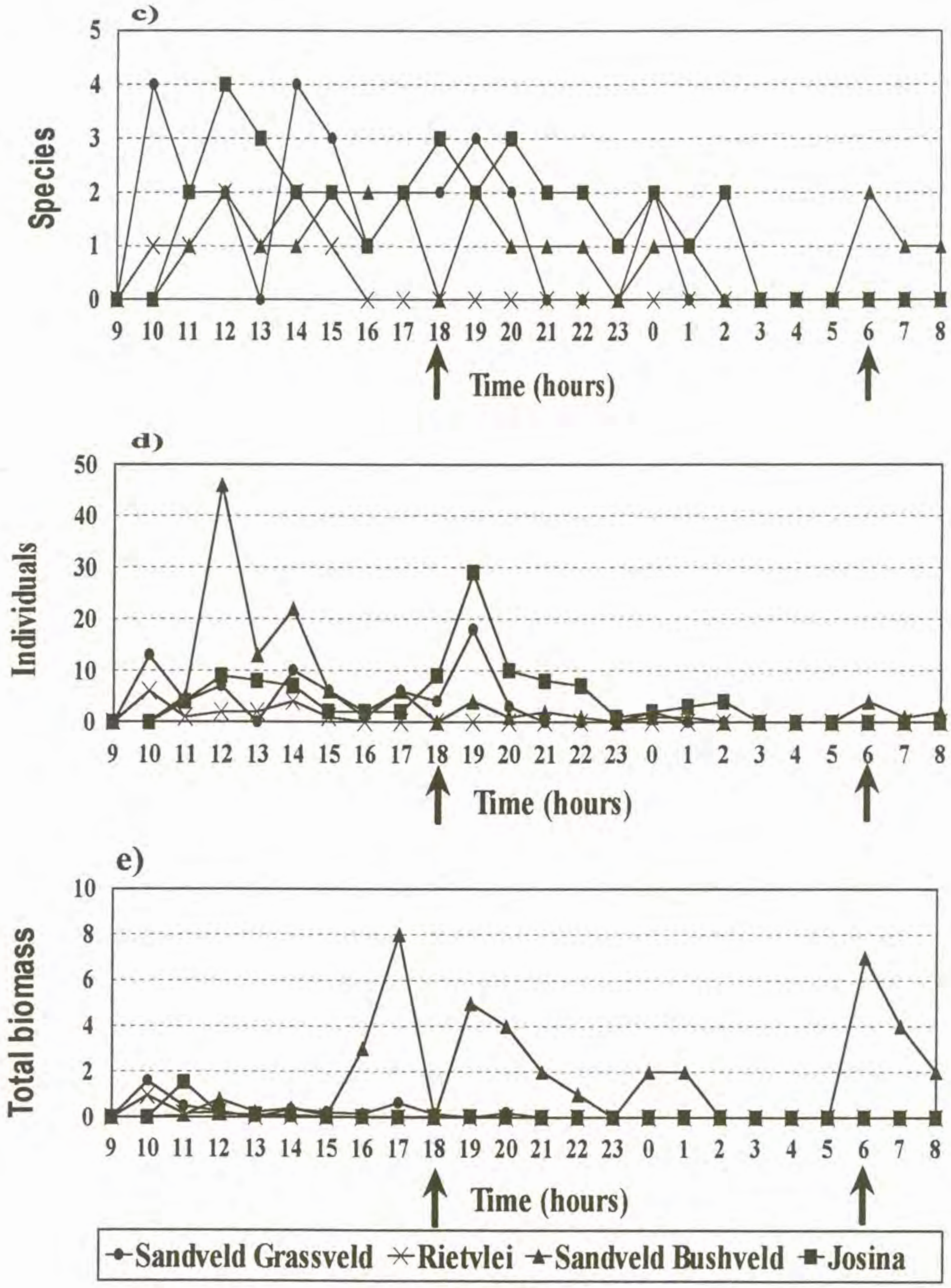


Fig. 5.1. Continued: Changes in species richness (c), number of individuals (d) and biomass (g) (e) of dung beetle assemblages over a 24-hour period during autumn (April 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

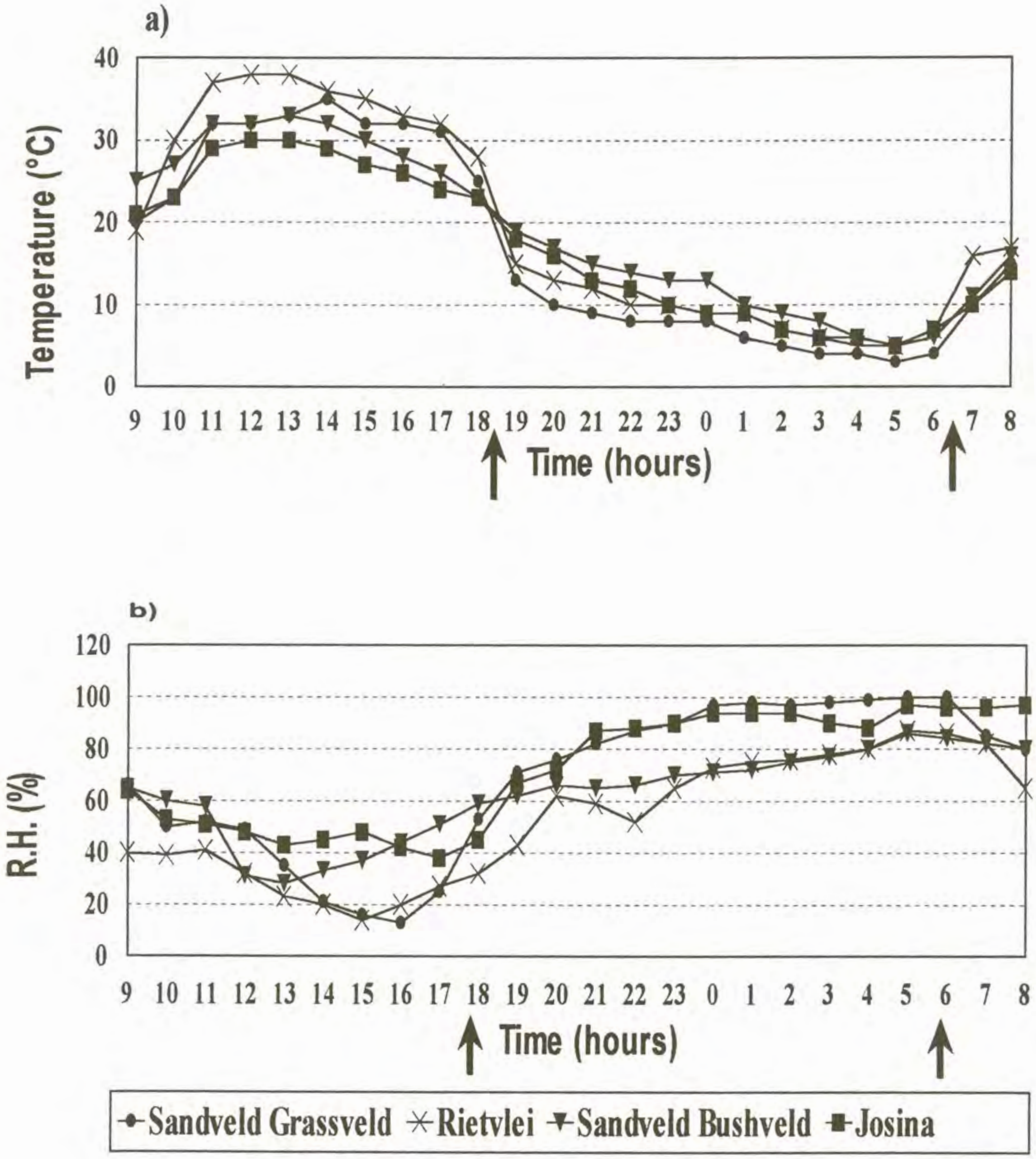


Fig. 5.2: Changes in ground temperature (°C) (a) and relative air humidity (%) (b) over a 24-hour period during spring (September 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

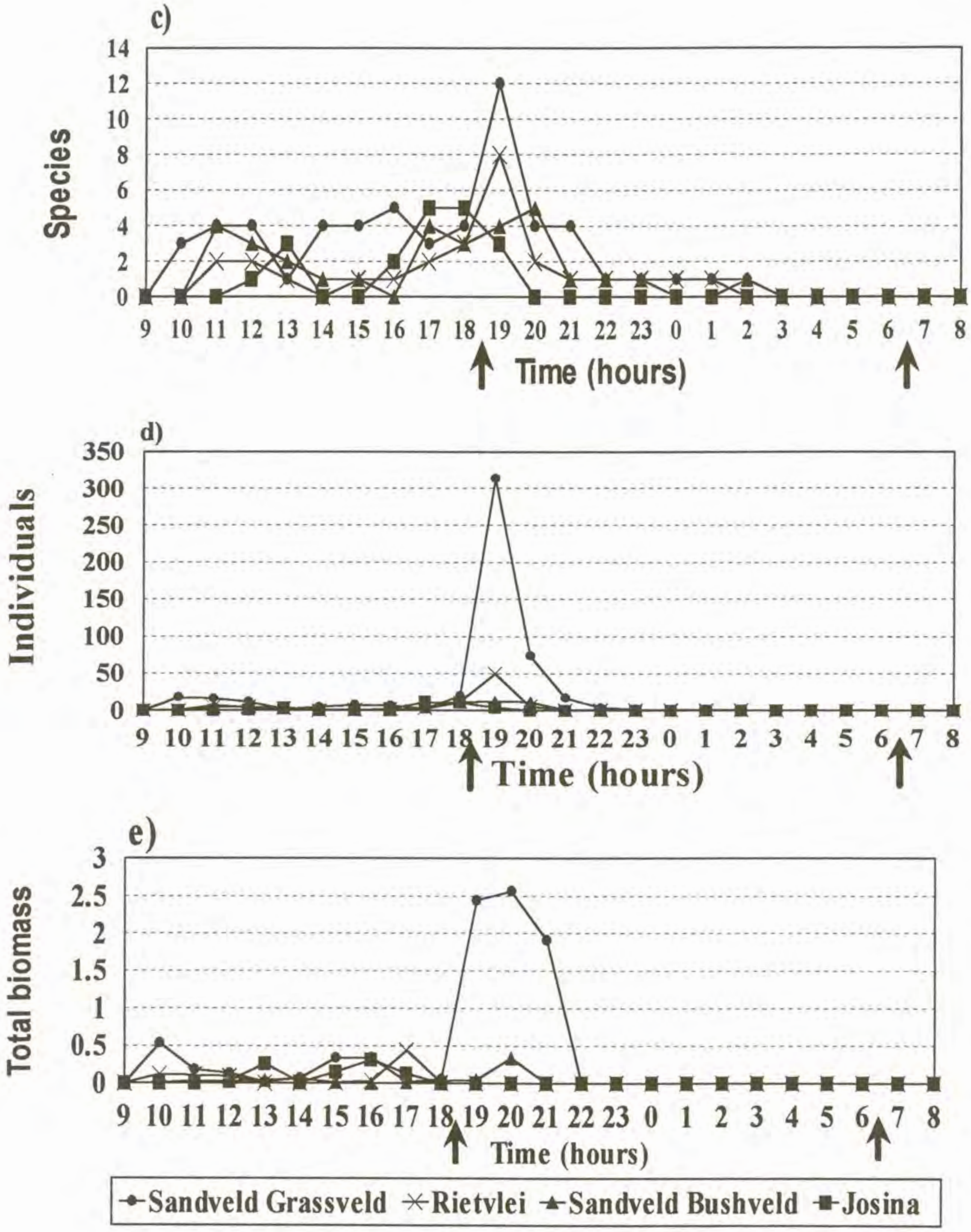


Fig. 5.2. Continued: Changes in species richness (c), number of individuals (d) and biomass (g) (e) of dung beetle assemblages over a 24-hour period during spring (September 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

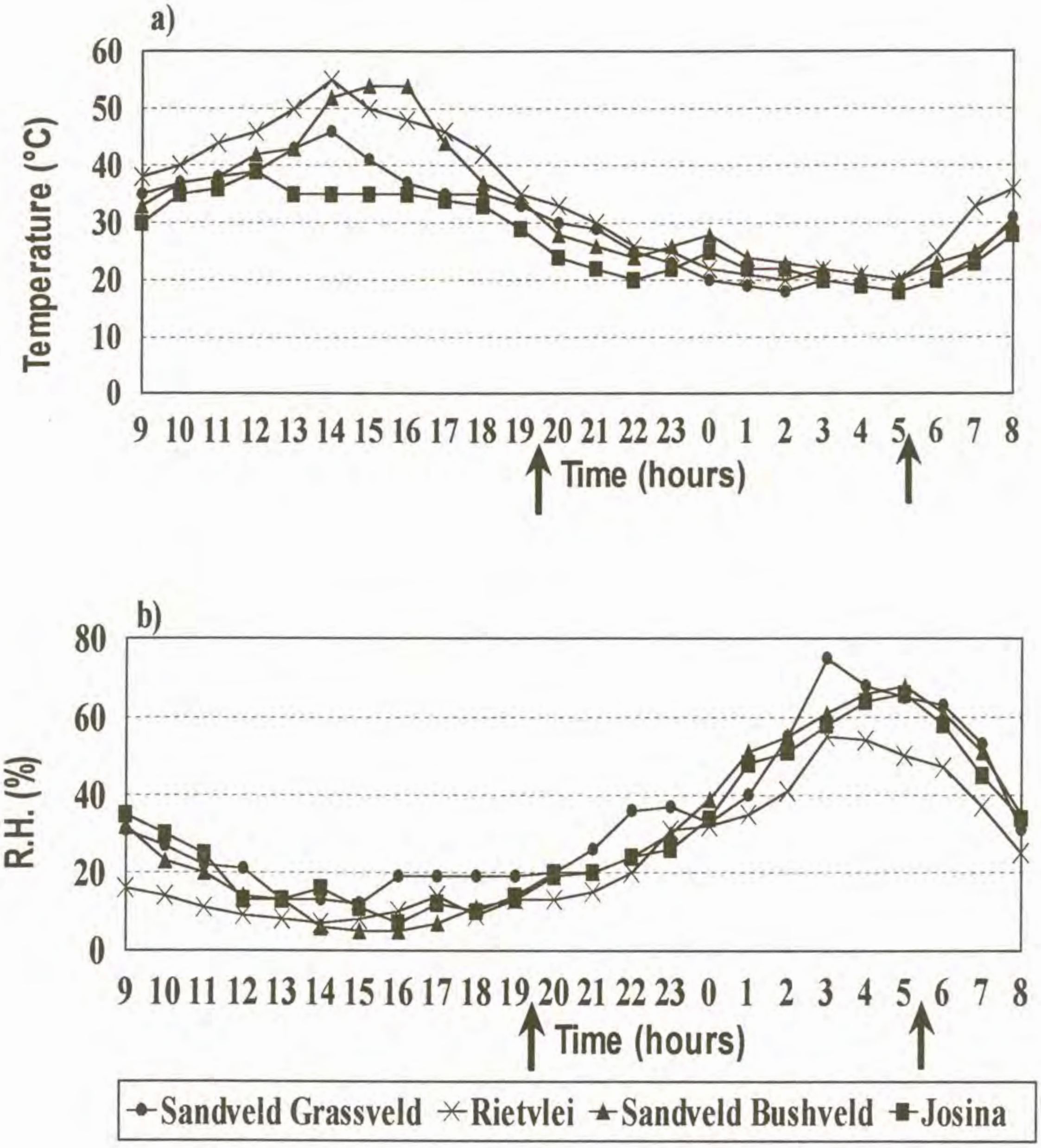


Fig. 5.3: Changes in ground temperature (°C) (a) and relative air humidity (%) (b) over a 24-hour period during summer (December 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

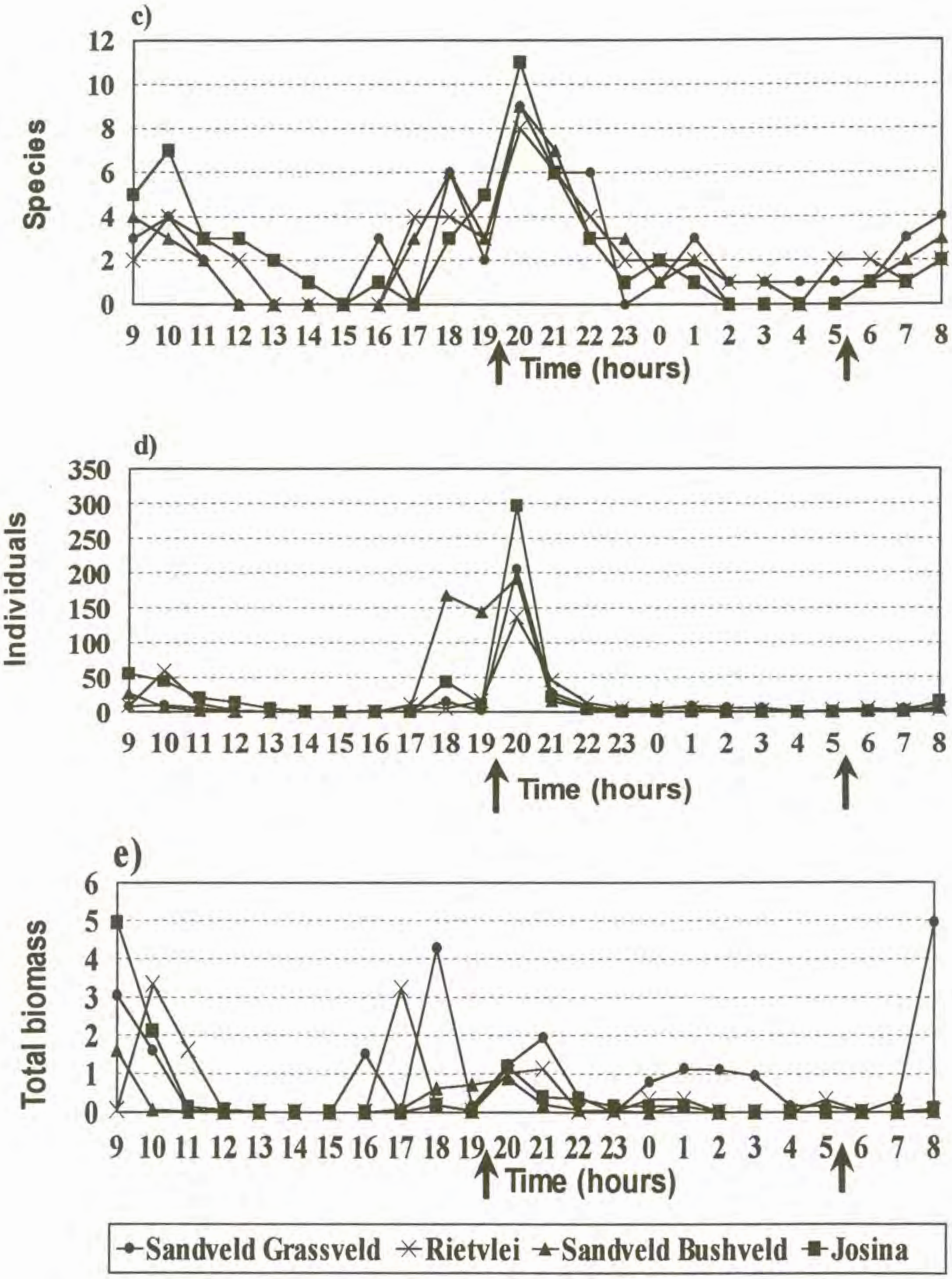


Fig. 5.3. Continued: Changes in species richness (c), number of individuals (d) and biomass (g) (e) of dung beetle assemblages over a 24-hour period during summer (December 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

Pattern of diel flight activity of different functional groups (F.G.)

Dung beetle communities typically have both diurnal and nocturnal species. There was variation in the occurrence of functional groups throughout the day in the four different habitats and during different seasons. According to Doube (1990) F.G. I, II, VI and VII are diurnal, F.G. III crepuscular/nocturnal and F.G. IV and V diurnal or crepuscular/nocturnal. In the present study slightly different activity patterns were found for the different functional groups. F.G. I was diurnal during summer in all the habitats (Fig. 5.6, a-d). F.G. II was diurnal/crepuscular during autumn and spring in the natural grassveld habitat (Fig. 5.4. a & Fig. 5.5 a) and diurnal in the disturbed grassveld habitat (Fig. 5.4. b & Fig. 5.5. b). There was no activity in this group from 12:00 to 13:00 and after 20:00 throughout the night (Fig 5.4. a, b & Fig. 5.5. a, b). During summer F.G. II was diurnal and crepuscular/nocturnal in all the habitats and the nocturnal activity period was longer than the diurnal activity period (Fig. 5.6. a-d). There was no activity in this group between 12:00 and 17:00 in the grassveld habitats (Fig. 5.6. a, b). This is probably because of very high temperatures during the day resulting in activity patterns restricted to early morning, late afternoon and at night. In the disturbed grassveld habitat the activity period for F.G. II was much shorter than in the natural habitat during all three seasons. F.G. IV was diurnal/crepuscular in both the natural habitats and diurnal in the disturbed habitats during autumn (Fig. 5.4. a-d). During spring this group was diurnal/crepuscular in the grassveld habitats and diurnal in the bushveld habitats (Fig. 5.5. a-d). During summer this group was diurnal and crepuscular/nocturnal in all the habitats (Fig. 5.6. a-d). During autumn F.G. V was diurnal in the natural grassveld habitat (Fig. 5.4. a), diurnal/crepuscular in the natural bushveld habitat (Fig. 5.4. c) and diurnal and crepuscular/nocturnal in the disturbed bushveld habitat (Fig. 5.4 d). During spring activity of this group was diurnal/crepuscular in the grassveld habitats with activity ceasing just after sunset at 19:00 (Fig. 5.5. a, b). This group was active for a longer period during the day in the natural habitat (Fig. 5.5. a). In the bushveld habitats activity of this group was diurnal and crepuscular/nocturnal with activity only ceasing at 21:00 (Fig. 5.5. c, d). Activity for this group was shorter in the disturbed bushveld habitat (Fig. 5.5. d).

During summer there was a short diurnal period for this group in the late afternoon in the grassveld habitats, but the activity was predominantly crepuscular/nocturnal with activity ceasing before 07:00 in the morning (Fig. 5.6. a, b). In the bushveld habitats this group was also active early in the morning, with the greatest activity during the crepuscular period and little nocturnal activity (Fig. 5.6. c, d). The activity period was shorter in the disturbed bushveld habitat (Fig. 5.6. d). F.G. VI showed little diurnal and nocturnal activity in the natural grassveld habitat (Fig. 5.4. a) and diurnal activity in the disturbed grassveld (Fig. 5.4. b) and bushveld (Fig. 5.4. d) habitats during autumn. This group showed diurnal activity in all the habitats during spring (Fig. 5.5. a-d). During summer F.G. VI showed diurnal activity in all the habitats, starting just after sunrise and ending before sunset (Fig. 5.6. a-d). F.G. VII was diurnal and crepuscular/nocturnal in the natural grassveld habitat during autumn, active early in the morning and late afternoon with a short activity period at night (Fig. 5.4. a). In the natural bushveld habitat this group was diurnal and crepuscular/nocturnal, occurring for longer periods during the day and night than in the grassveld habitat (Fig. 5.4. c, d). In the disturbed bushveld habitat this group also had diurnal and crepuscular/nocturnal activity, but only occurred diurnally during the late afternoon (Fig 5.4. d). During spring this group occurred diurnally for a short period during the late afternoon, but the activity was predominantly crepuscular/nocturnal in all the habitats (Fig. 5.5. a-d). During summer the activity of this group was crepuscular/nocturnal in all the habitats (Fig. 5.6. a-d).

The activity patterns of the functional groups seemed to be influenced by both the season and the habitat. Most functional groups seemed to have longer, more continuous activity periods in the natural habitats than in the disturbed habitats, except for F.G. VI, which had longer activity periods in the disturbed habitats. During spring and autumn most functional groups had a diurnal/crepuscular activity, with little nocturnal activity. The exception was F.G. VII, which consisted mostly of Aphodiinae. This group showed more nocturnal activity than the other groups during spring and autumn, but the nocturnal activity increased and diurnal activity decreased in summer. Fincher *et al.* (1971) found that in southern Georgia and Landin (1961) found that in Sweden most Aphodiinae were night flyers. In the other groups there was also a shift in activity during summer, with shorter diurnal activity periods and longer nocturnal activity periods. Diurnal activity in summer seemed to be restricted to short periods early in the morning and late afternoon. This is probably due to very high temperatures during midday. The temperatures at night were also higher during summer allowing species to be more active at night.

Pattern of diel flight activity of different species

All species of dung beetle show some variation in their activity throughout the 24 hours and some diurnal species fly from dawn to dusk, some nocturnal species fly throughout the night, whilst others have relatively restricted flight periods lasting only for a few hours (Doube, 1991; Cambefort, 1991). According to Caveney, *et al* (1995) intense competition for a limited resource favours a situation where each dung beetle species flies for a limited and often different period of the day. He found that in some species flight occurs only during a narrow range of light intensity at dusk, suggesting that the normal flight window in crepuscular fliers is demarcated by absolute light intensity. In the present study there were many species which flew only for short periods and few which had longer flight activity. Similar species seemed to have different activity periods. During autumn *Scarabaeus inoportunis* had the longest activity period in the natural grassveld habitat, occurring from 10:00 to 19:00 (Fig. 5.4. a). This species had a bimodal distribution with highest activity early in the morning and early evening. Other species belonging to the same functional group were *S. flavicornis*, which was active for a short period at 20:00 after the activity of *S. inoportunis* has ceased, and *S. bohemani*, which occurred for a brief period at 14:00 (Fig. 5.4. a). Species belonging to F.G. IV were also well-separated in their diel activity. *Metacatharsius sp. 1* was crepuscular and was active for a short period between 19:00 and 20:00, while *Onthophagus obtusicornis* was diurnal, active from 10:00 to 15:00 (Fig. 5.4. a). *O. pilosus* was active for a brief period early in the morning before *O. obtusicornis* became active (Fig. 5.4. a). *Onthophagus sp. 4, Caccobius seminulum, Pedaria sp. 4, Aphodius laterosetosus* and *A. teter* were active for very short periods, which did not overlap (Fig. 5.4. a). In the disturbed grassveld habitat there were fewer species and the diel activity was shorter for *S. inoportunis*, which occurred from 10:00 to 12:00 and *Onthophagus obtusicornis*, which occurred from 13:00 to 14:00 (Fig. 5.4. b). The diel activity of the other species was shorter with flight activity less than one hour (Fig. 5.4. b). In the natural bushveld habitat *Onthophagus obtusicornis*, belonging to F.G. IV, was active from 11:00 to 15:00 and *Onitis caffer*, belonging to the same functional group, was active for a short period at 19:00 (Fig. 5.4. c). *Metacatharsius sp. 3* and *Onthophagus variegatus* are smaller species belonging to F.G. V. These dung beetles use the dung in a similar way as the larger F.G. IV species. *Metacatharsius sp. 3* was active at 20:00, after activity of *Onitis caffer* ceased and *Onthophagus variegatus* was active from 16:00 to 17:00, between the activity periods of the two bigger species (Fig. 5.4. c). *Drepanocanthus eximius* and *D. rubicens*, both belonging to F.G. VII, occurred during the late afternoon, evening and early morning, but their diel flight was at different times with only slight overlap (Fig. 5.4. c). *Oniticellus planatus*, also belonging to F.G. VII, was active during the afternoon, its activity ceasing just before the diel flight of *D. rubicens* (Fig. 5.4. c). In the disturbed bushveld habitat *Onthophagus obtusicornis* and *D. eximius* had the longest diel flight, from 11:00 to 18:00 and from 17:00 to 2:00 respectively (Fig. 5.4. d). The other species had a shorter diel activity and there was considerable overlap between the diel periods of the different species (Fig. 5.4. d).

During spring *S. inoportunus* was active for a shorter period in the natural grassveld habitat occurring at 10:00 and again from 15:00 to 16:00 (Fig. 5.5. a). *S. anderseni* occurred during the period when *S. inoportunus* was inactive, from 11:00 to 14:00 (Fig. 5.5. a). *S. flavicornis* was active when activity of these two species ceased, from 18:00 to 21:00 (Fig. 5.5. a). *Onthophagus leucopygus* occurred diurnally from 10:00 to 17:00 with a short period of inactivity at 14:00. *Onthophagus quadraliceps* was active during this short period and *Onthophagus flavimargo* after activity of *Onthophagus leucopygus* has ceased at 19:00 and 22:00 (Fig. 5.5. a). *Onthophagus sugillatus* and *Onthophagus variegatus* are small species of similar size which use the dung in a similar way. These two species were, however, well-separated in it's diel activity with *O sugillatus* having diurnal activity ceasing at 17:00 and *O. variegatus* having crepuscular activity, only becoming active at 18:00 (Fig. 5.5. a). Species belonging to F.G. VII were all crepuscular. *Aphodius teter* occurred in high numbers during this period, but it's activity continued into the night, until 02:00 (Fig. 5.5. a). In the disturbed grassveld habitat species had roughly the same diel activity periods as in the natural habitat, but their activity periods were shorter than in the natural habitat (Fig. 5.5. b). In the bushveld habitats diel activity was also similar but, with the exception of *O. variegatus*, whose activity continued later into the night until 21:00, shorter than in the grassveld habitat (Fig. 5.5. c, d). *O. sugillatus* was active for a short period at 17:00, it's activity overlapping with that of *O. variegatus* (Fig. 5.5. c, d). The diel activity for most species was also shorter in the disturbed bushveld habitat than in the natural bushveld habitat (Fig. 5.5. d).

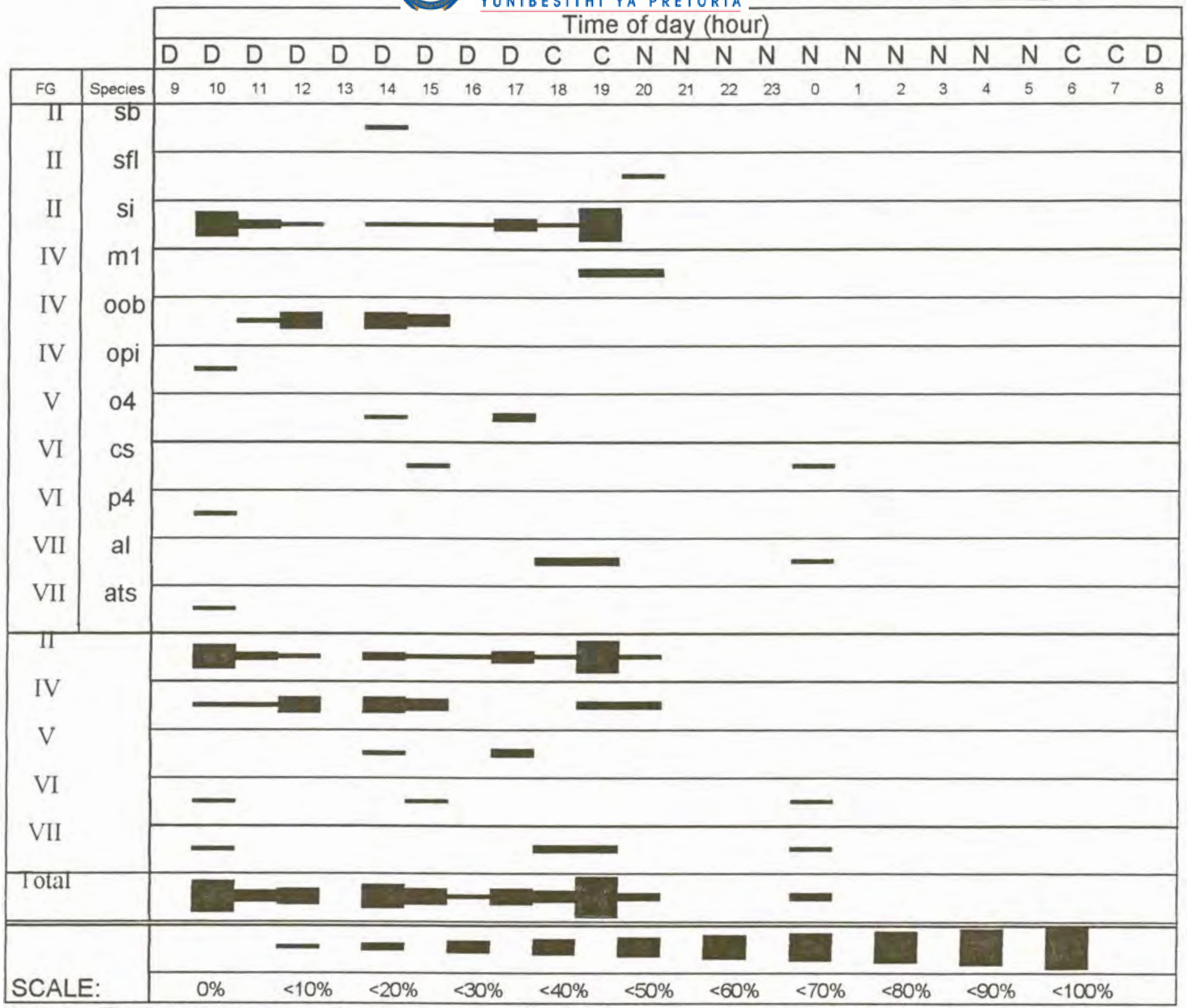
In the natural grassveld habitat during summer the diel flight activity of *S. anderseni* and *S. inoportunis* was much shorter than during the other seasons. *S. anderseni* was active for a short period early in the morning, while *S. inoportunis* was active for a short period in the late afternoon and early morning (Fig. 5.6. a). The diel activity of *S. flavicornis* was much longer than during the other seasons, starting after sunset at 20:00 and continuing through the night, ceasing just before sunrise at 5:00 (Fig. 5.6. a). *Pachylomerus femoralis* (FG I) activity was diurnal, from 8:00 to 10:00, at 16:00 and at 18:00 (Fig. 5.6. a). This is a large species and a highly effective competitor for dung. By having nocturnal activity *S. flavicornis* could successfully avoid direct competition and co-occur with this species. Most species belonging to F.G. IV and V were crepuscular/nocturnal, except for *O. aeruginosus* which occurred for a short period in the late afternoon at 18:00, *O. quadraliceps* which was active early in the morning, from 9:00 to 11:00 and late afternoon at 16:00 and 18:00 and *O. sugillatus,* which was active in the late afternoon from 18:00 to 19:00 just before the diel activity of *O. variegatus.* The diel activity of *A. teter* was shorter than during spring. This species occurred at sunset, with activity continuing until 21:00 and there was also a short period of activity at 8:00 in the morning (Fig. 5.6. a). In the disturbed grassveld habitat the diel flight of species in F.G. I and II was shorter than in the natural habitat. The activity of *P. femoralis* started later and ceased earlier and *S. flavicornis* was not active throughout the night as in the natural habitat (Fig. 5.6. b). *S. inopurtunis* had a short period of activity in the early evening at 18:00 (Fig. 5.6. b), while it had a bimodal activity in the natural habitat during the early morning and again in the late afternoon (Fig. 5.6. a). Most species in F.G. IV were active during late afternoon and early evening (Fig. 5.6. b). The diel activity of *O. quadraliceps* started earlier and ended later than in the natural habitat, but there was no activity during late afternoon (Fig. 5.6. b). All the species in F.G. V were crepuscular/nocturnal with longer, more continuous diel activities than in the natural habitat (Fig. 5.6. b). *Caccobius seminulum*, belonging to F.G. VI, and *A. teter*, belonging to F.G. VII, also had longer, more continuous diel activity in the disturbed habitat (Fig. 5.6. b). In the natural bushveld area most species had short diel activities lasting only one or two hours, with most species being active during the late afternoon, early evening or during the night (Fig. 5.6. c). The exception was *O. sugillatus*, which had longer diel activity beginning early, from 08:00 to 10:00, continued from 17:00 to 21:00 and at 01:00, with highest activity between 18:00 and 19:00 (Fig. 5.6. c). *A. teter* had a longer diel flight activity in the bushveld than in the grassveld habitats (Fig. 5.6. c, d). In the disturbed bushveld habitat. The diel flight activity of *O. sugillatus* was shorter and started later in the morning (at 10:00) than in the natural habitat. They were also less abundant between 18:00 and 19:00, while *O. variegatus* was more abundant at 20:00 (Fig. 5.6. d). *C. seminulum* had a longer more continuous flight activity in the disturbed bushveld habitat (Fig. 5.6. d).

Fincher *et al.* (1971) found that the flight activity of dung beetles begins at different times depending on the species, resulting in a succession pattern of the species arriving at dung. The beginning of this succession is dependent on the time the dung is deposited and the habitat in which it is dropped. In the present study it seems that similar species belonging to the same functional groups were fairly well-separated in their diel flight activities. Doube (1991) and Cambefort (1991) also found broad differences in diel activity among members of similar functional groups. Galante *et al.* (1993) found that although two species, *S. sacer* and *Gymnopleurus flagellatus*, which both belong to F.G. II, showed similar spatial distribution and annual activity, competition was minimal because of different daily flight periods. Otronen & Hanski (1983) also found that the activity patterns between two closely related species, living in the same environment, differed significantly. According to Hanski & Cambefort (1991b) the more similar two species are in their ecology, the greater not only the overlap in their resource use, but also the greater their spatial correlation across similar resource patches. Caveney *et al.* (1995) contributes the evolution of flight behaviour favouring intraspecific encounters over interspecific ones among similar dung beetle species to intense competition for a limited resource. Since fresh dung is deposited at different times during the day differences in diel activity of dung beetles is a very effective way to avoid interspecific competition and allowing co-existence of species of similar size and resource utilisation. Differences in diel activity give a species an advantage in the competition for dung deposited during its time of activity and better competitors cannot exclude species flying at different times (Hanski & Cambefort, 1991b).

The season as well as the habitat seemed to have a significant effect on the diel flight activity of dung beetle species, with shifts in the timing and duration of flight during different seasons and in different habitats. Diel activities were generally shorter in the disturbed habitats, beginning later and ceasing earlier. Diel activities were also shorter in the bushveld habitats. The exception was the smaller species, which seemed to have longer diel flight activities in the disturbed and bushveld habitats. According to Romoser (1981) insects placed in a temperature gradient will demonstrate a “preferred” temperature by locating themselves at a particular point along the gradient and this preferred temperature is roughly correlated with habitat preference. Differences in environmental conditions in the different habitats probably influenced the flight activities of different species, with the natural grassveld habitat more favourable for the continuous flight of larger species, while the disturbed grassveld habitat and the bushveld habitats were more favourable for the continuous flight of smaller species. Larger species may be better adapted to severe environmental conditions than smaller species. Chown *et al.* (1995) found that dung beetles of larger body mass, and therefore higher water content are capable of resisting desiccation for longer periods. Because of cooler conditions in the bushveld habitat, desiccation rates were probably slower and smaller dung beetle species could be active for longer periods. More intense competition in the natural grassveld habitat may explain the difference in this habitat and the disturbed grassveld habitat. In the natural grassveld habitat larger species were more abundant, restricting the smaller species to certain times of the day, while in the disturbed grassveld habitat where these larger species were less abundant, smaller species could be active for longer periods. During autumn and spring the activity generally started later and ceased earlier than in summer. Koskela (1979) also found that flight began earlier in the day in summer than in spring, and ceased later, while in autumn the flight period began later and ended earlier than during other times of the year. The activity of species, which were crepuscular during autumn and spring, became crepuscular/nocturnal during summer. The activity of *S. flavicornis* was crepuscular during autumn, ceased later in spring than in autumn and continued throughout the night during summer. Koskela (1979) concluded that both abiotic and biotic factors, as well as the size of the species, are important agents in modifying the strategies of dispersal flight in dung beetles. Temperature changes and aridity of the habitat may have a strong influence on species in the present study, higher temperatures in summer restricting certain species during the day, but also enabling species to be active for a longer period at night. Temperature will also influence different species differently. Species are differently adapted to extreme temperatures enabling them to occur successfully in different habitats, during different seasons and at specific times during the day. Diurnal species must be able to avoid desiccation during the day when temperatures are high and nocturnal species must be able to raise their thoracic temperature high enough for flight at night when the temperatures are low. Davis *et al.* (in preparation) found that dung beetle species are capable of altering their metabolic rates in response to seasonal changes, and that these metabolic rates were also different in different species. They concluded that these variations in metabolic rate between species were adaptive responses to different environments and that water conservation may be an important abiotic variable selecting for reduced metabolic rate. In addition dung beetles may also have morphological adaptations to withstand desiccation. Chown *et al.* (1998) found that by having a more rounded body shape certain dung beetle species lose less water because of a reduction in the surface area: volume ratio. Diurnal species, like *P. femoralis* probably have effective tolerance against desiccation because of its large body size, since the larger a species the better its desiccation tolerance (Schmidt-Nielsen, 1988). *P. femoralis* may also improve its desiccation resistance by reducing the rate at which water is lost. Chown *et al.* (1995) found that the rate of water loss of *P. femoralis* was similar to those found for Carabid beetles inhabiting xeric east African habitats. They also suggested that *P. femoralis* may be capable of thermoregulation, thus enabling this species to maintain a body temperature different from ambient temperature when temperatures become to high. Nocturnal dung beetles can raise and regulate their body temperature by endothermic means just before and during flight (Chown & Scholtz, 1993), but thoracic warm-up is particularly expensive in energetic terms for small beetles because of radiant heat loss (Caveney *et al.*, 1995). It seems, therefore, that larger species are better adapted to extreme environmental conditions than smaller species. In the present study the large dung beetle species, *P. femoralis*, was active during the day in summer, able to withstand high temperatures and desiccation successfully because of its large body size and its ability to thermoregulate. Because of a larger body size thoracic warm-up was probably less expensive in energetic terms for the nocturnal dung beetle species *S. flavicornis* than for the other smaller dung beetle species occurring in the same habitat. Larger size, therefore, probably gave these two species a competitive advantage above the other species because they could be active during times of the day and night when the environmental conditions were too extreme for the other smaller dung beetle species occurring in the same habitat.

According to Romoser (1981) several diurnal insect species, which display midday activity peaks under cool conditions, shift these activity peaks to early morning or evening in hot weather as a mechanism of ectothermic regulation. Dung beetles in the present study also showed these mechanisms to avoid extreme temperatures. During warmer seasons diurnal species were active earlier in the morning and later in the afternoon to avoid too high temperatures, while the activity of nocturnal species was crepuscular during the colder seasons to avoid too low temperatures that would affect flight. Koskela (1979) found that small species often fly in the morning and evening hours, whereas large species may be active throughout the day and Perez-Mendoza *et al.* (1999) found that in the beetle *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) flight activity was higher for strains of insects with higher body weight. The energy cost of flying has to be considered here. The cost of flying for smaller species is higher than for larger species and they therefore have ecological adaptations, restricting their flight times to certain times of the day. According to Hanski & Koskela (1979) small species are likely to spend more time in a single dung pat than large species, because of the higher cost of moving for these species.

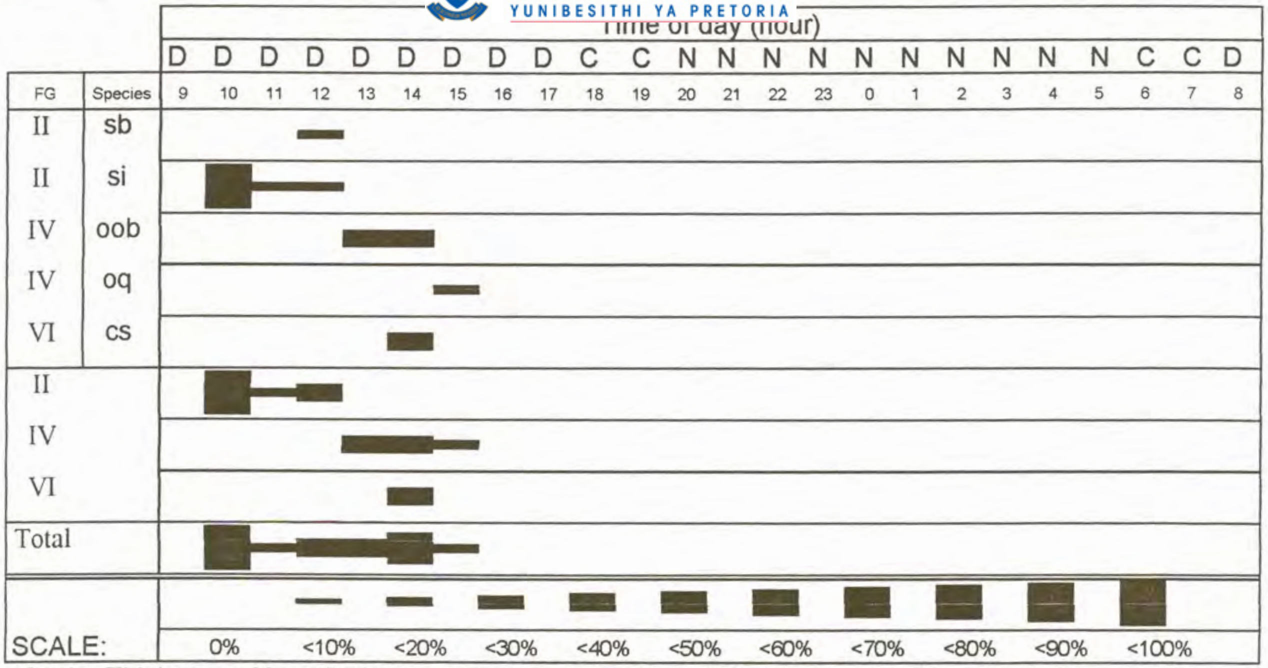
It can be concluded that the flight activity of dung beetles was influenced by temperature changes during the different seasons and different times of the day as well as by different environmental conditions in the different habitats. Conditions in the natural grassveld habitat were more favourable for the flight of large species than were the disturbed grassveld habitat and the bushveld habitats. Since larger dung beetle species belonging to FG 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 active for shorter periods than in the natural habitat. Doube (1991) ascribed the complete dung dispersal on sandy soils in the Hluluwe region (South Africa) to the dominance of large beetles (>1.024 mg dry wt), which bury large amounts of dung in a short time. The degradation of dung throughout a 24-hour period will therefore be most effective in the natural grassveld habitat during summer.



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

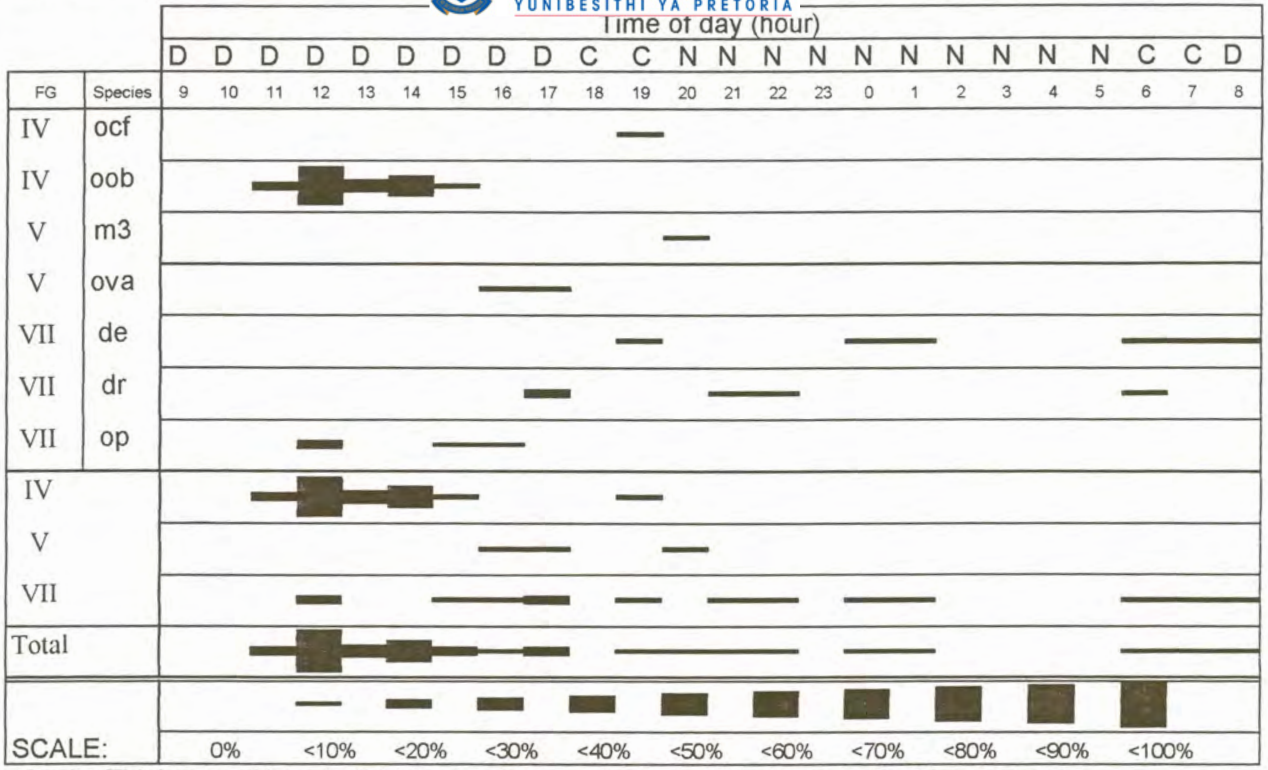
Fig. 5.4. Diel flight activity of different dung beetle species and functional groups over a 24-hour period during autumn (April 1997): a) Sandveld grassveld (natural grassveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

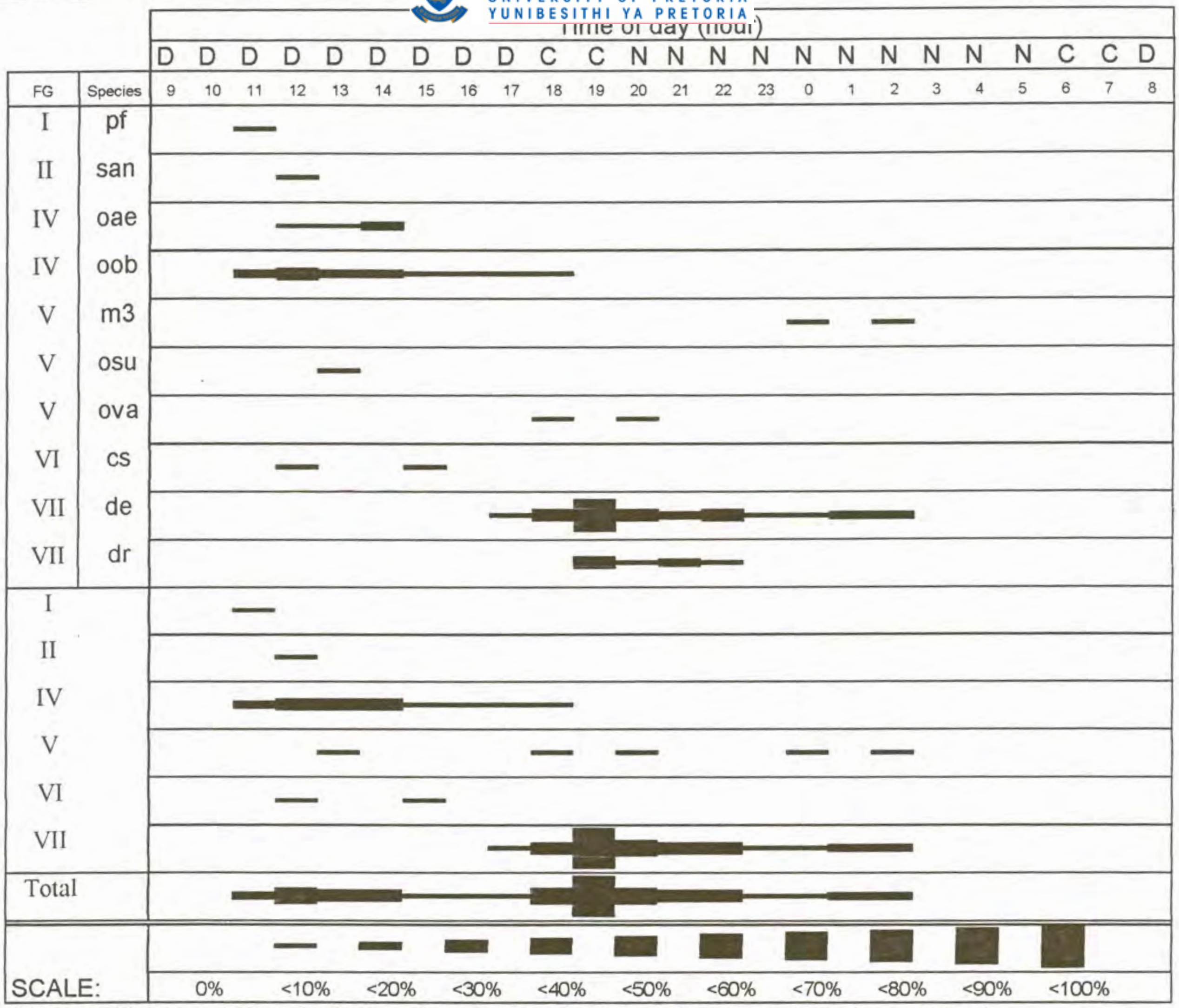
Fig. 5.4. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during autumn (April 1997): b) Rietvlei (disturbed grassveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

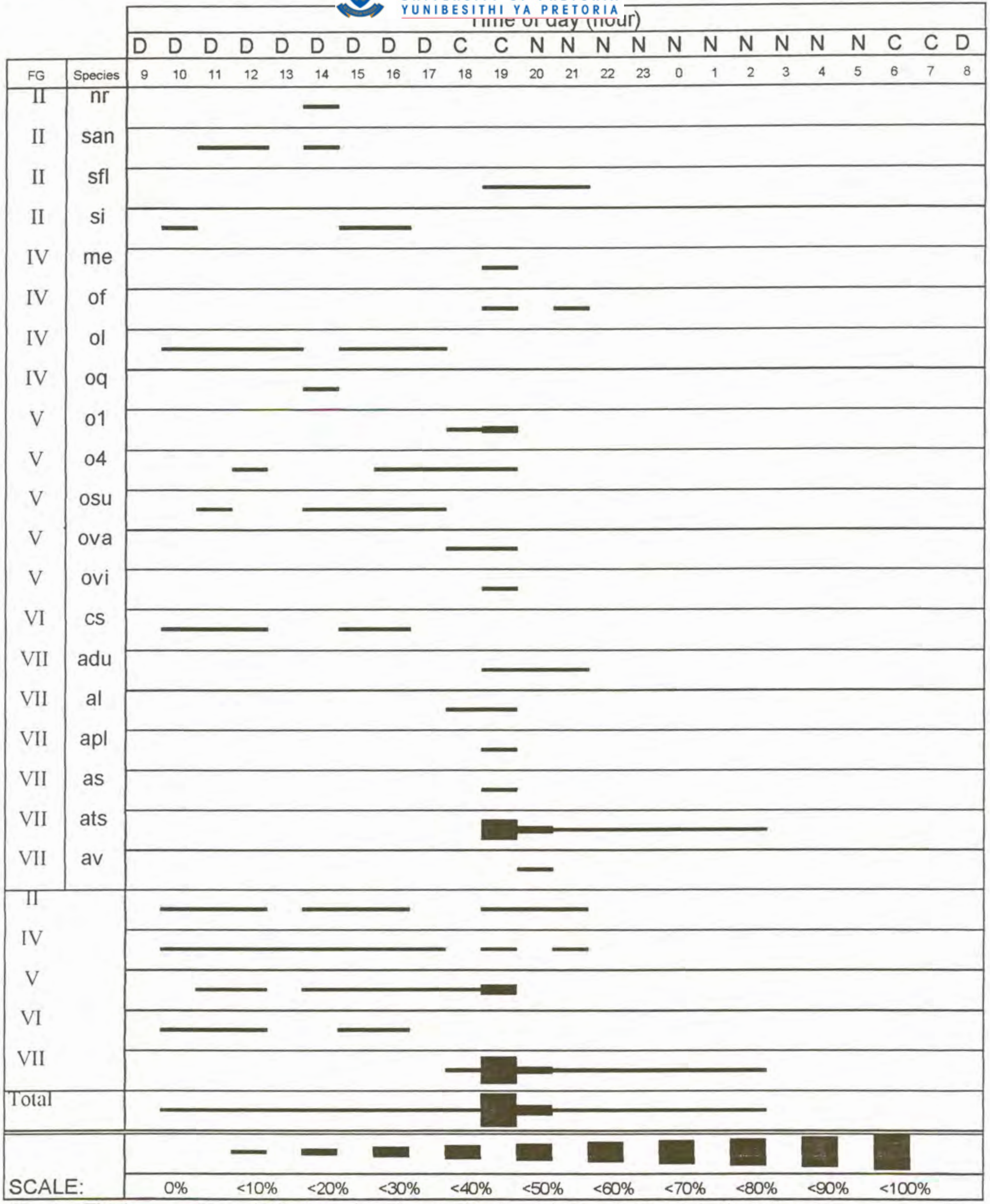
Fig. 5.4. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during autumn (April 1997): c) Sandveld bushveld (natural bushveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

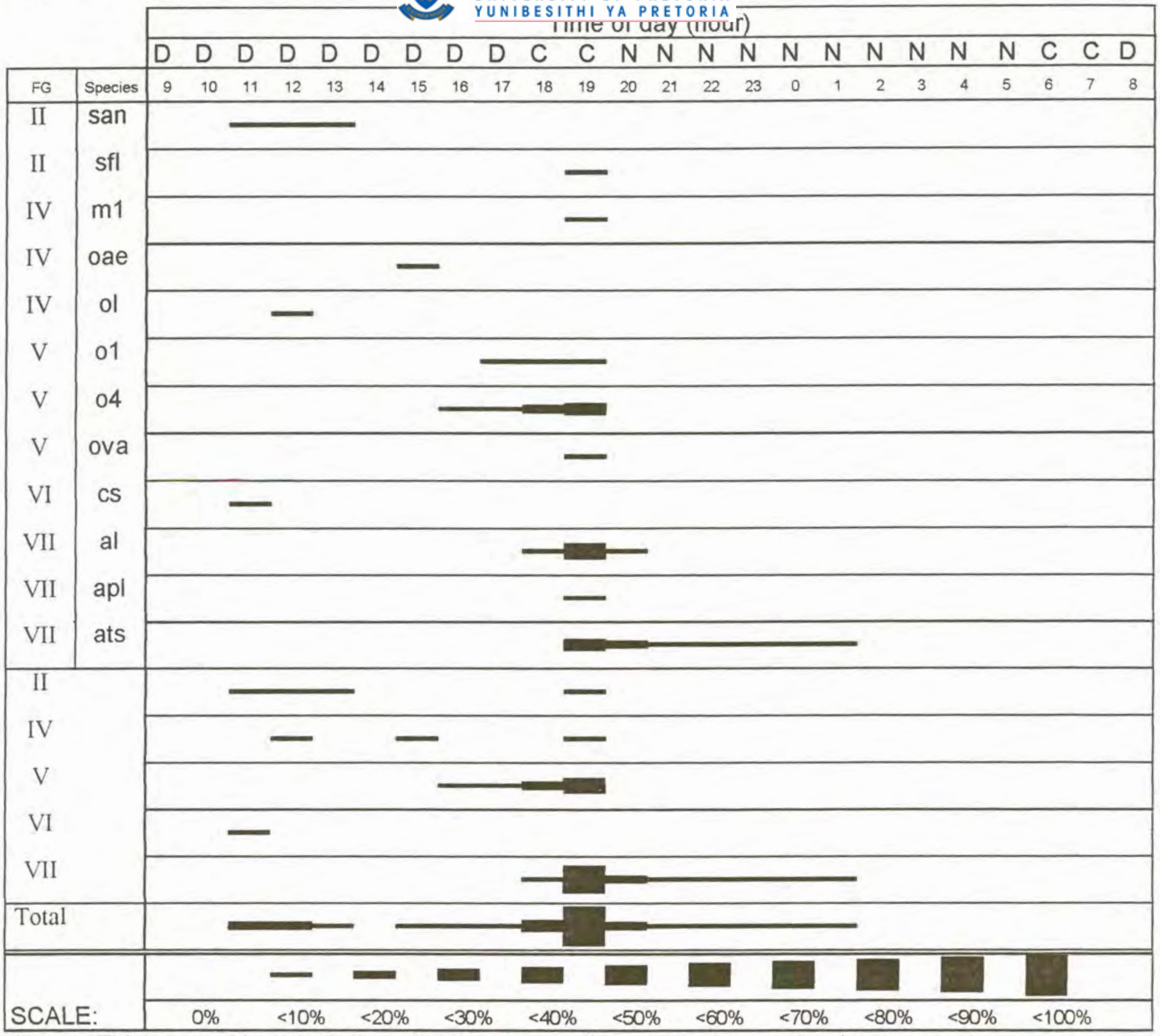
Fig. 5.4. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during autumn (April 1997): d) Josina (disturbed bushveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

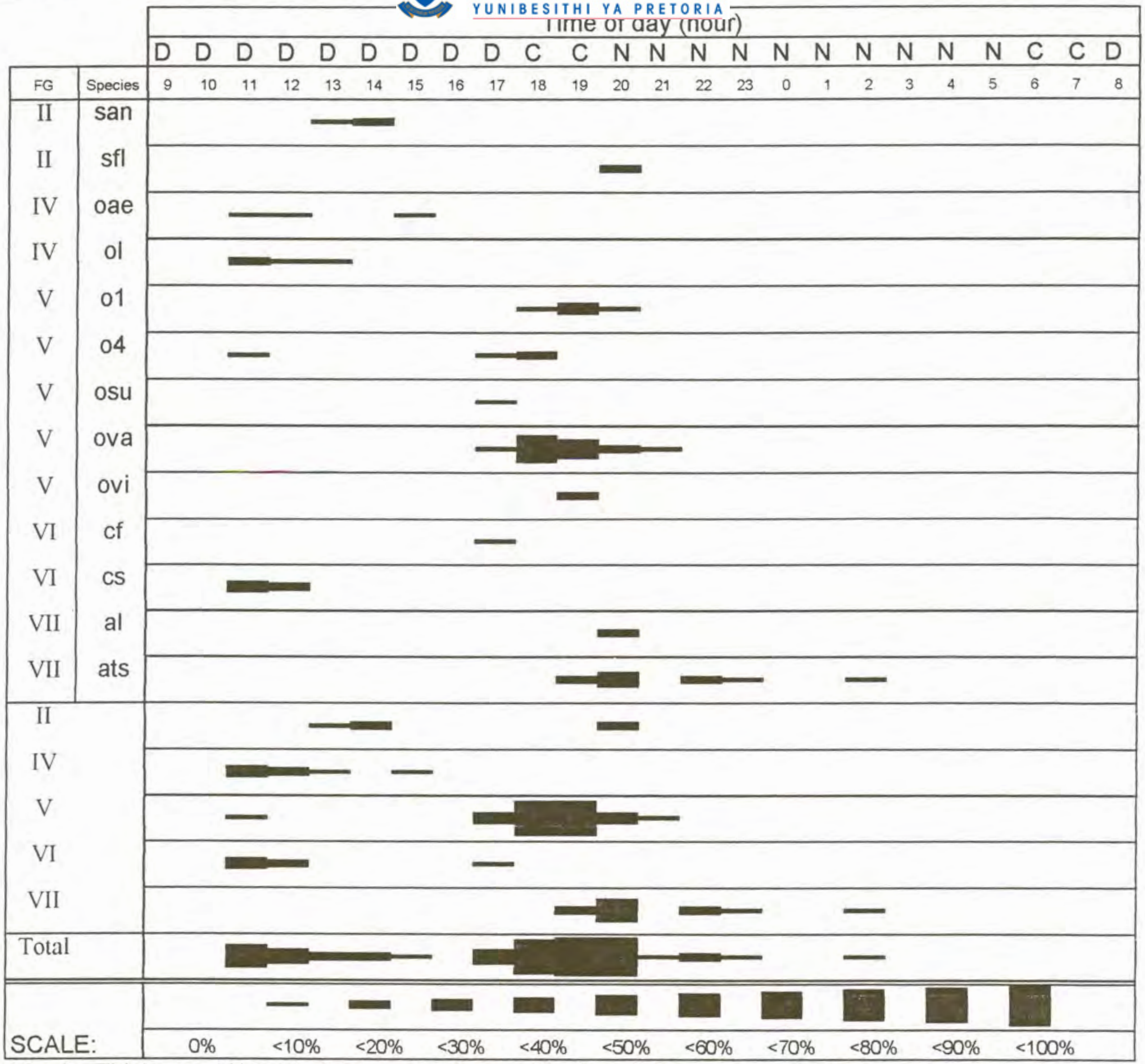
Fig. 5.5. Diel flight activity of different dung beetle species and functional groups over a 24-hour period during spring (September 1997): a) Sandveld grassveld (natural grassveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

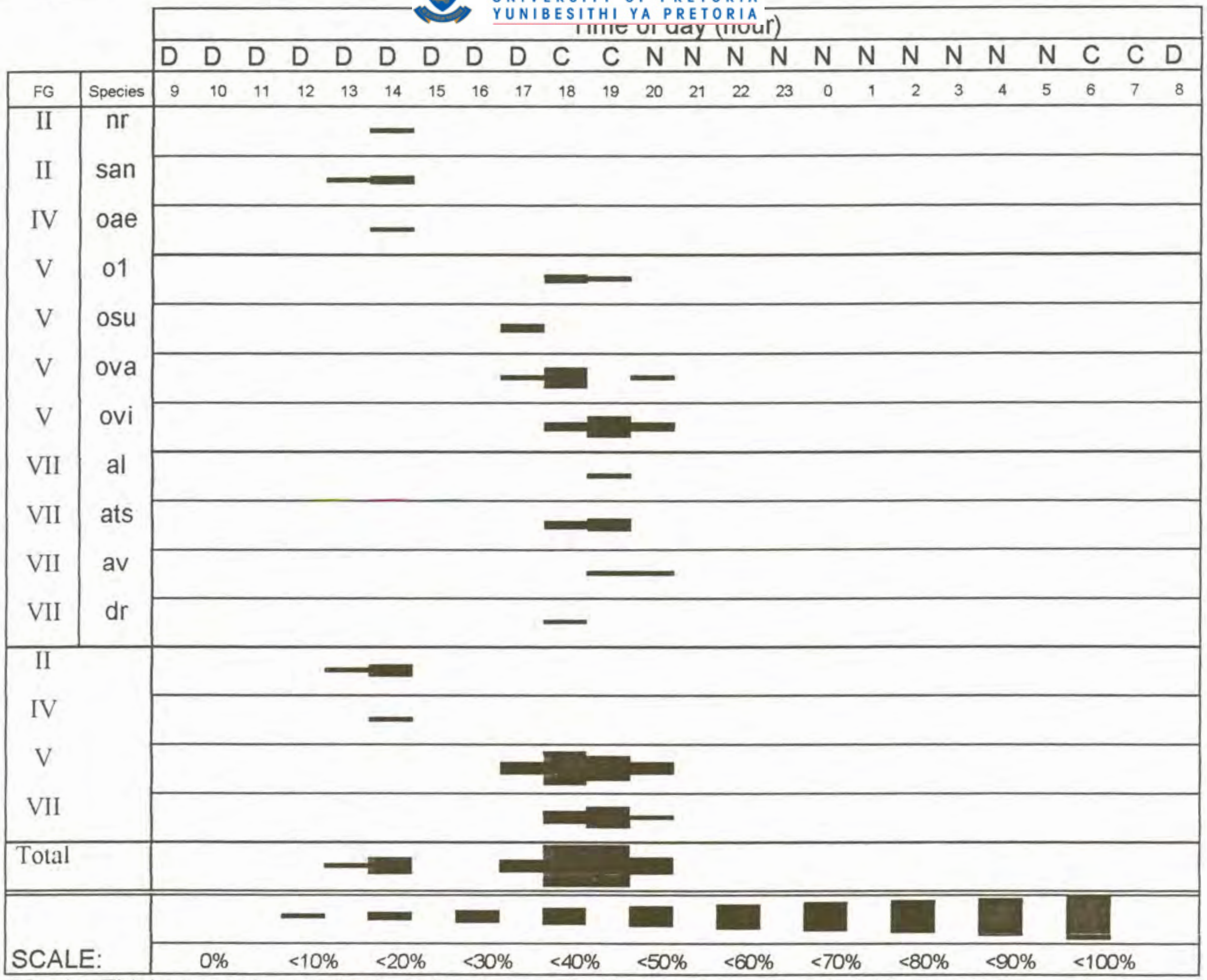
Fig. 5.5. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during spring (September 1997): b) Rietvlei (disturbed grassveld habitat).



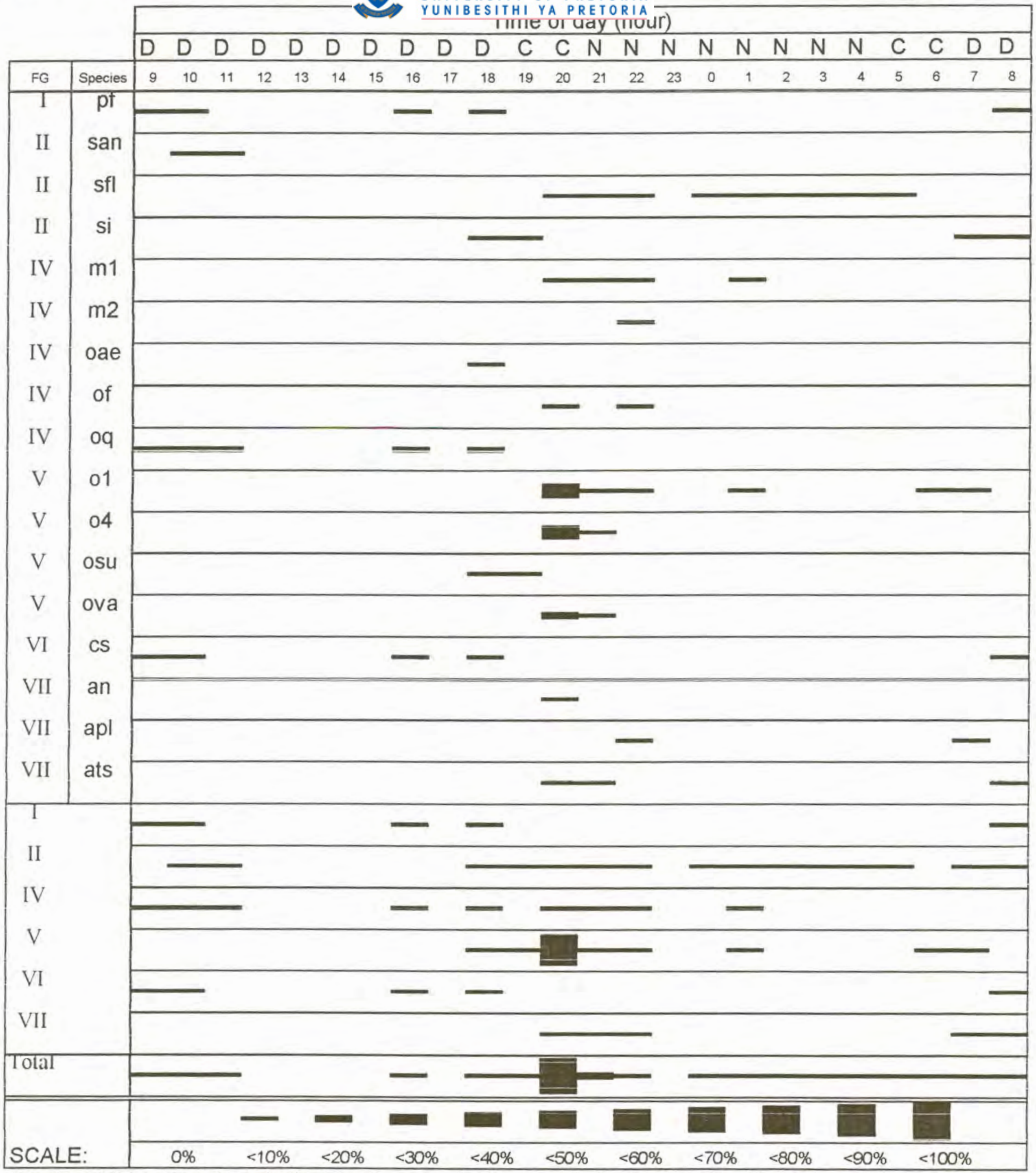
*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

Fig. 5.5. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during spring (September 1997): c) Sandveld bushveld (natural bushveld habitat).



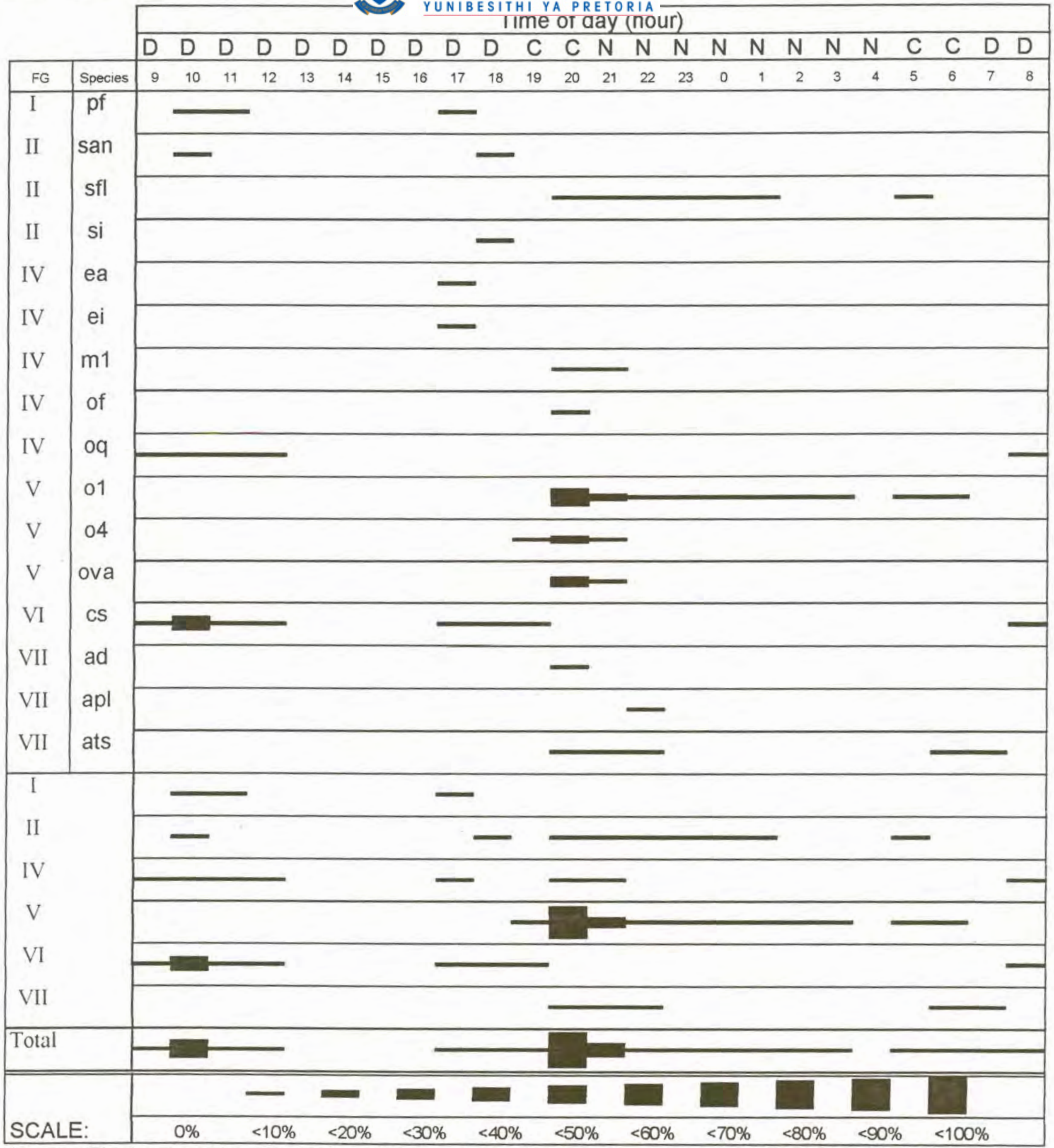
*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal
*For code of species names see Chapter 2 - Table 2.4.
Fig. 5.5. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during spring (September 1997): d) Josina (disturbed bushveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

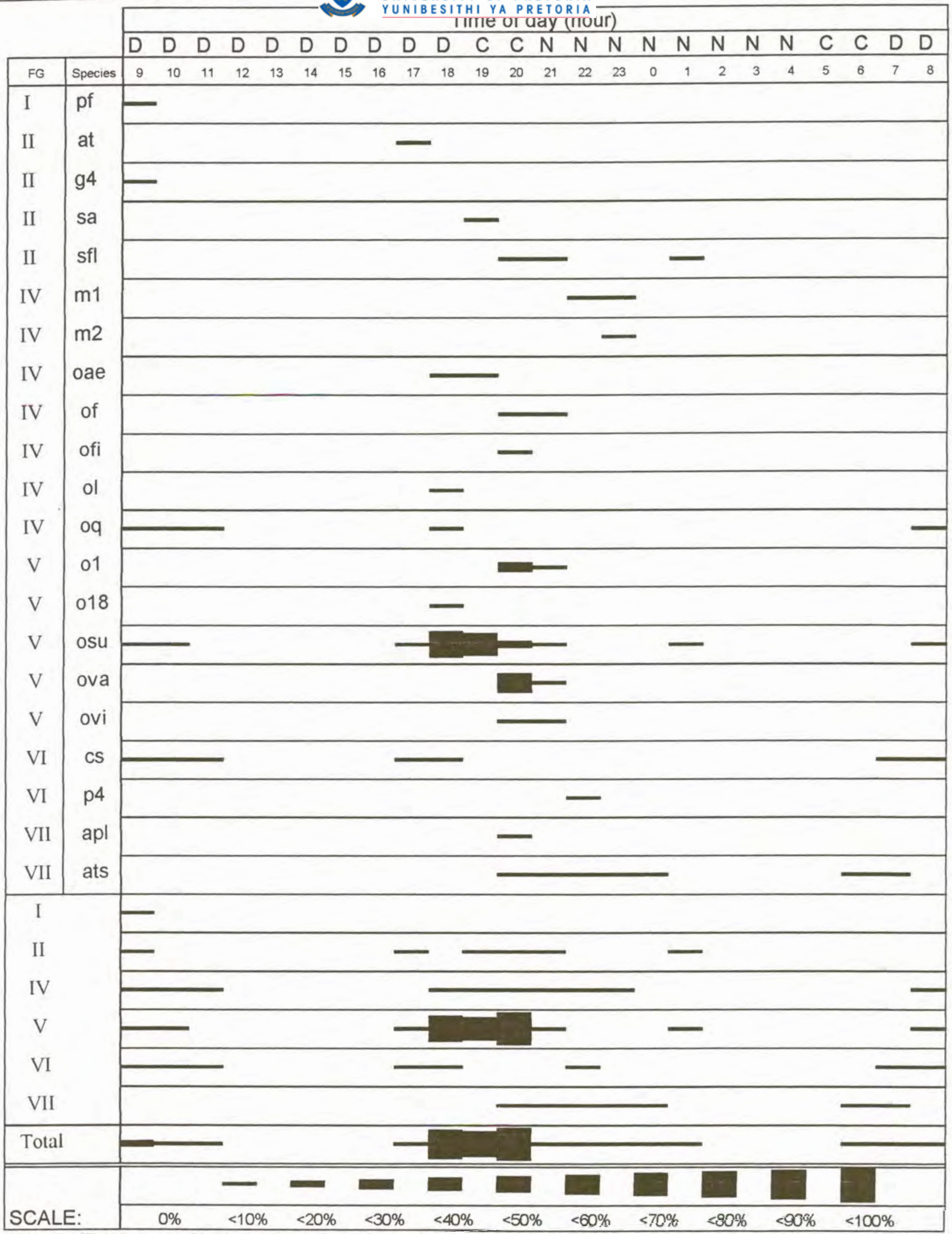
Fig. 5.6. Diel flight activity of different dung beetle species and functional groups over a 24-hour period during summer (December 1997): a) Sandveld grassveld (disturbed grassveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

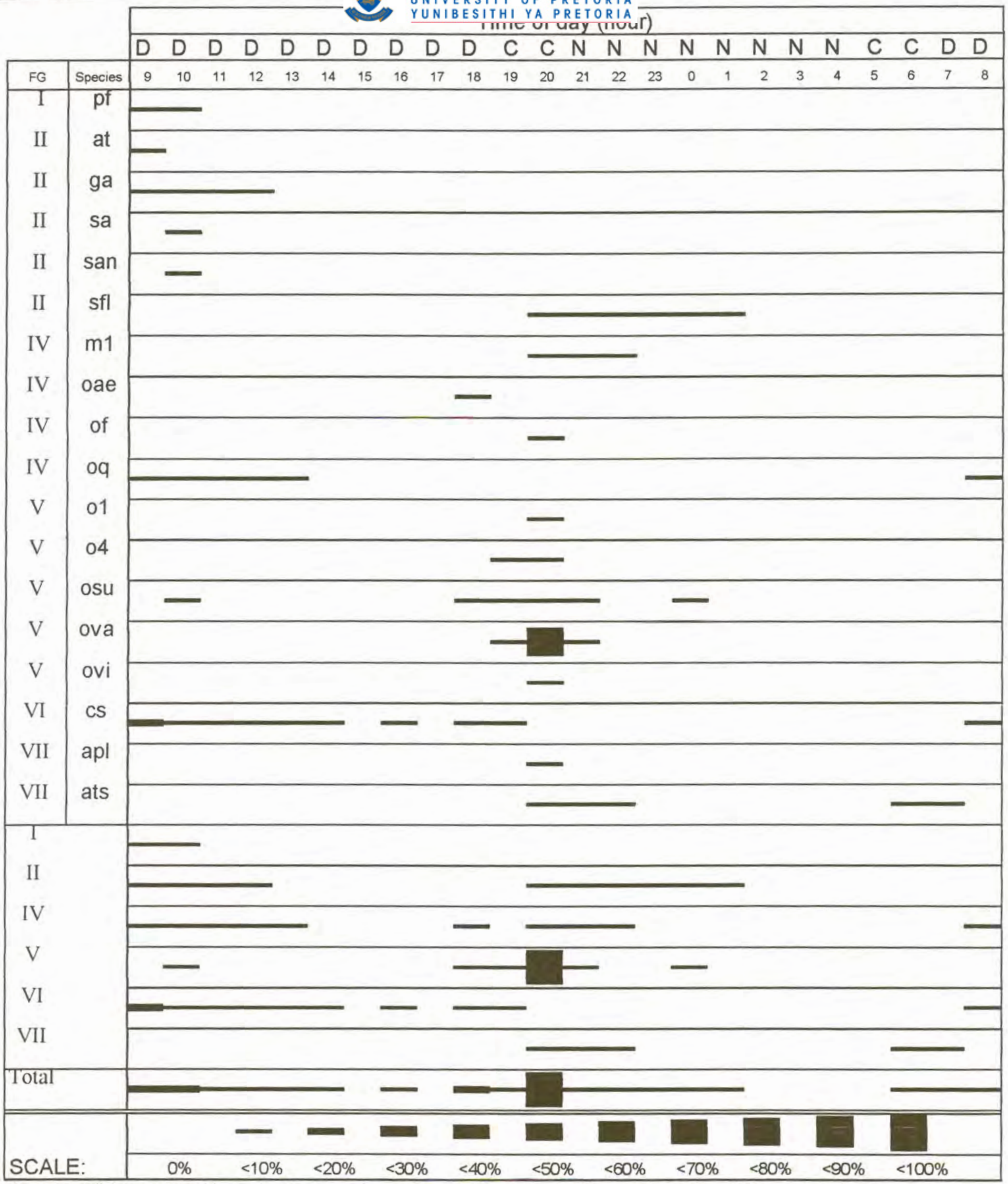
Fig. 5.6. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during summer (December 1997): b) Rietvlei (disturbed grassveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

Fig. 5.6. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during summer (December 1997): c) Sandveld bushveld (natural bushveld habitat).



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

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

Fig. 5.6. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during summer (December 1997): d) Josina (disturbed bushveld habitat).

Chapter 6

SUCCESSION IN DUNG BEETLE ASSEMBLAGES IN FOUR DIFFERENT HABITATS AND THEIR INFLUENCE ON DUNG DEGRADATION

6.1. INTRODUCTION

Dung decomposition is an indispensable process in any grazing ecosystem, because dung not efficiently recycled can lead to major problems of rejection and waste of grazing contaminated by dung. Several factors can affect the successful decomposition of dung in an area. Dung degradation is due primarily to decomposition of organic substances (Barth *et al.*, 1995) where material is lost from the pats by drainage and leaching, while microbial activity results in the destruction of both simple and complex organic molecules (Dickinson *et al.*, 1981). Macroinvertabrates (mainly dung beetles) play a vital role in the rapid destruction of dung pats. According to Stewart (1967) nature's sanitation system is largely dependent on the abundance of coprophagous beetles and Tyndale-Biscoe (1994) considers dung dispersal to be, in part, dependent on dung beetle numbers in the dung pat. Holter (1979b) also considered the rapid disappearance of dung to be brought about by the abundant dung insects in the fresh dung. These dung insects contribute to dung disappearance by direct metabolization, stimulation of microbial decomposition or dung burial.

Dung insects colonise the dung pat early and play an important role in the initial breakdown of the pat. Barth *et al.* (1994) found that adult Coleoptera and Diptera primarily invade the fresh pat, bacterial growth peaks between 5 and 14 days, thereafter arthropod larvae are most frequent, with earthworms appearing at a much later phase. Coleoptera seems to be the most important order colonising the dung pats in terms of abundance. Wingo *et al.* (1974) found that species belonging to the order Coleoptera were the most abundant species colonising dung. The successful colonisation and subsequent decomposition of dung by dung beetles is influenced by a variety of factors in the ecosystem. The rate of dung decomposition by dung beetles will mainly be determined by influences of both abiotic (season, rainfall, temperature, wind, sunlight, soil hardness, vegetation type) and biotic (competition and predation) factors. The external climatic conditions influence the nature of the dung environment, making it less suitable for the species which occupies it first, while macroinvertebrates alter the physical and chemical nature of the dung environment, causing an alteration in the type of population (Snowball, 1944). Marshall Lee & Peng (1981) found that the deteriorating effects of environmental factors such as sunbaking and exploitation by other organisms decrease the portion of the pat available to the beetles through time. In summer a hard crust forms on dung pats, which constitutes a refractory component during subsequent decomposition (Holter, 1979b). Valiela (1974) considers local alterations in the environment and in the dung itself to be the strongest influence on dung inhabiting insects. There are large differences in the decomposition of dung in different geographical areas and these differences can to a large extent be contributed to the dung beetle community of the area. The time required to remove most or all dung from the soil surface ranges from less than a day in Africa, to over 10 years in North American alpine areas (Herrick & Lal, 1996).

Because insects colonising dung affect their environment, Snowball (1944) considers this type of succession to be the active type. There are various ways of resource utilisation in a dung beetle assemblage, telecoprids remove the dung from the dung pat and bury it some distance from the pat, paracoprids bury the dung underneath the pat and endocoprids nest within the dung pat. Dung beetles also differ in their time of arrival at the dung and the tempo at which dung is removed. The wide range of different behaviours in a decomposer community can be expected to have very different impacts on the degradation process of the dung and the nutrients it contains, on the creation of biopores and on rates of soil transport and accumulation at the surface (Herrick & Lal, 1996). Doube *et al.* (1988) considered the time of arrival, capacity to remove dung and the rate of dung removal determinants of competitive ability. The difference in competitive ability of dung beetle species and different adaptations to different conditions in the dung will result in a successional pattern in the dung with different species influencing the success of others. Different adaptations and behaviour of dung beetle species also reflect different breeding strategies and allow a degree of resource partitioning between dung beetles in a pat (Doube *et al.*, 1988). Barth *et al.* (1994) found that qualitative and quantitative colonisation of dung pats varied considerably depending on climatic conditions such as temperature, wind, or sunlight. The pattern of arrival of species at the dung will also be strongly influenced by the age of the dung. Peck & Forsyth (1982) found interspecific differences in the responses of dung beetles to dung of different age. This may be related to food preference, odor perception, and foraging strategy. Doube *et al.* (1988) found differences in the amount of dung buried by different species. Many factors influence the success of dung beetles removing dung from the dung pat and burying it, but size probably plays the most important role in this respect. Larger dung beetles can compete better than smaller species and can remove larger quantities of dung from the pat within a short time. There is much evidence of dung-burying potential of dung beetles being related to the mean length or weight of a species (Doube *et al.*, 1988; Hallfter & Matthews, 1966; Nealis, 1977 and Marshall Lee & Peng, 1981). To determine dung degradation in a habitat, it is important to determine the effectiveness of the dung beetle assemblage at removing the dung in this habitat and also the influence of the habitat on the assemblage.

6.2. MATERIAL AND METHODS

Determination of dung beetle succession and degradation of dung

Sampling for this study was done on four separate occasions, December 1996 (summer), April 1997 (autumn), July 1997 (winter) and September 1997 (spring), in four different habitats. The study was carried out in Sandveld Nature Reserve (SNR) ($27^0$37'S; $25^0$46'E) and on two neighbouring farms Josina and Rietvlei. The four different habitats used for sampling were a natural bushveld habitat in SNR, a disturbed bushveld habitat on the farm Josina, a natural grassveld habitat in SNR and a disturbed grassveld habitat on the farm

Rietvlei. Fresh cattle dung 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 of the dung. 24 1l dung pats were placed on the soil in each of the four habitats. The dung pats were spaced 2m apart in two adjacent rows. Three sample pats were randomly collected in each habitat every six hours during the first day and every 24 hours until the fourth day. The degree of dung decomposition was assessed and different stages of dung degradation were determined. The mean ± SD stage of degradation in hours for three dung pats was determined for each stage. The dung beetles inside the dung pat and in the soil beneath the dung were collected by flotation and preserved in 70% alcohol for later identification. Dung beetles which did not enter the pat, but which fed on the pat and removed dung from the pat were also noted during the different stages of dung degradation. The mean ± SD species, individuals and biomass of the dung beetles colonising the dung during each stage were determined for the three sample dung pats. After the fourth day the dung pats were either completely removed or the pats were so desiccated that no adult dung beetles colonised the pat.

Analytical Methods

To determine whether beetles in different habitats and during different seasons colonised dung of different age, the successional mean occurrence (SMO, after Hanski 1980b) was calculated. SMO represents the mean of the colonisation curve (which gives the numbers of individuals of a species present in dung pats of different ages) and is calculated by:

$SMO=\Sigma pi(ti-ti_{-1})ti/\Sigma pi(ti- ti_{-1})$,

Where pi is the number of individuals colonising dung of age ti (in hours).

The dry mass per species was determined by calculating the mean ± SD mass of 20 specimens (10 males and 10 females) of each species. These were dehydrated at 80°C for 48 hours and were subsequently weighed on a precision balance. The rate of change in biomass during succession was determined by dividing the biomass of each successional stage by the total number of stages.

One estimate of pi, the potential amount of dung consumed by the scarabs in habitat i, is $p_i=\Sigma n_j l_j$, where n_j is the number of individuals of the jth species and l_j is the average length of the species. Nealis (1977) considers $p_i=\Sigma n_j w_j$, where w_j is the dry weight in grams of the jth species, a more suitable estimate of potential amount of dung consumed by dung beetles. The formula $p_i=\Sigma n_j w_j$ was used in the present study to determine the potential amount of dung consumed by dung beetle assemblages in the different habitats. Each habitat's contribution to the total potential dung disposal by dung beetle assemblages was expressed as pi/pt, where $p_t=\Sigma p_i$.

6.3. RESULTS AND DISCUSSION

Disappearance of dung pats in four different habitats

The decomposition process of dung is characterised by different stages. In the present study this process was divided into six stages:

Stage 1 (Fig. 6.1. a):

No dung removed from pat, whole dung pat moist, no sign of disturbance.

Stage 2 (Fig. 6.1. b):

No dung removed, dung covered by dry crust, moist inside, few holes in dung pat.

Stage 3 (Fig. 6.1. c):

± 20% of dung pat removed, covered by dry crust, moist inside, numerous holes.

Stage 4 (Fig. 6.1. d):

± 40% of dung removed, covered by dry crust, moist inside, numerous holes, holes filled with sand.

Stage 5 (Fig. 6.1. e):

± 60% of dung removed, crust shredded, dry inside.

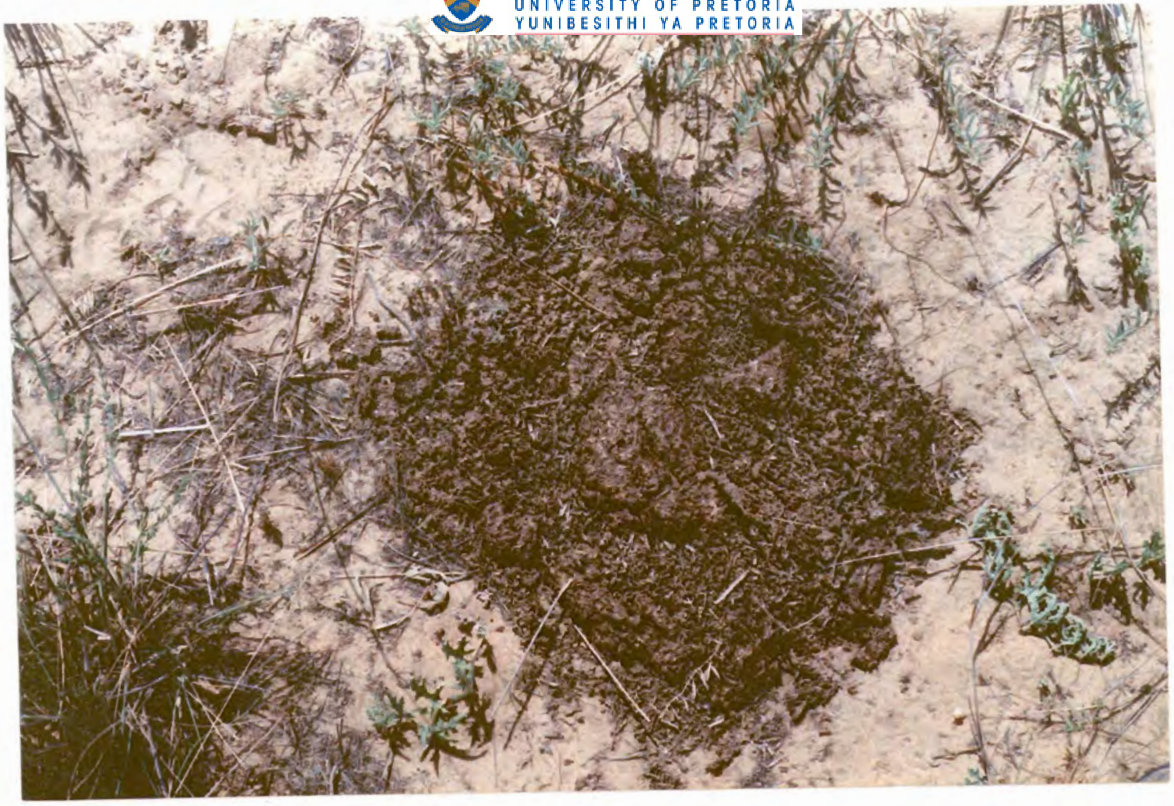
Stage 6 (Fig. 6.1. f):

Dung almost completely removed, few dry crusts remaining or dung totally shredded.

Fig. 6.1: General stages of dung degradation in a savanna ecosystem (SNR and neighbouring farms), a) stage 1 - No dung removed from pat, whole dung pat moist, no sign of disturbance; b) stage 2 - No dung removed, dung covered by dry crust, moist inside, few holes in dung pat.

Fig. 6.1. Continued: General stages of dung degradation in a savanna ecosystem (SNR and neighbouring farms), c) stage 3 -± 20% of dung pat removed, covered by dry crust, moist inside, numerous holes; d) stage 4 - ± 40% of dung removed, covered by dry crust, moist inside, numerous holes, holes filled with sand.

e)



f)

Fig. 6.1. Continued: General stages of dung degradation in a savanna ecosystem (SNR and neighbouring farms), e) stage 5 - ± 60% of dung removed, crust shredded, dry inside; f) stage 6 - Dung almost completely removed, few dry crusts remaining or dung totally shredded.

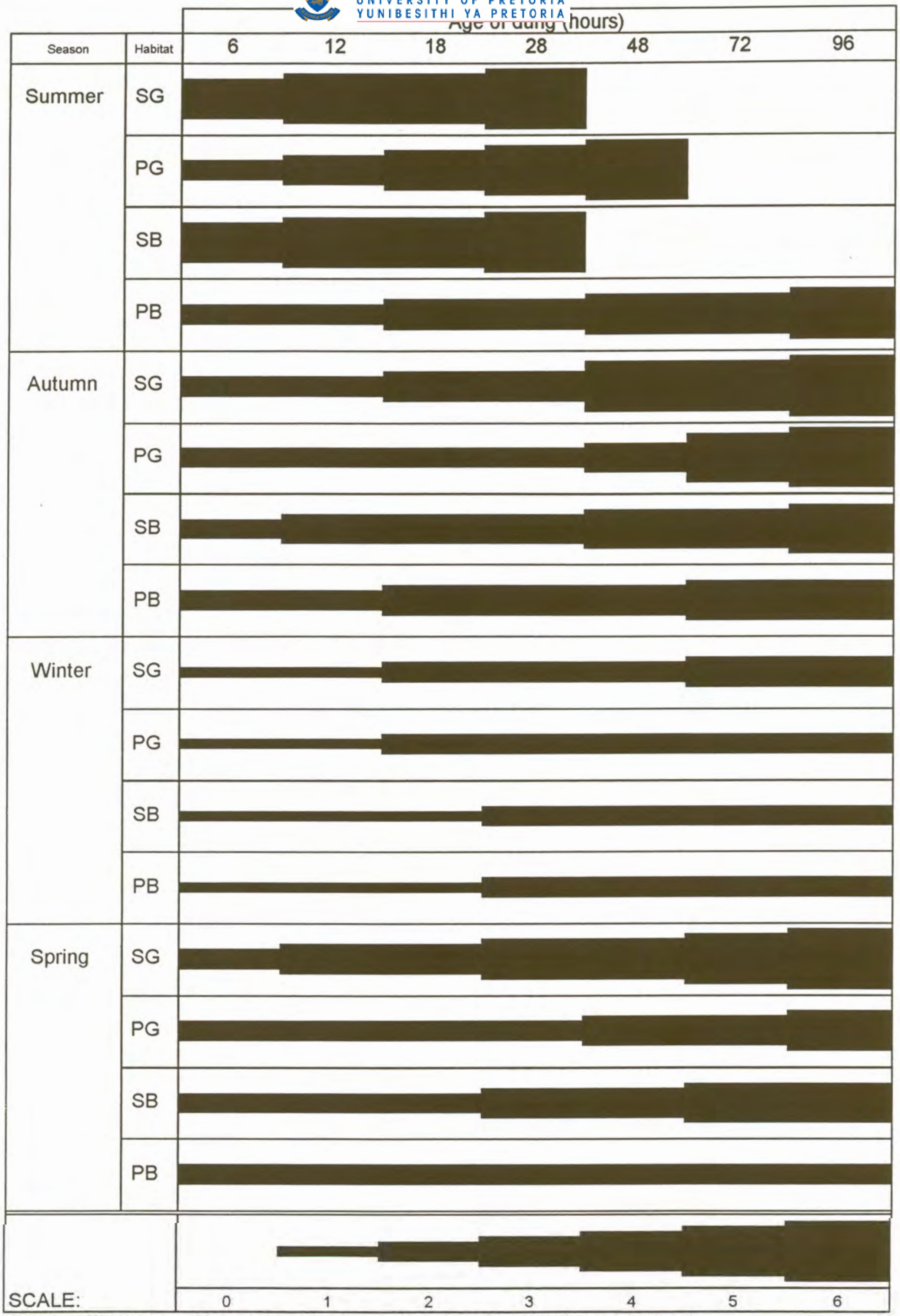
The rate of dung decomposition was very high during summer and higher in the natural grassveld habitats than the bushveld habitats. On the degradation index the dung in the natural grassveld habitat already reached stage 4 after 6 ± 1.4 hours, stage 5 after 12.5 ± 3.53 hours and was completely removed after 23 ± 4.24 hours (Fig. 6.2.a). Dung in the natural bushveld habitat reached stage 4 after 6 ± 1 hours, stage 5 after 12 ± 1 hours and was completely removed after 24.33 ± 1.53 hours (Fig. 6.2.a). In the disturbed grassveld habitat dung degradation only reached stage 4 after 18.33 ± 2.08 hours, stage 5 after 23 ± 1 hours and stage 6 after 46 ± 2 hours. In the disturbed bushveld habitat dung degradation reached stage 4 after 45.33 ± 2.51 hours and after 96 ± 2 hours dung was still in stage 5 (Fig. 6.2. a).

During Autumn dung degradation was much slower with dung in the natural grassveld habitat reaching stage 2 after 6.67 ± 0.58 hours, stage 3 after 17 ± 1 hours, stage 5 after 48.33 ± 0.58 hours and stage 6 after 95.67 ± 1.53 hours (Fig. 6.2. b). In the disturbed grassveld habitat dung degradation was slower with dung only reaching stage 3 after 48.33 ± 0.58 hours and stage 5 after 72.33 ± 1.53 hours (Fig. 6.2. b). In the natural bushveld habitat dung degradation was initially fast, reaching stage 3 after 12.33 ± 0.58 hours, but it slowed down and after 96 hours dung was still in stage 5 (Fig. 6.2. b). In the disturbed bushveld habitat dung degradation was slow with dung still in stage 4 after 96 hours (Fig. 6.2. b).

In winter dung degradation was very slow with dung in stage 3 after 96.33 ± 1.53 hours in the natural grassveld habitat and still in stage 2 in the other habitats (Fig. 6.2. c). An impenetrable crust had formed on the dung after 96 hours in all the habitats and no dung beetles colonised the dung after this time.

During spring in the natural grassveld habitat dung reached stage 3 after 11.67 ± 0.58 hours, stage 4 after 23.33 ± 1.53 hours, stage 5 after 71 ± 1 hours and was completely removed after 95.66 ± 1.53 hours (Fig. 6.2. d). Dung degradation was much slower in the disturbed grassveld habitat with dung only reaching stage 3 after 48 ± 1 hours and still in stage 4 after 96 hours (Fig. 6.2. d). In the natural bushveld habitat dung reached stage 3 after 23.66 ± 1.53 hours and stage 4 after 71.33 ± 1.15 hours, remaining in stage 4 after 96 hours (Fig. 6.2. d). In the disturbed bushveld habitat dung degradation was very slow, remaining in stage 2 after 96 hours (Fig. 6.2. d).

The rate of dung degradation differed with different seasons and in different habitats. Dung was degraded at the fastest rate during summer, with dung fully degraded after 24 hours, while dung was only fully degraded after 96 hours during the other seasons. Dung degradation was also much faster in the natural habitats than in the disturbed habitats during all four seasons. The faster rate of dung degradation during summer may be a result of higher temperatures and a higher abundance of dung inhabiting insects. According to Snowball (1944) high temperatures speed up the process of disintegration by accelerating the chemical and physiological processes within the dung and by stimulating the insects colonising the dung. The difference in degradation rates may also be a result of rainfall. Sandveld is a summer rainfall area with most of the rainfall in the area falling between November and April. Rainfall influences the occurrence of dung beetles with the highest abundance of dung beetles also during this time. Herrick & Lal (1996) also found that average decompositon rates for dung pats deposited during the wet-season were more than double than pats deposited in the dry-season. It seems most likely that the dung beetle fauna in a habitat and at a particular time influences the degradation of dung pats more strongly than any other factors. Herrick & Lal (1996) contribute the more rapid disappearance of dung during the wet-season to increased dung beetle activity during this time.



*Scale - Thickness of bars indicates stage of degradation (for stages see text)

Fig. 6.2: Rate of dung degradation in four different habitats during four different seasons, (SG-natural grassveld; PG-disturbed grassveld; SB-natural bushveld; Josina-distubed bushveld)

Population trends in dung beetle assemblages in terms of species, individuals and biomass in relation to age of the dung pat

The successional mean occurrence (SMO) of dung beetles differed in different habitats and during different seasons. Beetles colonised fresher dung in the natural habitats than the disturbed habitats and also fresher dung during the warmer seasons than the colder ones (Table 6.1).

Table 6.1: Successional mean occurrence (number of individuals) for dung beetles during four different seasons in four different habitats (S.G. - Sandveld Grassveld, natural grassveld habitat; Rietvlei – disturbed grassveld habitat; S.B. – Sandveld Bushveld, natural bushveld habitat; Josina – disturbed bushveld habitat).

	Summer (December)	**Autumn (April)**	**Winter (July)**	**Spring (September)**	**F**
S.G.	13.53	39.22	60.25	41.06	34.51, P<0
Rietvlei	19.81	73.52	72.00	50.46	
S.B.	15.003	58.80	86.4	52.03	
Josina	24.26	65.51	96	60.26	
F	4.3, P<0				

The colonisation of dung pats by dung beetles in terms of species richness, individuals and biomass differed according to season and habitat. During summer colonisation of dung was rapid in the natural grassveld and bushveld habitats. Species started colonising the dung within five minutes of deposition and species richness reached a peak 18 hours after deposition (Fig. 6.3a). After 24 hours no dung beetles were able to colonise the dung because it was completely broken down. Both number of individuals and biomass reached a peak after 12 hours (Fig. 6.3 b & c). The pattern of dung colonisation was similar in the natural bushveld habitat with early peaks in species richness, individuals and biomass and no dung remaining after 24 hours (Fig. 6.3. a-c). In the disturbed grassveld and bushveld habitats the initial colonisation of the dung was slower and species richness, individuals and biomass reached a peak only after 24 hours (Fig. 6.3. a-c). Dung beetles also remained in the pat for a longer time, until 72 hours after deposition in the disturbed grassveld habitat and 96 hours after deposition in the disturbed bushveld habitat (Fig. 6.3.a).

Peaks during autumn occurred later than during summer in all the habitats (Fig. 6.4 a-c). The peak in species richness, individuals and biomass was earlier in the natural grassveld habitat and dung beetles also remained in the dung for a shorter period in this habitat, than in the bushveld habitats and disturbed grassveld habitat (Fig. 6.4 a-c).

During winter, colonisation of dung by dung beetles was slow in all four habitats, but the earliest colonisation occurred in the natural grassveld habitat. In this habitat there was a peak in biomass after 24 hours (Fig. 6.5.c). In the disturbed grassveld habitat a peak in biomass only occurred after 48 hours (Fig. 6.5.c). In the natural bushveld habitat species richness, individuals and biomass reached a maximum only after 96 hours, while dung beetles in the disturbed bushveld habitat only started colonising the dung after 96 hours (Fig. 6.5.a-c).

During spring species richness, individuals and biomass reached a peak after 18 hours in the natural grassveld habitat and after 96 hours no dung beetles remained in the dung pat (Fig. 6.6. a-c). In the disturbed grassveld habitat species richness reached a peak after 24 hours (Fig. 6.6.a), individuals after 72 hours (Fig. 6.6. b) and biomass after 48 hours (Fig. 6.6 c), with dung beetles remaining in the pat after 96 hours. In the natural bushveld habitat species richness, individuals and biomass gradually increased after 24 hours, with a drop after 96 hours (Fig. 6.6. a-c). In the disturbed bushveld habitat species richness, individuals and biomass gradually increased, reaching a maximum after 96 hours (Fig. 6.6. a-c).

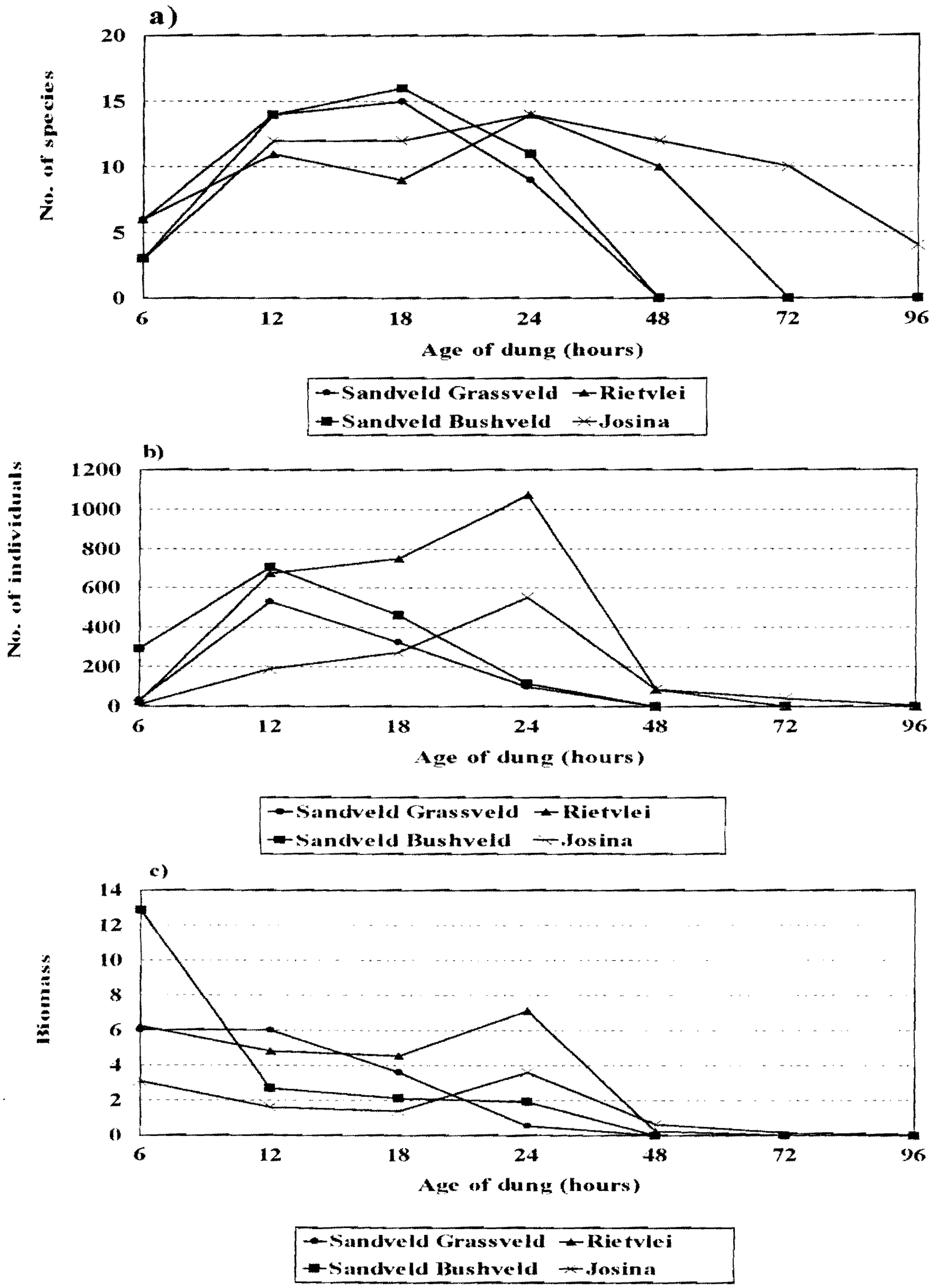


Fig. 6.3: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during summer (December 1996).

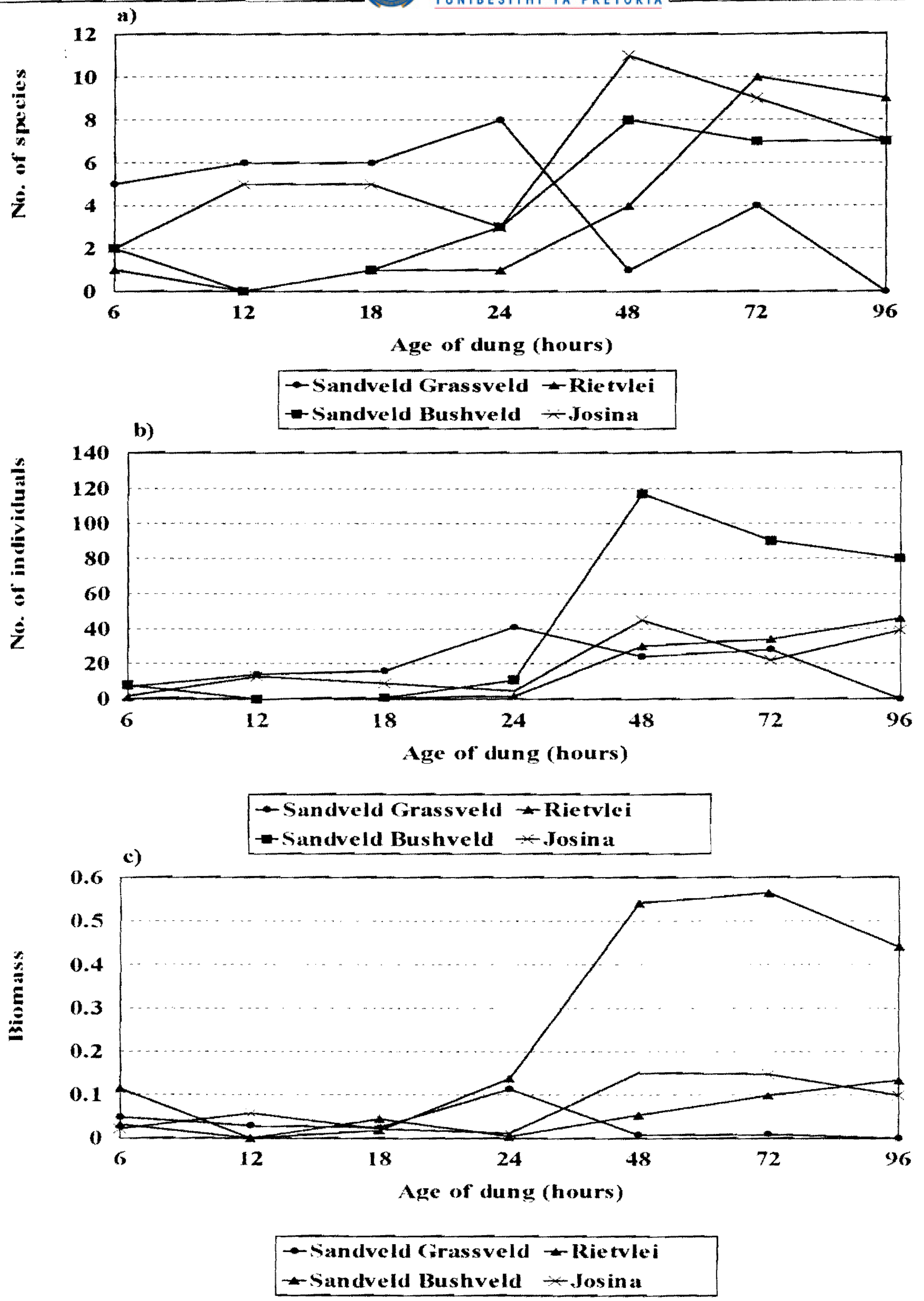


Fig. 6.4: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during autumn (April 1997).

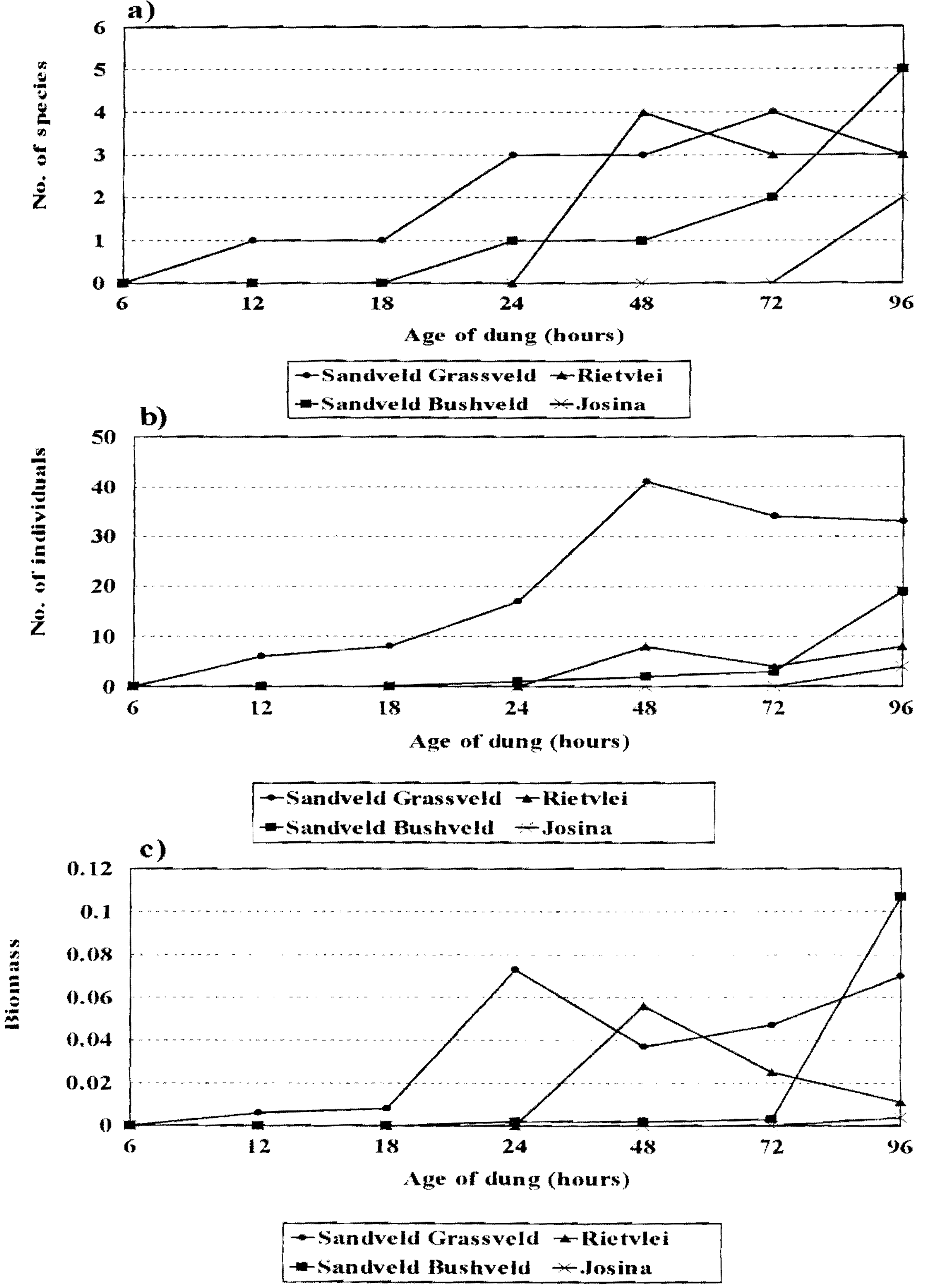


Fig. 6.5: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during winter (July 1997).

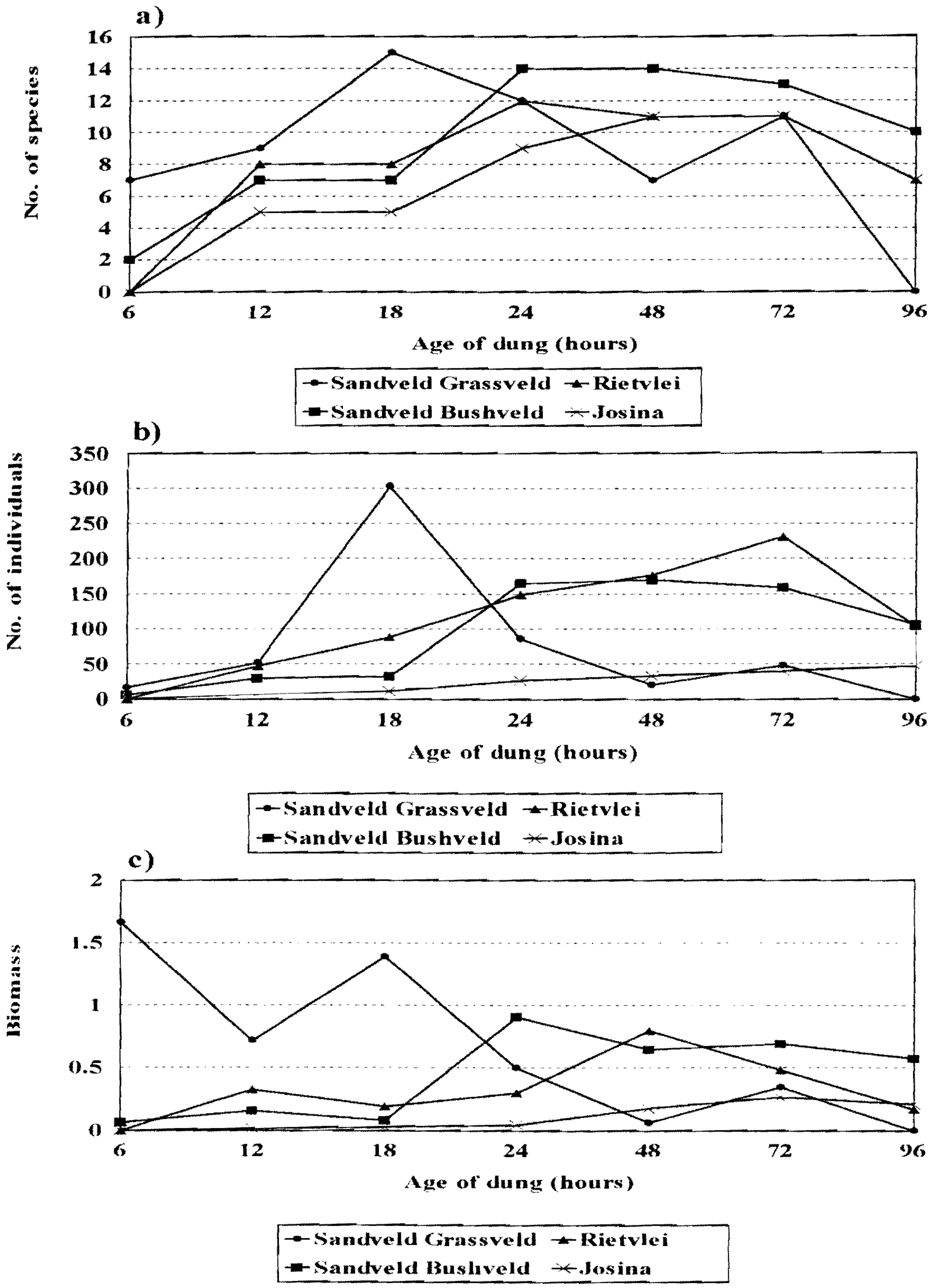


Fig. 6.6: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during spring (September 1997).

Howden & Nealis (1975) found that dung age was directly related to the number of individuals and species, decreasing as the dung aged. Cambefort (1991) found that most dung beetles reached their highest numbers in the pats during the first day and most species have left the pat during the fourth or even the third day. Similar results were found in the present study with no dung beetles left in the dung pat after four days. Dung age, however was not the only factor determining abundance of species, individuals and biomass. Time of colonisation of dung pats by dung beetles and peaks in species richness, individuals and biomass depended to a large extent on the habitat and the season. According to Koskela & Hanski (1977) macroenvironmental properties can determine the patterns observed in the numbers of species and diversity of the community during succession. In the present study differences in the macrohabitat had an important influence on the distribution of species, individuals and biomass in dung beetle assemblages during colonisation of the dung which could be contributed to various factors. The assemblage structure in the different habitats may differ, resulting in different species influencing one another differently and subsequently influencing the colonisation of the whole assemblage. The habitat may also have different influences on dung resulting in different temperature, humidity and rate of desiccation of dung, in turn influencing the succession of dung beetles. The natural grassveld habitat seemed to be most favourable for the early colonisation of large numbers of dung beetles. Dung was rapidly found and colonised by a large number of dung beetles at an early stage. The resource was quickly utilised and the duration of succession short. Small environmental differences in different habitats may have influenced the success of dung beetles and subsequently the succession in the dung. Valiela (1974) found that short-term localised conditions occurring during succession could greatly affect the course of events in dung beetle communities, while Koskela & Hanski (1977) found that in the later stages weather becomes the main factor determining the course of succession. Barth *et al* (1994) found that qualitative and quantitative colonisation of dung pats varied considerably depending on climatic conditions such as temperature, wind or sunlight, all of which can vary within short periods of time. In the present study the dung dried out very quickly during summer forming a hard crust within a short time resulting in a more rapid succession than during the colder months. As the temperatures dropped during the colder seasons desiccation rate of the dung was slower and it took a longer time to form a crust allowing dung beetles to colonise older dung.

Pattern of colonisation of dung pats by different functional groups

Dung beetles in different functional groups had different ways of utilising the dung and these groups also had different preferences for the age of dung they colonised. During summer in the natural grassveld habitat F.G. I, II, V and VI colonised the dung pats first, within the first six hours, while F.G. III, IV, and VII colonised 12 hour old dung (Appendix Fig. 6.1. a). Beetles belonging to F.G. I visited the dung pats only within the first six hours (Appendix Fig. 6.1. a). Beetles belonging to F.G. II and III colonised older dung and were found on the dung up to 18 hours old (Appendix Fig. 6.1. a). The dung beetles in F.G. IV, V, VI and VII stayed in the dung for longer than F.G. I, II and III, until the dung pat was broken down after 24 hours (Appendix Fig. 6.1. a). Dung beetles in F.G. IV and V spent some time in the dung pat, before burying it just beneath the pat, while F.G. VII made their nests inside the dung pat. F.G. VI occurred abundantly in the dung throughout the period until dung was broken down. These dung beetles used dung balls removed by telecoprids as food and breeding medium.

In the disturbed grassveld habitat all the functional groups colonised the dung before it was six hours old, whilst F.G. VII colonised the dung only after 12 hours (Appendix Fig. 6.1. b). The dung in this habitat was broken down later than in the natural grassveld habitat. F.G. I did not occur at the dung pat after six hours, but dung beetles in all the other groups occurred in the dung until it was 48 hours old, after which it was completely broken down (Appendix Fig. 6.1. b).

In the natural bushveld habitat beetles of all the F.G.'s were found at the dung pat after 24 hours (Appendix Fig. 6.1. c). Dung beetles occurred in the dung pat for the longest duration in the disturbed bushveld habitat and after 96 hours dung beetles belonging to F.G. IV, V and VII were still present (Appendix Fig. 6.1. d).

During autumn fewer dung beetles colonised the dung pat. In the natural grassveld habitat F.G. IV, V and VII colonised the dung before it was six hours old and all these groups were present in the dung after 72 hours (Appendix Fig. 6.2. a). In the disturbed grassveld habitat dung beetles generally colonised the dung later and only F.G. VII colonised the dung before it was six hours old. The other groups only colonised the dung after 72 hours and dung beetles occurred in the dung pats in this habitat until after it was 96 hours old (Appendix Fig. 6.2. b). In the natural bushveld habitat colonisation of the dung also occurred later with only F.G. V colonising the dung before it was six hours old. F.G. II, VI and VII occurred after 48 hours and F.G. IV after 18 hours (Appendix Fig. 6.2 c). F.G. IV, V, VI and VII were present in the dung after 96 hours (Appendix Fig. 6.2. c). In the disturbed bushveld habitat F.G. IV and V colonised the dung before six hours, F.G. VI colonised the dung after 48 hours and F.G. VII after 12 hours (Appendix Fig. 6.2. d). All the groups except F.G. VI were still present in the dung after 96 hours (Appendix Fig. 6.2. d).

During winter only dung beetles belonging to F.G. VII colonised the dung in the natural grassveld habitat. These dung beetles colonised 12 hour old dung and still occurred in the dung after 96 hours (Appendix Fig. 6.3. a). In the disturbed grassveld habitat beetles representing more functional groups colonised the dung, but these beetles colonised the dung very late, only after 48 hours and only stayed in the dung for a short period (Appendix Fig. 6.3. b). In the natural bushveld habitat dung beetles belonging to F.G. VII only colonised the dung after 24 hours and F.G. IV only after 96 hours (Appendix Fig. 6.3. c). In the disturbed bushveld habitat the only dung beetles colonising the dung belonged to F.G. VII and these dung beetles only occurred after 96 hours (Appendix Fig. 6.3. d).

During spring all the functional groups, except F.G. III colonised six-hour-old dung in the natural grassveld habitat. F.G. I occurred at fresh dung for only a short period, while the other groups occurred at the dung until it was 72 hours old (Appendix Fig. 6.4. a). In the disturbed grassveld habitat dung beetles occurred in the dung for a longer time, until it was 96 hours old (Appendix Fig. 6.4. b). In the natural bushveld habitat this group colonised the dung after 24 hours and in the disturbed habitat after 72 hours (Appendix Fig. 6.4. c and d). F.G. IV and V colonised the dung earlier in the natural habitat than the disturbed habitat (Appendix Fig. 6.4. c and d). In the natural habitat F.G. VI colonised the dung after 12 hours and F.G. VII after 18 hours (Appendix Fig. 6.4. c), while in the disturbed habitat F.G. VI colonised the dung after 18 hours and F.G. VII after 12 hours. In both habitats dung beetles stayed in the dung until it was 96 hours old (Appendix Fig. 6.4. c and d).

Different functional groups differed in their choice of dung age. The larger dung beetle species colonised the dung early and stayed in the dung for short periods. F.G. I colonised dung almost immediately after deposition and was rarely found in dung older than six hours. The exception was in the bushveld habitats where this group occurred in dung of up to 24 hours old. F.G. II also colonised fresh dung, but occurred at older dung pats than did F.G. I. Dung beetles in these two groups usually removed dung from the top of the dung pat and it is difficult to remove dung once a crust has formed. This is probably the reason why these groups colonised fresh dung and occurred at the dung pat for a relatively short period compared to the other groups. In the bushveld habitat, because of shade cover, dung stayed fresher and took longer to form a crust, enabling dung beetles to still remove moist dung after 24 hours. The other groups usually entered the dung from the basal edge of the pat, digging into the soil underneath the pats and staying in the pats for a relatively long period.

These findings are in agreement with Doube (1990) who found that, in southern Africa, F.G. I usually spent only 2-3 hours at the dung, F.G. II 2 to 24 hours, F.G. III 6-24 hours, F.G. IV up to 6 weeks, F.G. V up to several weeks and F.G. VII many weeks. Koskela & Hanski (1977) found that the mean weight per coprophage correlated positively with the moisture of the dung. They ascribed the decrease in the mean weight of coprophages during succession to a decreased amount of organic matter in the microhabitat and to changes in its structure. Small species are probably better adapted to cope with these changes than large ones. In the present study the initial time of colonisation of the other groups, representing the smaller dung beetles, was strongly affected by both the habitat and the season, with colonisation taking place later in the disturbed grassveld habitat and bushveld habitats than in the natural grassveld habitat and later during the colder seasons. It seems that the succession of dung beetles is influenced by external climatic conditions and also by small differences in vegetation type. The succession of dung beetles may also be determined by the abundance of the species that occupy the dung in the initial stages. These beetles may alter the physical and chemical nature of the environment and ultimately a stage is reached at which a primary species is displaced by one more adapted to the changed conditions.

Pattern of colonisation of dung pats by different species

Different dung beetle species colonised dung of different ages and also differed in the duration of their occurrence in the dung. During summer *Pachylomerus femoralis* and *Onthophagus sugillatus* colonised the dung early in all the habitats (Appendix Fig. 6.1. a-d). In the natural grassveld habitat *Caccobius seminulum*, *Neosisyphus ruber* and *Onthophagus sp. 4* also colonised the dung early (Appendix Fig. 6.1. a). The other species colonised older dung and some species such as *Aphodius pseudolividus*, *A. vestitus*, *C. ferrugineus*, *O. quadraliceps*, *Onitis uncinatus* and *P. femoralis* occurring only briefly in the dung (Appendix Fig. 6.1. a). Other species occurred in the dung for longer periods, with *C. seminulum* and *O. sugillatus* occurring in the dung until it was broken down. *N. ruber* and *P. femoralis* preferred fresher dung with *N. ruber* not occurring in dung older than 12 hours and *P. femoralis* not occurring in dung older than six hours (Appendix Fig. 6.1. a). *Scarabaeus flavicornis* colonised 12 hour old dung and occurred at the dung till it was 18 hours old (Appendix Fig. 6.1. a). The other, smaller species colonised older dung and stayed in the dung until it was broken down. In the disturbed grassveld habitat most species seemed to occur in the dung for longer periods than in the natural habitat. *N. ruber* colonised much older dung in this habitat than in the natural grassveld habitat. This species was observed at dung that was 48 hours old (Appendix Fig. 6.1. b). *O. quadraliceps* colonised fresh dung in the disturbed grassveld habitat and occurred in the dung until it was 24 hours old (Appendix Fig. 6.1 b), while in the natural habitat this species only occurred in older dung for a short period. *S. flavicornis* colonised the dung at the same time as in the natural grassveld habitat, but was observed at the dung for a shorter period (Appendix Fig. 6.1. b). In the natural bushveld habitat most species colonised the dung after 12 hours and only stayed for brief periods (Appendix Fig. 6.1 c). The only species occurring in fresher dung were *Euoniticellus intermedius*, *Onthophagus sugillatus* and *P. femoralis*. *Onthophagus sugillatus* stayed in the dung for the whole duration, while *E. intermedius* stayed in the dung till it was 18 hours old (Appendix Fig. 6.1 c). *E. intermedius* colonised the dung earlier and spend a much longer time in this habitat than in the grassveld habitat. *P. femoralis* occurred at the dung when it was still fresh, but also occurred at dung that was 24 hours old in the natural bushveld habitat (Appendix Fig. 6.1 c). Although there were species in the disturbed bushveld habitat which colonised the dung for only brief periods they seemed to stay in the dung for a longer time than in the natural bushveld habitat (Appendix Fig. 6.1. d). *O. sugillatus* colonised the dung before it was six hours old and stayed in the dung until it was 96 hours old (Appendix Fig. 6.1. d). *E. intermedius* did not occur in dung older than six hours in the disturbed habitat (Appendix Fig. 6.1. d).

During autumn most species colonised the dung within the first 12 hours in the natural grassveld habitat with *Aphodius laterosetosus*, *Onthophagus sp. 4*, *O. flavimargo* and *O. obtusicornis* colonisation within the first six hours (Appendix Fig. 6.2. a). In the disturbed grassveld habitat colonisation was much later than in the natural habitat and *A. laterosetosus* and *O. obtusicornis* only colonised the dung after 72 hours (Appendix Fig. 6.2. b). The only species present in fresh dung, for a short period, in this habitat was *Colobopterus sorex* (Appendix Fig. 6.2. b). In the natural bushveld habitat *O. sugillatus* was the only species colonising the fresh dung, with most of the other species only colonising the dung after 24 hours (Appendix Fig. 6.2. c). In the disturbed bushveld habitat *O. sugillatus* and *O. obtusicornis* colonised the fresh dung, with the other species occurring in older dung (Appendix Fig. 6.2. d).

During winter *A. separatus* was the first species to colonise the dung after 12 hours in the natural grassveld habitat (Appendix Fig. 6.3. a). *C. sorex and Drepanocanthus rubescens* colonised the dung after 24 hours, while *D. eximius* only colonised the dung after 48 hours (Appendix Fig. 6.3. a). All these species stayed in the dung for a relatively long period. In the disturbed grassveld habitat all the species only colonised the dung after 48 hours and stayed in the dung for only brief periods (Appendix Fig. 6.3. b). In the natural bushveld habitat *D. eximius* colonised the dung after 24 hours and *A. separatus* after 48 hours and these two species stayed in the dung for a relatively long period (Appendix Fig. 6.3. c). The other species in this habitat only colonised the dung after 96 hours (Appendix Fig. 6.3. c). In the disturbed bushveld habitat *A. calcaratus* and *D. eximius* colonised the dung after 96 hours (Appendix Fig. 6.3. d).

During spring *C. seminulum*, *C. sorex*, *N. ruber*, *Onthophagus sp. 4*, *O. leucopygus*, *O. quadraliceps* and *P. femoralis* colonised the dung early in the natural grassveld habitat (Appendix Fig. 6.4 a). *O. sugillatus* colonised older dung staying until it was 72 hours old (Appendix Fig. 6.4. a). In this habitat *N. ruber* also occurred at the dung for a much longer period during spring than during summer (Appendix 6.4. a). In the disturbed grassveld habitat no species colonised the dung before it was six hours old and *C. seminulum* and *N. ruber* only colonised the dung after 48 hours, while *C. sorex* colonised the dung after 72 hours (Appendix Fig. 6.4.b). These dung beetles also stayed in the dung for only brief periods. The other species in this habitat occurred in the dung until it was 96 hours old (Appendix Fig. 6.4. b). In the natural bushveld habitat *O. quadraliceps* and *O. sugillatus* colonised the dung after six hours and stayed in the dung until it was 96 hours old (Appendix Fig. 6.4. c). *O. sugillatus* colonised the dung later in the disturbed bushveld habitat, but also stayed in the dung until it was 96 hours old (Appendix Fig. 6.4. d).

There were differences between different species in their colonisation times and the time spent in the dung. Different species differed in their choice of dung age with some species preferring fresh dung, others preferring older dung and others not showing any preference. This is in agreement with Doube *et al.* (1988) who found that in Natal (South Africa) the pattern of arrival of species was strongly influenced by the age of the dung. In an Ecuadorian rain forest Peck & Forsyth (1982) also found differences in peak abundance between different species, with some species being more sensitive to dung age than others. They ascribed these differences to a difference in food preference, odour perception, and foraging strategy. This choice of dung age was also strongly influenced by the habitat and season. Species that colonised only fresh dung and staying for a short period in the natural grassveld habitat, colonised older dung in the disturbed habitat and stayed longer in the dung. During the colder seasons some species also occurred in the dung for longer periods than in summer. According to Peck & Forsyth (1982) competitive success to a large degree depends on the ability to rapidly locate dung. In the present study the competitive success of species might be influenced differently by habitats, which affect the pattern of succession of different species. Much of the competition is in the form of a scramble in the natural grassveld habitat, resulting in early colonisation of most species to secure dung fast enough before it is utilised by other species. The successional pattern was different for dung beetles in northern temperate countries where competition for dung was less severe. In northern Zealand (Denmark) where *Aphodius* is the dominant genus Holter (1982) found that invaders of fresh dung stay briefly, whereas late invaders have long residence times. This is not true for dung beetles in the present study, where late invaders also often occurred in the dung for short periods. This was probably the result of strong interspecific competition, which is stronger in the natural grassveld habitat than in the other habitats. In the other habitats the time dung beetles spent in the dung was often longer. Some genera have evolved behavioural strategies that decrease competition, such as removal and burial of dung in *P. femoralis*, *S. flavicornis* and *N. ruber*. These species are large, they arrive at the dung pat early and remove the dung quickly. According to Doube *et al.* (1988) effective competition for dung will be influenced by the timing of pad colonisation in relation to dung age, the rate and quantity of dung removal and beetle size. It is probably these species that have the greatest influence on the successional pattern of other species utilising the dung because, during summer months, under natural conditions colonisation and dung removal by these species were rapid. Although smaller species also colonised fresh dung they do not have a great impact on the dung. In the natural grassveld habitat during summer dung degradation was so rapid that little dung remained after 24 hours. This resulted in early colonisation of most species. In the other habitats and during the colder seasons these species were less abundant and subsequently had a smaller influence on the successional pattern resulting in slower dung decomposition and colonisation of older dung by other species.

Size of dung beetles in relation to dung decomposition

The amount of dung consumed by dung beetles (p) is a good measure to determine the effect of dung beetle specialisation on the habitat. The size and weight of individual dung beetles can be used to determine the efficiency of dung removal in habitats. Several studies confirm that the amount of dung buried by dung beetles is related to beetle size (Halffter & Matthews, 1966;. Lee & Peng, 1982; Doube *et al.*, 1988; Tyndale-Biscoe, 1994). Nealis (1977) and Kirk & Wallace (1990) used biomass of dung beetles as an indication of the quantity of dung removed. In the present study there were differences in the dung beetle biomass and hence amount of dung buried in the different habitats during the different seasons. During all four seasons the natural habitats had the highest p_i values (Table 6.2). The p_i values were also much higher during summer than during the other seasons. During summer p_i values made up 82.53% of the total, during autumn only 4.02%, during winter 0.64% and during spring 12.07% (Table 6.2). This indicates that more dung is buried in the natural habitats and considerably more dung is buried during summer. Nealis (1977) also found differences in the amount of dung buried in various habitats.

Table 6.2: Dung disposal over four different seasons in four different habitats (S.G. - Sandveld Grassveld, natural grassveld habitat; Rietvlei – disturbed grassveld habitat; S.B. – Sandveld Bushveld, natural bushveld habitat; Josina – disturbed bushveld habitat) as estimated by biomass measurements of the beetles in each habitat.

Season	Habitat	$p_i=\Sigma n_j w_j$	p_i as % total in different habitats	p_i as % total during different seasons
Summer (December)	Sandveld Grassveld	23	33.12	82.53
	Rietvlei	16.22	23.35	
	Sandveld Bushveld	19.643	28.28	
	Josina	10.599	15.25	
Autumn (April)	Sandveld Grassveld	0.741	21.92	4.02
	Rietvlei	0.313	9.25	
	Sandveld Bushveld	1.816	53.71	
	Josina	0.511	15.11	
Winter (July)	Sandveld Grassveld	0.241	45.05	0.64
	Rietvlei	0.092	17.2	
	Sandveld Bushveld	0.194	36.26	
	Josina	0.008	1.5	
Spring (September)	Sandveld Grassveld	4.679	43.39	12.07
	Rietvlei	2.258	20.94	
	Sandveld Bushveld	3.108	28.82	
	Josina	0.739	6.9	
Total	Sandveld Grassveld	28.66	34.05	
	Rietvlei	18.89	22.44	
	Sandveld Bushveld	24.76	29.42	
	Josina	11.86	14.09	

*F=44.78, $p<0.05$ *F=2.26, $p<0.05$

Rate of beetle biomass change during the course of succession

The rate of change in biomass during the course of succession was determined for dung beetle assemblages in four different habitats over four different seasons. The rate of change was most rapid in the natural habitats during summer. On the first day the colonisation rate was high during the first few hours when the dung was fresh in the natural habitats, with a sudden decrease after 12 hours (Fig. 6.7. a). In the disturbed habitats the colonisation rate was more gradual (Fig. 6.7. a). The colonisation rate was high in all four habitats over the four days of succession. The highest rate of colonisation occurred during the first day after which there was a sudden decrease (Fig. 6.7. b). During autumn the rate of increase was gradual in all four habitats during the first day (Fig. 6.8. a). Over the four days of succession the rate was highest in the natural habitats with highest colonisation during the first day, while the increase in biomass was more gradual in the disturbed habitats (Fig. 6.8. b). During winter the rate of succession was slow in all the habitats but was still higher in the natural habitats than the disturbed habitats during the first day (Fig. 6.9 a). Over the four days of succession the rate of colonisation was highest in the natural and disturbed grassveld habitats (Fig. 6.9. b). During spring the rate of succession was again highest in the natural habitats during the first day (Fig. 6.10. a) and highest in the natural grassveld habitat over the four day period of succession (Fig. 6.10. b).

Both the habitat and the season influenced the rate of succession. The rate of succession was higher in the natural habitats than the disturbed habitats and also higher in summer than during the colder seasons. According to Koskela & Hanski (1977) the rate of change is high in the early stages of succession giving species limited time for colonisation. During later stages of succession the rate of change decreases, resulting in more time for colonisation of the later succesional stages. In the present study the rate of succession is very high in the natural habitats during summer, resulting in the total breakdown of the dung and leaving little time for colonisation in the later stages of succession. The rate of change is, however, slower during the early stages of succession in the disturbed habitats resulting in more time for colonisation in these habitats.

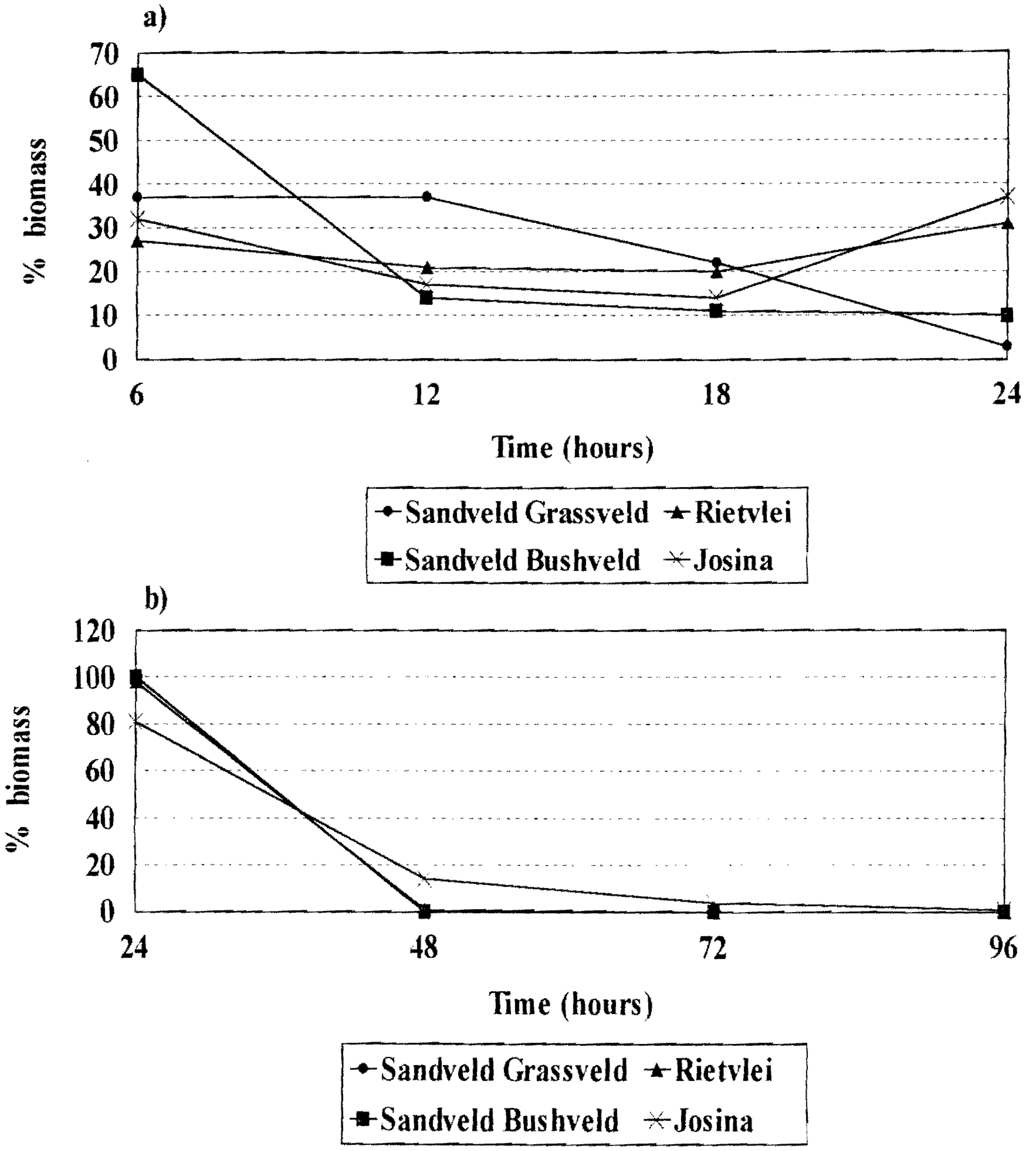


Fig. 6.7: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina – disturbed bushveld) (Summer - December 1996).

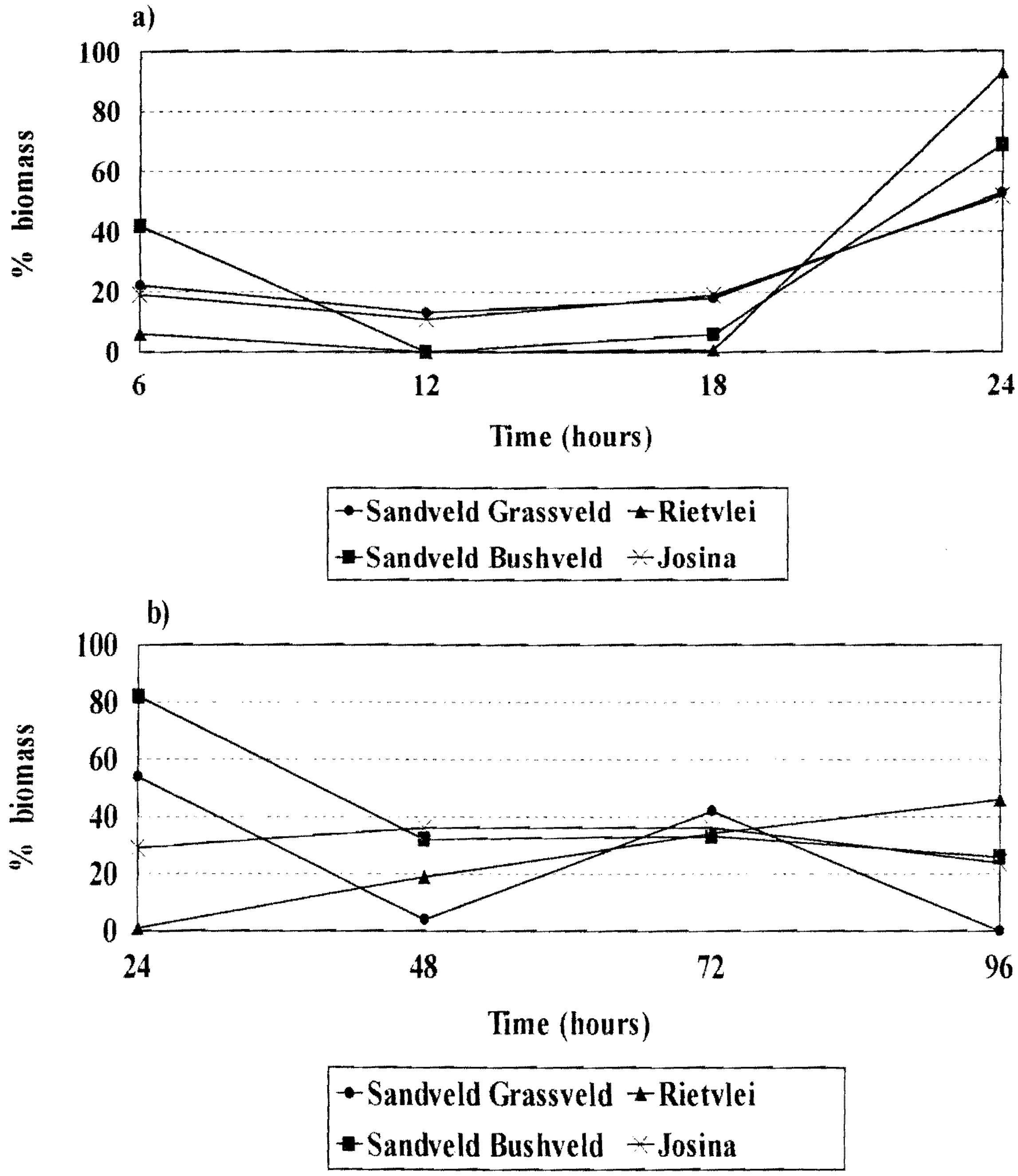


Fig. 6.8: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina – disturbed bushveld) (Autumn - April 1997).

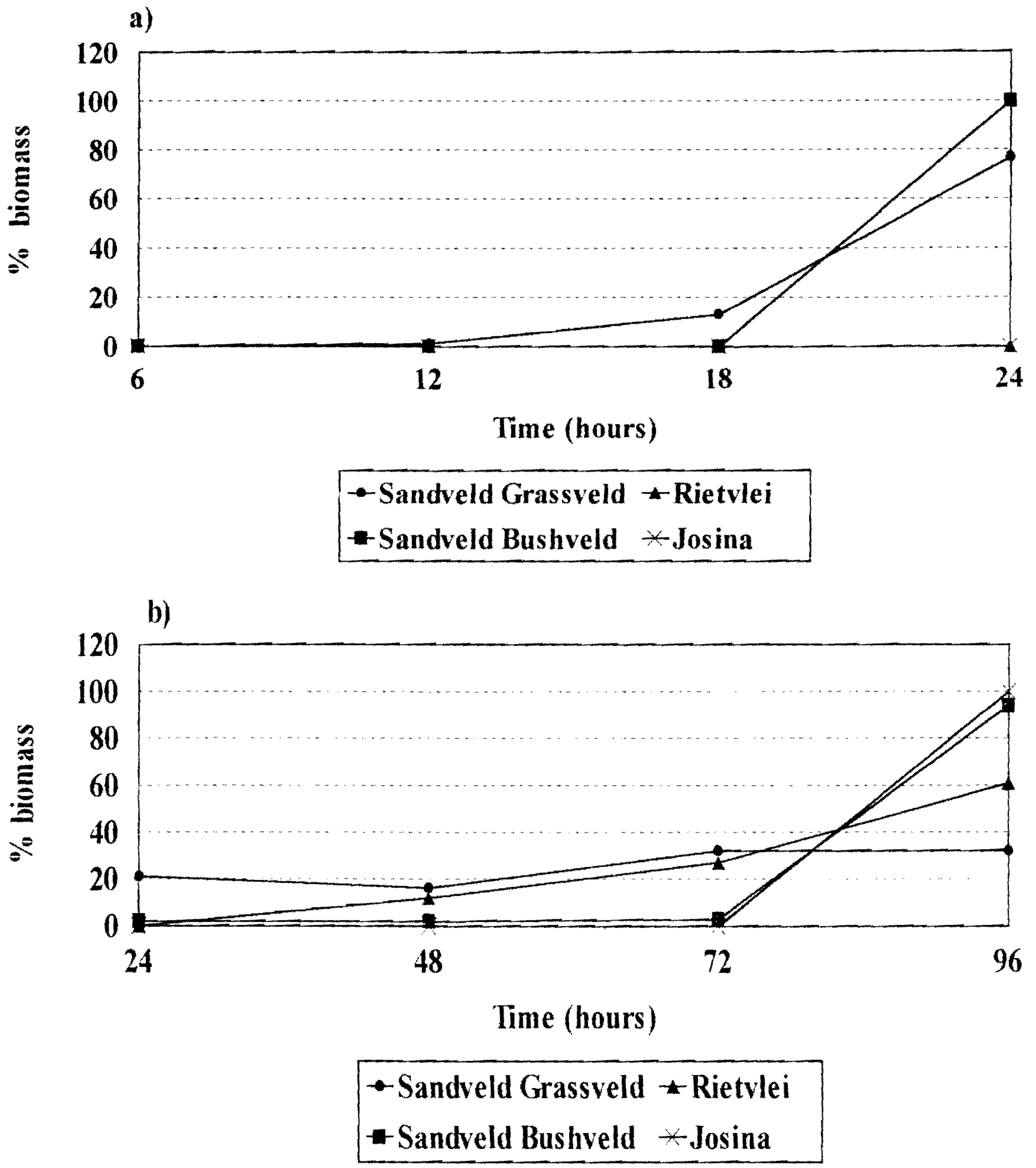


Fig. 6.9: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina – disturbed bushveld) (Winter - July 1997).

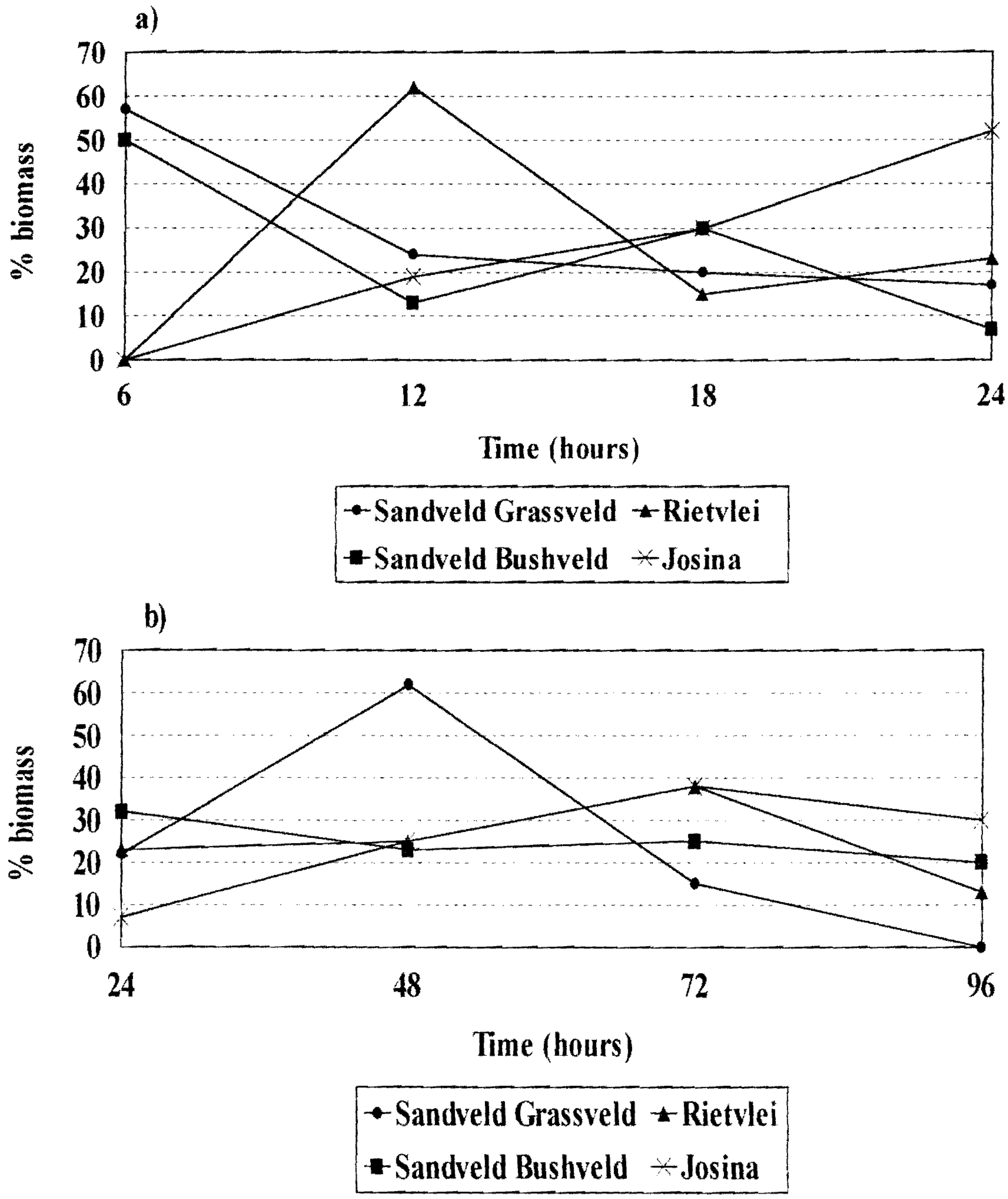


Fig. 6.10: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina – disturbed bushveld) (Spring - September 1997).

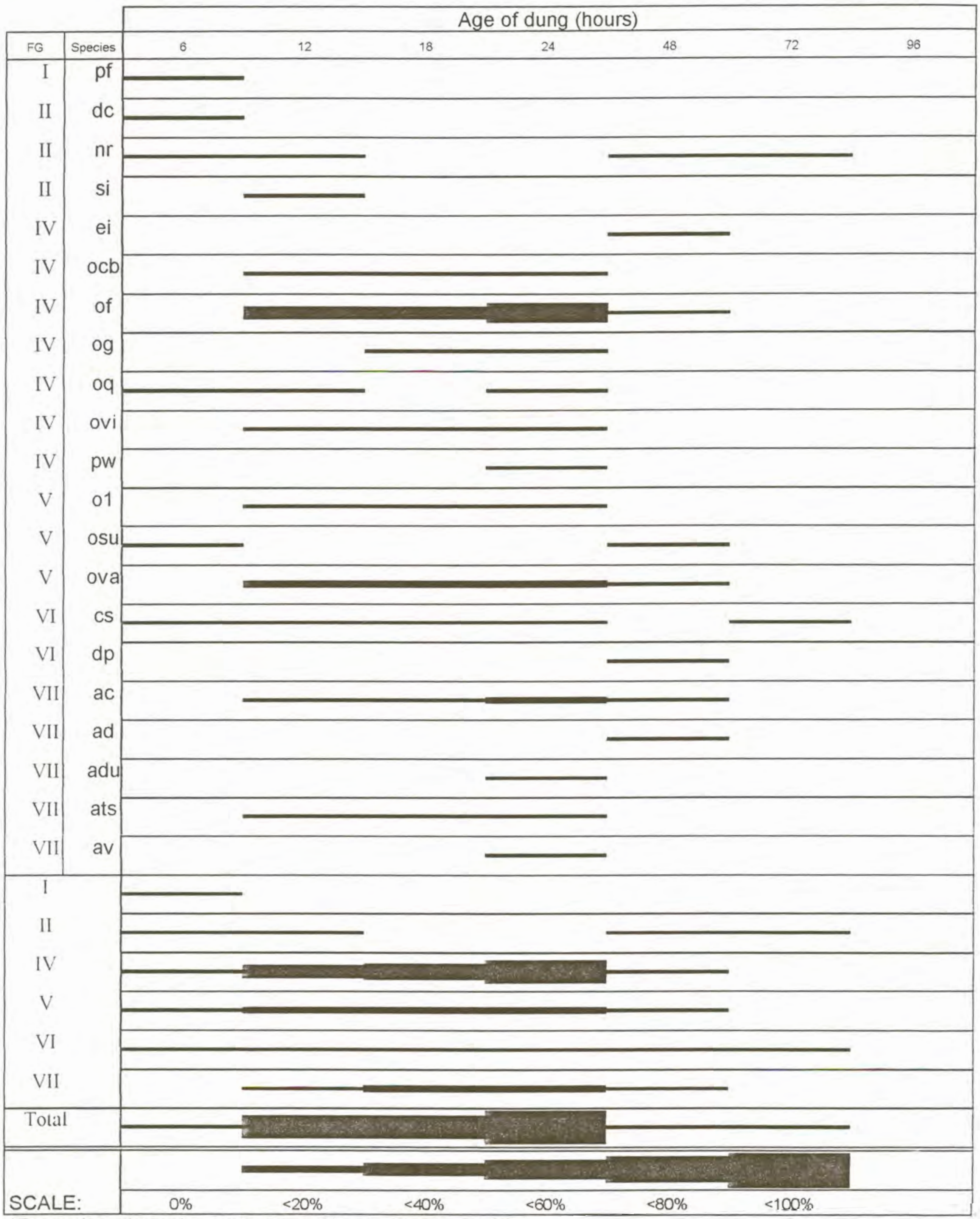
6.4. CONCLUSION

Valiela (1974) found that food was not a limiting factor for dung invertebrates, but that local changes in the environment and in the dung itself may have a limiting influence. In the present study the season and the habitat in which the dung was dropped had a strong influence on the succession of dung beetles and subsequently also the rate of dung decomposition. Dung degradation was faster during the warmer summer months and also faster in the natural habitats. Dung degradation was probably most strongly influenced by the colonisation of dung beetles, because the maximum species richness, biomass and number of individuals were also reached earlier in summer and also earlier in the natural habitats. Different functional groups differed in their choice of dung age, but habitat and season also influenced this choice, with colonisation of functional groups occurring earlier in the natural grassveld habitat and earlier in summer. Different species differed in the time of colonisation and also in the time spent in the dung. Species generally colonised fresher dung in the natural grassveld habitat and stayed in the dung for shorter periods than in the disturbed grassveld habitat. Dung beetles also stayed longer in the dung during the colder seasons. This might be an indication of stronger interspecific competition during summer in the natural grassveld habitat. In the present study *P. femoralis* (F.G. I), *S. flavicornis* (F.G. II) and *N. ruber* (F.G. II) probably have the strongest influence on the course of succession. According to Doube (1990) removal of dung by dung beetles of F.G. I and II is rapid. These larger dung beetles were more numerous in the natural grassveld habitat resulting in a larger amount of dung buried in this habitat within a short time. The rate of change in succession was also more rapid in the natural habitats during summer.

6.5. APPENDIX

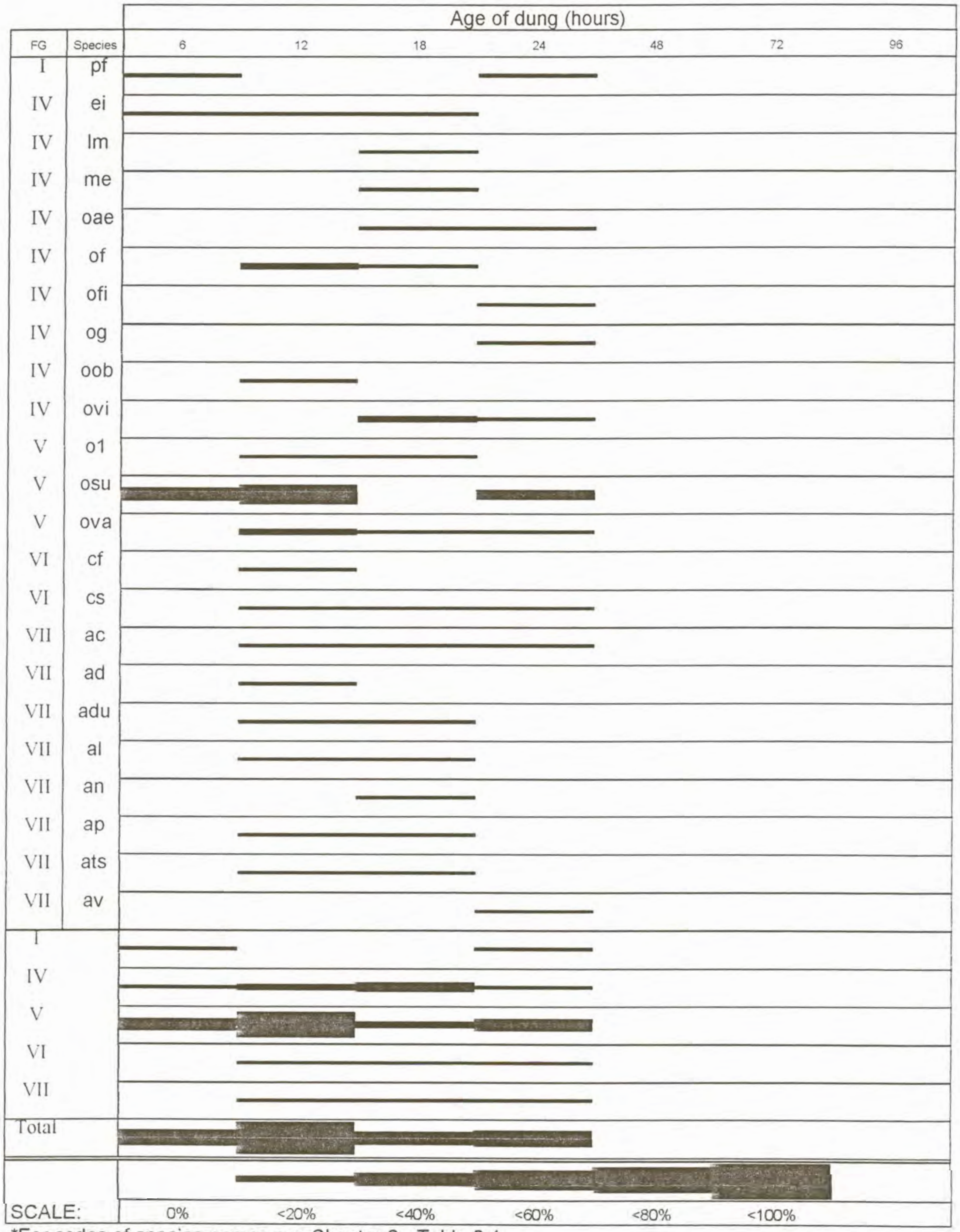
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.1. Successional pattern of dung beetle species and functional groups (F.G.'s) during summer (December 1996): a) Sandveld grassveld (natural grassveld habitat).



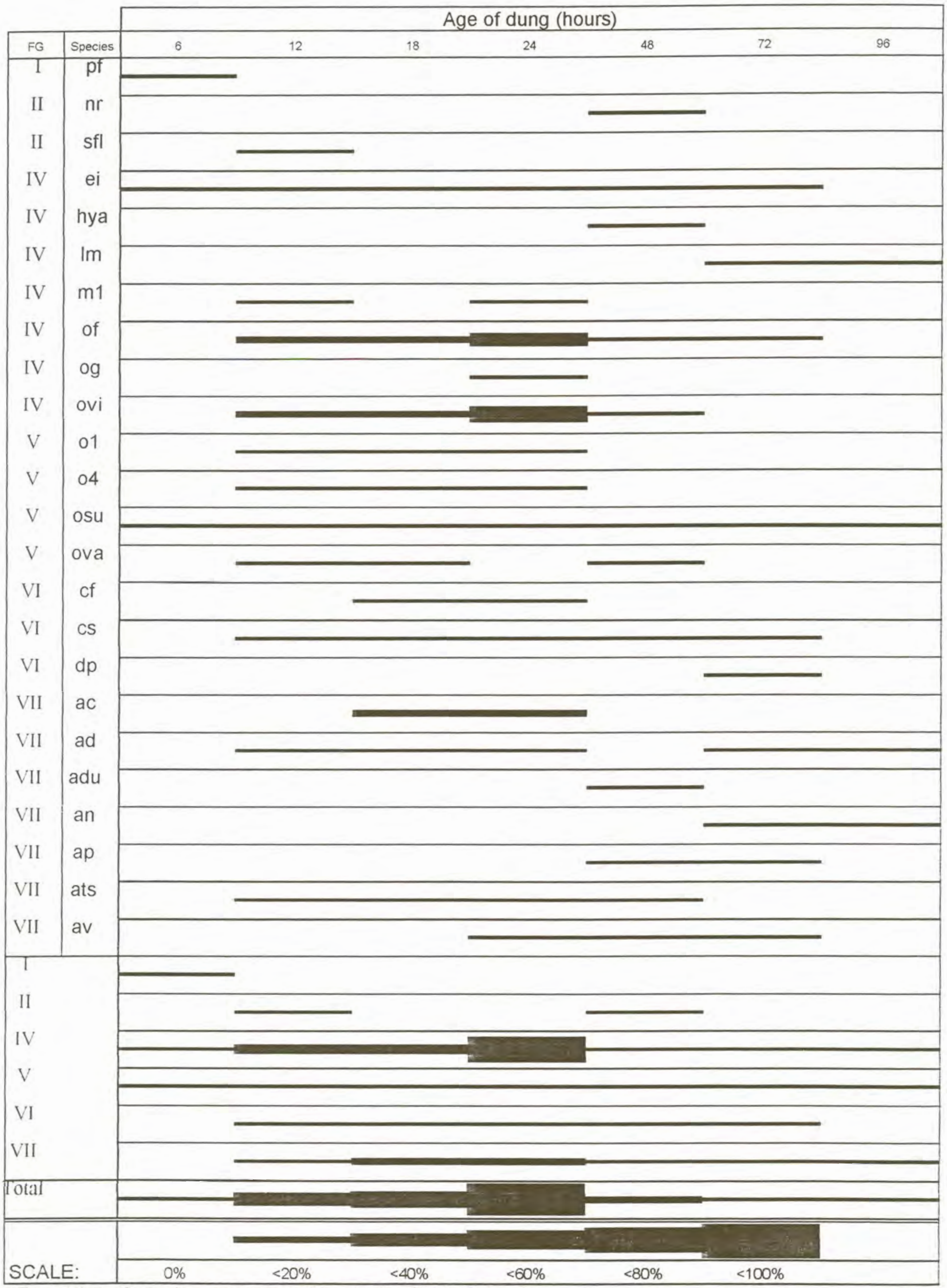
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.1. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during summer (December 1996): b) Rietvlei (disturbed grassveld habitat).



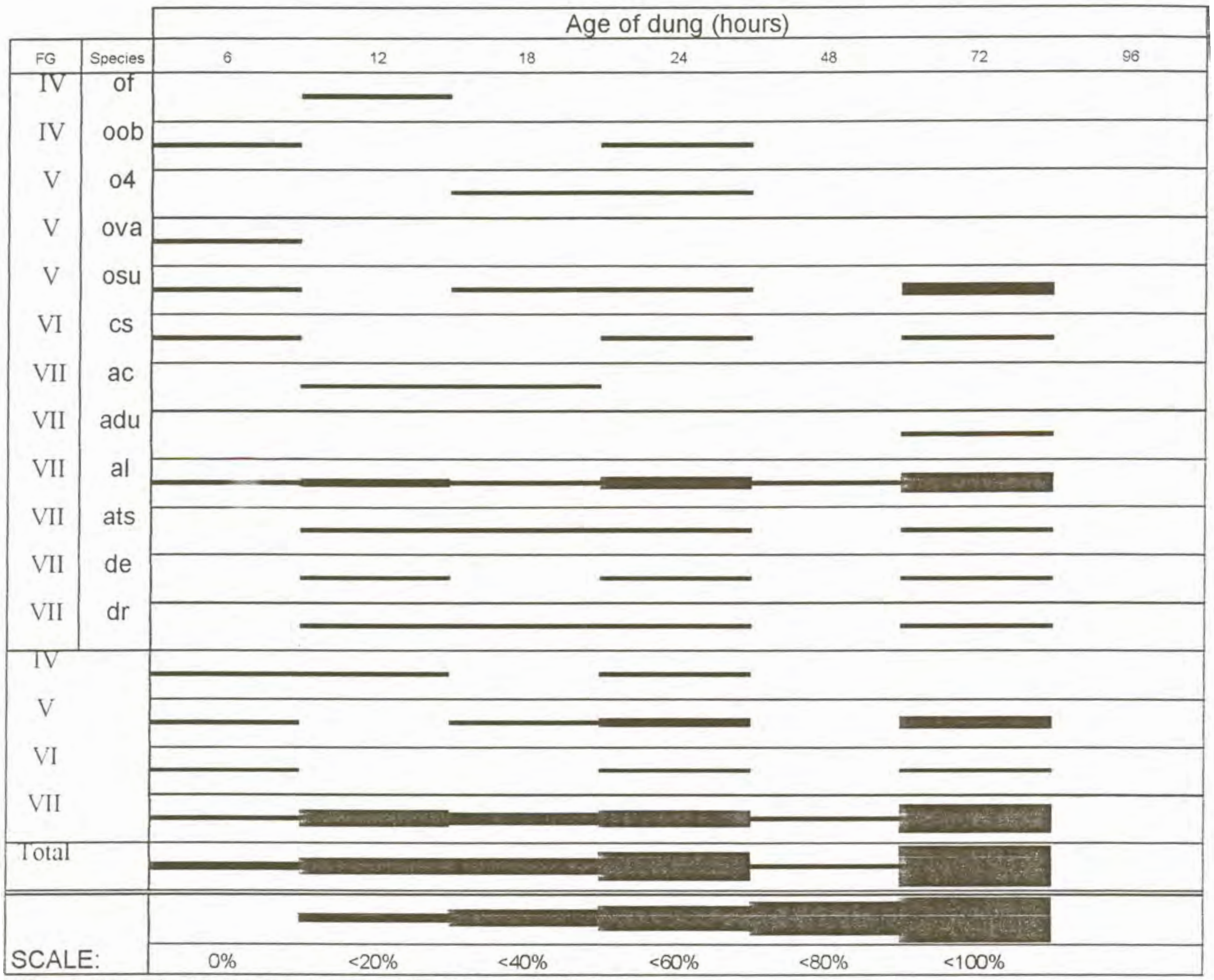
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.1. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during summer (December 1996): c) Sandveld bushveld (natural bushveld habitat).



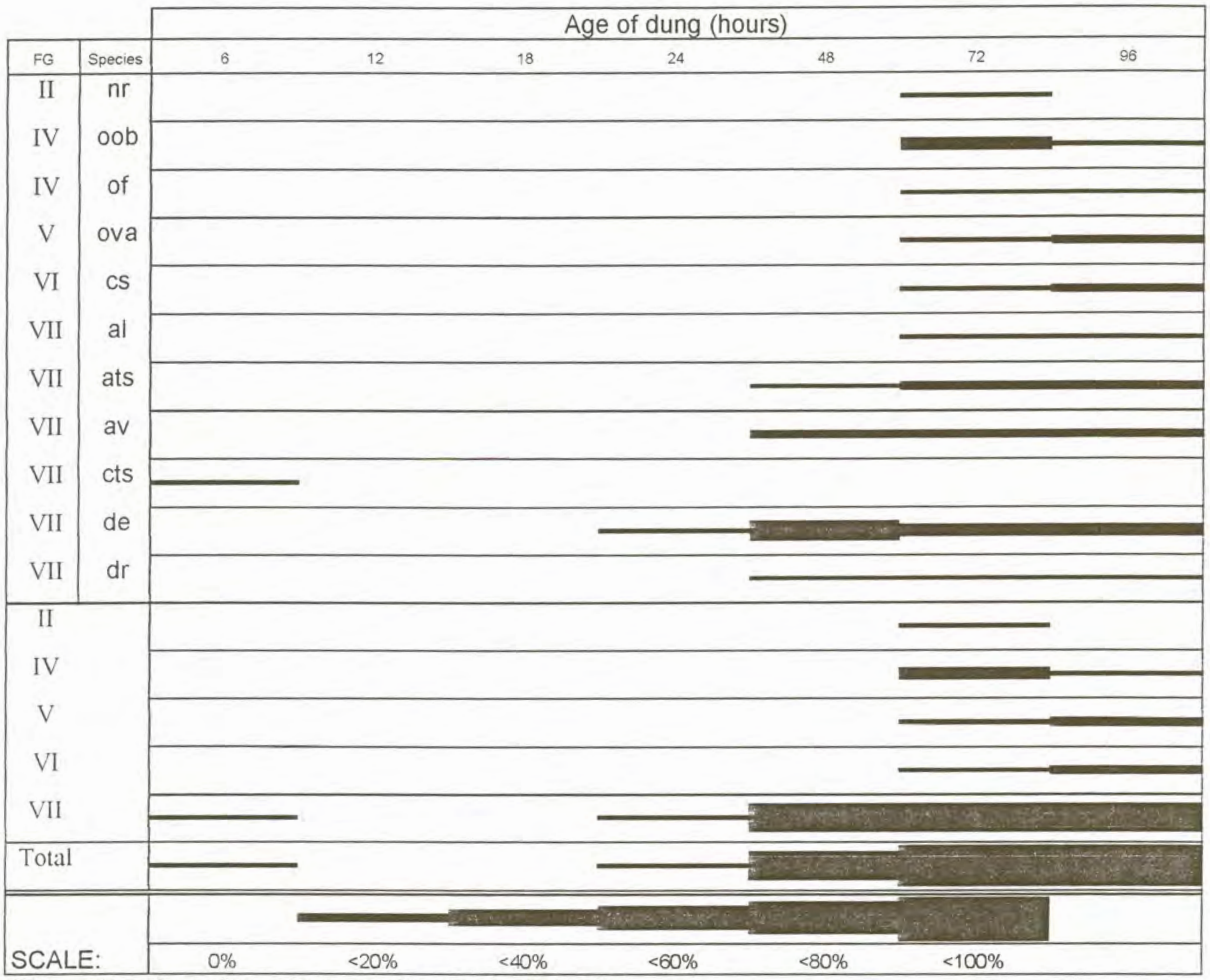
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.1. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during summer (December 1996): d) Josina (disturbed bushveld habitat).



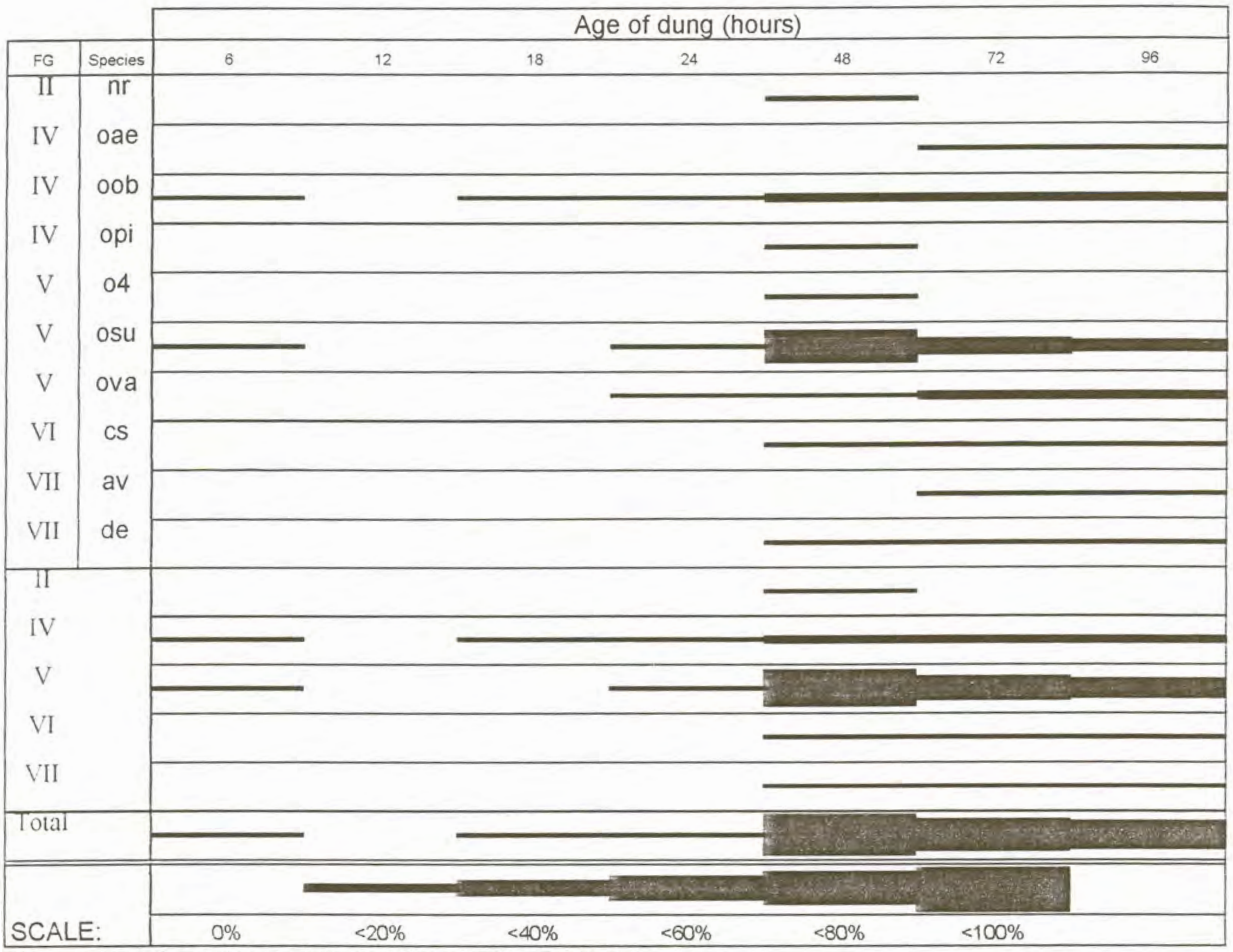
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.2. Successional pattern of dung beetle species and functional groups (F.G.'s) during autumn (April 1997): a) Sandveld grassveld (natural grassveld habitat).



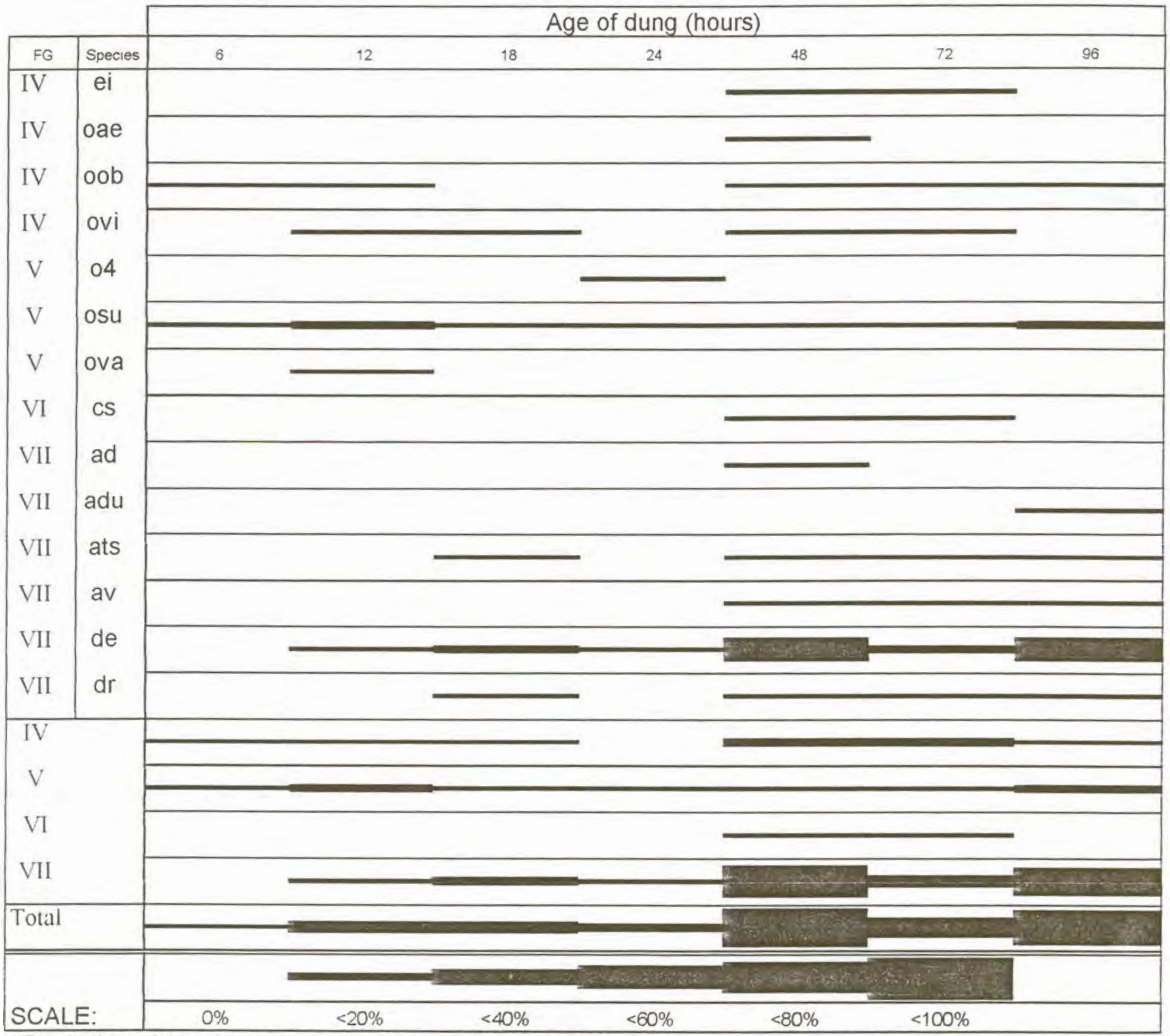
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.2. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during autumn (April 1997): b) Rietvlei (disturbed grassveld habitat).



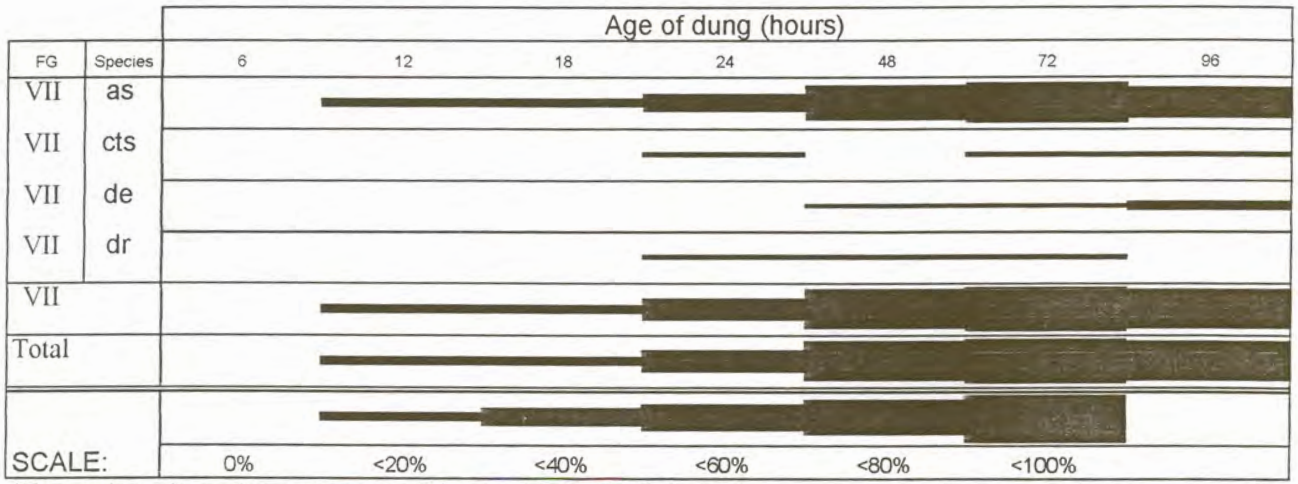
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.2. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during autumn (April 1997): c) Sandveld bushveld (natural bushveld habitat).



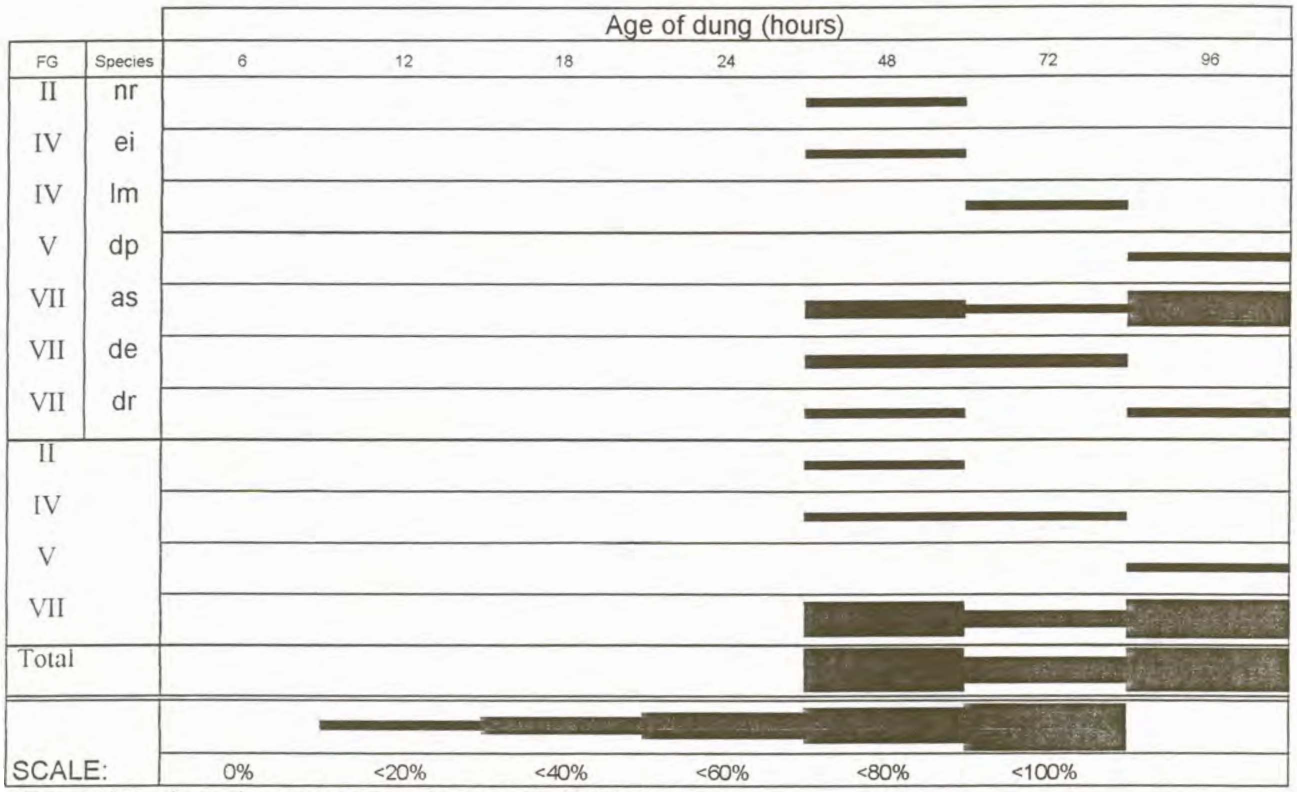
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.2. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during autumn (April 1997): d) Josina (disturbed bushveld habitat).



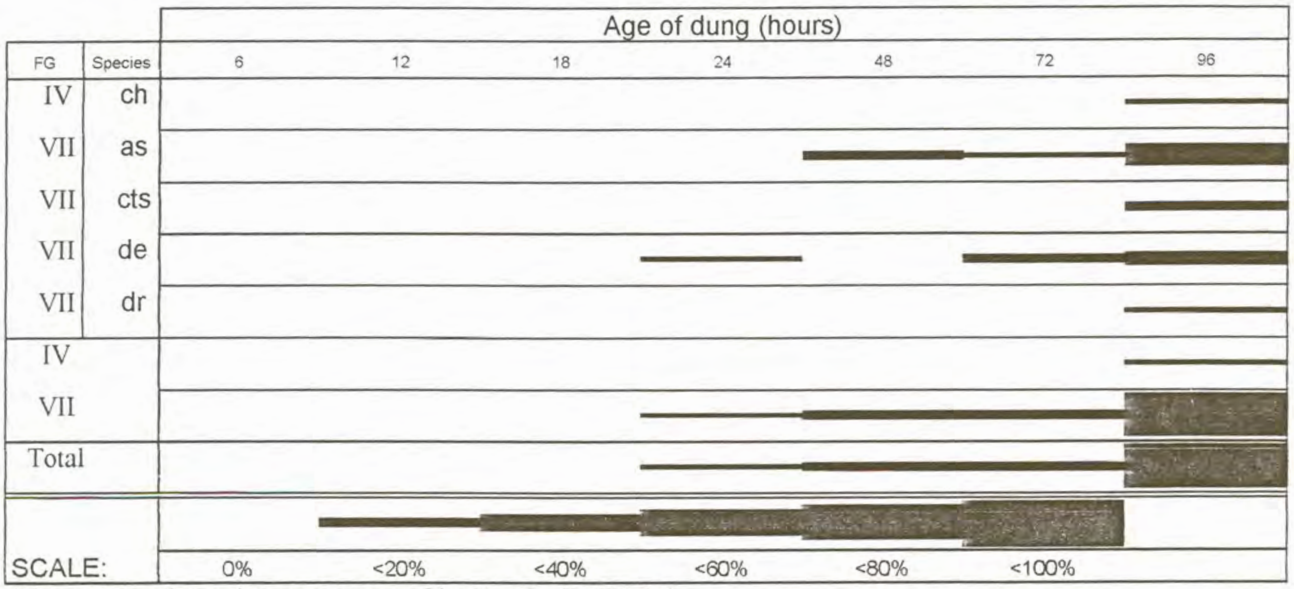
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.3. Successional pattern of dung beetle species and functional groups (F.G.'s) during winter (July 1997): a) Sandveld grassveld (natural grassveld habitat).



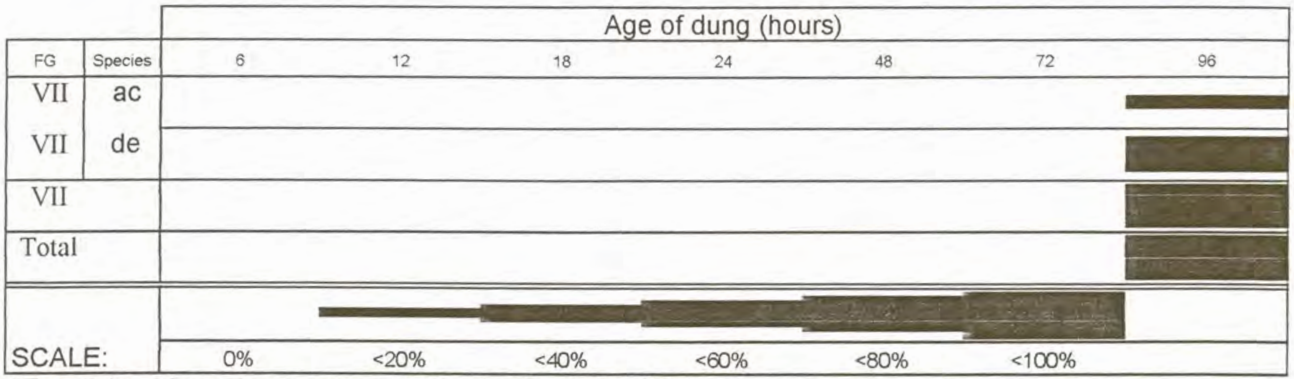
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.3. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during winter (July 1997): b) Rietvlei (disturbed grassveld habitat).



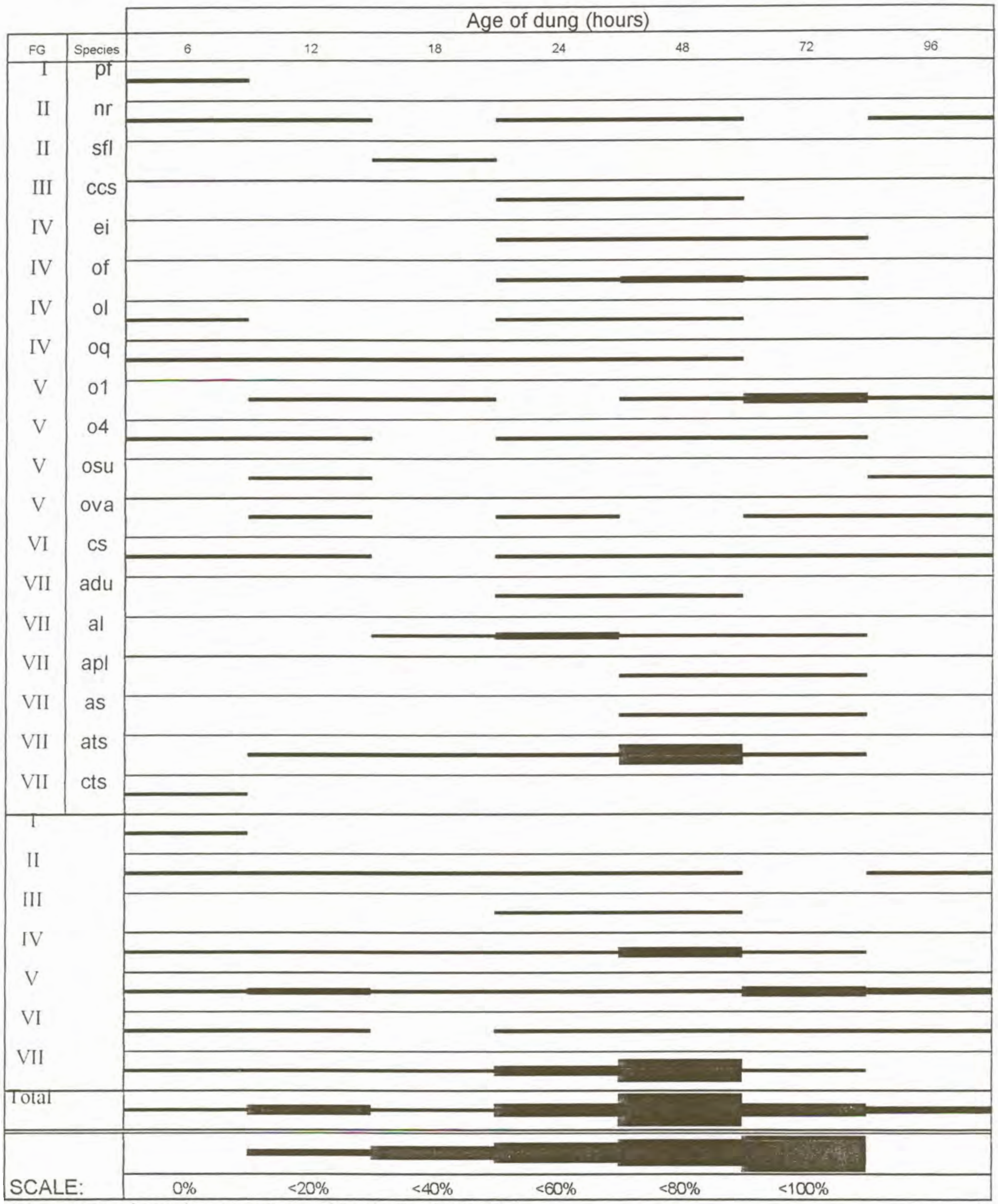
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.3. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during winter (July 1997): c) Sandveld bushveld (natural bushveld habitat).



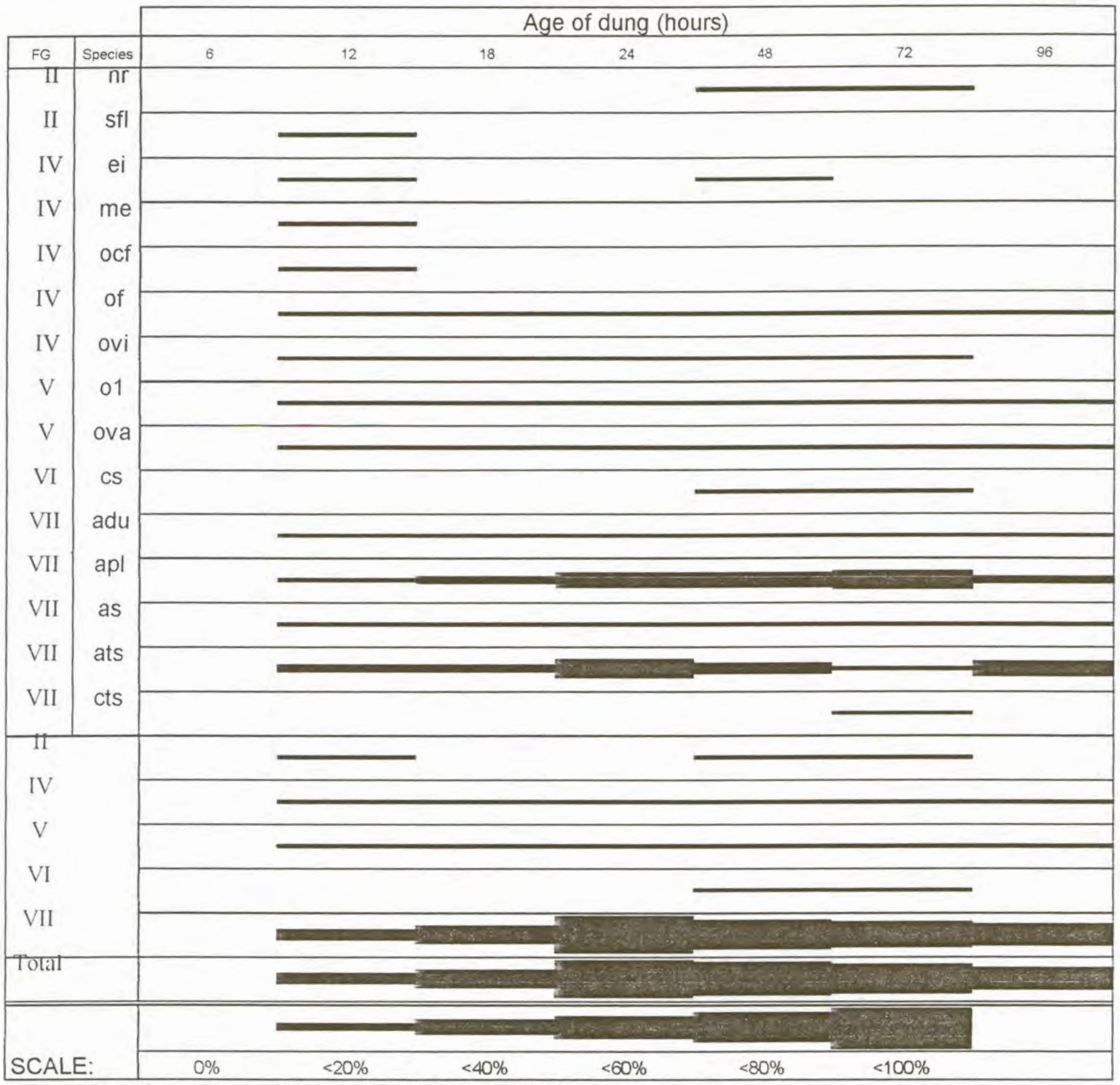
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.3. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during winter (July 1997): d) Josina (disturbed bushveld habitat).



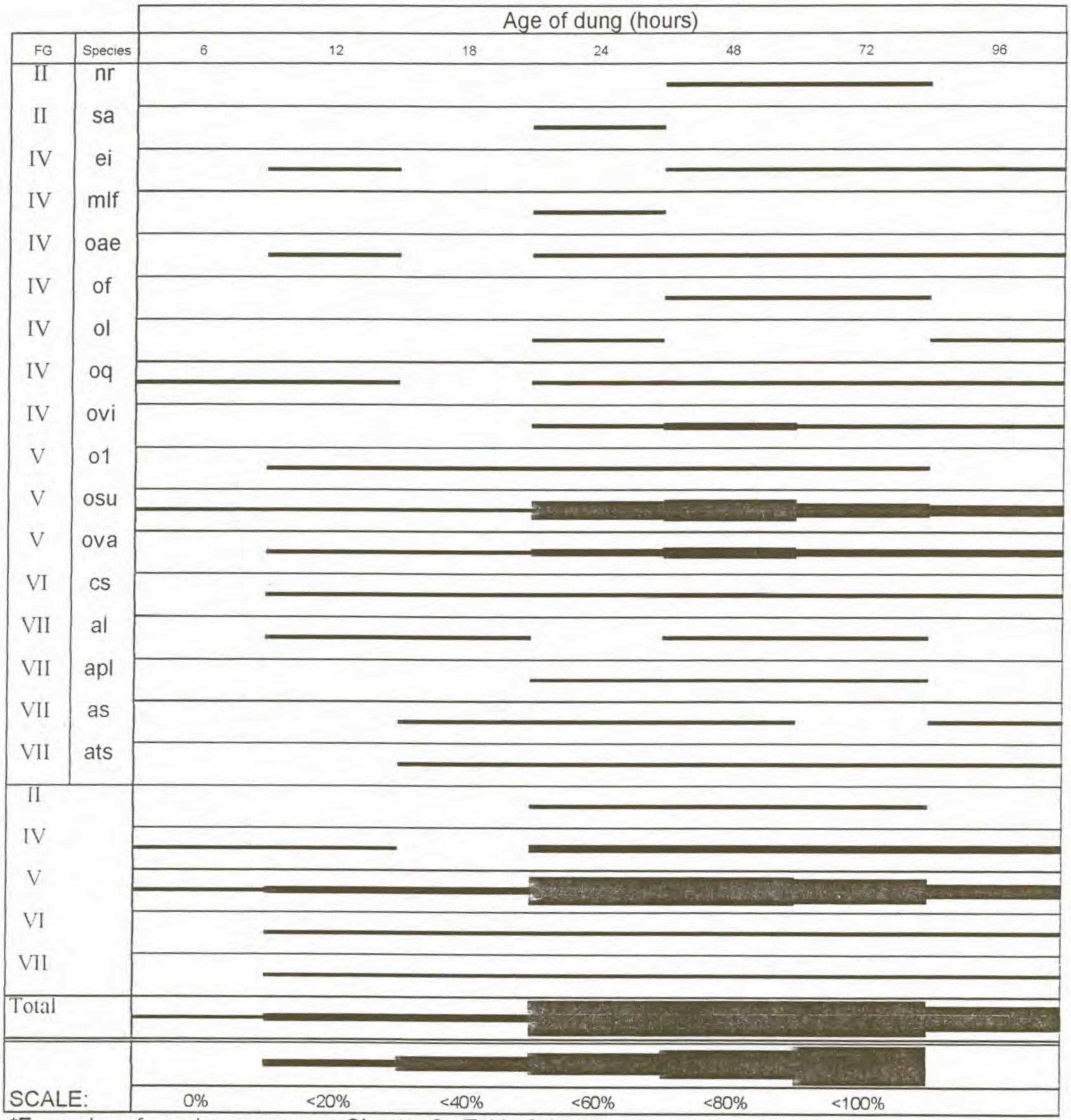
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.4. Successional pattern of dung beetle species and functional groups (F.G.'s) during spring (September 1997): a) Sandveld grassveld (natural grassveld habitat).



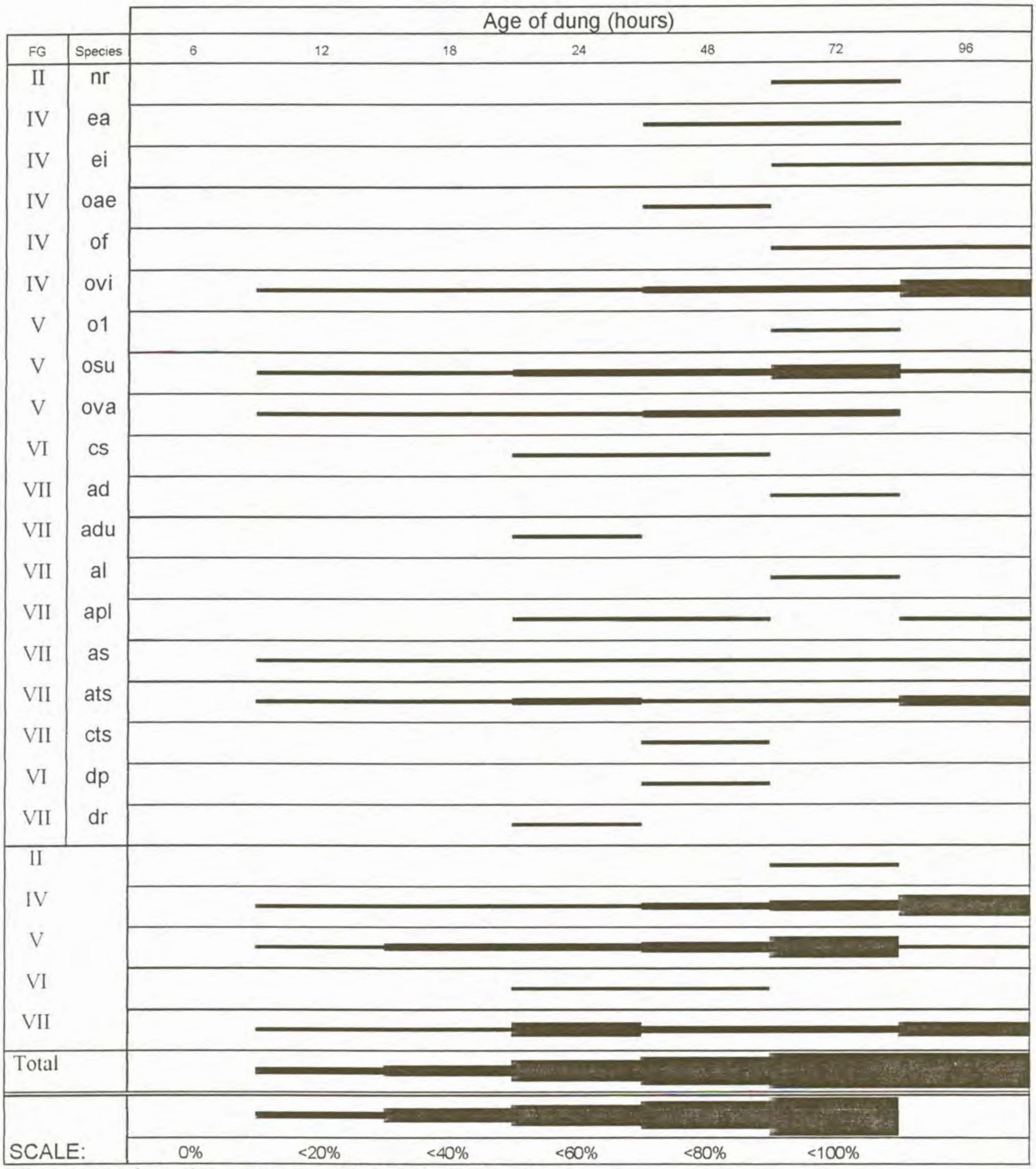
*For codes of species names see Chapter 2 - Table 2.4.

Fig. 6.4. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during spring (September 1997): b) Rietvlei (disturbed grassveld habitat).



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

Fig. 6.4. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during spring (September 1997): c) Sandveld bushveld (natural bushveld habitat).



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

Fig. 6.4. Continued: Successional pattern of dung beetle species and functional groups (F.G.'s) during spring (September 1997): d) Josina (disturbed bushveld habitat).

Chapter 7

DUNG PREFERENCES OF DUNG BEETLES IN FOUR DIFFERENT HABITATS

7.1. INTRODUCTION

Different animals are adapted to feed on a large variety of food plants. The vegetation upon which they graze affects the chemical composition of the dung they produce (Al-Houty & Al-Musalam, 1997). Consequently dung types which vary in texture, consistency, moisture content, microbial content, odour and quantity are produced. Rainio (1966) found that beetles usually feed on vertebrate dung, mostly on that of ungulates, such as domestic animals. The suitability of dung as an insect food is influenced by the species of animal that produces it (Edwards, 1991). Due to fencing and farming of previously open areas in southern Africa over the last century, the distribution of most mammals was dramatically affected (Du Plessis, 1969). Today large game concentrations occur only in game reserves and this has an effect on the distribution of dung beetles (Tribe, 1976). Fincher, Stewart & Davis (1970) also found that the alteration in the habitat affects the dung beetle community through changes in numbers and species of food-producing vertebrate animals. The original food source of dung beetles was gradually replaced by dung of domestic animals. The shift from wild herbivore dung to the dung of domesticated animals was, however, easily achieved by most dung beetles. In this regard Gordon (1983) and Tyndale-Biscoe (1988) state that the nature of the dung on which both adults and larvae of dung beetles feed may determine their distribution in different habitats. On the other hand, Landin (1961) and Nealis (1977) maintained that the distribution of dung beetles in different habitats does not depend on the kind of dung. The size of the dung pat is more significant to dung beetles than quality and kind of dung (Cambefort, 1991). The presence of large mammals will therefore have the greatest influence on dung beetles.

Most dung beetle species are coprophagous, but there are records of species utilising other types of food such as carrion and rotting plant material (Doube, *et al.* 1991; Gill 1991; Hanski & Cambefort 1991a). The two main types of food resource used by dung beetles are large herbivore dung and omnivore dung (Hanski & Cambefort, 1991a). Relatively few dung beetles are attracted to carnivore dung (Hanski 1987a; Rainio 1966). Davis (1977) suggested that a viable population of endocoprids can only be maintained where there is a sufficient density of large, intact, dung masses of larger herbivores. Stewart (1967) found that *Phanaeus* species showed a preference for pig dung, while opossum dung was second choice and even in an environment dominated by cattle, the preference was for pig or opossum dung.

Some dung beetle species are stenophagous, feeding only on a certain type of dung. The majority, however, are euryphagous, feeding indiscriminately or with a low degree of preference, on the various types of dung available (Halffter & Matthews, 1966). Rainio (1966) reported that in Helsinki (S. Finland) none of the dung beetle species he investigated are entirely specialised to a particular kind of dung.

The question is whether different resources have a significant influence on the distribution of dung beetles in different habitats. The dung preferences of dung beetles in four different habitats were determined in an attempt to answer this question.

7.2. MATERIAL AND METHODS

Sampling methods

Sampling for this study was done during January 1997 with four different dung types as bait in four different habitats. The four different habitats used for sampling were a natural bushveld habitat in Sandveld Nature Reserve, a disturbed bushveld habitat on the farm Josina, a natural grassveld habitat in Sandveld Nature Reserve and a disturbed grassveld habitat on the farm Rietvlei. 11 Plastic pitfall traps were baited with four different dung types, i.e. 200g of fresh cattle, buffalo, white rhinoceros and horse dung. Fresh cattle dung was collected on the dairy farm Bospré, near Bloemfontein (26°00'S; 29°00'E). Fresh horse dung was collected at stables in Bainsvlei (29°07'S,25°12'E) near Bloemfontein and fresh buffalo and white rhinoceros dung was collected at the Bloemfontein Zoo. The dung was transported in plastic buckets, covered tightly with lids to avoid desiccation and oxidation of the dung. In each habitat there were four sampling sites spaced 1 km apart and each site contained three plots, spaced 50 metres apart, each containing four traps. The traps were spaced 2m apart and each of the four traps in a plot was randomly baited with a different dung type. The traps were buried up to the rim and the bottom filled with salt water. A container with 200g of fresh dung was put inside the trap to attract the dung beetles. Both flying and walking dung beetles could be caught in these traps. Dung beetles attracted by the dung fell into the traps and could be collected later. The traps were left for 24 hours before the dung beetles were collected. They were preserved in 70% alcohol and kept for later identification.

Analysis of different dung types

The mean pH ± SD of five fresh dung samples of each dung type was measured with a pH meter. The mean percentage moisture ± SD of five fresh dung samples was determined by weighing fresh dung, oven-drying it for a period of 48 hours and weighing the dried dung. The percentage moisture could then be determined from the difference between the wet and dry weight of the sample. In another trail dung was dried in sunlight for about a month and then ground into a fine powder. Mean fibre ± SD and mean nitrogen ± SD content of the different dung types were then determined according to analytical procedures described by AOAC (1984).

7.3. RESULTS AND DISCUSSION

Differences in species richness, diversity, number of individuals, and total biomass of dung beetle assemblages attracted to four different dung types in four habitats

The same order of preference in terms of number of species colonising the dung types was observed in all four habitats. Cattle dung was preferred by most species, while buffalo dung was second in preference followed by horse and white rhinoceros dung (Table 7.1). There was a large difference in the number of individuals, the maximum number of individuals, as well as the biomass of dung beetles colonising the different dung types. In all the habitats the number of individuals, maximum number of individuals and biomass of dung beetles attracted to cattle dung were more than double that of dung beetles attracted to the other dung types (Table 7.1). In the grassveld habitats buffalo dung was second in preference followed by horse and finally white rhinoceros dung, while in the bushveld habitats white rhinoceros dung was second in preference, followed by horse and buffalo dung (Table 7.1). This difference in dung preference between the bushveld and grassveld habitats might be explained by the shade cover in the bushveld habitat, which results in slower drying out of the drier dung types than in the open habitats.

There were slight differences in the Berger-Parker indices for dung beetle assemblages attracted to the different dung types in the different habitats, but these differences were not significant. This indicates that although there is a drastic difference in species richness, individuals and biomass of dung beetles attracted to different dung types, the dominance of dung beetle assemblages attracted to different dung types does not necessarily differ (Table 7.1).

Table 7.1: Differences in species richness (S), number of individuals (N), maximum number of individuals (Nmax), Berger Parker dominance index (1/d) and biomass (g) of dung beetles attracted to four different dung types in four different habitats.

Habitat	Dung type	S	N	N max	1/d	Biomass (g)
Sandveld grassveld (natural grassveld)	Cattle	13	632	197	3.21	172.48
	Horse	7	37	12	3.08	18.19
	White rhinoceros	5	25	15	1.66	22.44
	Buffalo	12	211	104	2.02	23.64
Rietvlei (disturbed grassveld)	Cattle	15	407	106	3.84	62.30
	Horse	7	79	30	2.63	15.02
	White rhinoceros	7	57	20	2.85	14.05
	Buffalo	10	344	201	1.7	26.53
Sandveld Bushveld (natural bushveld)	Cattle	20	590	212	2.78	50.43
	Horse	10	170	78	2.18	2.60
	White rhinoceros	10	178	99	1.8	5.80
	Buffalo	15	132	39	3.38	4.20
Josina (disturbed bushveld)	Cattle	16	290	103	2.82	30.12
	Horse	10	97	35	2.77	0.905
	White rhinoceros	8	106	39	2.72	0.977
	Buffalo	11	49	13	3.77	2.118
		F=41.08 P<0.05	F=11.01 P<0.05	F=8.94 P<0.05	F=2.81 P>0.05	F=5.71 P<0.05

For herbivores, interspecific variability in dung characteristics arises from the major dichotomies in herbivore feeding and digestion, namely grazing vs browsing, and rumination vs non-rumination (Edwards, 1991). These sources of variation result in dung that differs in characteristics such as texture and size and water, nitrogen and fibre content. Cattle dung, because of its richness in organic material and its microclimatic conditions, is an ideal medium for the establishment of a specific, rich and varied community (Galante *et al.* 1993). Cattle dung also has high water content and the outer crust prevents evaporation of water. Results in the present study indicate that a greater variety of species and also more individuals are attracted to cattle dung than to the other dung types tested, irrespective of the habitat. Cattle dung had the highest moisture content and buffalo dung the second highest, while white rhinoceros and horse dung had lower moisture content than cattle and buffalo dung with horse dung having the lowest (Table 7.2.). The pH did not differ much between the different dung types, but cattle dung had a slightly lower pH (Table 7.2.). The fibre content of cattle and buffalo dung was lower and nitrogen higher than that of horse and white rhinoceros dung (Table 7.2). These characteristics might explain the preferences of dung beetles for certain dung types. Edwards (1991) considers the moisture content of dung the most important attribute for coprophagous insects. Since adult dung beetles feed on the fluid component of dung (Halffter & Matthews, 1966), cattle dung will be most favourable as this dung type has the highest percentage moisture. Al-Houty & Al-Musalam (1997) found that dung of low moisture content is unsuitable for telecoprid dung beetles because it is difficult for these beetles to form and roll dung balls when the dung is too dry, while Edwards (1991) found that dung of low moisture content is unsuitable for dung beetles since the adults cannot extract the dung fluid from the dung. The fibre content might also have an influence in the present study with cattle and buffalo dung, with a lower fibre content, easier for the formation of balls than horse and white rhinoceros dung. Dung beetles of the other functional groups might also be influenced by the desiccation rate of the dung. Horse and white rhinoceros dung is more fibrous and has a looser structure than cattle and buffalo dung and will consequently dry out more rapidly than cattle dung. Species that stay in the dung for longer periods will therefore choose a dung type that will be more consistent and dry out slower.

Table 7.2: pH and mean percentages of moisture, fibre and nitrogen in the four different dung types used as bait.

n=5	% Moisture ± SD	PH ± SD	% Fibre ± SD	Nitrogen (N) ± SD
Cattle	82.15±0.94	6.88±0.74	34.75±0.56	10.27±0.65
Buffalo	78.24±0.77	7.42±0.91	35.72±0.76	9.38±0.98
White Rhinoceros	76.06±0.52	7.83±0.45	42.15±0.91	7.27±0.93
Horse	74.45±0.52	7.12±0.63	41.23±0.43	6.99±0.68

Dung beetles attracted to cattle dung were most abundant in terms of species richness, individuals and biomass in all the habitats. Dung beetle abundance and biomass were highest in the natural grassveld habitat and second highest in the natural bushveld habitat with the abundance in numbers and biomass much lower in the disturbed habitats (Table 7.1). Even though there are no cattle present in the natural habitats dung beetles in these habitats still showed a stronger preference for cattle dung than white rhinoceros and buffalo dung, which occur naturally in these areas. The association with particular habitats is therefore not a reflection of the distribution of a certain type of food. Although dung beetles show a preference for a certain dung type they are very adaptable and are able to survive successfully on any dung type available. Dung beetles have thus adapted successfully to a change in dung type on the farms but are, however, less successful in these habitats than in the natural habitats. There are other factors in the habitats, which influence this success of dung beetles, and the dung type is not necessarily an important one. This is in agreement with Nealis (1977) who concluded that food is not an important determinant in local distributions for most species. This is supported by Lumaret *et al.* (1992) who found that numbers and biomass of dung beetles rather depended on the quantity of the trophic resources.

Functional group structure of dung beetle assemblages attracted to different dung types in different habitats

In the natural grassveld habitat dung beetles belonging to all functional groups were most strongly attracted to cattle dung (Fig. 7.1 a). Of all the functional groups dung beetles belonging to F.G. II showed the strongest preference for cattle dung with almost no dung beetles in this group attracted to other dung types (Fig. 7.1 a). This was also the case in the other habitats (Fig. 7.1 b-d). In the natural bushveld habitat and both the disturbed habitats the different functional groups showed a stronger preference for the horse, white rhinoceros and buffalo dung than in the natural grassveld habitat (Fig. 7.1). It also seems that F.G. I and II, containing the larger, better competitors, preferred cattle dung exclusively with almost no attraction to the other dung types. F.G. IV, V, VI and VII, containing the smaller less effective competitors, were more attracted to other dung types than F.G. I and II (Fig. 7.1). Cattle dung is dropped in large pats and has a high moisture content and a smooth texture. Horse is dropped in more scattered pats and is also drier and more fibrous than cattle dung. Although white rhinoceros dung occurs in large heaps, it is more fibrous and drier than cattle dung. Smaller species of F.G. IV, V, VI and VII are more generalist in their preferences and able to utilise many different food sources. Dung beetles of these functional groups also do not roll dung balls, but feed at the dung pat, making it easier to utilise more fibrous dung. These smaller species are less abundant in the natural grassveld habitat than the other habitats explaining the lower attraction to other dung types in this habitat. Larger dung beetles need larger amounts of dung for feeding and breeding and because cattle dung pats provide a large amount of dung with the right texture and moisture content it is ideal for these dung beetles. Dung beetles in F.G. I and II roll balls and cattle dung is also easier to form into a dung ball. Lumaret *et al.* (1992) found that in southern Europe larger species, owing to their preference for large pats, were favoured by a change in resource from sheep to cattle dung.

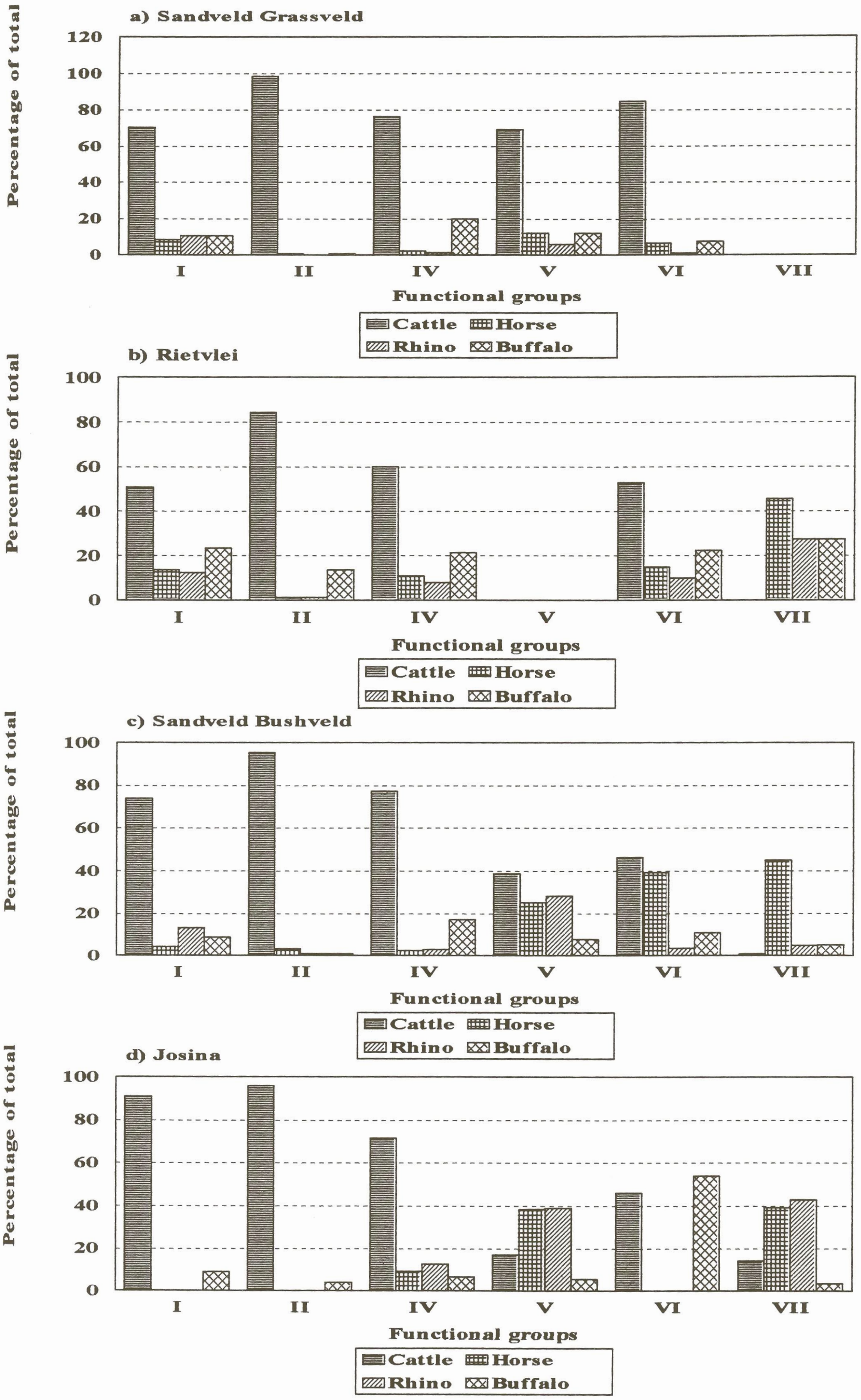


Fig. 7.1: Functional group structure of dung beetles attracted to different dung types in four different habitats.

Abundance of different dung beetle species attracted to different dung types in four different habitats

Abundance of different species differed in the different habitats, but the respective species all preferred cattle dung in all these habitats (Table 7.3). *Pachylomerus femoralis* was also attracted to the other dung types in the grassveld habitats, while there was very little attraction to other dung types in the bushveld habitats (Table 7.3). *Scarabaeus flavicornis* and *Scarabaeus ambiguus* seemed to be exclusively attracted to cattle dung, with little or no attraction to other dung types in all the habitats (Table 7.3). *Neosisyphus ruber*, which only occurred in the disturbed grassveld habitat, preferred cattle dung, but was also attracted to buffalo dung (Table 7.3). *Onthophagus quadraliceps* was attracted to all the dung types in the natural grassveld habitat, to cattle and buffalo dung in the disturbed grassveld habitat and only to cattle dung in both the bushveld habitats (Table 7.3). In the grassveld habitats *O. obtusicornis* was only attracted to cattle dung, while in the bushveld habitats they were attracted to different dung types (Table 7.3). *O. pilosus* occurred most abundantly in the disturbed grassveld habitat where they were attracted to all the dung types (Table 7.3). *O. xanthopterus*, which occurred most dominantly in the natural grassveld habitat, preferred cattle dung with only very slight attraction to buffalo dung (Table 7.3). *Liatongus militarus*, which occurred only in the bushveld habitats, was the only species which preferred buffalo dung over cattle dung. No individuals of this species were attracted to cattle dung (Table 7.3). Both *O. variegatus* and *O. sugillatus* occurred most abundantly in the bushveld habitats, where they were attracted to all the dung types (Table 7.3). These species were attracted to cattle dung in the natural grassveld habitat, but in much lower numbers. They were also attracted in much lower numbers to other dung types than in the bushveld habitats (Table 7.3). *Caccobius seminulum* was most abundant in the disturbed grassveld habitat and was also more attracted to dung types other than cattle dung in this habitat than in the other habitats (Table 7.3).

The degree of dung preference differed between species and between different habitats. It seems that the more abundant a species in a habitat the wider the dung preference becomes. This is in agreement with Hanski & Krikken (1991) who found that the most abundant species in the local community have more diverse food habits than the less abundant ones. This might be explained by intraspecific competition when the species is abundant in a habitat. In such a scenario the preference might be for cattle dung, but because of strong competition for this dung type, individuals of this species might be forced to feed on other dung types. It is this adaptability of dung beetle species to utilise different food sources under extreme conditions that determines their success in an environment. Howden & Nealis (1975) found that most dung beetle species in Colombia, they studied seemed capable of utilising several dung types, with only slight preferences and Rainio (1966) found that none of the dung beetle species in S. Finland was wholly specialised to any particular kind of dung.

7.4. CONCLUSION

Differences in the characteristics of cattle, horse, white rhinoceros and buffalo dung reflects differences in the feeding ecology and digestion of these animals. These differences influenced the preferences of dung beetles for a particular dung type. Although dung beetles showed preferences for certain dung types, this did not reflect association with a particular habitat. Dung beetles seem to be very adaptable and will colonise the most favourable dung type when it is available. The dung type will, however, not limit the dung beetles to a particular habitat because they are able to adapt to feeding on many different dung types. According to Lumaret *et al.* (1992) dung beetles, which have evolved over a long time to cope with ungulate dung, are quickly and easily able to react to sudden changes in the type of dung. The degree of dung preference also differed between species and between different habitats with the more abundant species in a habitat showing a wider dung preference. This might be a result of strong intraspecific competition within a habitat. Because of the adaptability of dung beetle species to utilise different dung types dung beetles of the same species can successfully co-occur in similar macrohabitats.

Table 7.3: Abundance of different dung beetle species in different dung types (cattle, horse, white rhinoceros and buffalo) in four different habitats: S.G. – Sandveld grassveld, natural grassveld; Rietvlei – disturbed grassveld; S.B. – Sandveld bushveld, natural bushveld; Josina – disturbed bushveld.

Species	S.G.				Rietvlei				S.B.				Josina			
	Cattle	Horse	Rhino	Buffalo	Cattle	Horse	Rhino	Buffalo	Cattle	Horse	Rhino	Buffalo	Cattle	Horse	Rhino	Buffalo
FGI																
pf	100	12	15	15	32	10	9	17	17	1	3	2	10	0	0	1
FGII																
sfl	113	1	0	1	28	0	0	0	108	4	1	0	42	0	0	0
sa	2	0	0	0	10	0	0	2	7				24	0	0	1
nr	0	0	0	0	40	1	1	11	0	0	0	0	0	1	0	1
FGIV																
m1	20	0	0	1	18	1	2	1	12	0	0	2	2	2	1	0
m2	2	0	0	1	8	2	0	0	3	1	0	1				
oae	0	0	0	0	0	0	0	0	4	0	0	1	27	0	0	4
of	0	0	0	0	7	0	0	0	17	0	2	1	0	0	0	0
oq	197	7	5	63	31	0	0	16	11	0	0	0	2	0	0	0
oob	21	0	0	0	11	0	0	0	212	4	5	39	103	15	28	2
opi	2	2	0	6	106	30	20	45	8	0	1	5	5	0	0	0
ox	41	0	0	3	2	0	2	3	15	0	0	3	32			
lm	0	0	0	0	0	0	0	0	0	4	3	10	0	4	0	10
FGV																
ova	18	4	1	1	1	0	0	0	52	22	14	6	10	28	25	2
osu	27	4	3	7	0	0	0	0	103	78	99	25	18	35	39	7
FGVI																
cs	88	7	1	8	106	30	20	45	13	11	1	3	6	0	0	7
FGVII																
al	0	0	0	0	0	5	3	0	0	0	0	0	0	2	3	0
at	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
apl	0	0	0	0	0	0	0	0	0	5	0	5	1	0	0	0
adu	0	0	0	0	0	0	0	0	1	40	49	0	0	0	0	0
an	0	0	0	1	0	0	0	0	0	0	0	0	3	3	1	1
ats	0	0	0	0	0	0	0	0	0	0	0	0	0	6	8	0

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

Chapter 8

CO-OCCURRENCE AND AGGREGATION OF DUNG BEETLES COMPETING FOR EPHEMERAL RESOURCES IN FOUR HABITATS

8.1. INTRODUCTION

Dung pats are discrete, ephemeral patches or 'islands' of highly concentrated energy, which are widespread throughout a variety of habitats over the surface of the landscape. These units exist only until the energy they contain has been consumed or dispersed. One would expect these dung pats to be colonized by a great number of species taking advantage of a resource with such a high energy content. Because of the temporary nature of dung a scramble for this resource can be expected. In ecosystems where dung beetles are less abundant this would pose no problem. In many biotopes in southern Africa, however, dung beetles are often very abundant, especially in the warm rainy season, and there is potential for strong competition for dung here. According to Hanski & Cambefort (1991b) intraspecific and interspecific competition occur at least occasionally in nearly all communities of dung beetles and in some situations competition is severe and undoubtedly greatly influences the structure of communities. Ridsdill-Smith (1990) states that competition occurs when resources become limiting, and would be expected to be particularly important in populations living in dung. He also agrees that competition is one of the important regulating factors in determining the size of the population. Hudson & Stiling (1997) found that in a phytophagous insect community *Trirhabda bacharidis* played a major role, depressing densities of the most common insect herbivores on *Baccharis halimifolia*. They ascribed the reduced densities to interspecific, exploitative competition facilitated by *T. bacharidis* herbivory. Ward & Seely (1996) found that in a detritivorous tenebrionid community in the Namib desert interspecific competition was an important organizing force. Reeve *et al.* (1998) state that although competition is not the most important force in the dynamics of the southern pine beetle, *Dendroctonus frontalis*, in the southern U.S.A., intraspecific competition could be a source of immediate density dependence in the beetle's population dynamics.

Competition for dung can take a number of forms, ranging from direct combat, in which beetles fight over the possession of dung, through resource pre-emption, in which priority of access determines the winner, to scramble competition, in which the beetles' activity at high densities prevents most individuals acquiring sufficient resources for breeding (Doube, 1991). Competition can either be intraspecific or interspecific and may be either symmetric or asymmetric. Symmetric interspecific competition occurs when both species are negatively effected, while asymmetric competition has a negative effect on one species, but no detectable effect on the other (Ridsdill-Smith, 1990). Competition in dung beetle assemblages is mostly asymmetric, with a superior competitor occurring dominantly and many inferior competitors occurring less abundantly.

If competition is so strong in dung beetle assemblages, how can we then explain the often high species diversity of assemblages that exploit this discrete ephemeral resource? One would expect that in these situations the superior competitors would cause the weaker competitors to become extinct, resulting in lower species diversity. Because there are large numbers of species in most dung communities there are numerous potential interspecific interactions, but there is frequently much variation in the behaviour of different species, which might influence the outcome of competition. Differences in diel activity, time of colonization, seasonality, habitat preference and dung preference can enable weaker competitors to co-exist with stronger competitors. Doube (1987) found that the majority of interactions occur only infrequently, if at all, because most species are relatively rare, are restricted to particular habitats in specific seasons of the year and have specific diets. Dung is, however, a relatively homogenous resource and thus presents beetles with little opportunity for specialization within a single resource patch (Giller & Doube, 1989) and despite a high level of niche partitioning in dung beetles on various scales there are still species with similar biological characteristics that occur together. Dung is patchily distributed in both time and space. Patchy environments may be unstable at one spatial scale, but stable on another scale. The instability of populations in habitat patches may contribute to stability on a larger scale in competitive and predator-prey systems (Hanski, 1987b). Species must occupy the same pat in order to compete with one another and some species show independently aggregated spatial distributions among patches, which reduces the probability of potential competitors occurring together on the same resource. Aggregation refers to the degree to which insects are clumped among the patches. If most of the individuals of one species occur in a few of the patches, causing a high variance in the number of dung beetles per patch, then the distribution is intraspecifically aggregated, while interspecific aggregation is the degree to which two different species occur in the same patches, producing positive covariance between the distributions of the two species (Ives, 1991). Several authors agree that the patchiness of dung and the aggregation of dung beetles in discrete habitat patches will reduce interspecific competition and facilitate co-existence of different species, resulting in higher species diversity. Ives (1991) considers aggregation a general mechanism that may explain co-existence in any insect community in which species compete for patchily distributed resources. Doube (1987) suggests that the independent aggregated distribution of species over discrete patches of resource favours the co-existence of competing species by reducing the intensity of interspecific competition. Atkinson & Shorrocks (1981) also found that two processes could lead to more prolonged coexistence, viz. increasing patchiness of resources and increased aggregation of the competitor. They found that the maximum time of co-existence between competitors resulted when both the degree of their aggregation over sites and patchiness of the resource were at their maximum. Hanski (1990) reasons that many dung and carrion communities are exceptionally rich in species because habitat patchiness facilitates coexistence. Patchiness leads to independently aggregated spatial distributions in the competitors and differences in foraging behavior affect the probabilities of colonization of individual habitat patches. Hanski & Cambefort (1991b) argue that when habitat patchiness increases and the durational stability of individual patches decreases, the level of spatial aggregation in the insect populations further increases. Further to this Kneidel (1985) found that under high patchiness, where aggregation was high and the species were distributed independently, overlap was reduced, the effect of interspecific competition was reduced and the level of intraspecific competition was increased.

On farms there is normally an unlimited supply of dung because of a concentration of large herbivores in a small area. This is usually not the case in a nature reserve where dung is distributed randomly because of a larger area through which the large herbivores are able to move. This will probably influence the aggregation of dung beetles in an area and subsequently the outcome of competition.

3.2. MATERIAL & METHODS

Sampling procedure

During the sampling period the species richness, total abundance of dung beetles and the maximum number of individuals were highest during February 1997 in all four habitats. The interspecific and intraspecific interaction in the dung beetle assemblages can be expected to be most pronounced during this time and data collected during this month was therefore used to determine the aggregation of dung beetles in the four different habitats. Dung beetle sampling was done in four different localities within two different habitat types, comprising a grassveld area and a bushveld area. In these two habitat types dung beetle assemblages in a natural habitat (Sandveld Nature Reserve) 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 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. 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 200g of fresh cattle dung was put inside the trap to attract the dung beetles and was considered sufficient to attract both flying and walking dung beetles. Dung beetles attracted by the dung fell into the traps and could be collected later. Freshly dropped 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 of the dung. 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.

Analytical Methods

Intraspecific aggregation was determined between plots, which were spaced 50m apart and between sites, which were spaced 1 km apart. Ives' measure of aggregation (J) (Ives, 1991) was used to determine the intraspecific aggregation of species of dung beetles attracted to pitfall traps:

$$J=\{[\Sigma\ n_{i\,(}n_i - 1/(NL)] - N\}/N$$

Where L is the number of traps, n_i the number of dung beetles attracted to trap i (i = 1 to L), and N the mean number of dung beetles. A value of J=0.75 indicates a 75% increase in the expected number of conspecifics attracted to the same trap above what the expected number would be if dung beetles were randomly and independently distributed. J=0.75 thus means an increase in crowding by 75% (Ives, 1991).

Interspecific aggregation was determined between sites, which were spaced 1 km apart. To measure interspecific aggregation between sp. A and sp. B Ives' measure of interspecific aggregation (C) was used (Ives, 1991):

$$C_{A.B}=\{[\Sigma\ n_i m_i/(NL)]-M\}/M$$

Where L is the number of traps, n_i and m_i are the numbers of dung beetles of each species attracted to trap i (i = 1 to L), and N and M the mean number of dung beetles. A value of $C_{A,B}$=0.5 indicates that there is a 50% increase in the expected number of heterospecific competitors in the same trap above the expected number if sp. A and sp. B were distributed independently.

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 size and abundance of different dung beetle species and level of intraspecific aggregation in a species 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.

8.3. RESULTS & DISCUSSION

Species richness, abundance and dominance in four different habitats

Because of a concentration of large mammals in a small area on the farms Rietvlei and Josina there is an unlimited supply of dung. One would therefore expect that these farms would support more species and higher abundance of dung beetles than in the nature reserve where dung is more widely distributed across a larger area. This is, however, not the case. The highest number of species occurred in the grassveld area at SNR and the species richness is higher in both the grassveld and bushveld areas in the nature reserve (Table 8.1). The total abundance and maximum number of individuals are higher in the grassveld area than the bushveld area and also higher in the nature reserve than on the farms (Table 8.1).

Table 8.1: Species richness (S); number of individuals (N) and maximum number of individuals (Nmax) in four different habitats: Sandveld Grassveld – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; Sandveld bushveld – natural bushveld habitat; Josina – disturbed bushveld habitat.

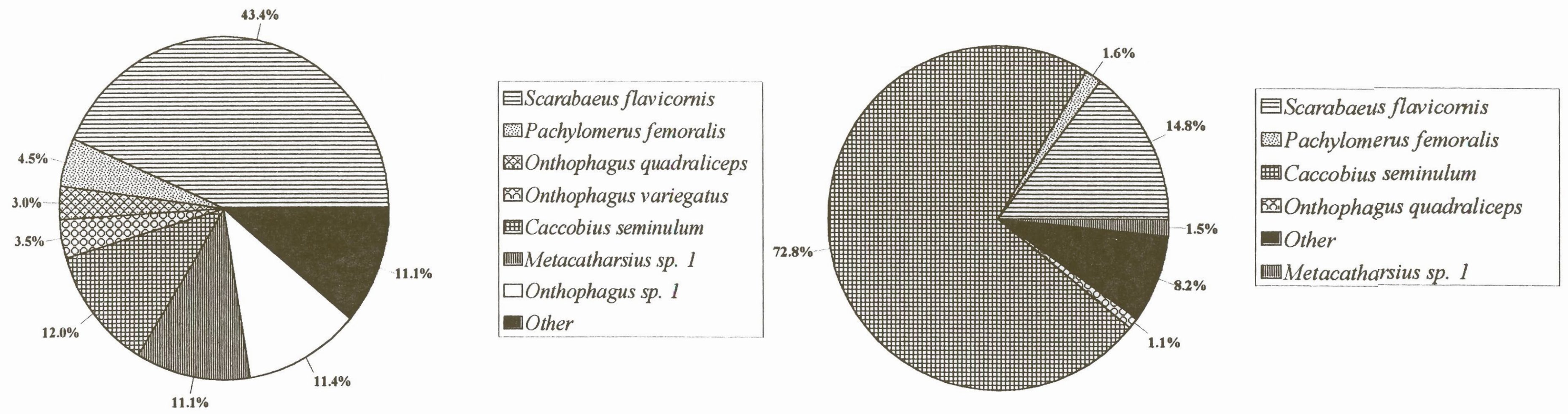
	S	N	Nmax
Sandveld Grassveld	31	3657	1588
Rietvlei	22	1402	1016
Sandveld Bushveld	28	979	364
Josina	25	718	312

Although many species occurred in the study area only a few species were dominant, with many rare species. In the grassveld area at SNR seven species were dominant, making up 88.9% of the total abundance (Fig. 8.1.a). *Scarabaeus flavicornis* was the most dominant species making up 43.4% of the total population (Fig. 8.1 a). In the disturbed grassveld area (Rietvlei) six species were dominant, making up 91.8% of the total abundance. There was a much higher dominance in this area than in the natural grassveld area, with *Caccobius seminulum* making up 72.8% of the total population (Fig. 8.1. b). In the natural bushveld area at SNR there were seven dominant species, making up 83.1% of the total abundance. *Onthophagus variegatus* was dominant making up 36.3% of the total population (Fig. 8.1. c). Five dominant species occurred in the disturbed bushveld habitat, making up 72.5% of the total abundance. *Onthophagus variegatus* was dominant, making up 44.1% of the total population (Fig. 8.1 d). Due to the dominance of a single species in all the habitats we can expect competition, if it occurs, to be asymmetric. Denno *et al.* (1995) found that interspecific competitive interactions in phytophagous insects were also mostly asymmetric. They ascribed the tendency for intraspecific competition to diminish interspecific interactions to this asymmetry. In the present study there was a high dominance of one species in all the habitats but the degree of dominance and the dominant species varied between the habitats. There is a clear difference between the different functional groups in their ability to compete for dung. The best competitors are the large telocoprids (FG I) and the fast-burying paracoprids (FG III), whilst the small telocoprids (FG II) are also good competitors because they remove the dung soon after arrival at the pat (Doube, 1991). Compared to these groups the paracoprids (FG IV and V) are subordinate and the endocoprids (FG VI) are especially likely to have their breeding activities disrupted by members of the other functional groups, while kleptocoprids (FG VI) use the dung buried by other groups (Doube, 1991). The natural grassveld habitat was dominated by a superior competitor belonging to FG II, which removes large amounts of dung at a fast rate, while the disturbed habitat was dominated by an inferior competitor belonging to FG VI, which use the dung buried by other dung beetles as food source. Both the bushveld habitats were dominated by an inferior competitor belonging to FG V, which is small and removes dung at a slow rate.

In the natural grassveld habitat the dominant species has a competitive advantage through its ability to rapidly gain control over dung, causing resources to be limiting in this area. Although *P. femoralis* were not as abundant as *S. flavicornis*, this was a large superior competitor, removing large amounts of dung at a fast rate. There was pre-emptive competition between these two species where the resource was limited, with one species utilizing all the dung voided at certain times of the day leaving no resource for the other species. Despite abundance of superior competitors in the natural grassveld habitat there were many other species able to co-exist with them (Table 8.1). There must be some mechanism, which enables these species to occur together in the same area despite strong interference. The dung beetle assemblages here are structured by variance-covariance dynamics, where many species occupy the same dung pat. In assemblages obeying variance-covariance dynamics, regional species richness may be high in spite of competition.

a) Sandveld Grassveld

b) Rietvlei



c) Sandveld Bushveld

d) Josina

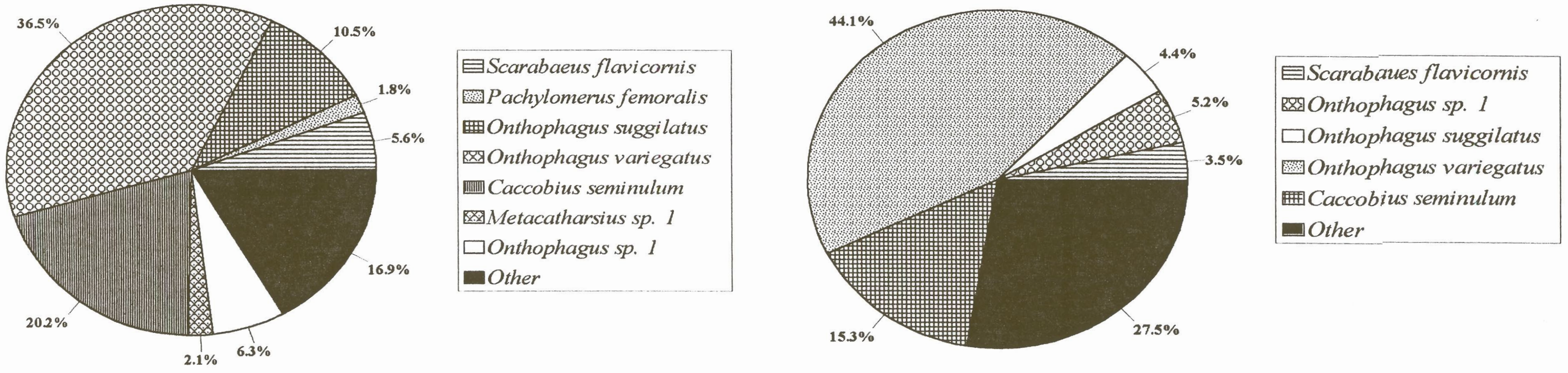


Fig. 8.1:Distribution of dominant species in dung beetle assemblages in four different habitats: a) Sandveld Grassveld – natural grassveld habitat; b) Rietvlei – disturbed grassveld habitat; c) Sandveld Bushveld – natural bushveld habitat; d) Josina – disturbed bushveld habitat.

Intraspecific and interspecific aggregation of dung beetle species in four different habitats

Intraspecific aggregation may play an important role in structuring dung beetle assemblages. In northern Germany Hirschberger (1998) found that intraspecific competition played an important role in the small dung beetle species *Aphodius ater*. She found that this species aggregate, possibly to facilitate mate finding, but between-pat distribution was more even in older pats, leading to a more even distribution of eggs and minimal larval competition. In southern Africa the dung beetle assemblages differ from those in temperate climates. There is an abundance of larger dung beetle species and intraspecific aggregation may play a completely different role to enable smaller species to co-exist with larger, superior competitors. In the present study intraspecific aggregation differed between plots and sites and also between habitats. Hanski & Cambefort (1991b) found that average distance between traps or dung pats affects the level of aggregation. In the present study and depending on the species, the level of aggregation differed with varying degrees between plots and sites (Table 8.2). Between both plots and sites *Pachylomerus femoralis* was more aggregated in the disturbed grassveld habitat than in the natural habitat (Table 8.2). The level of aggregation for this species was higher between sites than plots, indicating that it tended to be more aggregated over larger than smaller areas (Table 8.2). *Scarabaeus flavicornis,* which was the dominant species in the natural grassveld habitat, was more aggregated over a small area, while they were more aggregated over a larger area in the disturbed habitat (Table 8.2). This species was also more aggregated over a larger area in the disturbed bushveld habitat than in the natural bushveld habitat (Table 8.2). *Metacatharsius sp. 1* also showed a higher level of aggregation over a small area in the natural grassveld habitat and a higher level of aggregation in the disturbed grassveld habitat (Table 8.2). Between sites the level of aggregation for *Onthophagus quadraliceps* was higher in the natural grassveld habitat than in the disturbed grassveld habitat (Table 8.2). Both between plots and sites *Onthophagus variegatus, Onthophagus sugillatus* and *Onthophagus sp. 1* all showed a higher level of aggregation in the disturbed bushveld habitat than the natural bushveld habitat (Table 8.2). *Caccobius seminulum* showed a higher level of aggregation in the natural grassveld habitat than the disturbed habitat, both between plots and sites and also showed a higher level of aggregation between plots in the disturbed bushveld habitat than the natural bushveld habitat, whilst between sites there was similar aggregation in these two habitats (Table 8.2). *Scarabaeus flavicornis* showed a high level of aggregation over small areas in the natural grassveld habitat. This species was dominant here and the aggregation probably enabled smaller less effective competitors to utilise the resource where this species did not occur over a small area. According to Giller & Doube (1994) co-existence is facilitated by increased aggregation of the competitively superior species, as this leaves more low density or empty sites in which the inferior species can breed. Atkinson & Shorrocks (1981) argue that co-existence should depend much more on the aggregation of the superior competitor than on the inferior one. Over a larger area in the natural grassveld habitat, however, the opposite was found in the present study, where there seemed to be a smaller level of aggregation of larger superior competitors, while the level of aggregation for the smaller species seemed to be larger. This might be explained by a better dispersal ability of the inferior competitors. Giller & Doube (1994) state that species may co-exist either due to good dispersal or good competitive abilities and Keough (1984) found that the best competitors tended to exclude other species from large patches, while the latter species, usually good dispersers, survive in small patches. The smaller inferior competitors in the present study therefore probably have good dispersal abilities enabling them to locate the few patches not colonised or carrying a lower density of superior competitors over a large area. The inferior competitors can therefore adjust their own spatial distribution to minimise the effects of competition with larger superior competitors. In the disturbed grassveld habitat the situation seemed to be reversed. The larger more effective competitors seemed to be more aggregated than the smaller less effective competitors. In this habitat the co-existence seemed to be dependent on the aggregation of the superior competitor allowing the inferior competitor to become more dominant. This might explain the dominance of the small cleptocoprid *Caccobius seminulum* in this habitat. There seemed to be a higher level of intraspecific aggregation over a large area in the disturbed grassveld habitat than in the natural grassveld habitat. The level of intraspecific aggregation was also higher in the disturbed bushveld habitat than in the natural bushveld habitat. It would seem therefore that the habitat influences the level of intraspecific aggregation and consequently also the structure of the assemblage. This is reflected by the difference in dominance of different species in the different habitats (Fig. 8.1).

In the natural grassveld habitat interspecific aggregation was stronger between the smaller, less effective competitors belonging to FG IV and FG V, while the larger superior competitors belonging to FG I and FG II did not show such strong interspecific aggregation (Table 8.3 a). Interspecific aggregation was, however, stronger between the larger species than between the larger and smaller species (Table 8.3 a). Cambefort (1991) found that the greater the size difference between two species, the lower their spatial correlation. In the present study small species of similar habits and size, like the species belonging to FG IV and V, compete for breeding space in the soil underneath the dung pat and therefore affect the spatial distribution of one another. According to Hanski & Cambefort (1991b) paracoprids have two essential requirements for successful breeding, namely food for the larvae and a space in the soil, below the dung, to construct their nest. The larger species belonging to FG I and FG II are unaffected by this because dung is buried at a distance from the dung pat. The intraspecific aggregation of the larger competitors was also stronger than the interspecific aggregation between larger, superior competitors and smaller inferior competitors. According to Hanski (1991) increasing intraspecific aggregation amplifies intraspecific competition relative to interspecific competition. Co-existence will depend on the relative magnitudes of intraspecific and interspecific competition and increasing intraspecific aggregation of the superior competitor relative to interspecific aggregation between this competitor and inferior competitors will facilitate co-existence. In the disturbed grassveld habitat the interspecific aggregation was stronger between species belonging to FG I and FG II than in the natural grassveld habitat (Table 8.3 b). Trampling and overgrazing of the habitat probably influences the breeding space of these species in the habitat resulting in a more aggregated distribution. In the natural Bushveld habitat there was also stronger interspecific aggregation between smaller species belonging to FG V (Table 8.3 c), while interspecific aggregation was stronger between larger superior competitors in the disturbed bushveld habitat than in the natural bushveld habitat (Table 8.3 d).

According to Giller & Doube (1994) co-existence is facilitated by increased aggregation of the competitively superior species. This was true for dung beetles in the disturbed habitats, but in the natural habitats the inferior competitors were more aggregated than the superior competitors. Atkinson & Shorrocks (1981) suggest two processes, which can lead to more prolonged coexistence, increased patchiness of resources, and increased aggregation of competitors. According to Begon, *et al.* (1995) the heterogeneous nature of the environment can facilitate co-existence without the presence of a marked differentiation of niches. They argue that interspecific competition often proceeds not in isolation, but under the influence of, and within the constraints of, a patchy, impermanent or unpredictable world. Gittings & Giller (1998) reason that dung quality preferences can also lead to reduced interspecific aggregation in naturally dropped dung pats of varying moisture and nitrogen content. In the present study there were differences in the habitats and these differences influenced the distribution of resources and consequently the distribution of dung beetle species. In the natural habitats the resources were more randomly distributed than in the disturbed habitats, probably facilitating co-existence even if species were less aggregated. The habitat seems to have a very strong effect on the level of intra-and interspecific aggregation of species, competition and co-existence. Atkinson & Shorrocks (1981) found that the outcome of competition is as much determined by the way the individuals respond to the environment as by the competitive interactions between species. Dung beetle species tended to be more intra- and interspecifically aggregated in the disturbed habitats than in the natural habitats. The larger superior competitors were more aggregated in the disturbed habitats than in the natural habitats. This enabled the smaller less effective competitors to become more dominant in the disturbed habitats. Trampling and overgrazing in the disturbed habitat might influence the distribution of the species here, forcing them to become more aggregated, and thereby influencing the structure of the assemblage. The more aggregated distribution of dung beetles in the disturbed habitats may also be explained by the movement of cattle and the resultant pat-deposition between camps. Giller & Doube (1994) argue that cattle are moved between paddocks several times per year and some paddocks are not stocked for a substantial period of time, resulting in instantaneous density of potential colonist beetles emerging from previous resource patches.

Table 8.2: Level of intraspecific aggregation (J) of dung beetle species distributed between plots and sites in four different habitats: S.G. – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; S.B. – natural bushveld habitat; Josina – disturbed bushveld habitat.

Species	**Dry mass (g)**	**Intraspecific aggregation (J)**							
		Between Plots				**Between Sites**			
		S.G.	**Rietvlei**	**S.B.**	**Josina**	**S.G.**	**Rietvlei**	**S.B.**	**Josina**
F.G. I:									
Pachylomerus femoralis	1.49 ± 0.27	0.01	0.18	TS	TS	0.18	1.17	TS	TS
F.G. II:									
Scarabaeus flavicornis	0.158 ± 0.31	1.82	0.02	-0.04	0.09	0.19	1.14	-0.01	0.35
F.G. IV:									
Metacatharsius sp. 1	0.028 ± 0.002	0.16	0.04	0.07	TS	0.18	0.39	0.24	TS
Onthophagus quadraliceps	0.014 ± 0.005	0.08	0.07	TS	TS	0.66	0.306	TS	TS
F.G. V:									
Onthophagus sugillatus	0.003 ± 0.0008	TS	TS	0.49	1.04	TS	TS	0.24	0.46
Onthophagus variegatus	0.003 ± 0.0006	1.14	TS	0.47	0.6	1.39	TS	0.74	1.4
Onthophagus sp. 1	0.005 ± 0.001	0.58	TS	0.09	1.04	0.33	TS	-0.02	0.83
F.G. VI:									
Caccobius seminulum	0.001 ± 0.003	0.31	0.28	0.09	0.35	0.1	0.02	0.36	0.3

***TS – Samples to small**

Table 8.3: Average association values (C) between individual species between sites in four different habitats

a) Sandveld Grassveld –natural grassveld habitat

Species	**Interspecific aggregation (C)**						
	FG I	FG II	FG IV		FG V		FG VI
	Pachylomerus femoralis	*Scarabaeus flavicornis*	*Onthophagus quadraliceps*	*Metacatharsius sp. 1*	*Onthophagus variegatus*	*Onthophagus sp. 1*	*Caccobiu seminulu*
F.G. I:							
Pachylomerus femoralis		0.19	0.19	0.19	0.07	0.07	0.03
F.G. II:							
Scarabaeus flavicornis			0.12	0.18	-0.06	0.01	0.01
F.G. IV:							
Onthophagus quadraliceps				0.23	0.89	0.46	0.15
Metacatharsius sp. 1					0.14	0.11	0.04
F.G. V:							
Onthophagus variegatus						0.68	0.21
Onthophagus sp. 1							0.11
F.G. VI:							
Caccobius seminulum							

Table 8.3. Continued: Average association values (C) between individual species between sites in four different habitats

b) Rietvlei – disturbed grassveld habitat

Species	**Interspecific aggregation (C)**					
	FG I	FG II	FG IV		FG V	FG VI
	Pachylomerus femoralis	*Scarabaeus flavicornis*	*Onthophagus quadraliceps*	*Metacatharsius sp. 1*	*Onthophagus sp. 1*	*Caccobius seminulum*
F.G. I:						
Pachylomerus femoralis		-0.61	-1.73	-0.6	-0.87	-0.06
F.G. II:						
Scarabaeus flavicornis			-0.27	0.72	1.5	-0.7
F.G. IV:						
Onthophagus quadraliceps				-0.31	-0.8	-0.05
Metacatharsius sp. 1					1.00	2.12
F.G. V:						
Onthophagus sp. 1						-0.9
F.G. VI:						
Caccobius seminulum						

Table 8.3. Continued: Average association values (C) between individual species between sites in four different habitats

c) Sandveld Bushveld – natural bushveld habitat

Species	**Interspecific aggregation (C)**					
	FG II	FGIV	FG V			FG VI
	Scarabaeus flavicornis	*Metacatharsius sp. 1*	*Onthophagus variegatus*	*Onthophagus sugillatus*	*Onthophagus sp. 1*	*Caccobius seminulum*
F.G. II:						
Scarabaeus flavicornis		-0.1	-0.08	0.05	-0.02	-0.07
F.G. IV:						
Metacatharsius sp. 1			-0.1	-0.3	0	-0.2
F.G. V:						
Onthophagus variegatus				0.27	0.16	0.53
Onthophagus sugillatus					0.05	0.26
Onthophagus sp. 1						0.1
F.G. VI:						
Caccobius seminulum						

Table 8.3. Continued: Average association values (C) between individual species between sites in four different habitats

d) Josina – disturbed bushveld habitat

Species	**Interspecific aggregation (C)**				
	FG II	FG V			FG VI
	Scarabaeus flavicornis	*Onthophagus variegatus*	*Onthophagus sugillatus*	*Onthophagus sp. 1*	*Caccobius seminulum*
F.G. II:					
Scarabaeus flavicornis		-0.71	-0.41	0.54	0.1
F.G. V:					
Onthophagus variegatus			0.88	-0.48	-0.49
Onthophagus sugillatus				-0.22	-0.34
Onthophagus sp. 1					-0.19
F.G. VI:					
Caccobius seminulum					

Correlation between the size and abundance of different dung beetle species and the level of intraspecific aggregation in a species

In the natural grassveld habitat there was a negative correlation between the dry mass of a species and the level of aggregation, with the smaller species tending to be more aggregated (r=-0.27; Fig. 8.2). The opposite was true for dung beetle species in the disturbed grassveld habitat. There was a very high positive correlation between the dry mass of a species and the level of aggregation, with the larger species more aggregated (r=0.68; Fig. 8.2). In both the natural and disturbed bushveld habitats there was a negative correlation between the dry mass of species and the level of aggregation (r=-0.51; r=-0.47; Fig. 8.2). Hanski & Cambefort (1991b) found that large Coprini interfere with one another and become distributed more evenly among the dung pats than the small paracoprids Onthophagini and Oniticellini, and Giller & Doube (1994) also found that in West Africa the larger Coprini tend to be more evenly distributed than the smaller tunnelling species. Hanski & Cambefort (1991b) concluded that the size of the beetle, not the tribe, significantly affects aggregation. From the present study it can be concluded that the habitat influences species of different sizes differently and consequently influence their distribution and aggregation differently.

The correlation between abundance and aggregation (J) also differed between the habitats. In both the natural and disturbed grassveld habitats there was a negative correlation between the abundance and aggregation with aggregation increasing with decreasing abundance (r=-0.335; r=-0.534; Fig. 8.3). The most abundant species probably utilised most of the resource, while the less abundant species tended to be aggregated in the patches less occupied by the more abundant species. In both the natural and disturbed bushveld habitats the situation was reversed. There was a very high positive correlation between abundance and aggregation in both habitats, with the more abundant species being more aggregated (r=0.89; r=0.81; Fig. 8.3). Tree cover might influence the distribution of the more abundant species causing a more aggregated distribution of abundant species in the bushveld habitats than in the grassveld habitats.

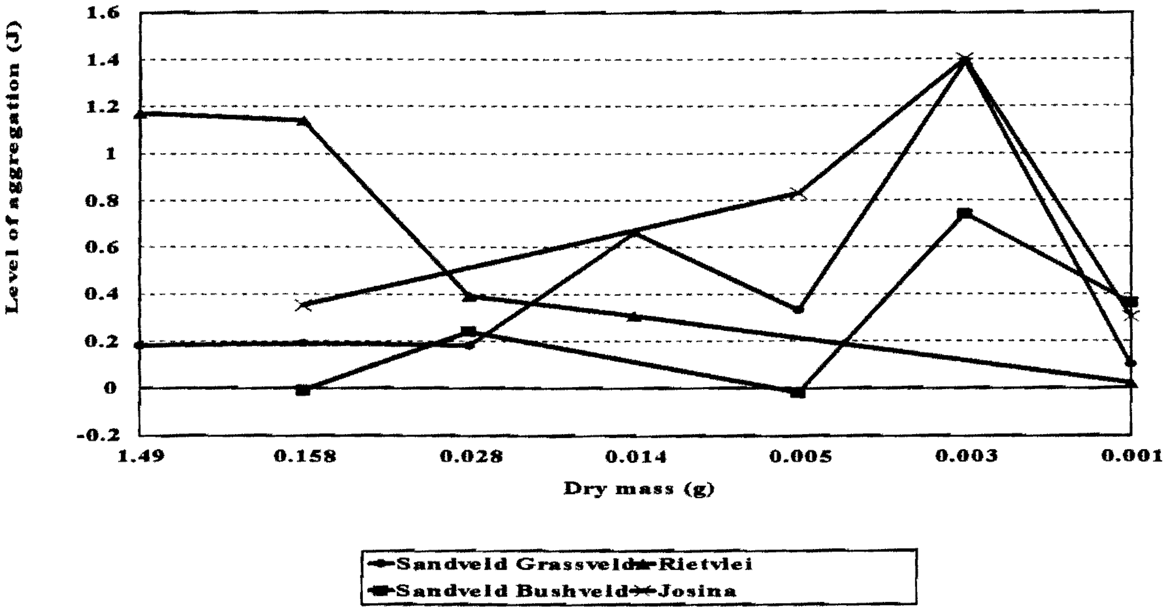


Fig. 8.2: Correlation between dry mass (g) of dung beetles and level of aggregation (J) in four different habitats: Sandveld Grassveld – natural grassveld habitat (r=-0.27); Rietvlei – disturbed grassveld habitat (r=0.68); Sandveld Bushveld – natural bushveld habitat (r=-0.51); Josina – disturbed bushveld habitat (r=-0.47).

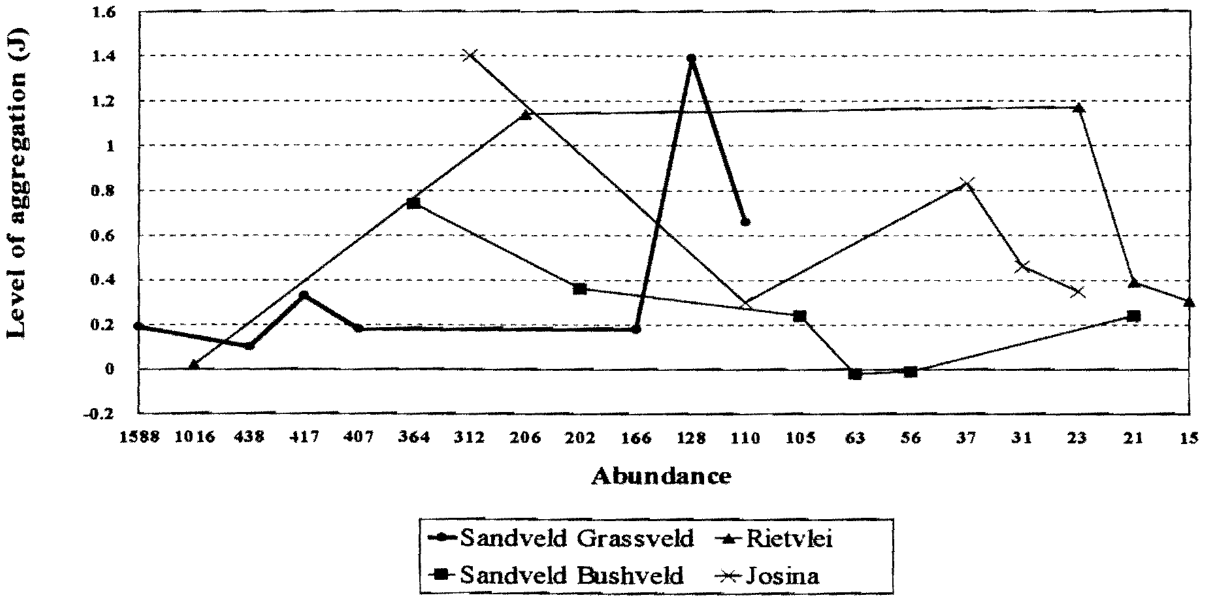


Fig. 8.3: Correlation between abundance of dung beetles and level of aggregation (J) in four different habitats: Sandveld Grassveld – natural grassveld habitat (r=-0.355); Rietvlei – disturbed grassveld habitat (r=-0.534); Sandveld Bushveld – natural bushveld habitat (r=0.89); Josina – disturbed bushveld habitat (r=0.81).

8.4. CONCLUSION

Aggregated distribution of dung beetle species and patchiness of resources is just one of the many mechanisms allowing the co-existence of inferior competitors with superior competitors in a dung beetle assemblage. It is, however, an important mechanism determining the structure of the assemblage in a particular habitat. The habitat seems to have an important effect on the aggregation of dung beetle species. In the present study the degree of dominance and also the dominant species differed with different habitats. In the natural grassveld habitat the assemblage was dominated by a superior competitor belonging to FG II, while the assemblages in the disturbed grassveld habitat was dominated by an inferior competitor belonging to FG VI. The assemblages in both the bushveld habitats were dominated by an inferior competitor belonging to FG IV. In the natural grassveld habitat the larger, superior competitors showed a lower level of intraspecific aggregation, while in the disturbed grassveld habitat these competitors were more aggregated intraspecifically and there was also stronger interspecific aggregation between superior competitors, allowing a higher dominance of the smaller inferior competitors. There was a correlation between size and level of aggregation with aggregation decreasing with increasing size in the natural grassveld habitat and aggregation increasing with increasing size in the disturbed grassveld habitat. Size thus seems to have a significant effect on aggregation. Different habitats influence dung beetles of different sizes differently. Larger, superior competitors are more severely effected in disturbed habitats than in the natural habitats. This will influence the aggregation of these species and subsequently the structure of the whole assemblage.

CHAPTER 9

MODEL AND CONCLUDING REMARKS

9.1. INTRODUCTION

The need to formulate general rules in complex systems in ecology often result in the construction of qualitative, mathematical or graphical models. According to Price (1984) a model should represent a simplified view of the system being modeled, and yet capture the essence of the system such that the model has explanatory and predictive power. According to Begon *et al.* (1995) there are four reasons for constructing a model.

i) Models bring together in terms of a few parameters, the important, shared properties of unique examples.

ii) Models force us to try to extract the essentials from complex systems. If each example can be expressed in a common language, then their properties relative to one another will be more apparent.

iii) Models can provide a standard of idealized behaviour against which reality can be judged and measured.

iv) Models can shed light on the real world.

These four reasons for constructing models are also criteria by which any model should be judged. A model will only be useful if it performs one or more of these four functions (Begon *et al.* 1995).

After a series of life tables has been developed, covering a wide range of conditions, it is likely that one or two key variables will be revealed that are mainly responsible for population changes. According to Price (1984) the basis for understanding the population dynamics of any organism lies in the identification of these key factors.

According to Dempster (1991) the largest single cause of changes in the distribution and abundance of insects in Britain over the past 50-100 years is loss of habitat resulting from changing land use. Humans tend to create a patchy landscape of numerous ecosystem types ranging from crop monocultures to botanical gardens (Odum, 1993). Environmental resource patches are patches of vegetation left behind despite environmental change and these are important refugia for many insects (Samways, 1994). In a patchy landscape, patch size is an important factor in determining what species of animals are able to survive. A patchy landscape would not necessarily result in a decrease of diversity because there are a host of rare species, which are able to adapt to new conditions in these habitat patches. These edge species can adapt to changed conditions and become abundant in the absence of dominant species. According to Samways (1994) the disturbed landscape, if not too severe to cause deterministic extinction, will set in motion a chain of events that may lead to at least increased extinction risks. For insects, with their small size and generally high susceptibility to adverse environmental influences, it is the fragmentation of the population and decrease in abundance in the population, making it vulnerable to further disturbances, that is significant. Farmers control most of the land which act as matrix for nature reserves and provides good insect habitat and potential corridors (Moore, 1991). Pastoralism is not new and grazing both by domestic cattle and indigenous megaherbivores has continued side by side for centuries. Many grassland insect species have adapted and diversified under these conditions. It is, however, major disturbances such as ploughing and heavy overgrazing that leads to declining population levels and a loss of insect populations (Samways, 1994).

An ecosystem is composed of many individuals interacting among themselves and with their physical environment. Preservation of varying and overlapping ecosystems is necessary because insect species and other biota are an intrinsic part of it (Samways, 1994). Dung beetle assemblages are important for the successful functioning of any grazing ecosystem. Continued adverse environmental disturbances caused by farming activities such as overgrazing have placed stress on dung beetle assemblages on farms. These disturbances have influenced the dung beetle assemblages on farms in such a way that their ecological role in the grazing ecosystem has been affected. It is therefore important to determine the key variables responsible for these changes, species influenced and to construct a simple model to describe the most important factors influencing dung beetle assemblages and to shed some light on changes in these assemblages. This will enable us to make predictions and recommendations to farmers and managers of nature reserves.

9.2 Factors influencing the success of dung beetle assemblages in a grazing ecosystem

Ecosystems are complex, gradually changing over time and subject to many abiotic and biotic influences. Change in an ecosystem is one of the most obvious attributes, particularly in vegetational attributes, but also in the kinds of animals that reside in the ecosystem. Usher & Jefferson (1991) consider the process of ecological succession the single most important factor causing change in an arthropod community. Ecological succession is usually predictable and directional so that a pattern of change can be observed (Price, 1984). The dung beetle assemblages at Sandveld nature reserve and on the neighbouring farms are subject to many natural changes over time. These changes can be both allogenic (external) and autogenic (internal) (Fig. 9.1). Odum (1993) proposed a general systems model of succession where the internal or autogenic inputs and the periodic external allogenic inputs both affect the progress of a system developing toward climax. The autogenic forces tend to drive the system toward equilibrium, while strong allogenic inputs tend to disrupt progress toward equilibrium and set back the succession to a younger stage (Odum 1993). Begon, *et al.* (1995) distinguishes between successions that occur as a result of biological processes that modify conditions and resources (autogenic successions) and successions occurring as a result of external forces (allogenic successions). Natural allogenic changes are periodic and dung beetle assemblages can continue to exist without severe changes to the assemblage. Many insect populations show quick recovery from naturally adverse conditions, but it is when conditions are severe and prolonged that populations begin to fragment (Samways, 1994). Situations created by human impacts such as overgrazing is often severe and prolonged.

There are many variables to consider when looking at the success of a dung beetle assemblage in an ecosystem (Fig. 9.1):

Allogenic factors

The allogenic variables influencing dung beetle assemblages in an ecosystem are: the human impact, season and habitat.

*Human impact:

According to Goudie (1990) humankind has possibly had a greater influence on vegetation than on any of the other components of the environment. Through inducing vegetation change, whole landscapes have been transformed. Human induced changes such as overgrazing, trampling of vegetation and fragmentation of habitats transform the microhabitat (Fig. 9.1). These microhabitat changes can have severe effects on the dung beetle assemblages. Degradation of vegetational ground cover will influence the cover for dung beetles and trampling will affect the breeding space in the soil. Fragmentation will isolate dung beetle assemblages increasing the chances for extinction.

*Season:

Seasonal variables, which have the greatest influence on dung beetle assemblages, are temperature and rainfall. Increased temperatures and higher rainfall will be favourable for dung beetle assemblages. There is, however an upper threshold, with too high temperatures and rainfall having a negative effect on the dung beetle assemblages. The study area is an unpredictable habitat with wet and dry seasons of varying length, and downpours alternating with extended periods of drought (Chapter 2). Dung beetles in the study area seemed to be adapted to arid conditions and high temperatures. Temperature seemed to be a key factor in the distribution of dung beetle assemblages, while rainfall was less important (Chapter 4). Dung beetle assemblages were able to survive adverse seasonal periods of low temperatures, high temperatures and drought, because these periods were periodic and assemblages recovered quickly afterwards.

Seasonal changes have an indirect influence on the dung beetle assemblages by causing changes in the habitat (Fig. 9.1). Changes in temperature and rainfall will cause changes in the vegetational ground cover. These, in turn, will influence the composition of the dung beetle assemblage (Fig. 9.1). Seasonal changes influences the dung beetle assemblages directly with temperature, rainfall and length of day influencing the succession, diel, aggregation and dung preferences of dung beetles (Fig. 9.1).

*Habitat:

Both seasonal and human impacts have a great influence on the habitat (Fig. 9.1). It appears that drought is a normal phenomena in the study area (Chapter 2). According to Skinner (1981) semi-arid grassveld is particularly susceptible to drought. Seasonal impacts on the habitat are periodic and the habitat is able to recover after periods of drought. It is the human impact, however, that has the greatest influence on the condition of the veld. Danckwerts & Stuart-Hill (1988) found a slower rate of recovery on grazed than on ungrazed veld and attribute this to the ill-effect grazing had on seedling establishment and tuft regeneration from a limited number of secondary tillers. Veld condition is primarily related to its ecological status such as succession stage, species composition and cover density (Nel, 1991). The veld in the disturbed habitat on the farm Rietvlei in the study area is still in a pioneer stage, while the veld in the nature reserve is in subclimax (Table 2.1, Chapter 2). The basal cover and relative veld condition is also much lower on the farm than in the nature reserve (Table 2.1, Chapter 2). Without human impact plants will be able to survive periodic adverse seasonal impacts. Combined seasonal and human impacts, however, can be detrimental to plant cover. Excessive trampling when conditions are dry will reduce the size of soil aggregates and plant litter to a point where they are subject to aeolian deflational processes and heavy grazing can kill plants or lead to a marked reduction in their level of photosynthesis (Goudie, 1990). A change in vegetation caused by heavy grazing and the soil caused by trampling will influence the composition of the dung beetle assemblage in this habitat by determining the size and competitive ability of the dominant species (Fig. 9.1). This in turn will influence processes in the dung beetle assemblage such as succession in the dung, diel flight during a 24-hour period, interspecific and intraspecific aggregation of species and individuals and the dung preferences of the dung beetles (Fig. 9.1). These processes will in turn influence the recycling of dung in a habitat. The size and competitive ability of the dominant species will determine the rate and amount of dung removed. The success of the dung beetle assemblage will ultimately determine the success of the habitat by improving the recycling of nutrients (Fig. 9.1). Dung decomposition has been widely associated with inprovement in soil fertility (Petersen, *et al.*, 1956; Dickinson *et al.*, 1981; Omaliko, 1984; Herrick & Lal, 1996; Lovell & Jarvis, 1996). Herrick & Lal (1996) found that processes associated with dung decomposition play a role in reducing surface compaction by increasing the volume of soil macropores and that these changes appear to be tied to macroinvertebrate activity. According to Lovell & Jarvis (1996) the substantial amounts of nutrients that are contained in cattle dung can potentially be recycled back to the soil in an available form. Fast breakdown and mixing of dung with the soil increases the size and the activity of the soil microbial biomass, whereas slow breakdown and release of nutrients from dung pats does not (Lovell & Jarvis, 1996). Fast breakdown of dung by dung beetles will therefore release nutrients back into the soil, improving the plant growth, before it is lost. In a system where recycling of dung is ineffective undegraded dung will accumulate in the environment, with little nutrients being released back into the soil. According to Waterhouse (1974) dung deposited on the soil can eventually cause serious damage because it deteriorates the pastureland by preventing plant growth. It also causes the loss of nitrogen by volatilization, which then cannot be incorporated into the soil.

Autogenic factors:

Dung beetles do not divide resources along one resource dimension at one time but, like the populations of most animals and plants, populations of dung beetles are affected by several dimensions simultaneously (Hanski & Cambefort, 1991a). There are many biological and behavioral differences between co-occurring species within a dung beetle assemblage, which influences the interactions within the assemblage and which may facilitate co-existence. There are differences in the type of dung used and how it is used;

succession in the dung differs in terms of the age of dung colonized by different species and functional groups; there are differences in diel activity of different species during a 24-hour period and habitat selection at small and large spatial scales differ. All these processes are interrelated and a change along one resource dimension might result in changes in the others (Fig. 9.1). These processes are also influenced by outside factors such as the season (Fig. 9.1). The season also influences the composition of dung beetle assemblages and subsequently succession, diel, aggregation and dung preference. The habitat and the human impact, by influencing the habitat, will also influence these activities (Fig. 9.1).

***Succession:**

Both the season and the habitat in which the dung was dropped had a strong influence on the succession of dung beetles in the dung (Fig. 9.1). Maximum species richness, biomass and number of individuals of dung beetles were reached earlier in summer. Dung beetles also stayed in the dung for longer periods during the colder seasons (Chapter 6). By influencing the habitat the human impact also influenced the succession of dung beetles. The maximum species richness, biomass and number of individuals were reached earlier in the natural habitats (Chapter 6). Species generally colonized fresher dung in the natural grassveld habitat and stayed in the dung for shorter periods than in the disturbed grassveld habitats (Chapter 6). The rate of change in succession was also more rapid in the natural habitats (Chapter 6). The habitat determines the size and competitive ability of the dominant species and this will in turn influence the succession. Larger dung beetles belonging to FG I and II were more abundant in the natural grassveld habitat and this resulted in earlier colonisation of dung by other species to ensure a part of the resource. The abundance of larger dung beetles in the natural habitat will also result in a larger amount of dung buried within a shorter time (Fig. 9.1).

***Diel activity:**

Although many species had specific flight times, because of specific physiological adaptations, there were minor changes influenced by season and habitat. Activity periods for the community as a whole were shorter during autumn and spring and also occurred later in the morning and earlier in the afternoon during these seasons (Chapter 5). The habitat influenced the diel activity of larger dung beetle species, whose activity periods were longer in the natural habitats, while smaller species had longer diel flight activity in the disturbed habitats (Chapter 5). Dung degradation would therefore be more effective throughout a 24-our hour period in the natural habitat.

***Aggregation:**

The habitat had a very important influence on the aggregation of dung beetle species. In the natural grassveld habitat the larger superior competitors showed a lower level of intraspecific aggregation, while in the disturbed grassveld habitat these competitors were more aggregated intraspcifically and there was also stronger interspecific aggregation (Chapter 8). In the natural grassveld habitat aggregation decreased with increasing size and in the disturbed grassveld habitat increased with increasing size (Chapter 8).

***Dung preferences:**

Although dung beetles showed preferences for certain dung types this did not reflect association with a particular habitat. Dung beetles seem to be very adaptable and will colonize the most favourable dung type when it is available (Chapter 7).

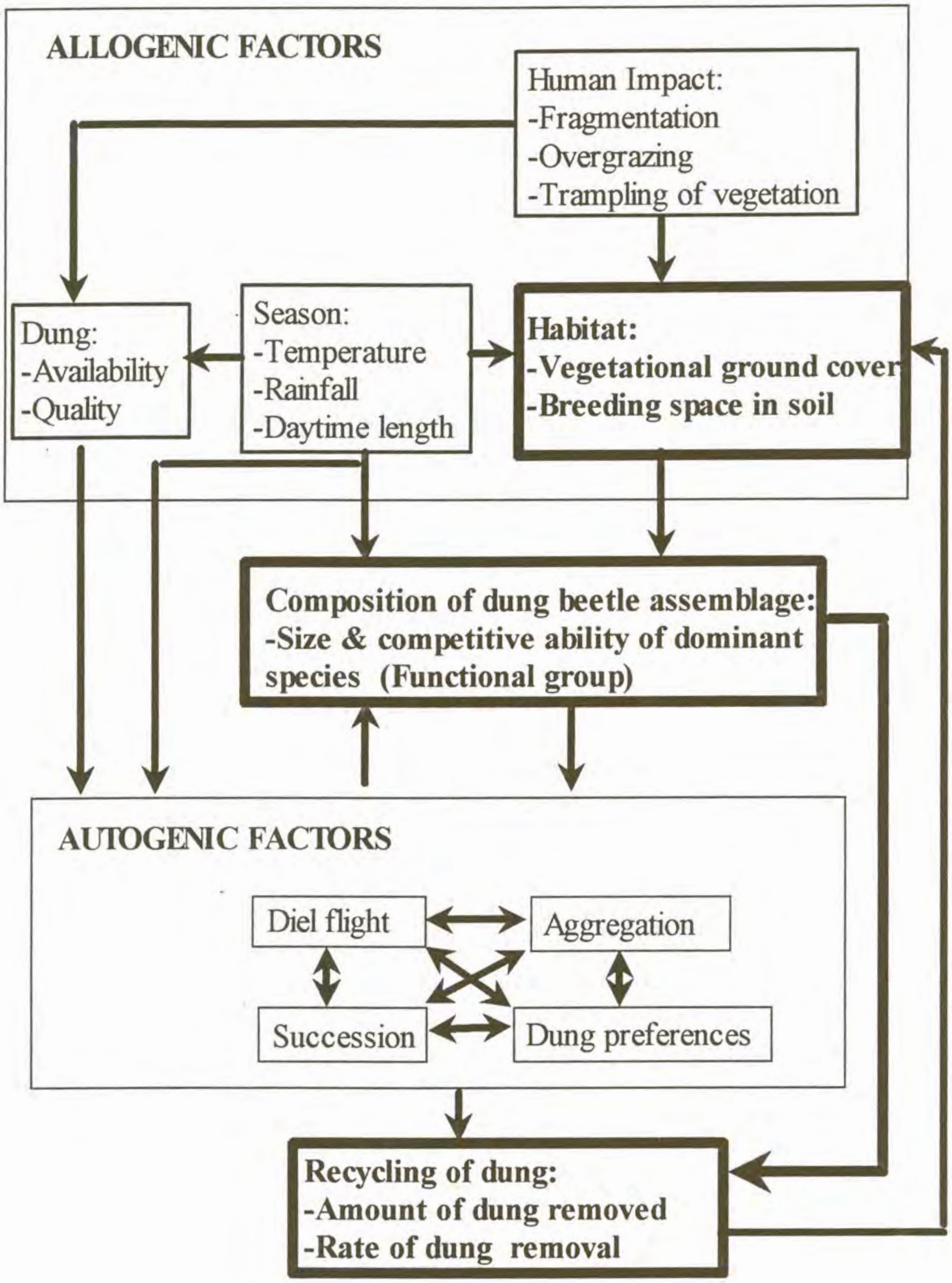


Fig. 9.1: Autogenic and allogenic factors influencing the success of a dung beetle assemblage in a grazing ecosystem

9.3. The importance of size in a dung beetle assemblage

The key factors in these dung beetle assemblages seem to be the habitat and size of the dominant species within this habitat. The size and competitive ability of the dominant species influences the succession, diel activity and aggregation in a dung beetle assemblage. This in turn will influence the rate of dung decomposition in a habitat. Human impact on a habitat such as overgrazing and trampling influences the composition of the dung beetle assemblage in this habitat. Here size of dung beetles played an important role because the change in habitat, caused by human impact, affected the larger better competitors more severely, while the smaller less effective competitors did not seem to be affected by human impact on a habitat (Chapter 3). According to Begon, *et al.* 1995) individual size is perhaps the most apparent aspect of an organism's life-history. Large size may increase an organism's competitive ability and large organisms are also better able to maintain a constancy of body function in the face of environmental variation because their smaller surface-to-volume ratio makes them less 'exposed' to the environment. Larger size, however, can increase some risks. Larger individuals require more energy for maintenance, growth and reproduction, and may therefore be more prone to a shortage of resources (Begon, *et al.*, 1995). Larger dung beetles need more breeding space in the soil and also better vegetation for cover. Larger dung beetles will therefore be more prone to disturbances in the habitat than smaller dung beetles. The larger dung beetles belonging to functional groups I, II and III, which are the better competitors in an assemblage, can therefore be considered as the key species. It is these species which will be affected first by a disturbance in a habitat. These species can therefore be used as early indicators of disturbance. Dufrêne & Legendre (1997) found that when local consequences of habitat fragmentation needs to be determined and this information cannot be obtained by bird or botanical studies, studies on invertebrates will be the best alternative.

A simple size index is proposed to determine the influence of a disturbance in the habitat on ecological role of the dung beetle assemblage as a whole in this habitat:

Size index = B/N

Where B is the total biomass of a dung beetle assemblage in a habitat and N is the total number of individuals in this habitat.

When applying this index to the dung beetle assemblages at Sandveld Nature Reserve and the neighbouring farms we find that the value for the size index is much higher for dung beetle assemblages in the natural grassveld habitat than in the disturbed grassveld habitat (Fig. 9.2). In both the bushveld habitats the value for the size index is low (Fig. 9.2). The size index reflects the degree of dominance in biomass in a habitat and therefore the abundance of larger species in the habitat. This is related to the ecological role, the recycling of dung, of dung beetles in an ecosystem. Merritt & Anderson (1977) found that biomass per dung pat was more important than the number species or individuals per pat in influencing the rate of dung degradation. Larger dung beetles will remove more dung at a faster rate than small dung beetles. The higher the size index the nearer the dung beetle assemblage would be to its full ecological potential in a specific habitat. The recycling of dung will, therefore, be more effective in the natural grassveld habitat than in the disturbed grassveld habitat and also more effective in the natural grassveld habitat than in the bushveld habitats. Because of a difference in vegetation in the bushveld habitats the dung beetle assemblage differ from the dung beetle assemblage in the grassveld habitat. Because of tree cover, which may influence searching success the larger dung beetle species are much less abundant in the bushveld habitats. To determine the effect of habitat disturbance on dung beetle assemblages this model is more applicable to grassveld habitats where larger dung beetle species are abundant. Disturbance of a habitat results in a decrease of the size index and a dung beetle assemblage moving away from its full ecological potential (Fig. 9.2).

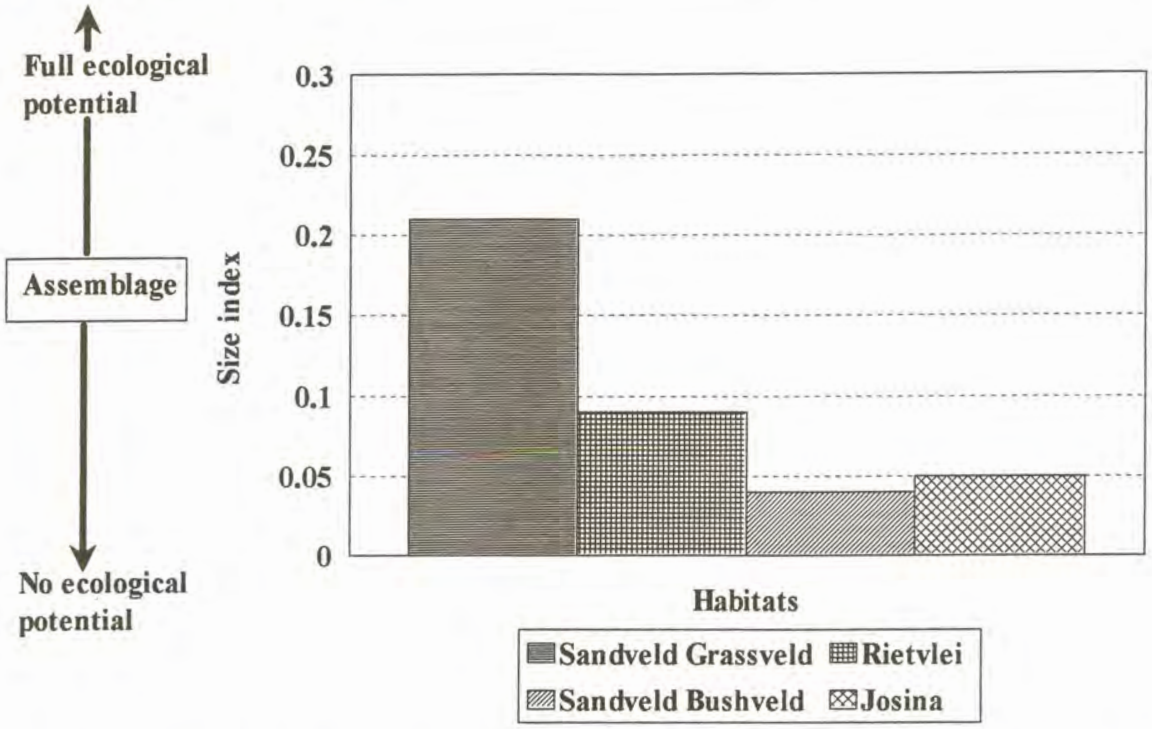


Fig. 9.2: Size index, indicating the ecological role of dung beetle assemblages in four different habitats: Sandveld Grassveld – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; Sandveld Bushveld – natural bushveld habitat; Josina – disturbed bushveld habitat.

Seasonal changes can also cause slight disturbances in a habitat. The size index for dung beetle assemblages changed with seasonal changes throughout the year (Fig. 9.3). There were peaks in the index from October to November and from January to February (Fig. 9.3). There was a drop in the index during December, when the temperatures became too high. It also dropped from March to July and was low during the cold, dry winter months (Fig. 9.3). Seasonal disturbances caused a decrease in the size index. During times of adverse seasonal impacts such as too high or too low temperatures and periods of drought there was very little difference between the size index for the natural grassveld habitat and the disturbed grassveld habitat (Fig. 9.3). As seasonal conditions improved there was an increase in the size index in both habitats but there was a marked difference in size index with the size index being much higher in the natural habitat (Fig. 9.3). Dung beetle assemblages in a habitat experience natural seasonal disturbances, but because these disturbances are periodic they are able to recover quickly when seasonal conditions change. A combination of human and natural impacts, however, might influence the dung beetle assemblage in such a way that they recover more slowly when seasonal conditions change and a stage might be reached where the human disturbances influence the assemblage in such a way that it could no longer recover. At this stage larger species will be replaced by smaller generalist species which are better able to cope with adverse conditions and the assemblage will near a stage where it no longer has ecological potential in the habitat. This will have an effect on the recycling of dung because the dung beetle assemblage is no longer able to fulfill its ecological role successfully resulting in dung left undegraded in the ecosystem. This will place further stress on the habitat because nutrients are not recycled effectively and pastures are fouled by undegraded dung.

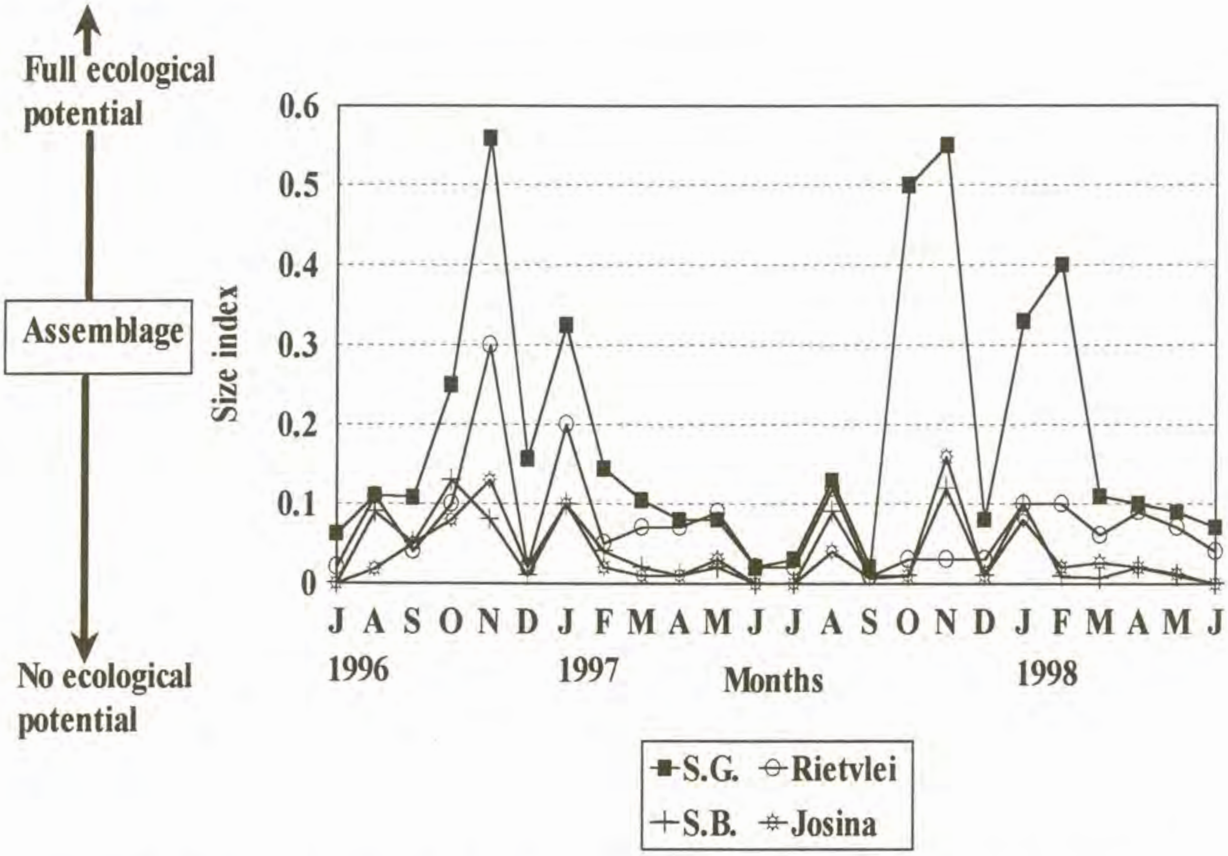


Fig. 9.3: Seasonal change in size index of dung beetle assemblages in four different habitats: Sandveld Grassveld – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; Sandveld Bushveld – natural bushveld habitat; Josina – disturbed bushveld habitat.

9.4. Conclusion

The focus of this study was the dung beetle assemblages in a particular habitat and their ecological role in an ecosystem. The important shared parameters in this system was the human impact, season and habitat as external factors and succession, diel activity, aggregation and dung preferences in dung beetle assemblages as internal factors. All these parameters are interrelated with a change in one resulting in a change in another. These parameters cannot be separated from one another but two key variables could be extracted. These key variables are the influence of habitat and the size of the dominant species in this habitat. These two key variables represent the essentials of the system and by looking at them predictions can be made as to in which direction the dung beetle assemblage in a habitat will move. This will then enable us to make predictions about the condition of the habitat.

Conservation of insects cannot be separated from the conservation of the other biota of the habitats in which those insects live. Conservation action should focus on the conservation of whole ecosystems and this includes insects, because insects play an important role in any ecosystem. Dung beetles are an intrinsic part of any grazing ecosystem, especially open grassveld systems. Traditional pasture improvement strategies for reducing compaction are frequently not practicable because of financial, equipment, and topographic limitations (Herrick & Lal, 1995). When managing natural resources there are two issues of concern: productivity and sustainability. In the management of ecosystems in nature reserves as well as on farms maintaining dung beetle population, which are able to fulfill their ecological role successfully, can provide a cheap and effective alternative for improvement of pastures in a way that will increase productivity as well as sustainability. In looking at the ecological role of dung beetles, diversity alone is not an effective indication of success of a dung beetle assemblage in an ecosystem. The key indicator species are the larger dung beetles. A drop in numbers of these species might act as an early warning. Continued and severe impacts on the habitat might eventually result in the total disappearance of these species consequently leading to impoverished pastures. Improving the habitat will automatically improve the success of the key species. This will improve the recycling of dung and subsequently the quality of the grazing. By limiting disturbances in the habitat with better management practices such as rotation grazing and putting less pressure on the veld during times of periodic natural disturbances such as droughts, the quality of the ecosystem will automatically improve. Resting the veld for as long as possible after a drought is very important and farmers should weigh the costs of supplementary feeding for their livestock after a drought versus their long-term losses associated with reduced veld condition as a result of injudicious grazing. It is important to consider the conservation of habitats rather than species. Not only ecosystems in nature reserves should be focussed on, but also ecosystems on farms. Better communication with farmers is therefore a prerequisite for conservation of dung beetles. By the conservation of whole ecosystems farmers will also benefit by improvement of their grazing pastures, soil fertility, less accumulation of dung and fouling of pastures and less insect pests breeding in dung. By these actions ecological corridors, acting as shelter for dung beetle assemblages, will be created. Connecting these corridors to nature reserves will ensure the future well being of grazing ecosystems in both nature reserves and on farms.

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