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:

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

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.

a)

b)

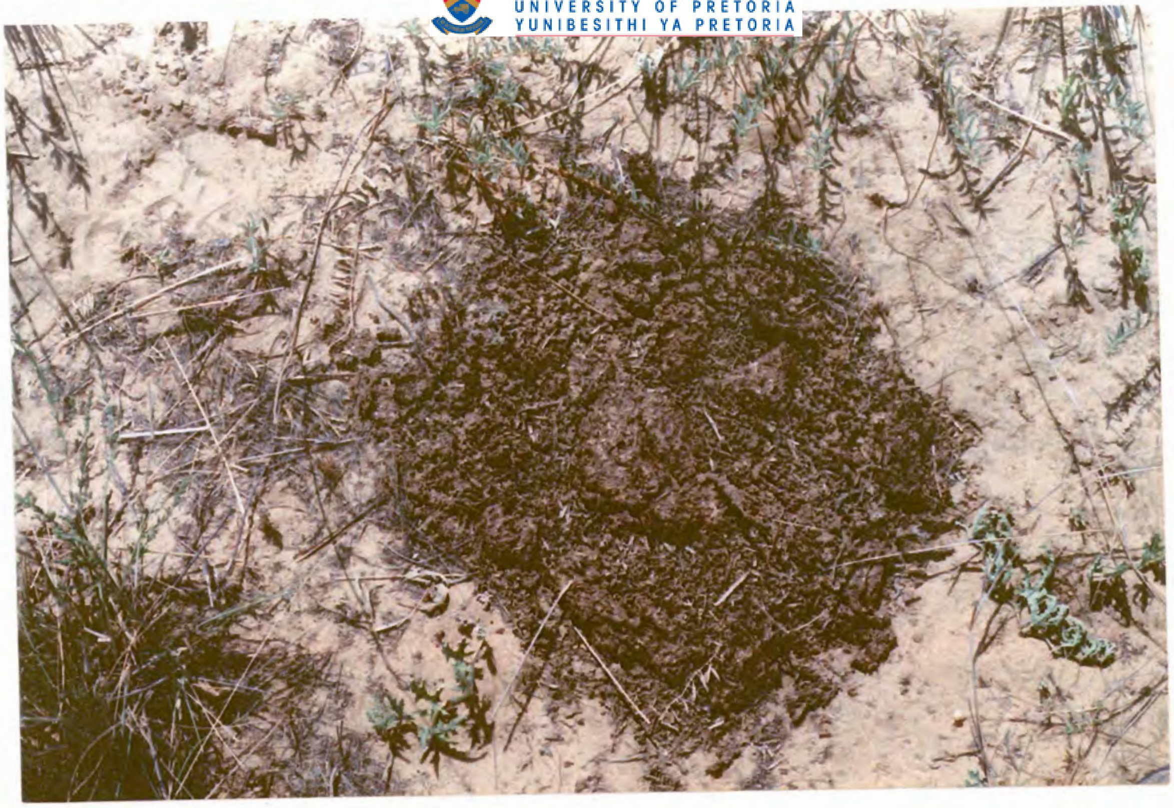
Fig. 6.1: General stages of dung degradation in a savanna ecosystem (SNR and neighbouring farms), a) stage 1 - No dung removed from pat, whole dung pat moist, no sign of disturbance; b) stage 2 - No dung removed, dung covered by dry crust, moist inside, few holes in dung pat.

c)

d)

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.

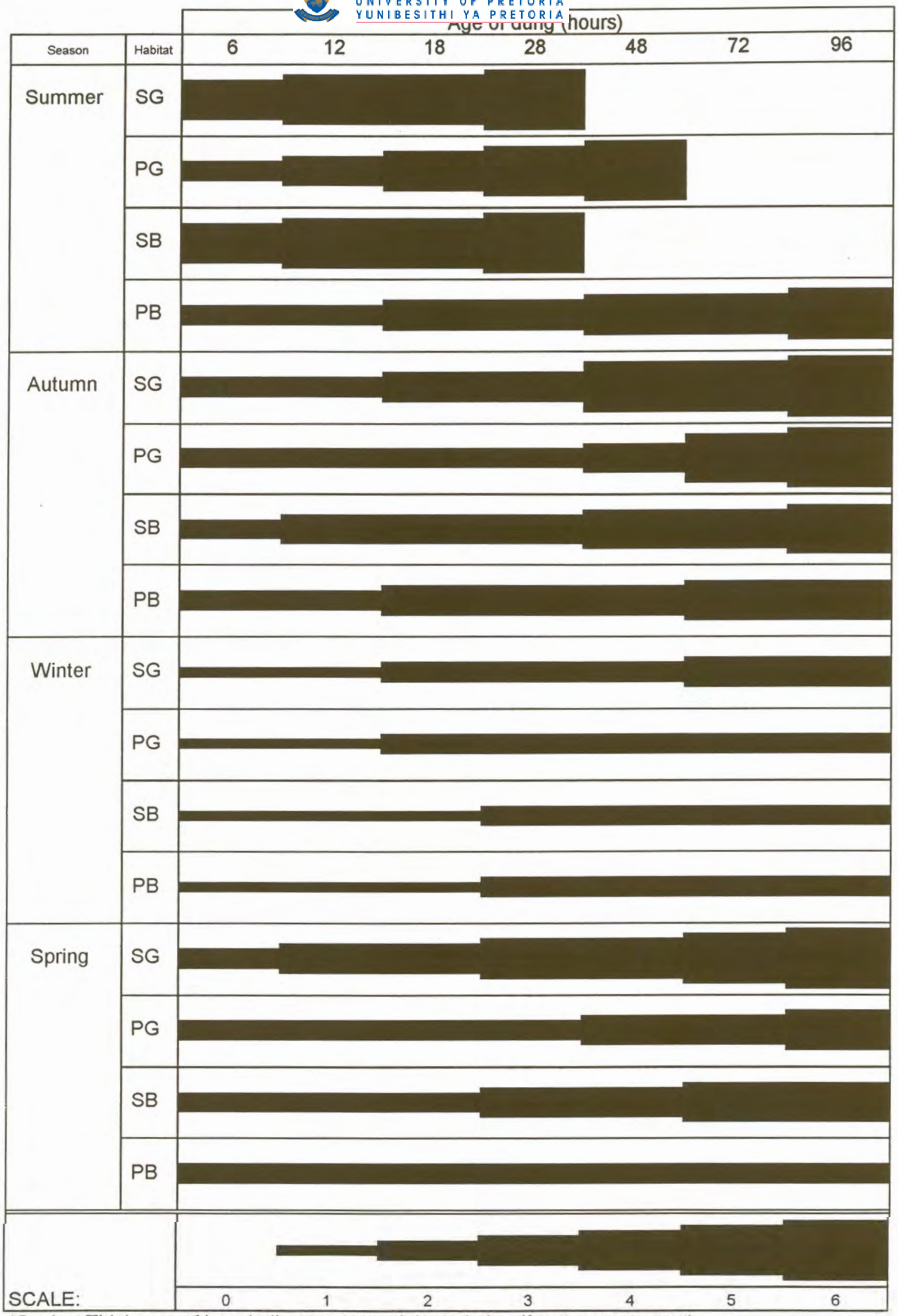
The rate of dung decomposition was very high during summer and higher in the natural grassveld habitats than the bushveld habitats. On the degradation index the dung in the natural grassveld habitat already reached stage 4 after 6 ± 1.4 hours, stage 5 after 12.5 ± 3.53 hours and was completely removed 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).

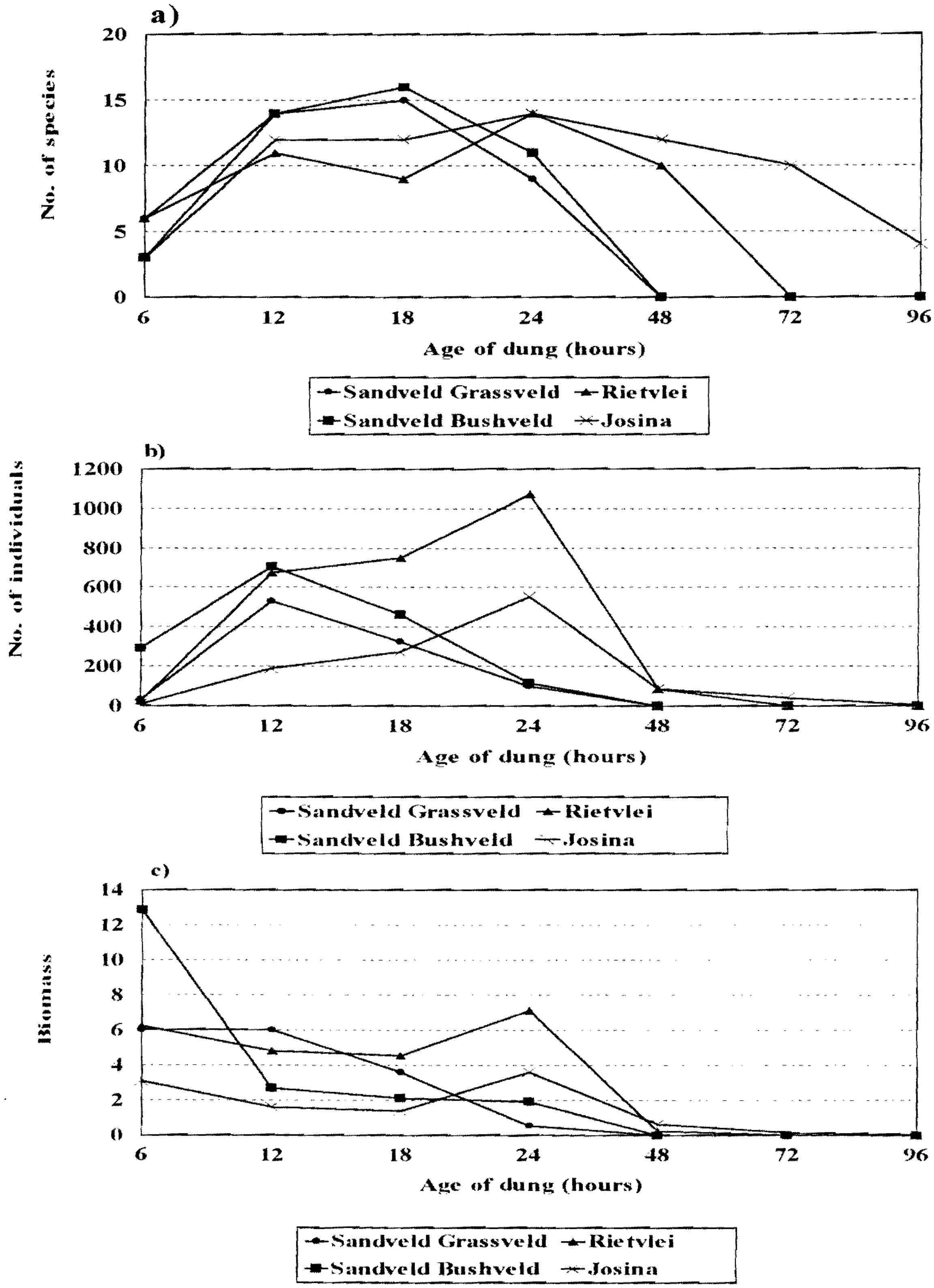


Fig. 6.3: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during summer (December 1996).

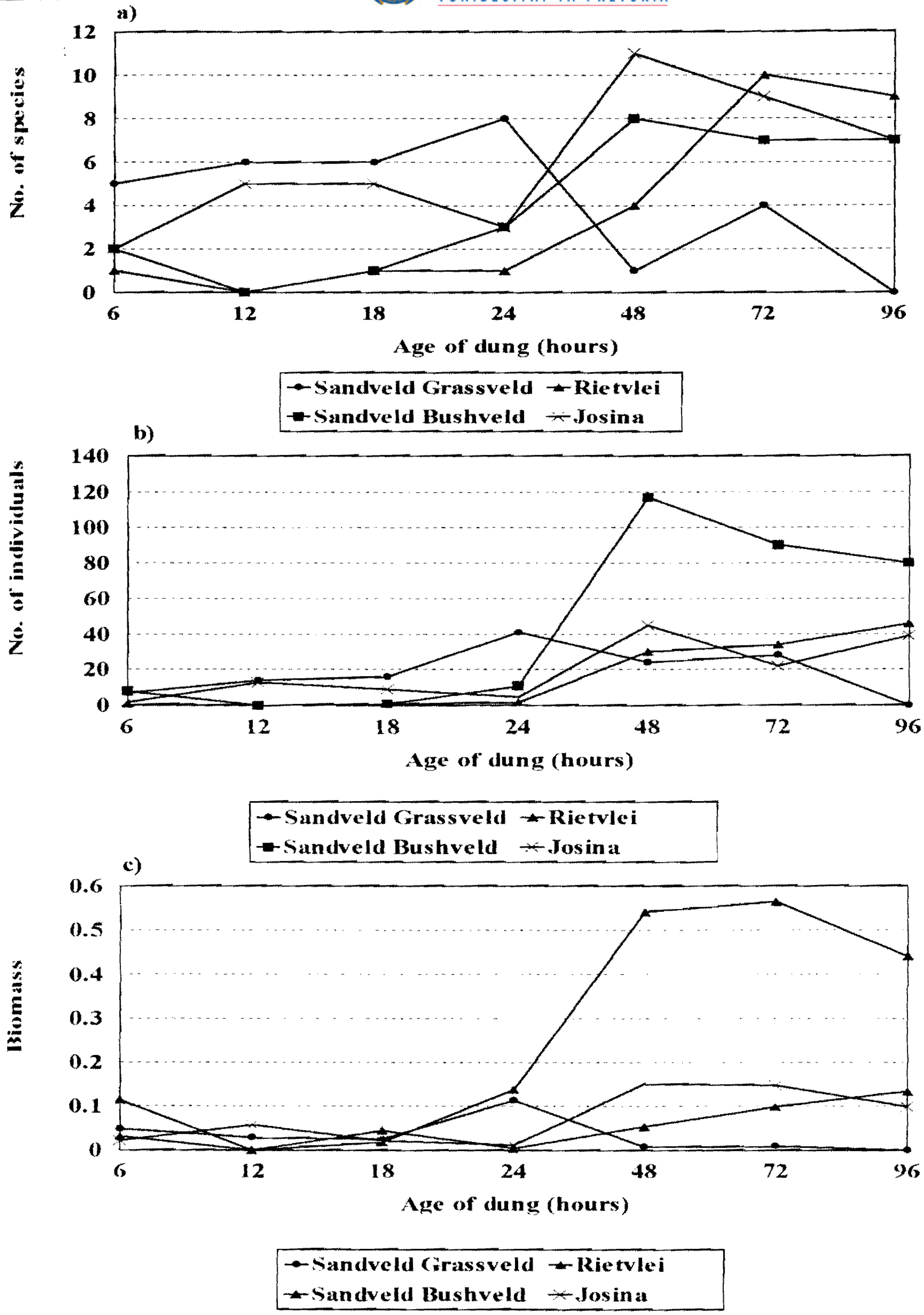


Fig. 6.4: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during autumn (April 1997).

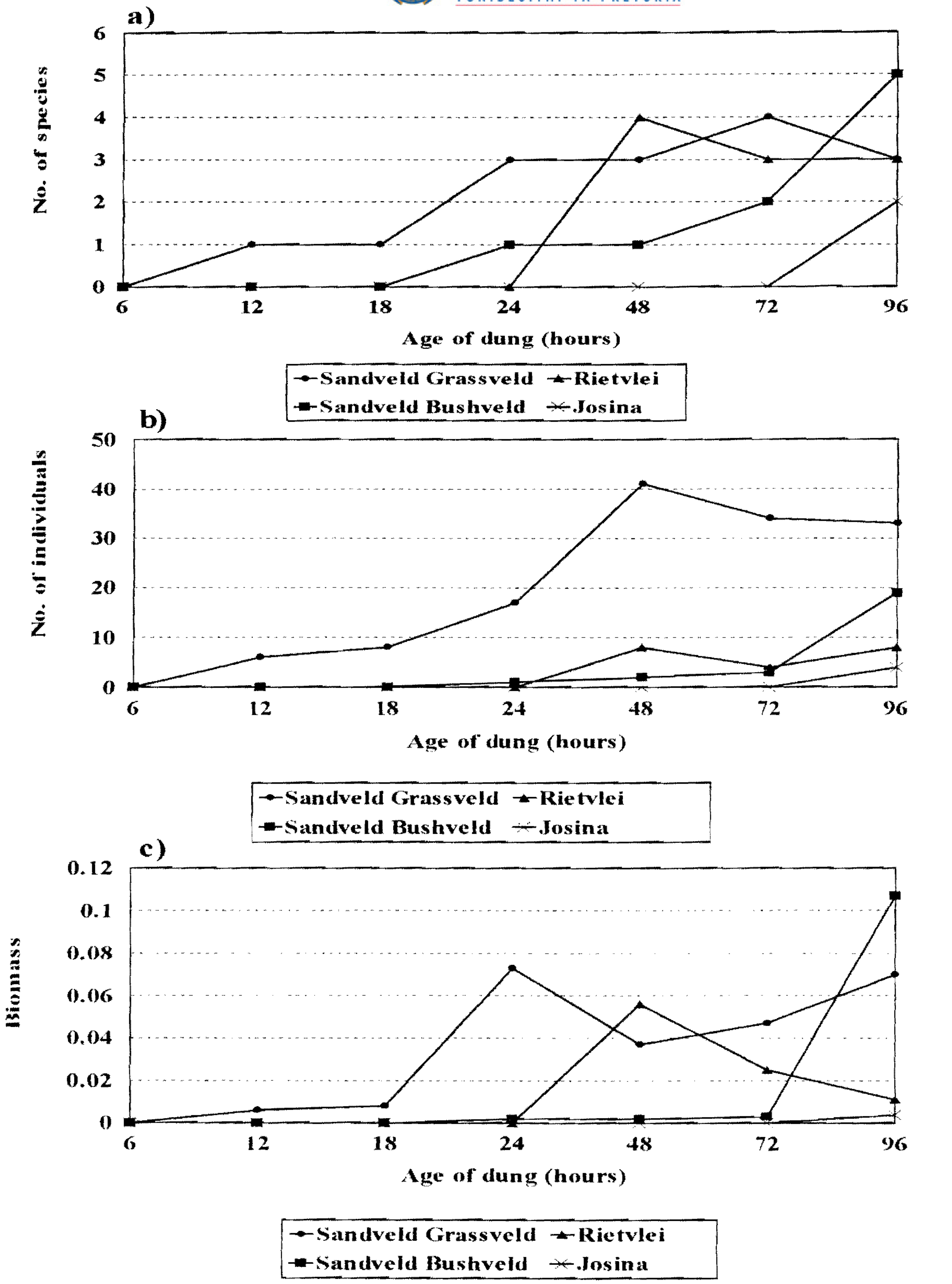


Fig. 6.5: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during winter (July 1997).

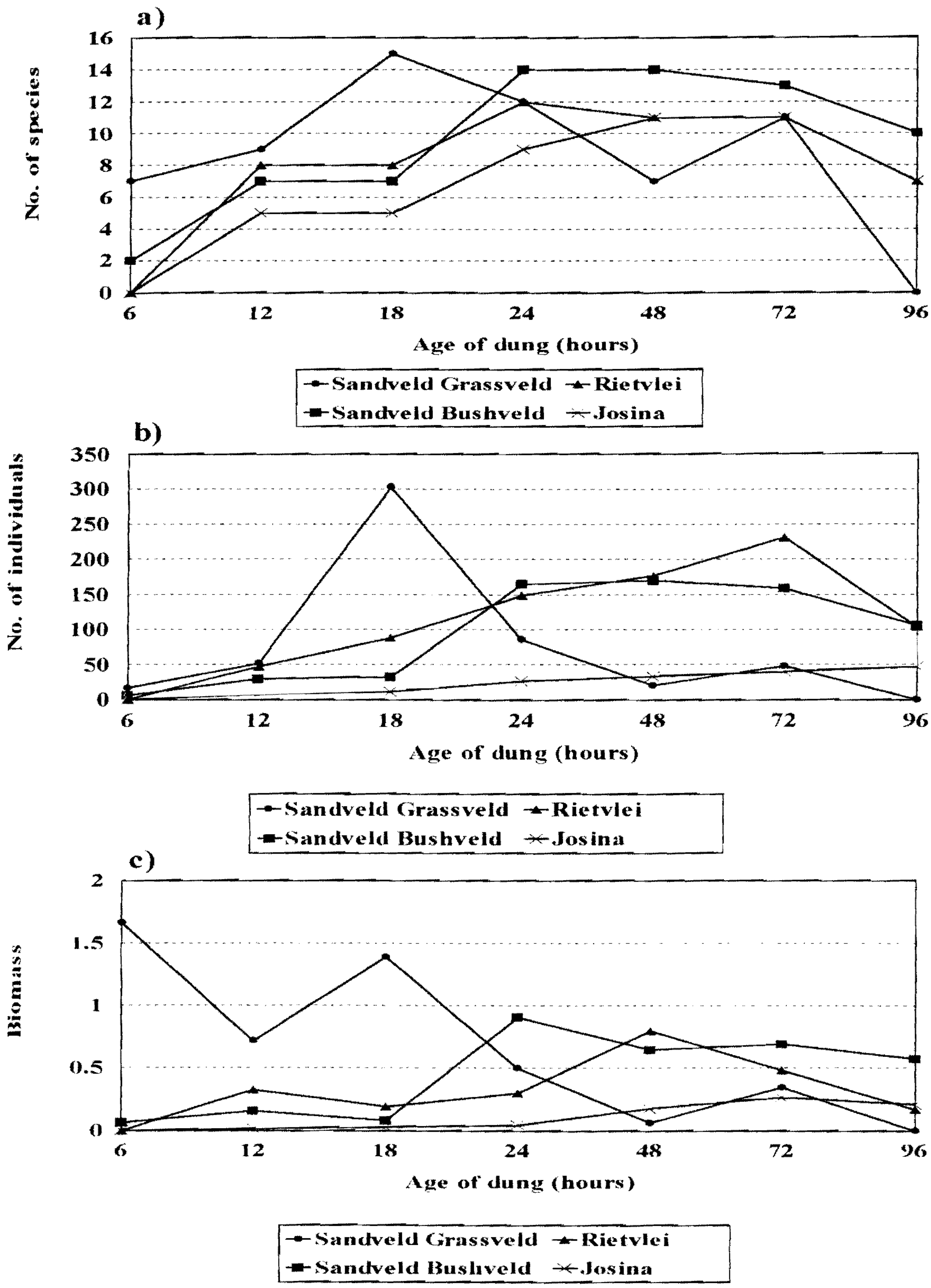


Fig. 6.6: Changes in species richness (a), number of individuals (b) and biomass (c) in relation to dung age in dung beetle assemblages in four different habitats during spring (September 1997).

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. ferruginus, 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.

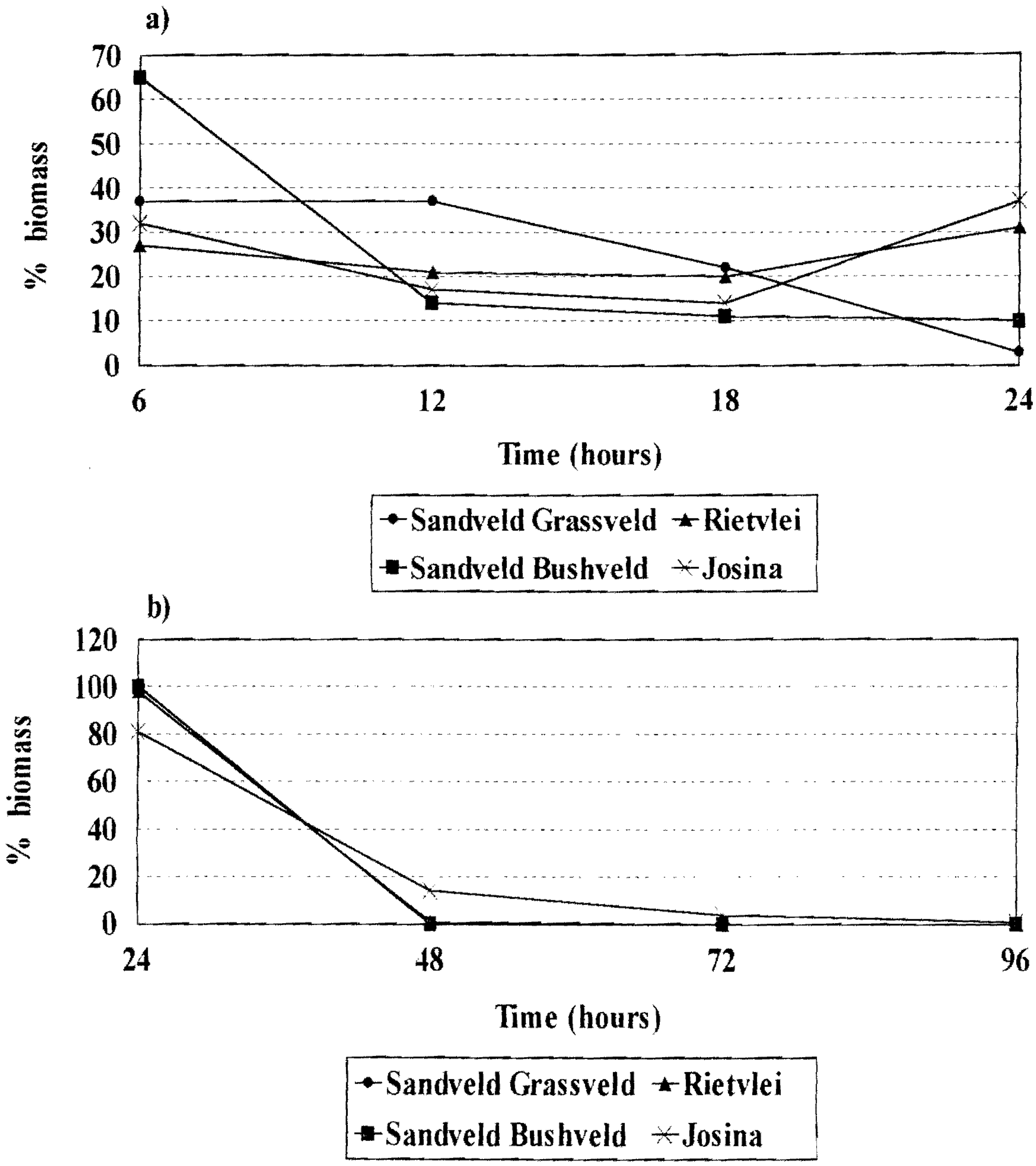


Fig. 6.7: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina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

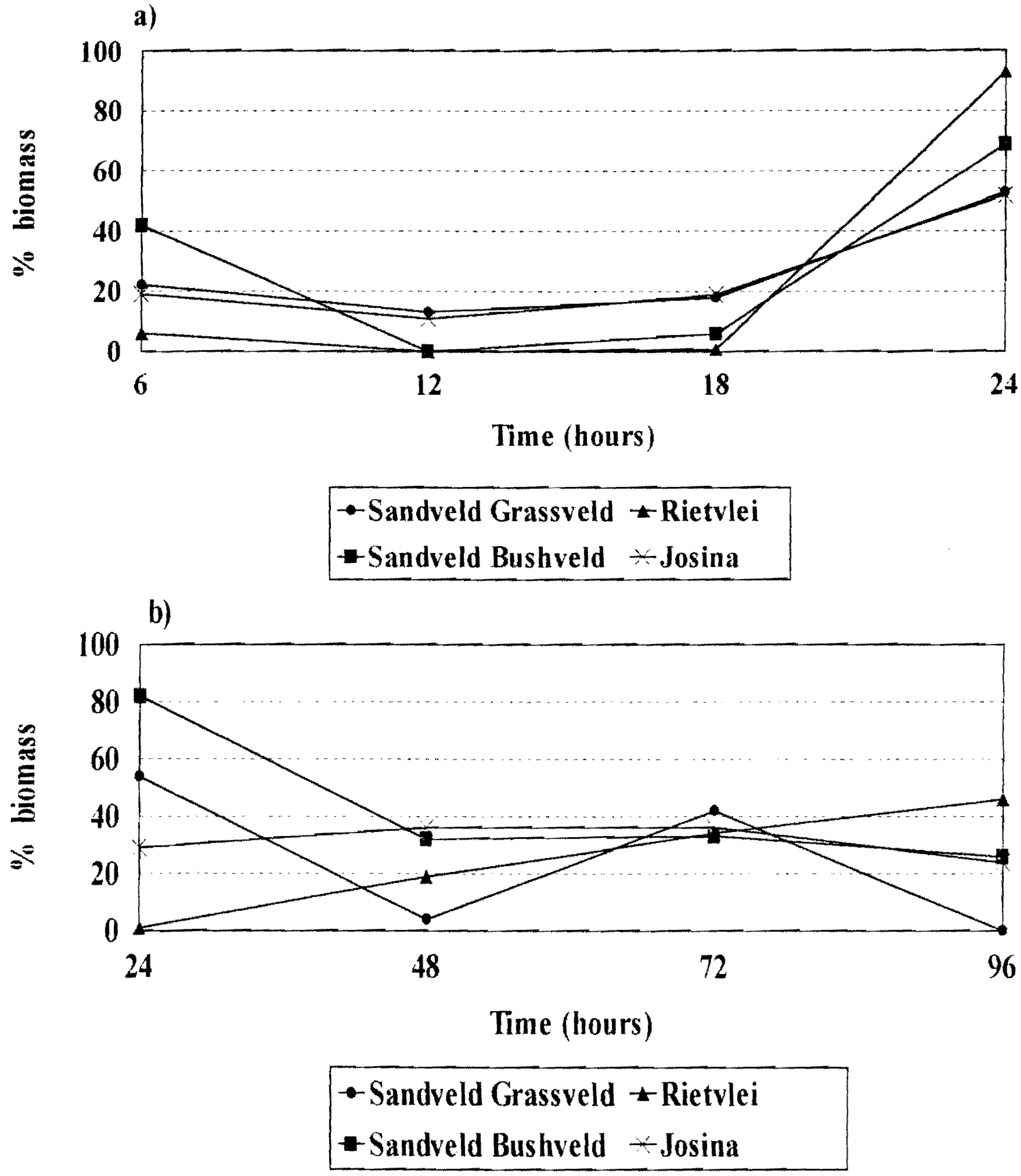


Fig. 6.8: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina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

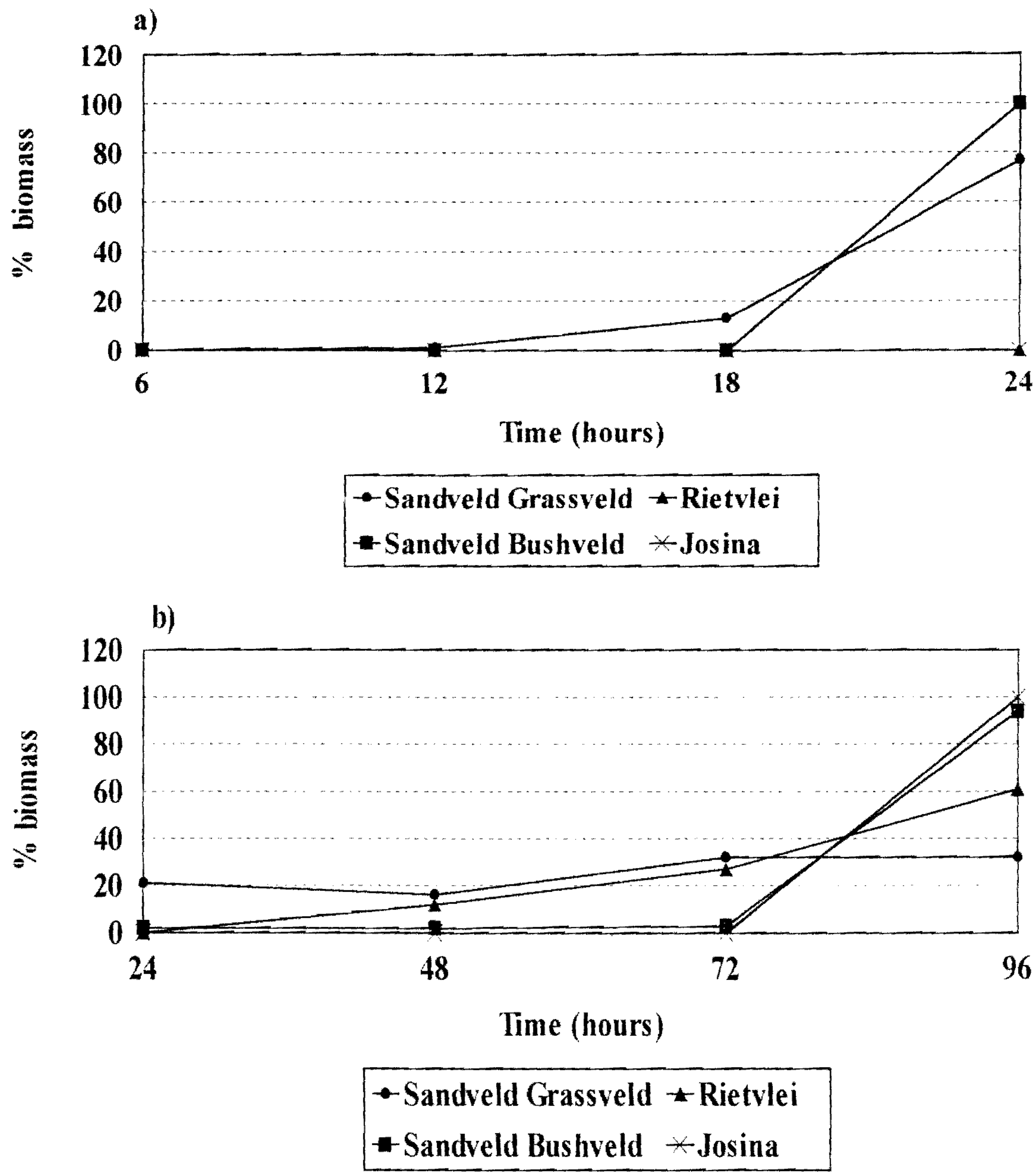
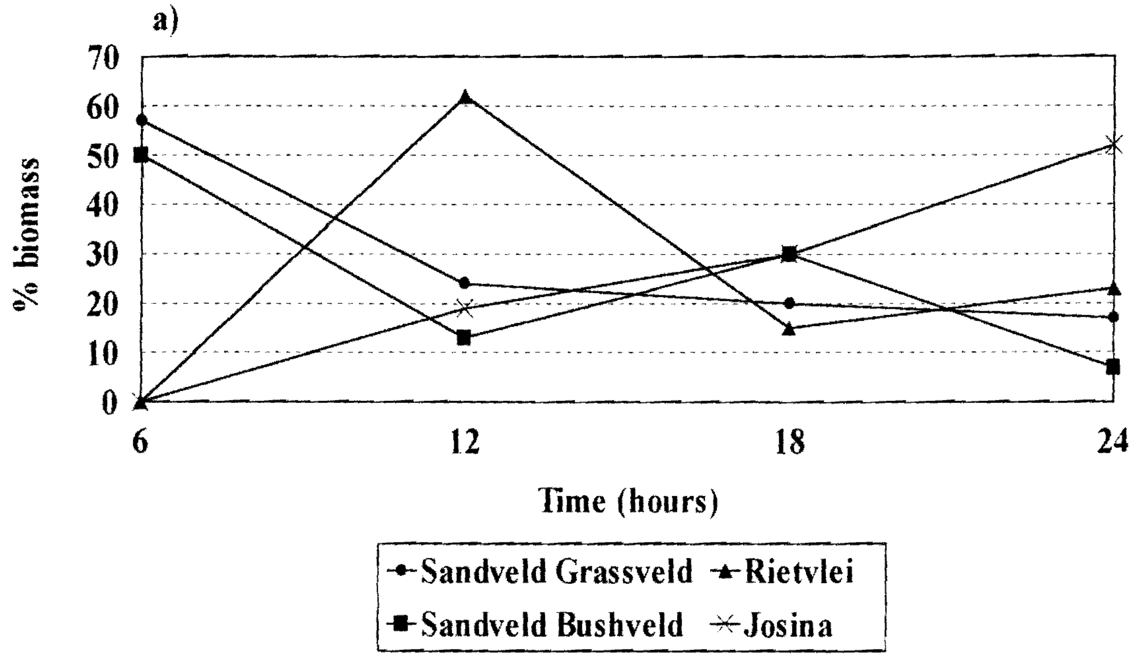


Fig. 6.9: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina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



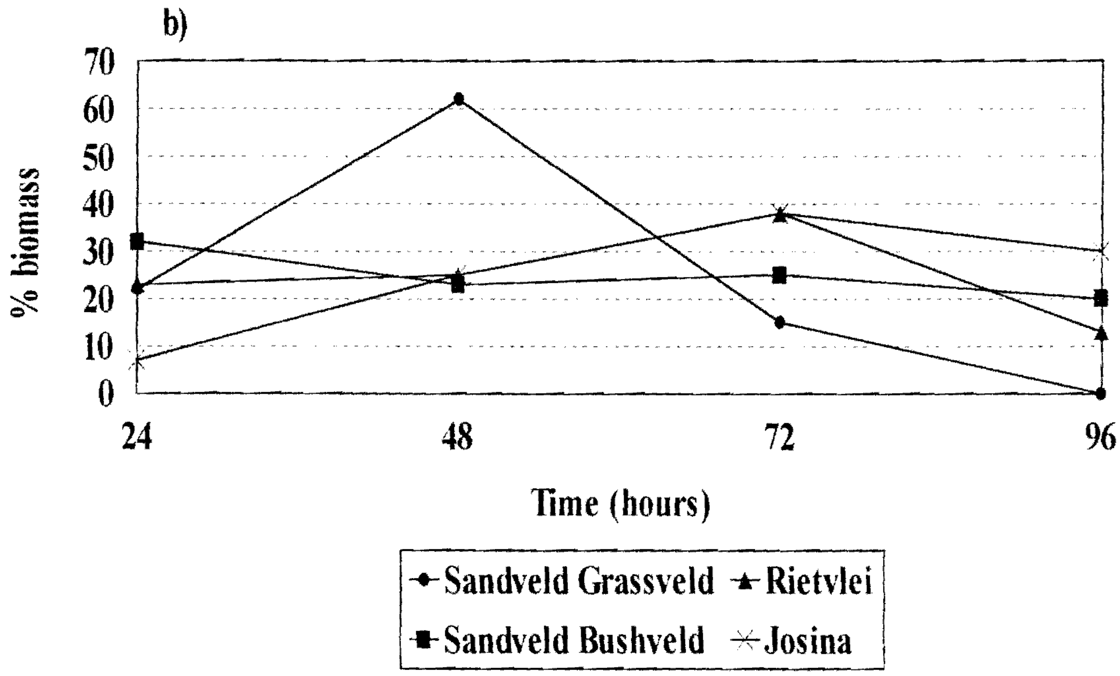


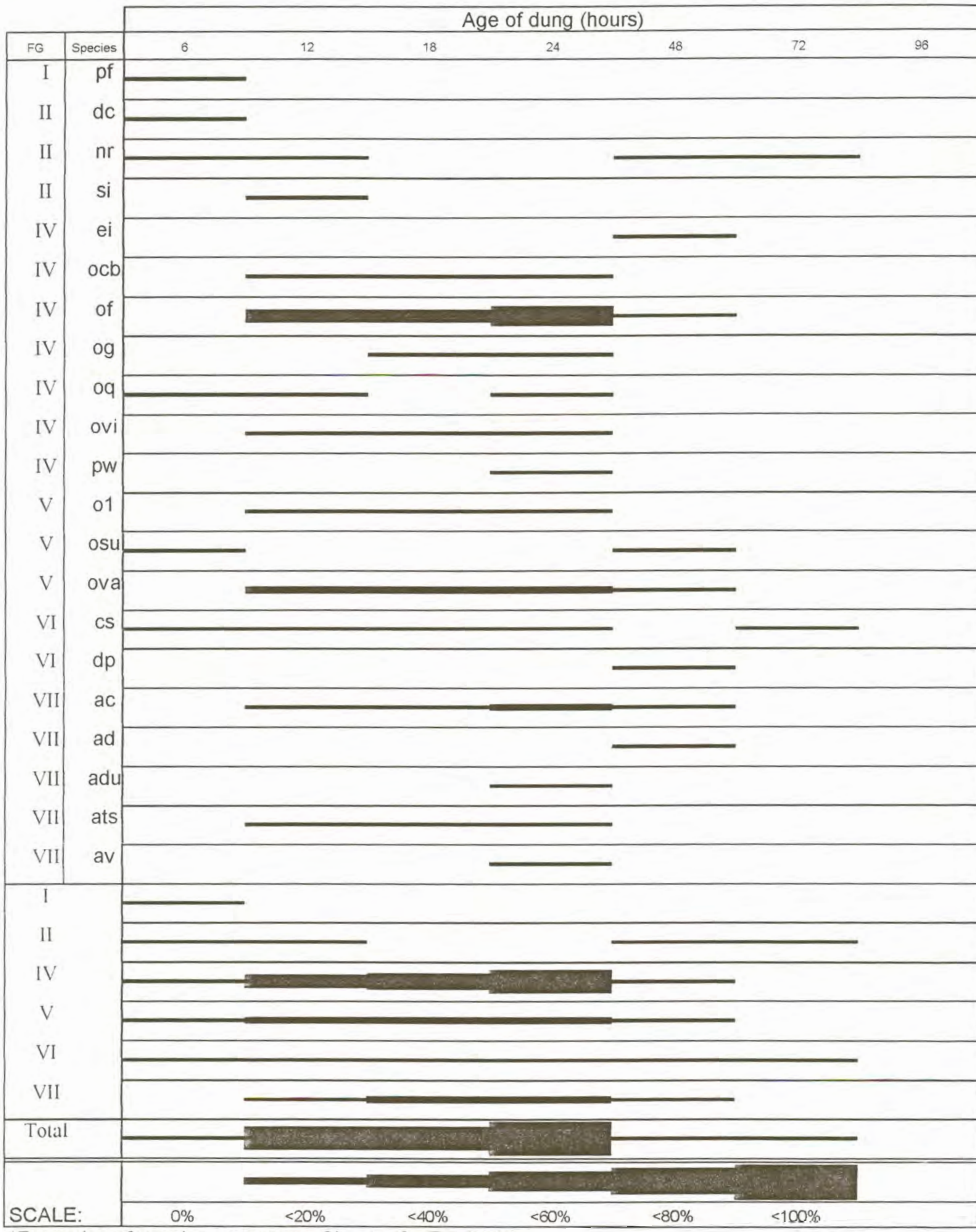
Fig. 6.10: Change in rate of dung pat colonisation by dung beetles based on biomass: a) during the first day and b) during the first four days of succession in four different habitats (Sandveld Grassveld – natural grassveld, Rietvlei – disturbed grassveld, Sandveld Bushveld – natural bushveld, Josina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

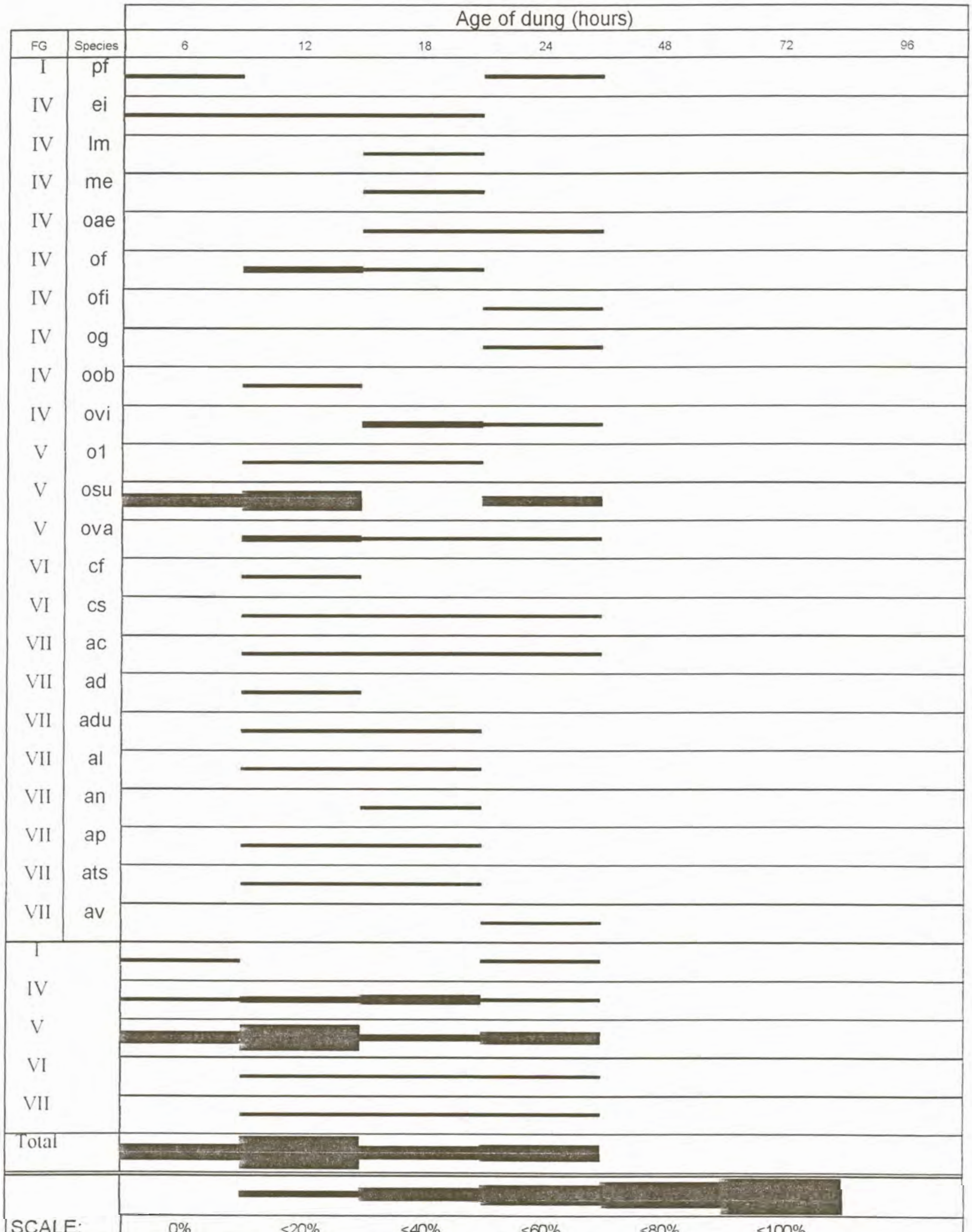
*For codes of species names see Chapter 2 - Table 2.4.

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).



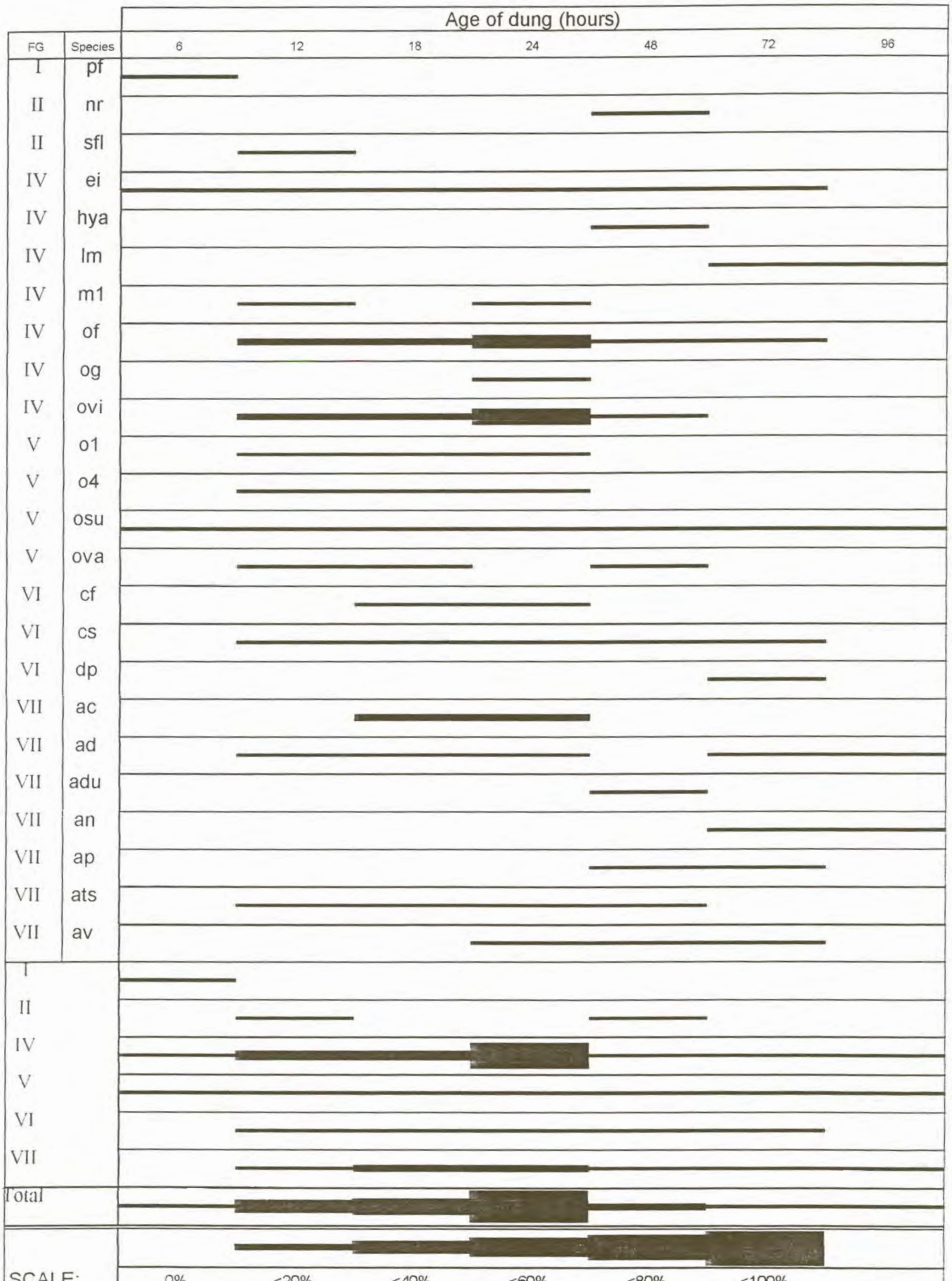
*For codes of species names see Chapter 2 - Table 2.4.

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).



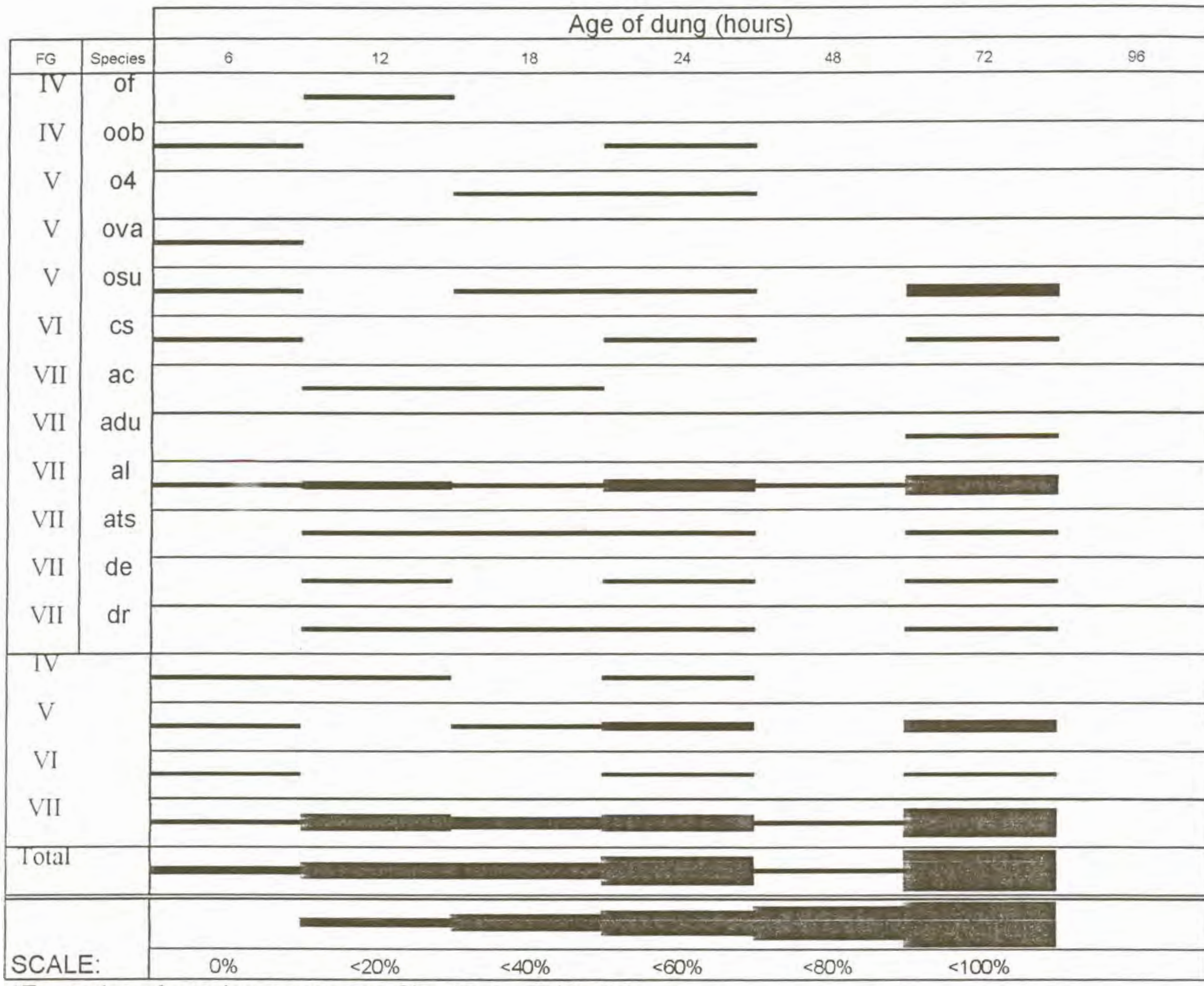
*For codes of species names see Chapter 2 - Table 2.4.

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).



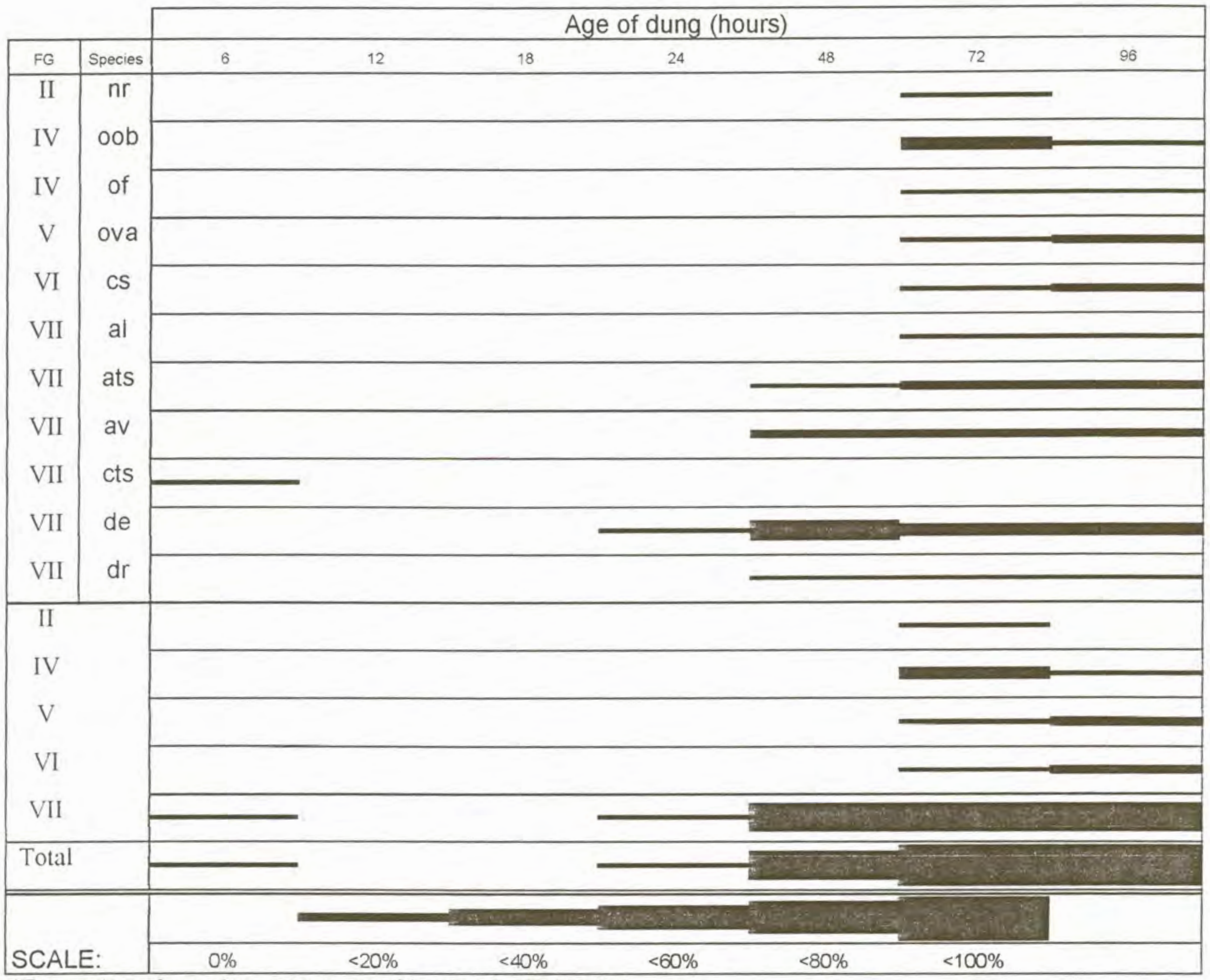
*For codes of species names see Chapter 2 - Table 2.4.

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).



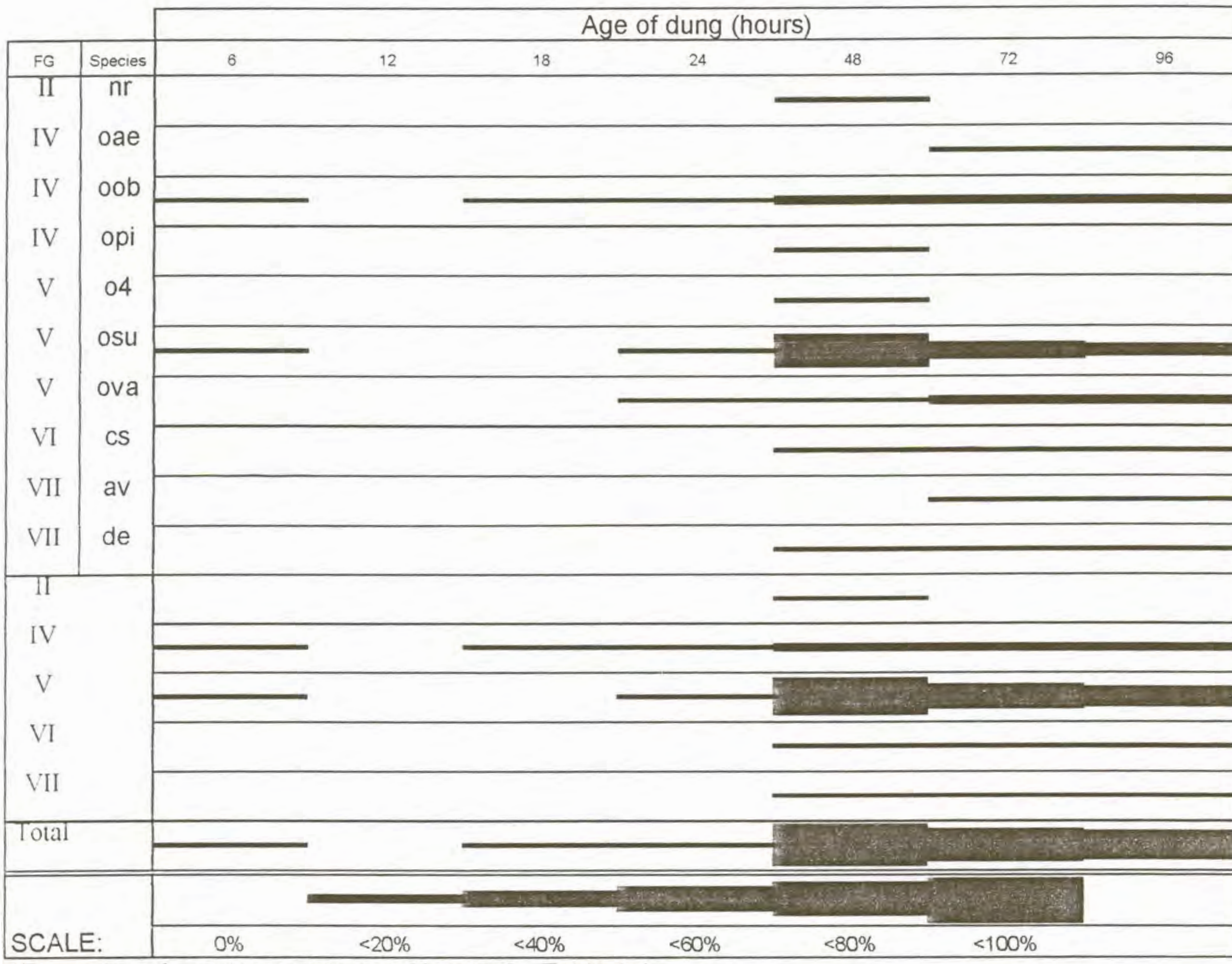
*For codes of species names see Chapter 2 - Table 2.4.

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).



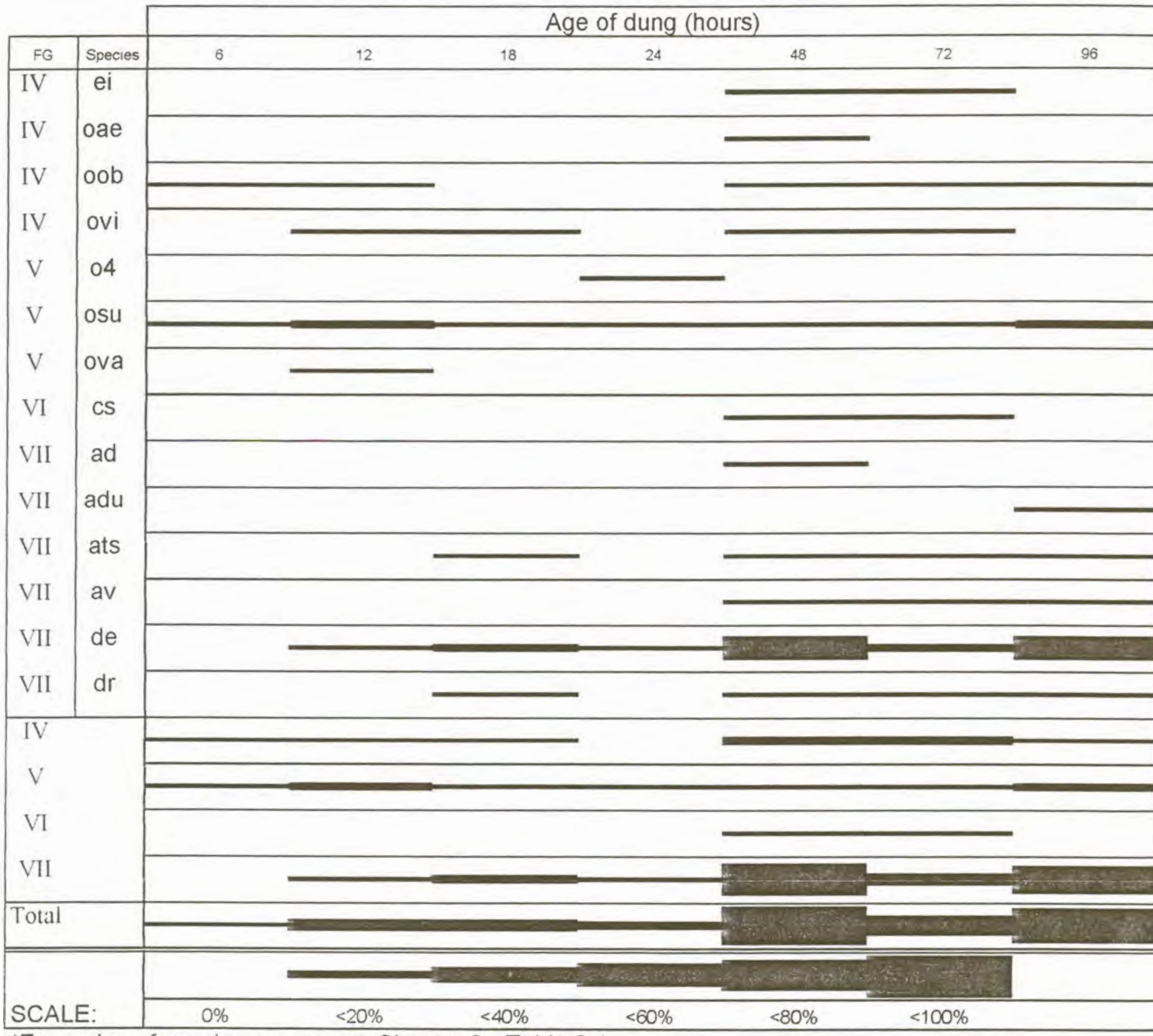
*For codes of species names see Chapter 2 - Table 2.4.

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).



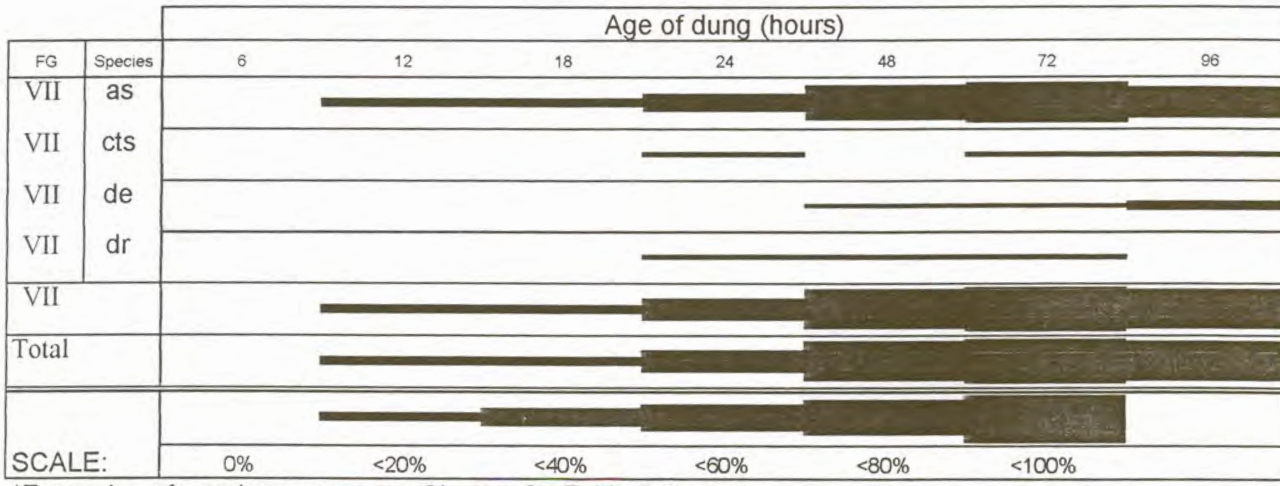
*For codes of species names see Chapter 2 - Table 2.4.

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).



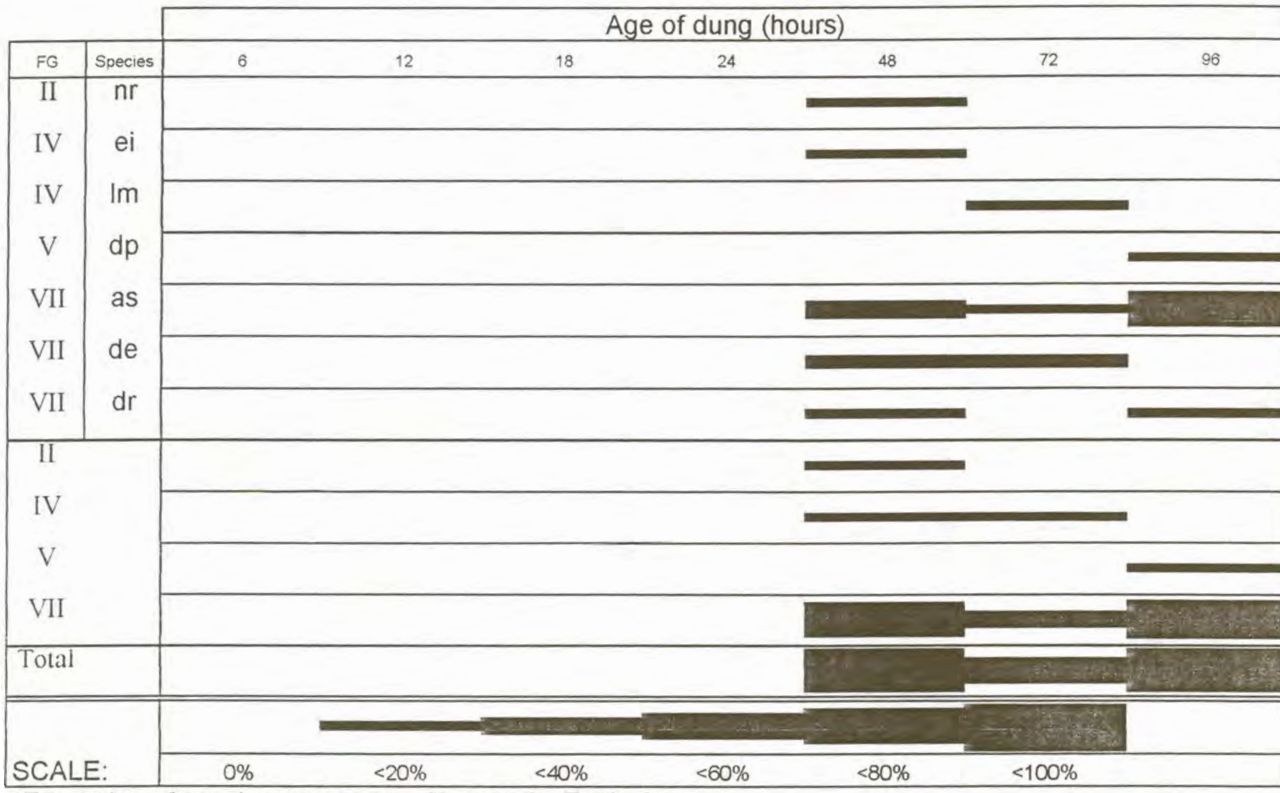
*For codes of species names see Chapter 2 - Table 2.4.

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).



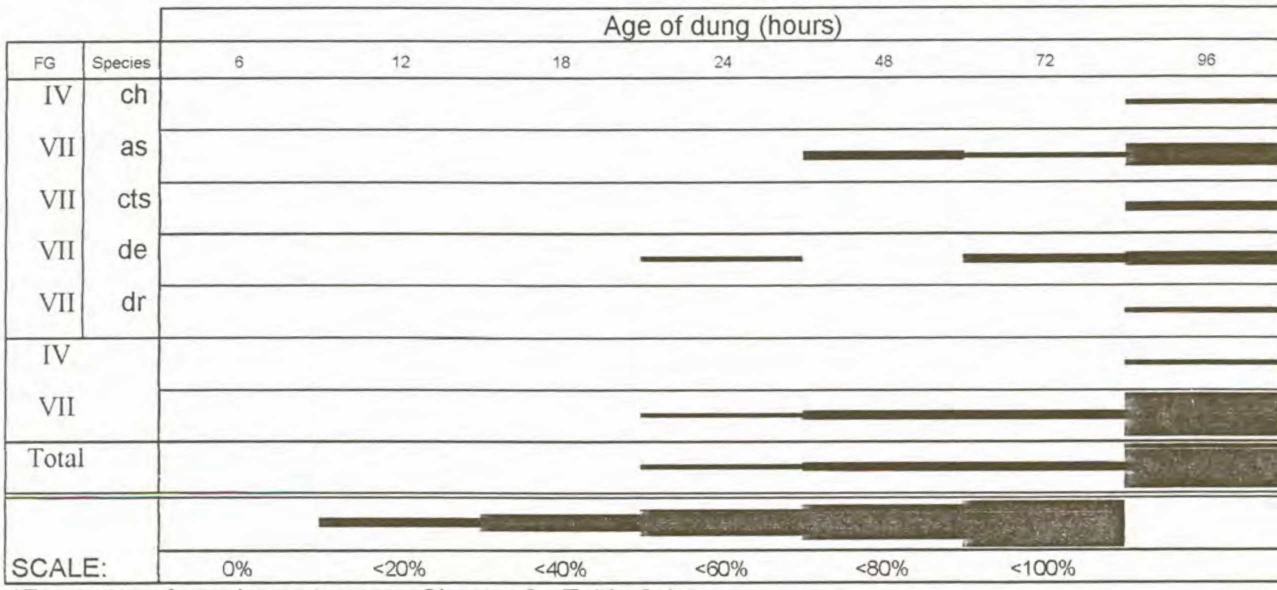
*For codes of species names see Chapter 2 - Table 2.4.

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).



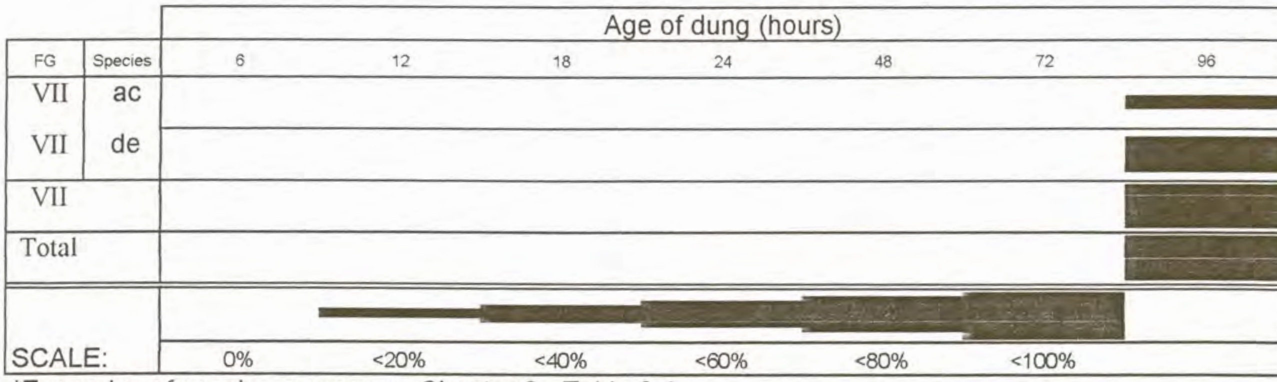
*For codes of species names see Chapter 2 - Table 2.4.

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).

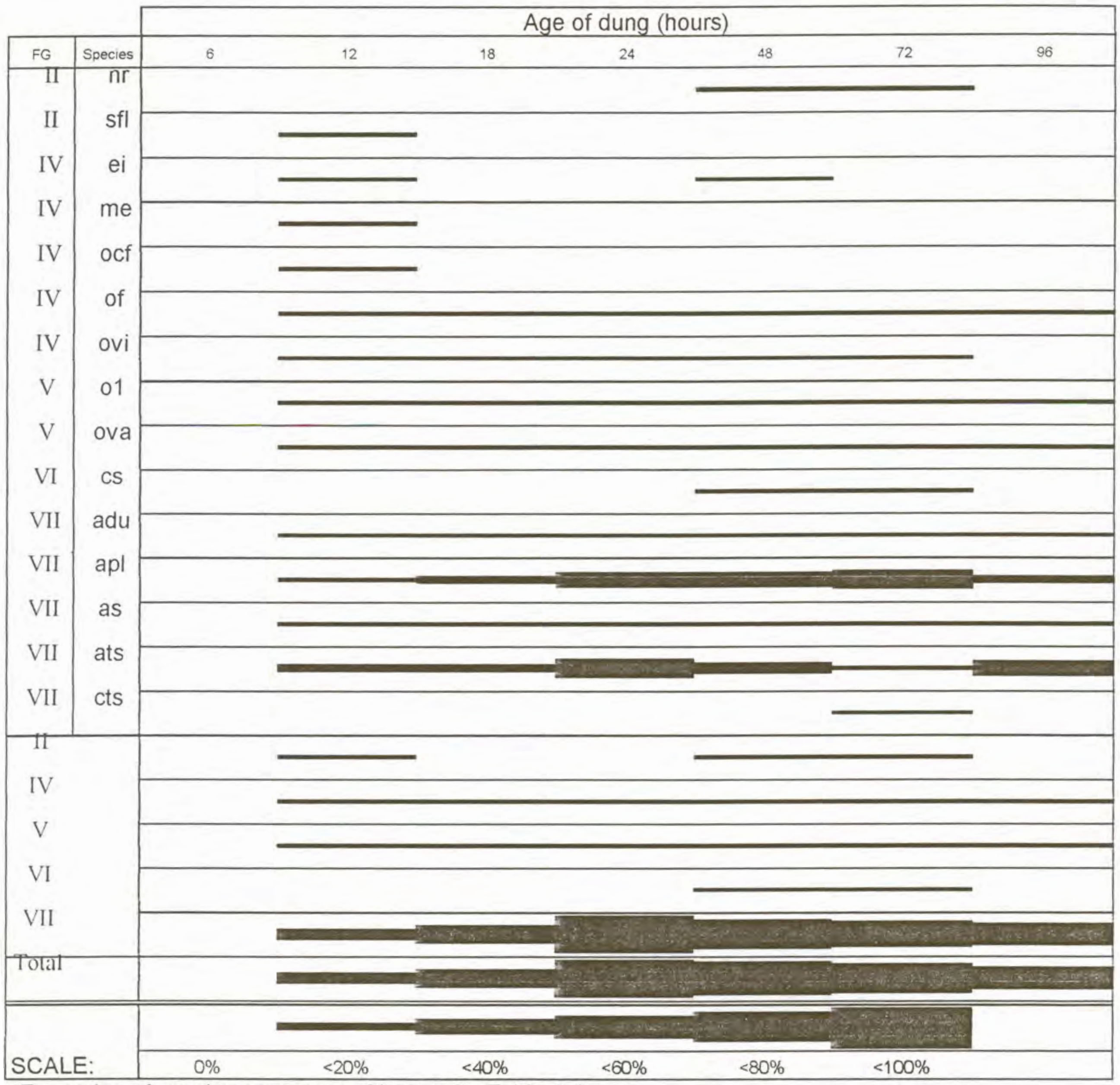


*For codes of species names see Chapter 2 - Table 2.4.

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).

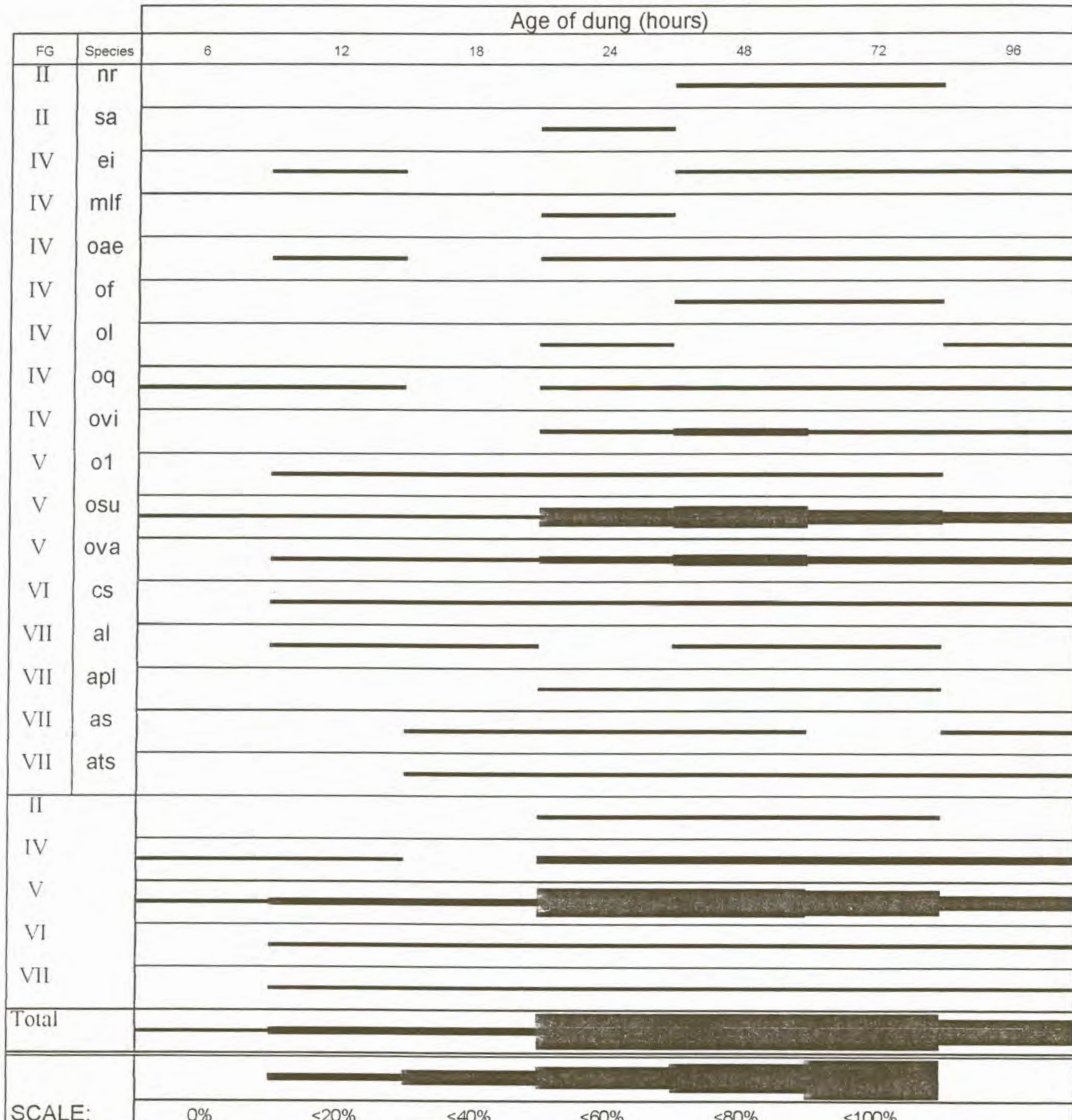
*For codes of species names see Chapter 2 - Table 2.4.

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).



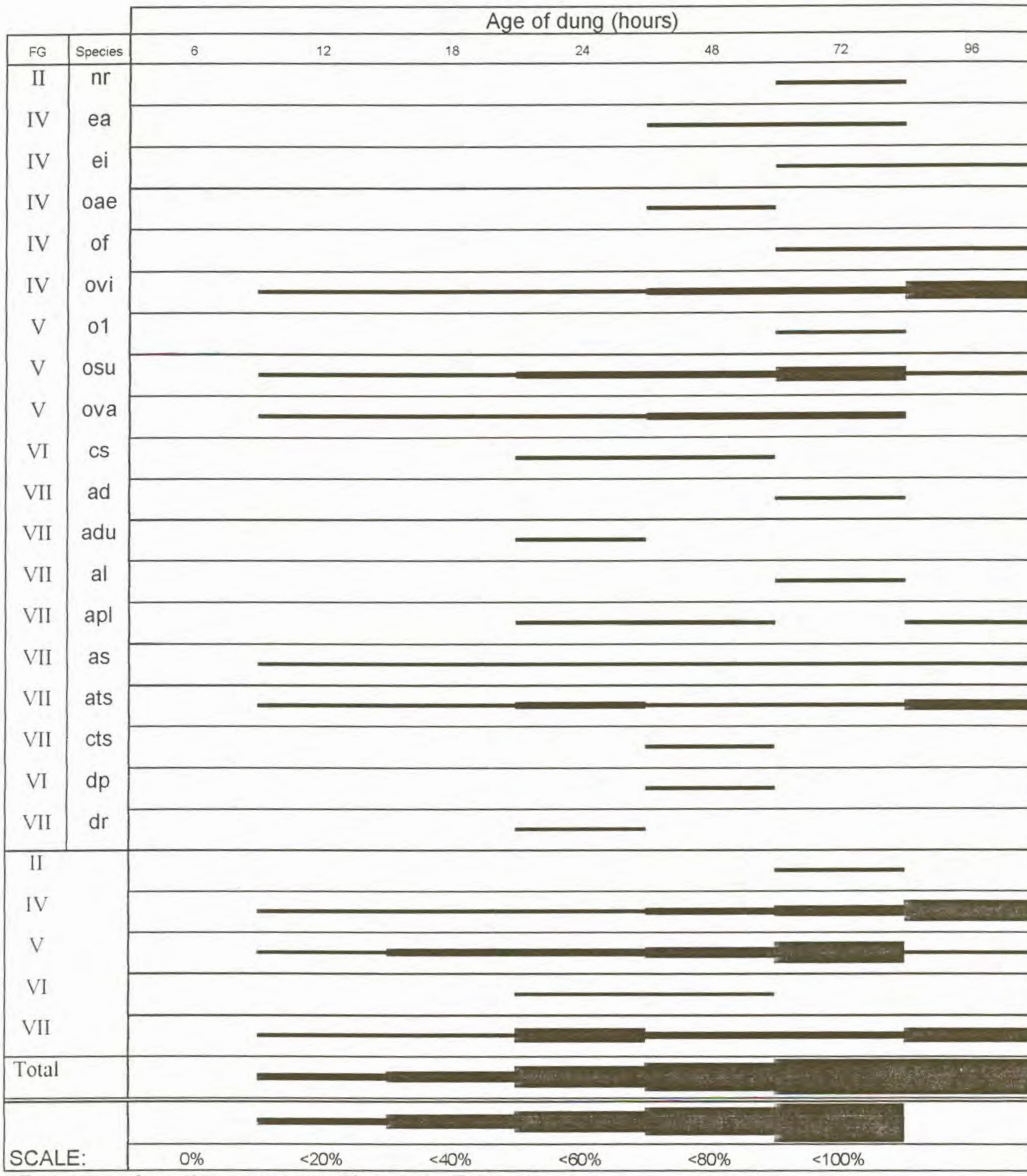
*For codes of species names see Chapter 2 - Table 2.4.

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).