UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

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

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

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

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

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.

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

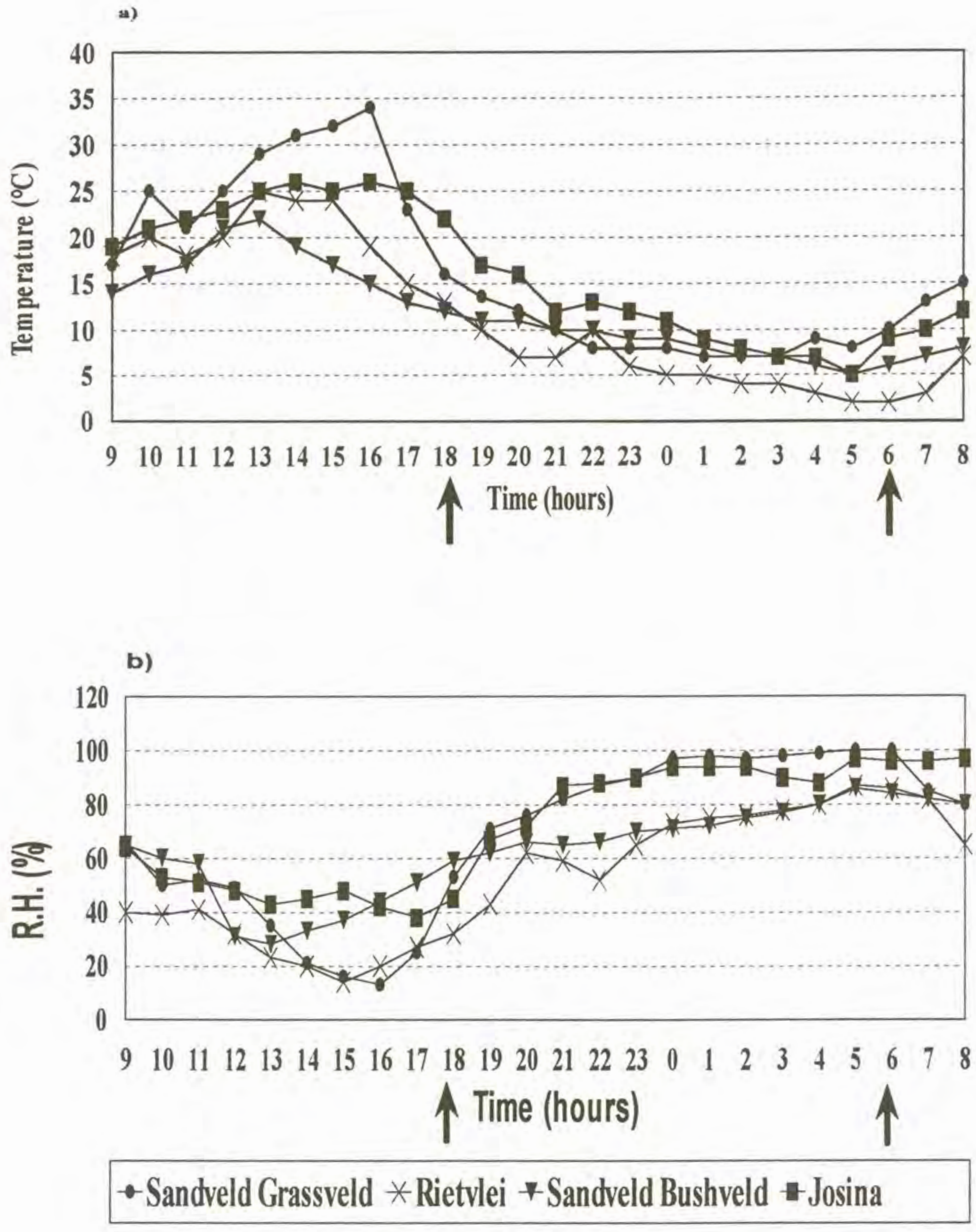


Fig. 5.1: Changes in ground temperature (°C) (a) and relative air humidity (%) (b) over a 24-hour period during autumn (April 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

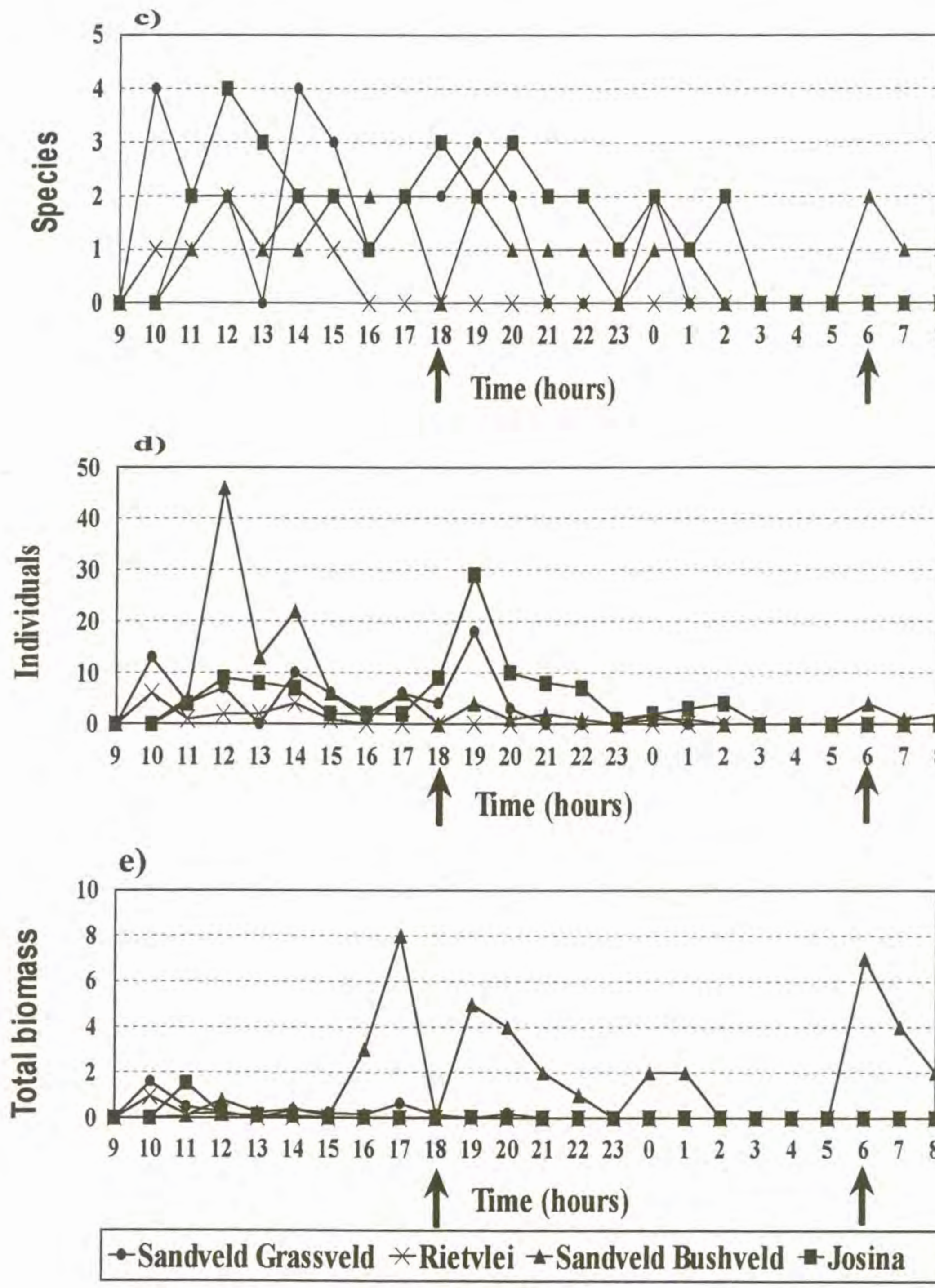


Fig. 5.1. Continued: Changes in species richness (c), number of individuals (d) and biomass (g) (e) of dung beetle assemblages over a 24-hour period during autumn (April 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

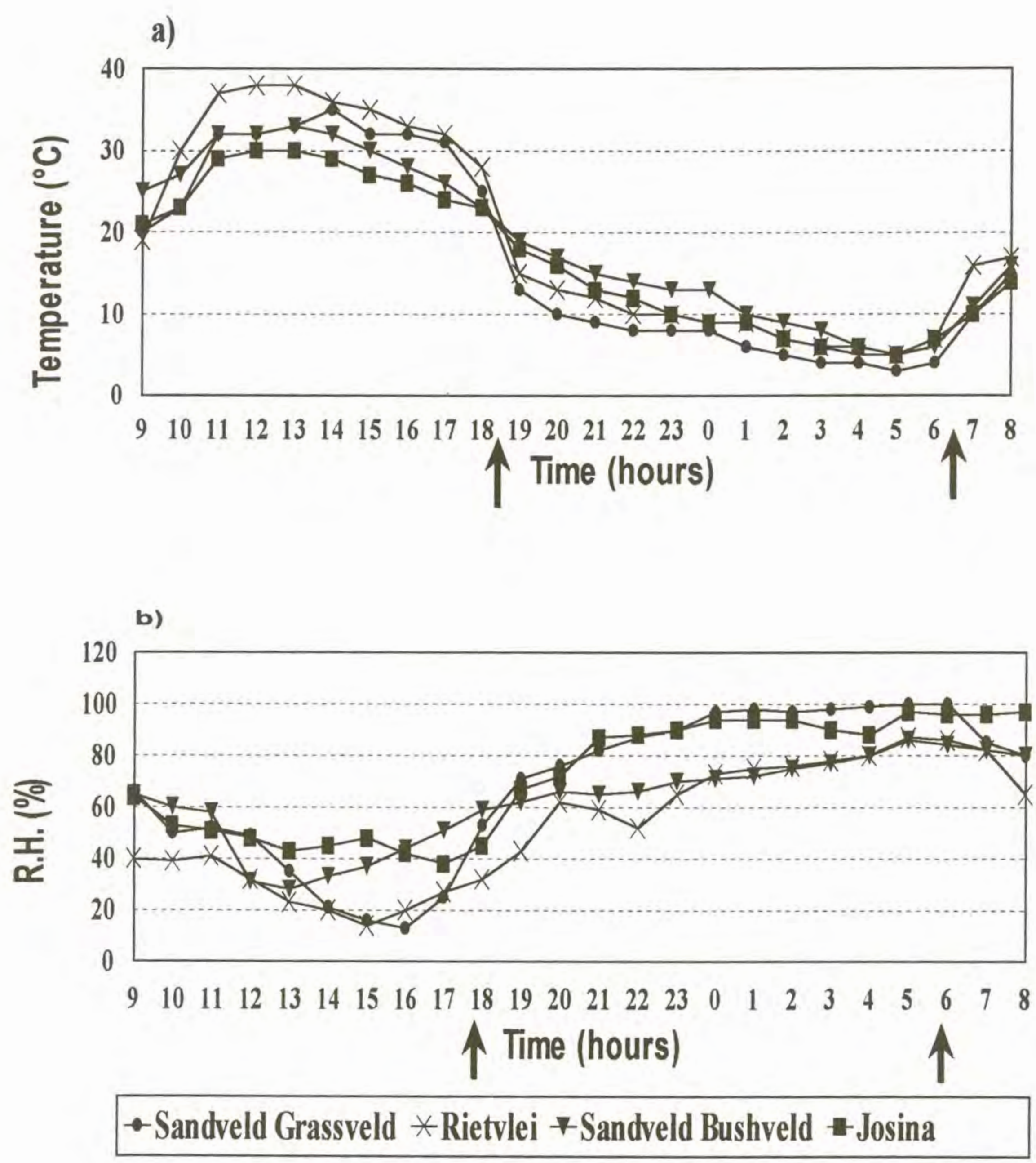


Fig. 5.2: Changes in ground temperature (°C) (a) and relative air humidity (%) (b) over a 24-hour period during spring (September 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

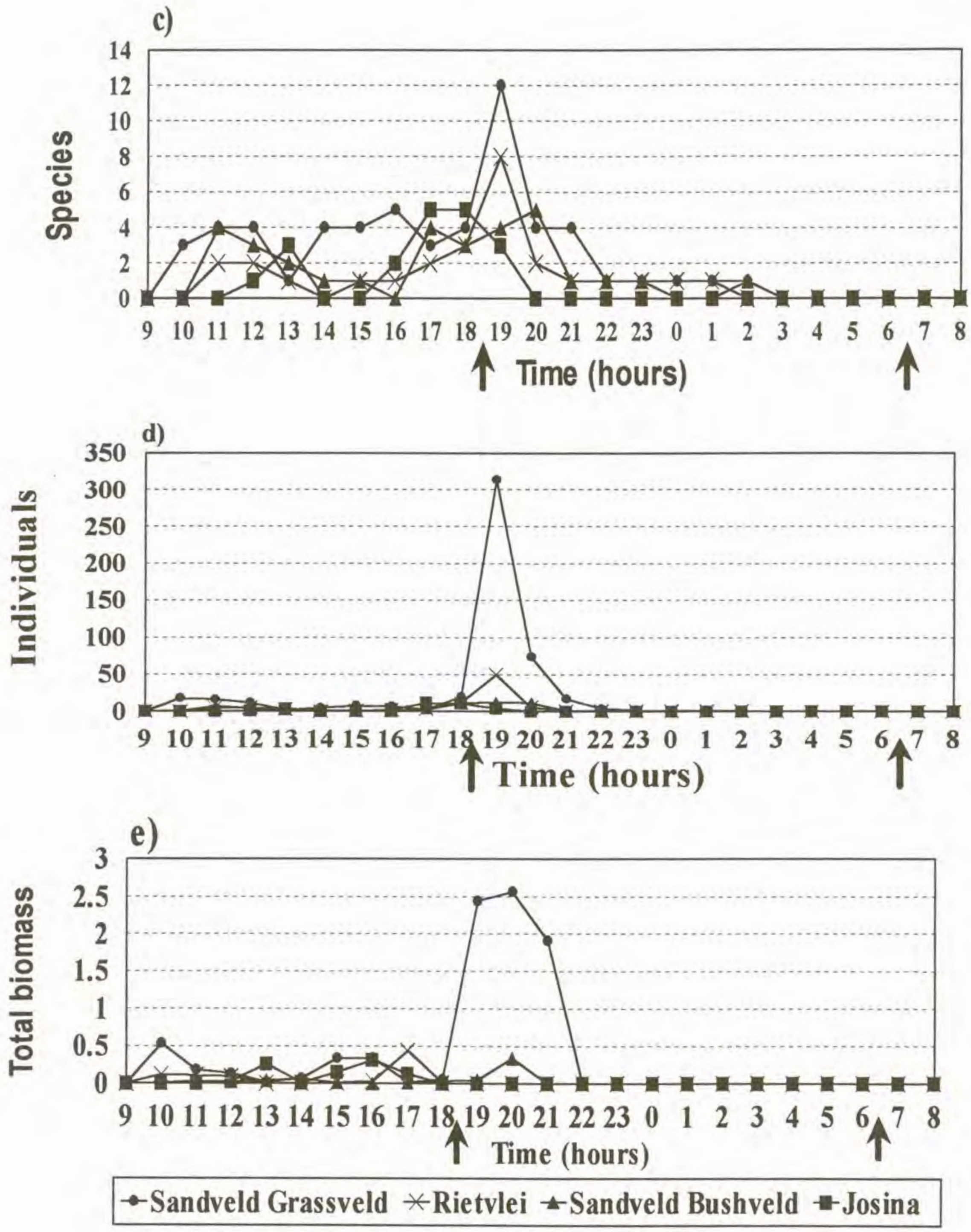


Fig. 5.2. Continued: Changes in species richness (c), number of individuals (d) and biomass (g) (e) of dung beetle assemblages over a 24-hour period during spring (September 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

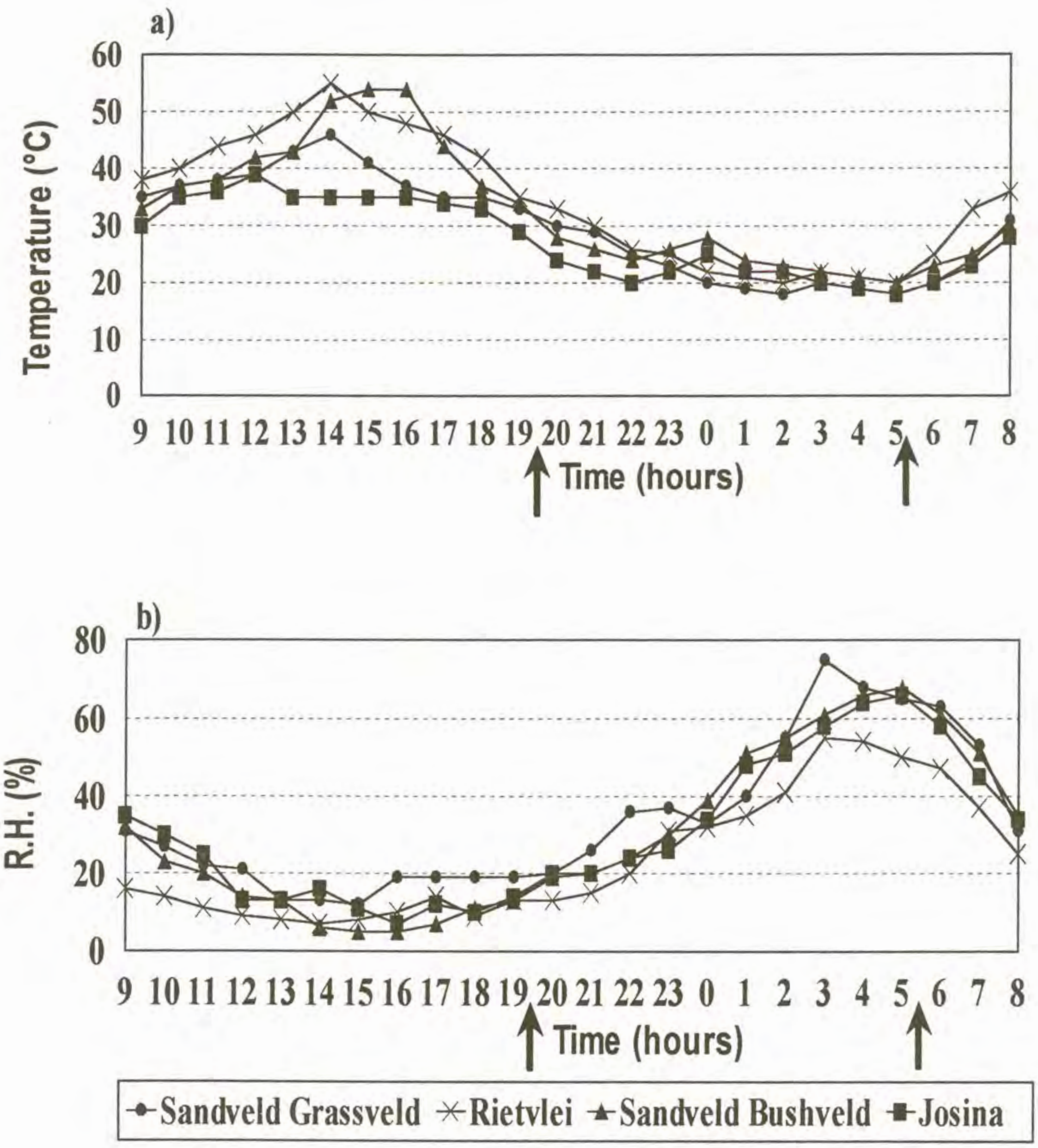


Fig. 5.3: Changes in ground temperature (°C) (a) and relative air humidity (%) (b) over a 24-hour period during summer (December 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

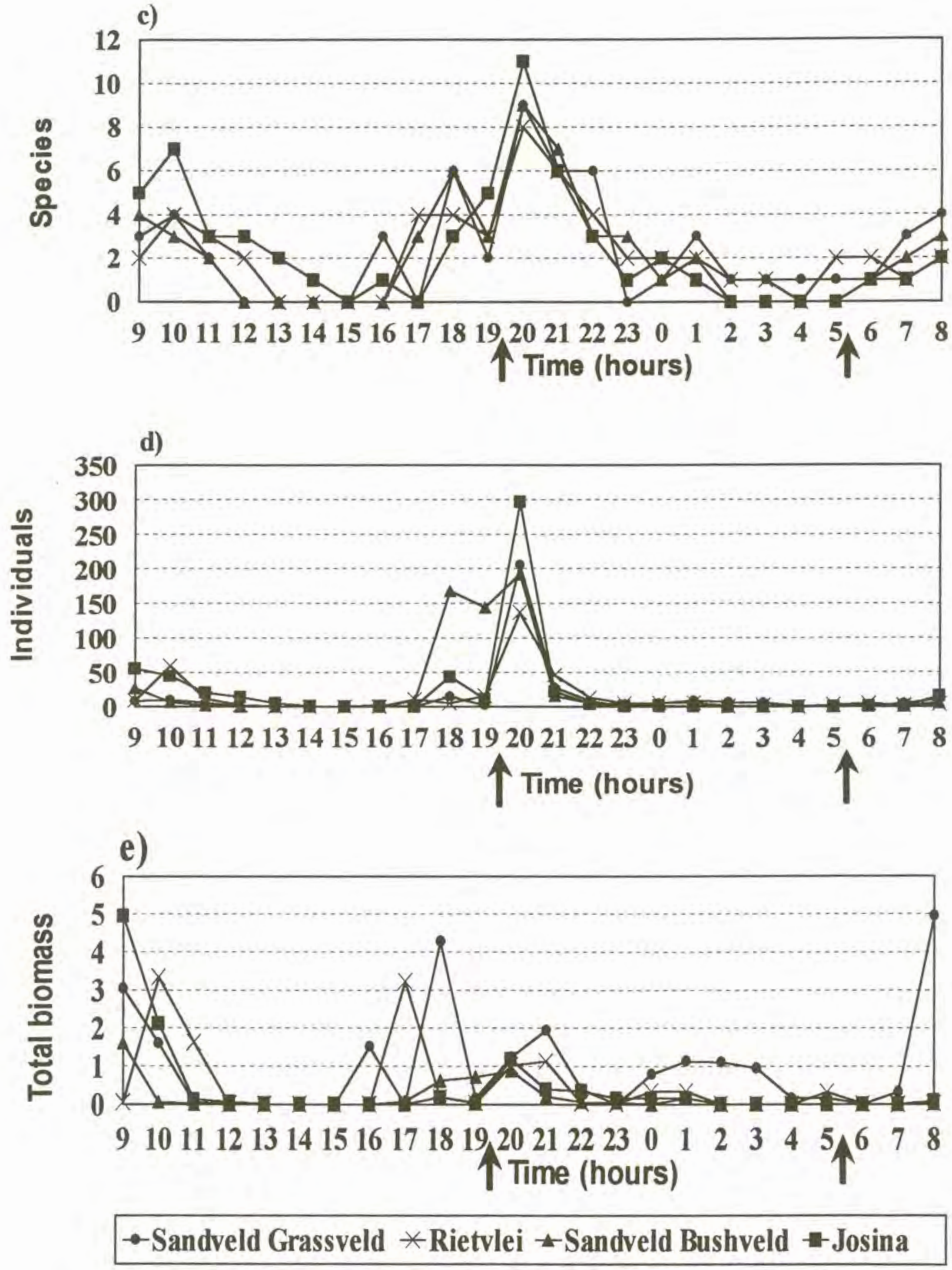


Fig. 5.3. Continued: Changes in species richness (c), number of individuals (d) and biomass (g) (e) of dung beetle assemblages over a 24-hour period during summer (December 1997) in four different habitats (see text for details). Sunrise and sunset indicated by arrows.

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

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

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

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

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

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

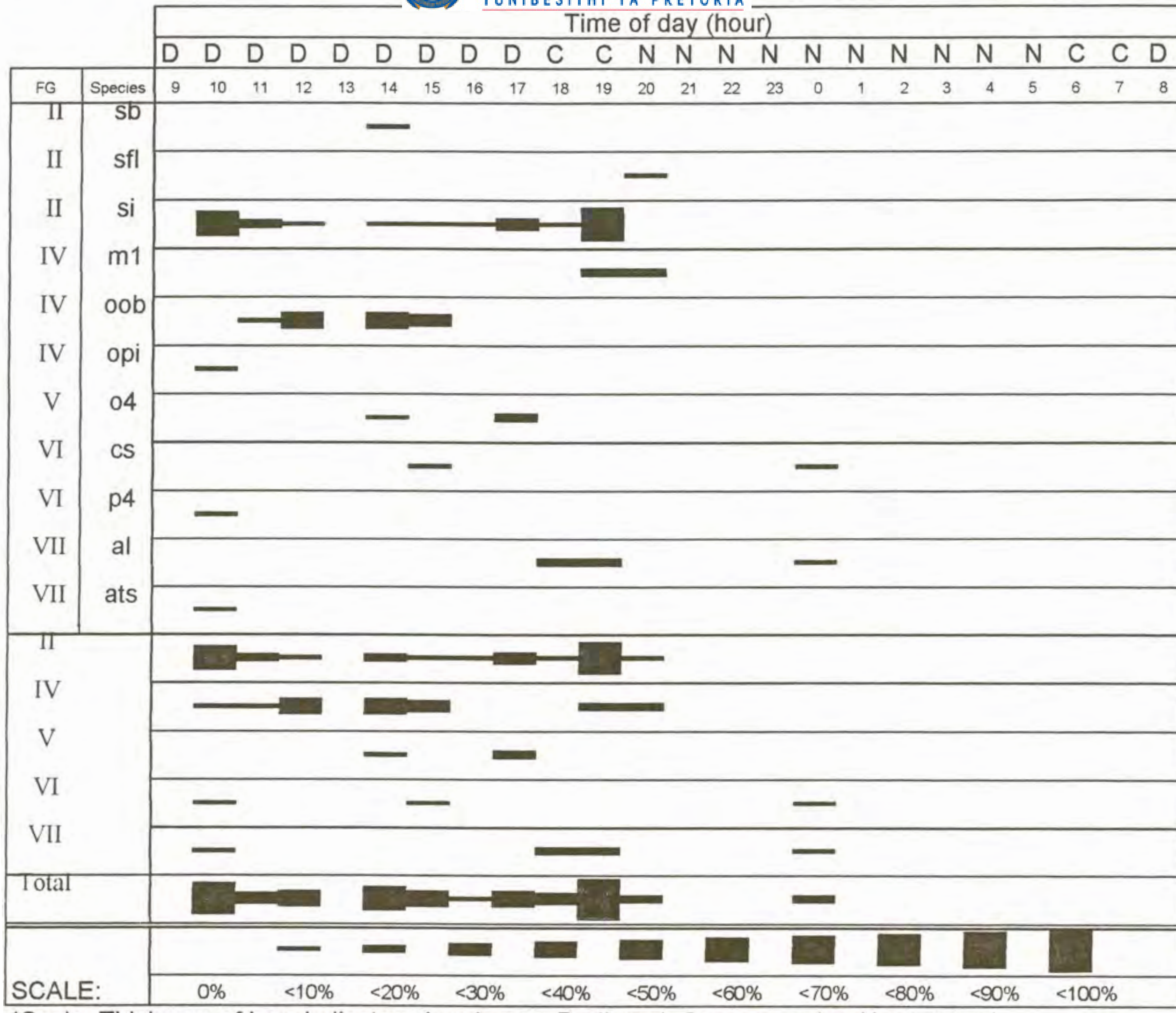
bushveld habitat, desiccation rates were probably slower and smaller dung beetle species could be active for longer periods. More intense competition in the natural grassveld habitat may explain the difference in this habitat and the disturbed grassveld habitat. In the natural grassveld habitat larger 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

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

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.

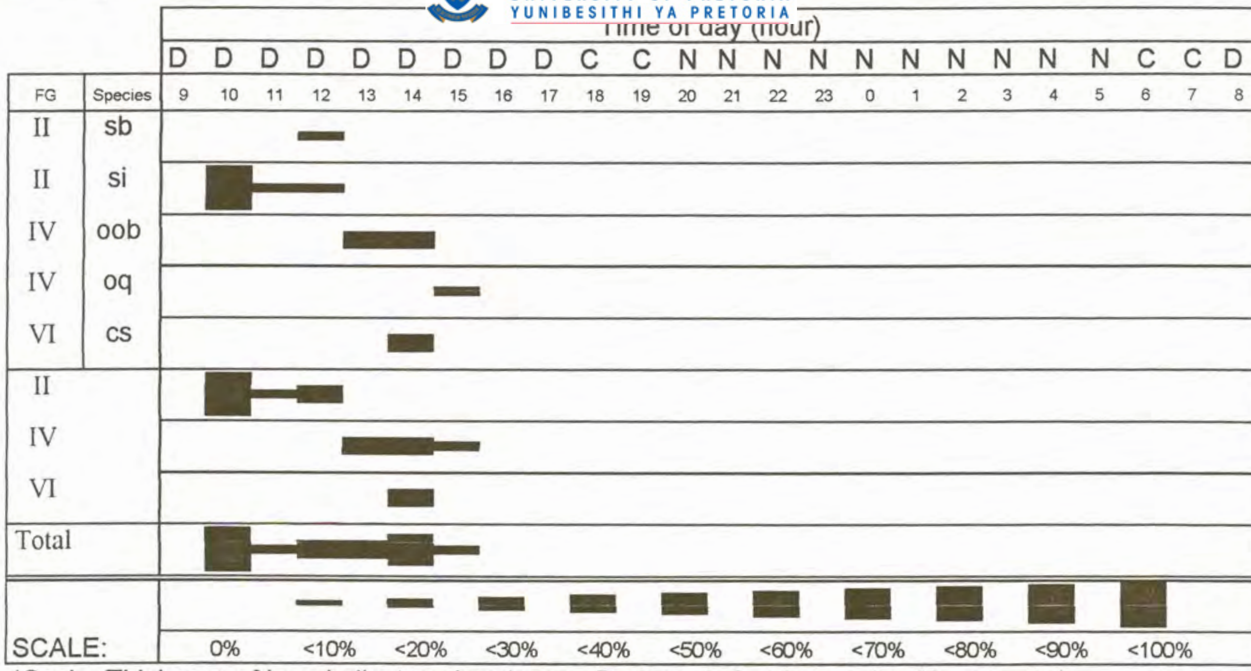
According to Romoser (1981) several diurnal insect species, which display midday activity peaks under cool conditions, shift these activity peaks to early morning or evening in hot weather as a mechanism of ectothermic regulation. Dung beetles in the present study also showed these mechanisms to avoid 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.

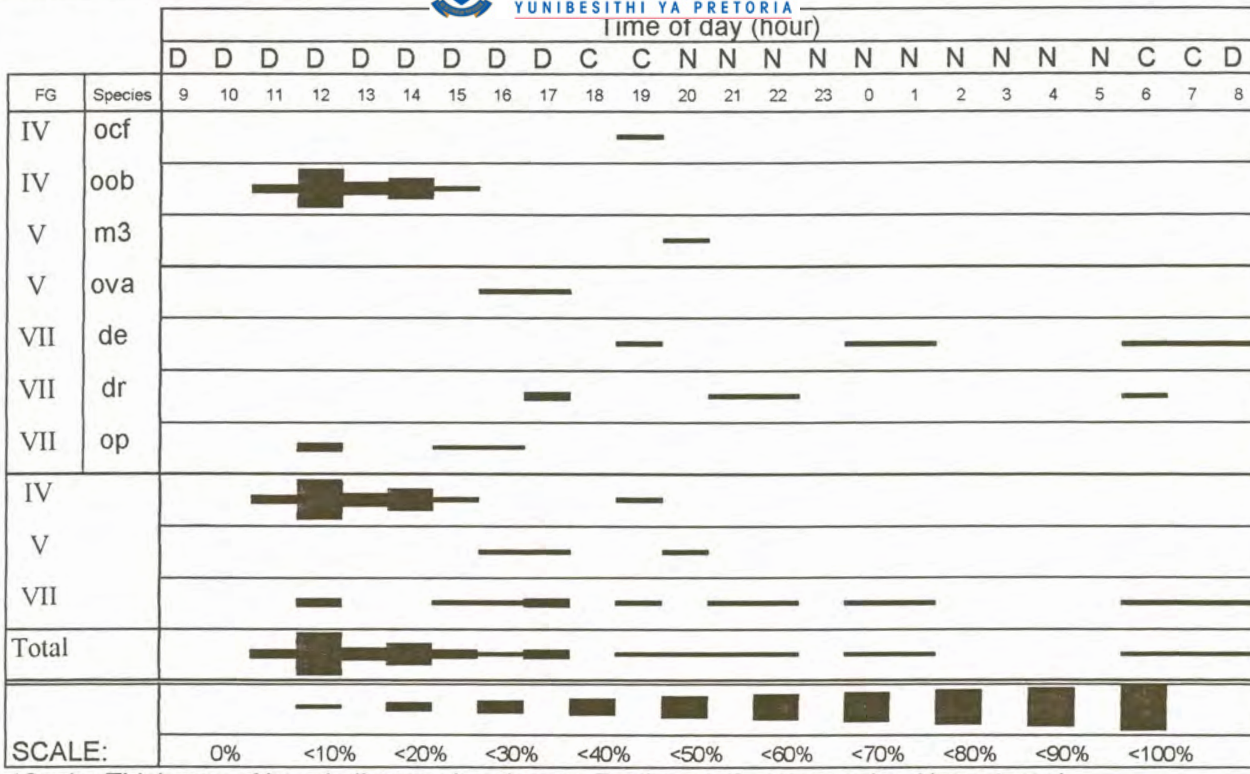
Fig. 5.4. Diel flight activity of different dung beetle species and functional groups over a 24-hour period during autumn (April 1997): a) Sandveld grassveld (natural grassveld habitat).



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

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

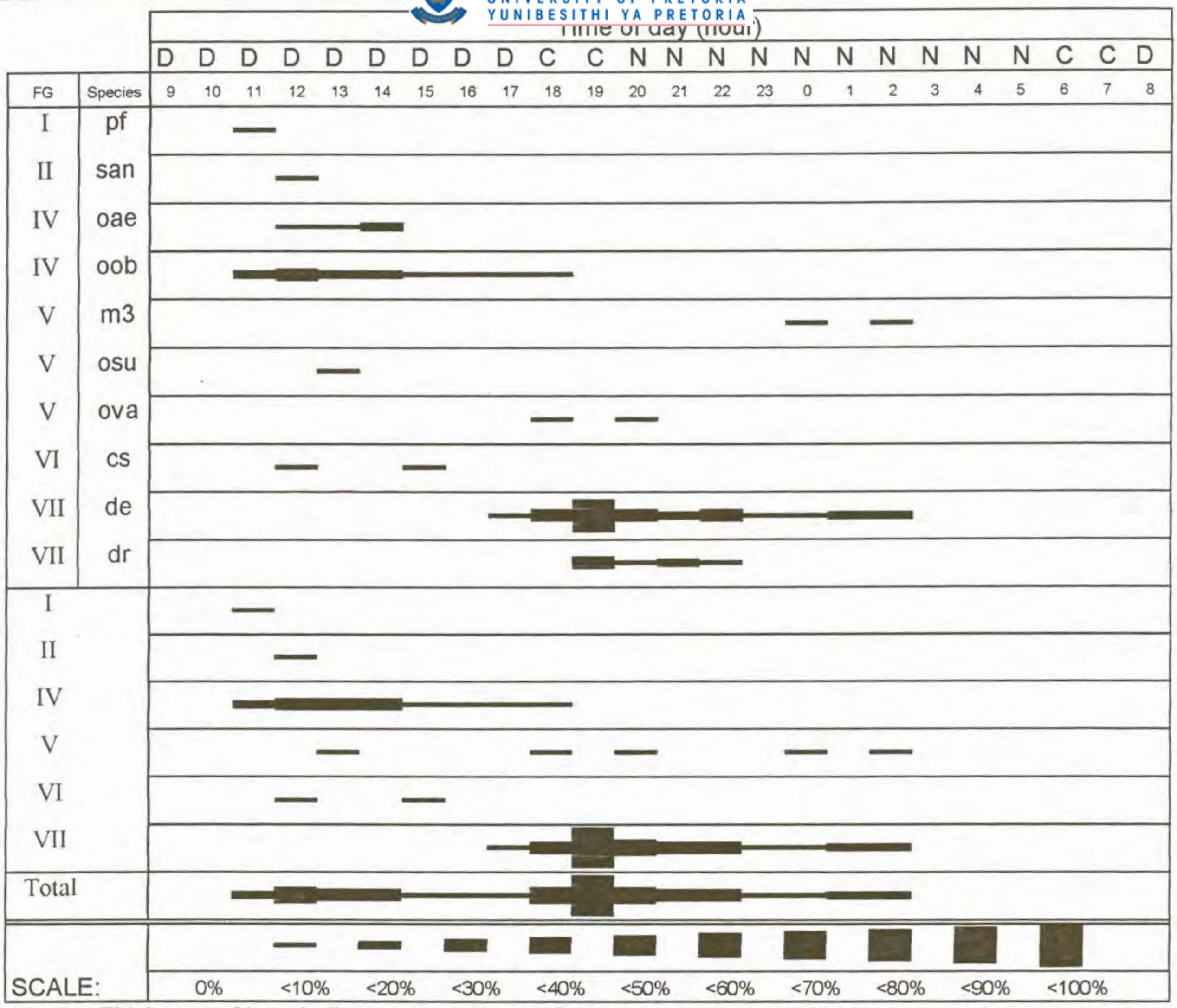
Fig. 5.4. Continued: Diel flight activity of different dung beetle species and functional groups over a 24-hour period during autumn (April 1997): b) Rietvlei (disturbed grassveld habitat).



*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).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

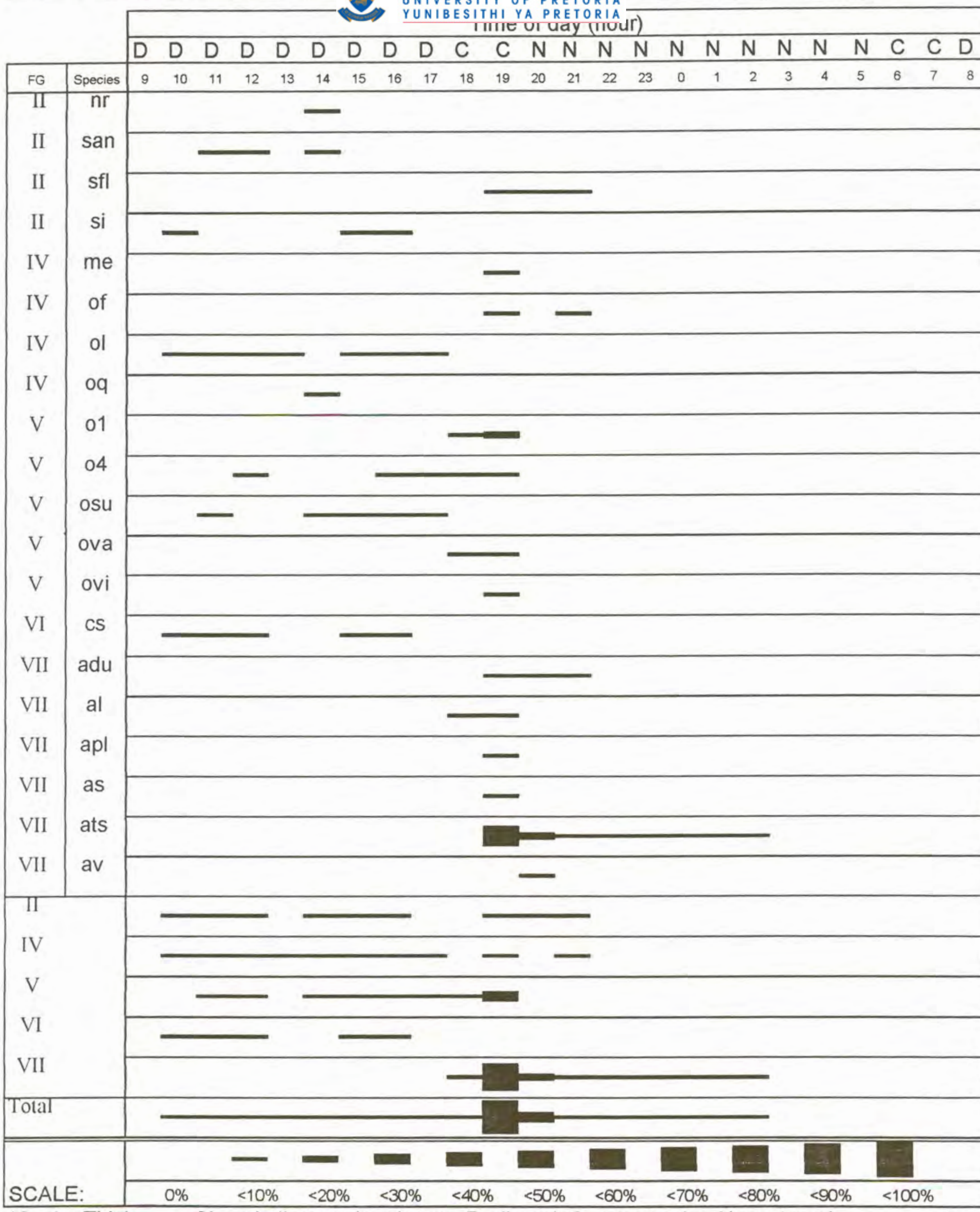


*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

*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).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

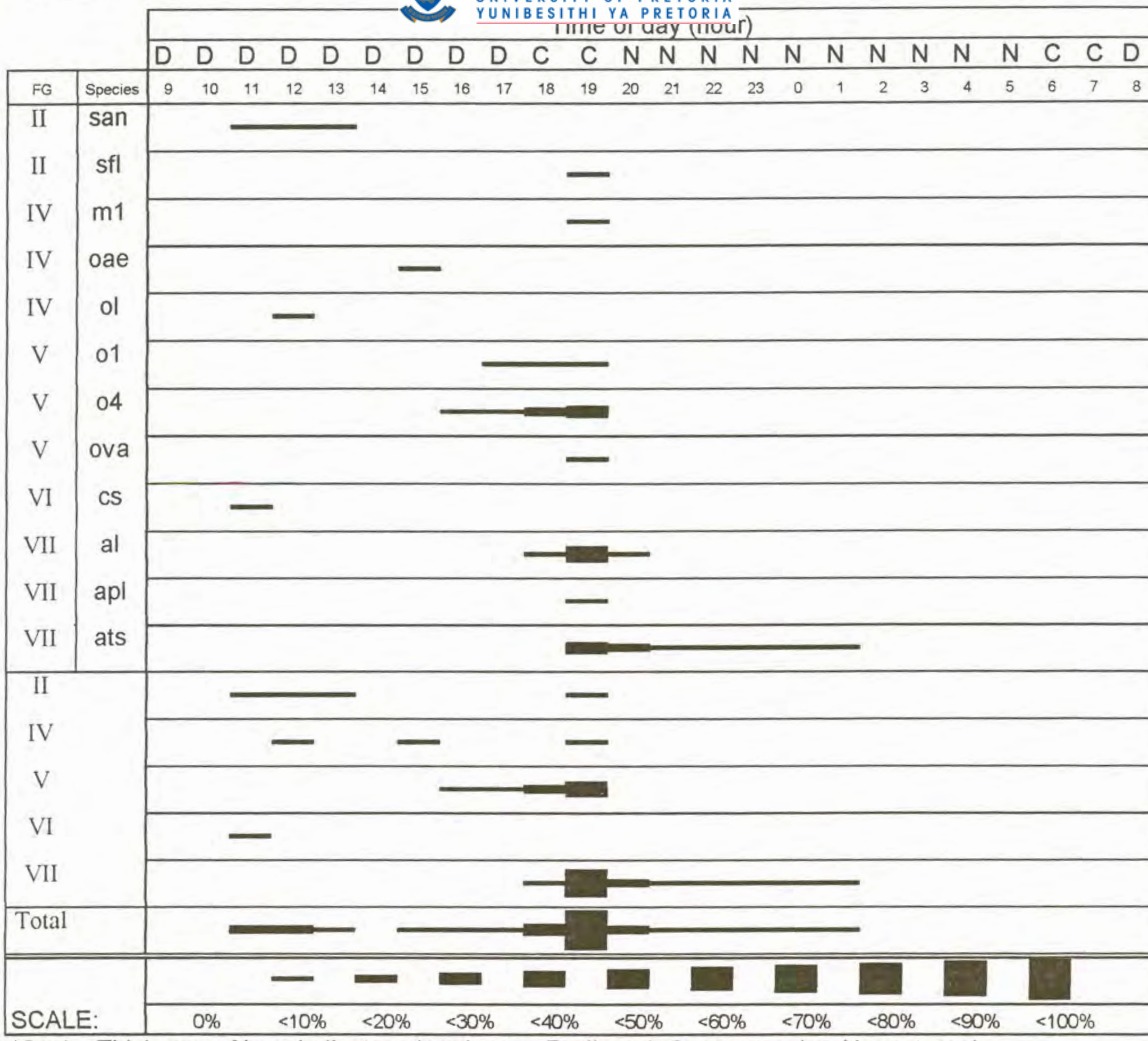


*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

*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).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

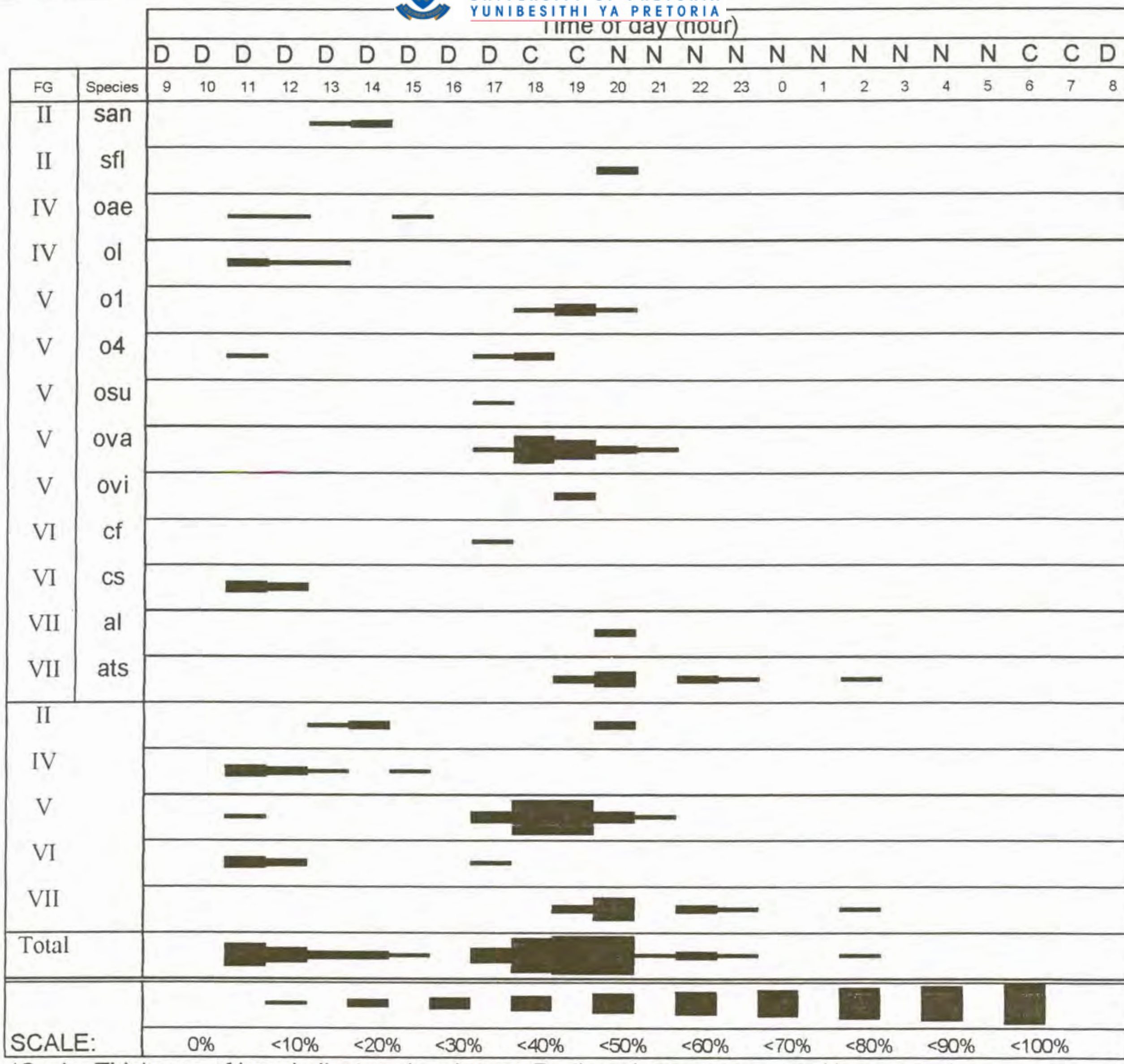


*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

*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).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

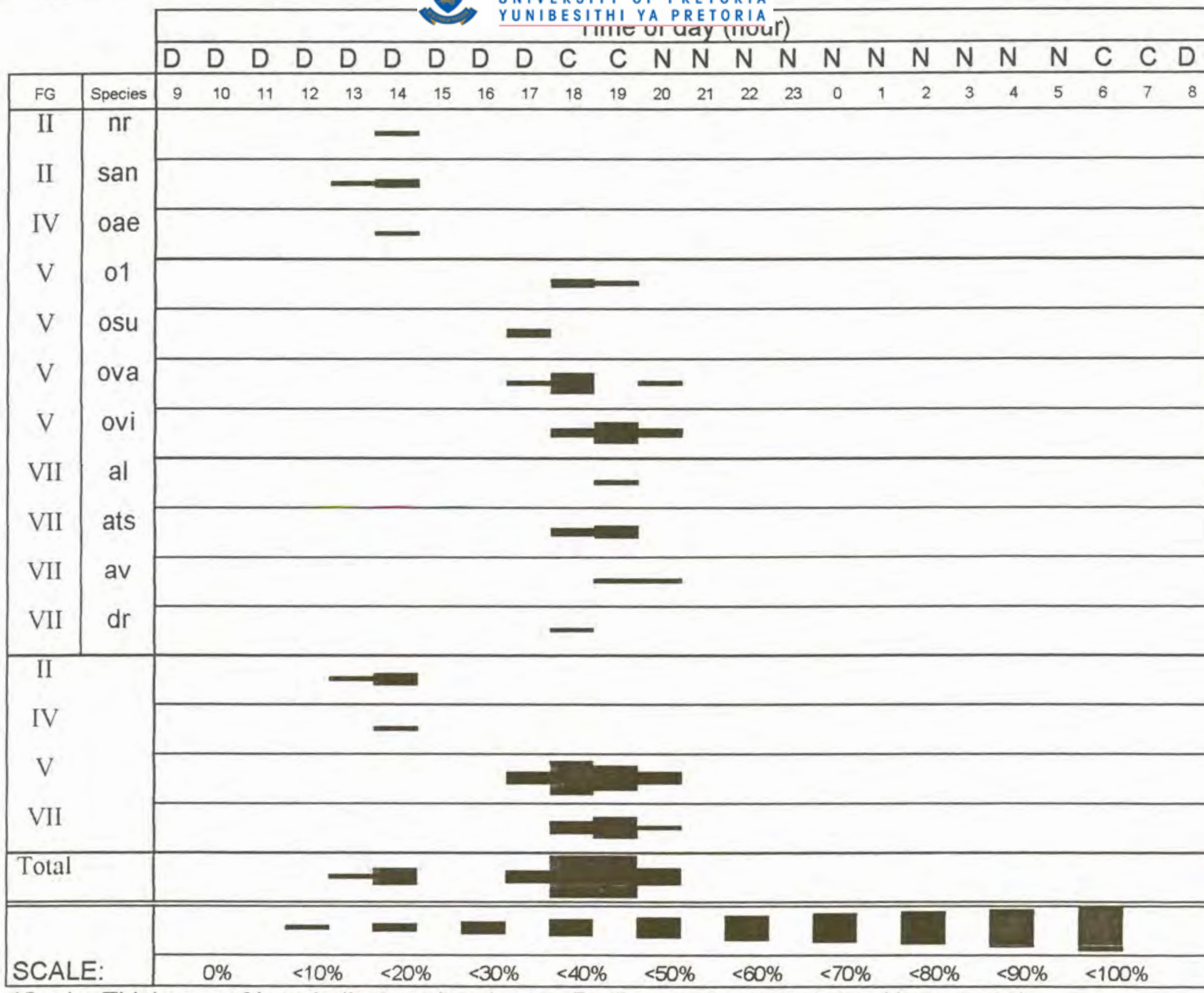


*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

*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).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

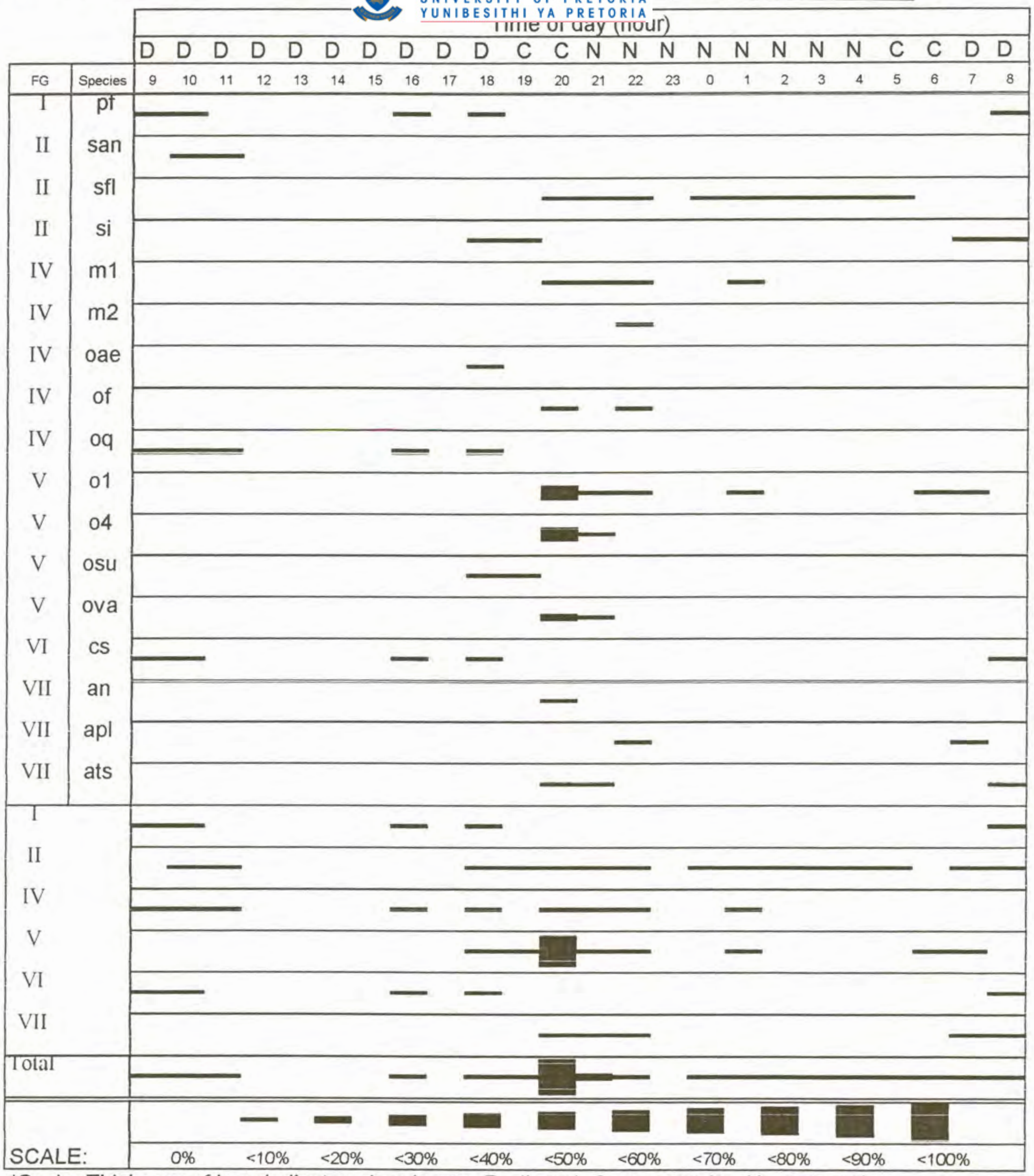


*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

*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).

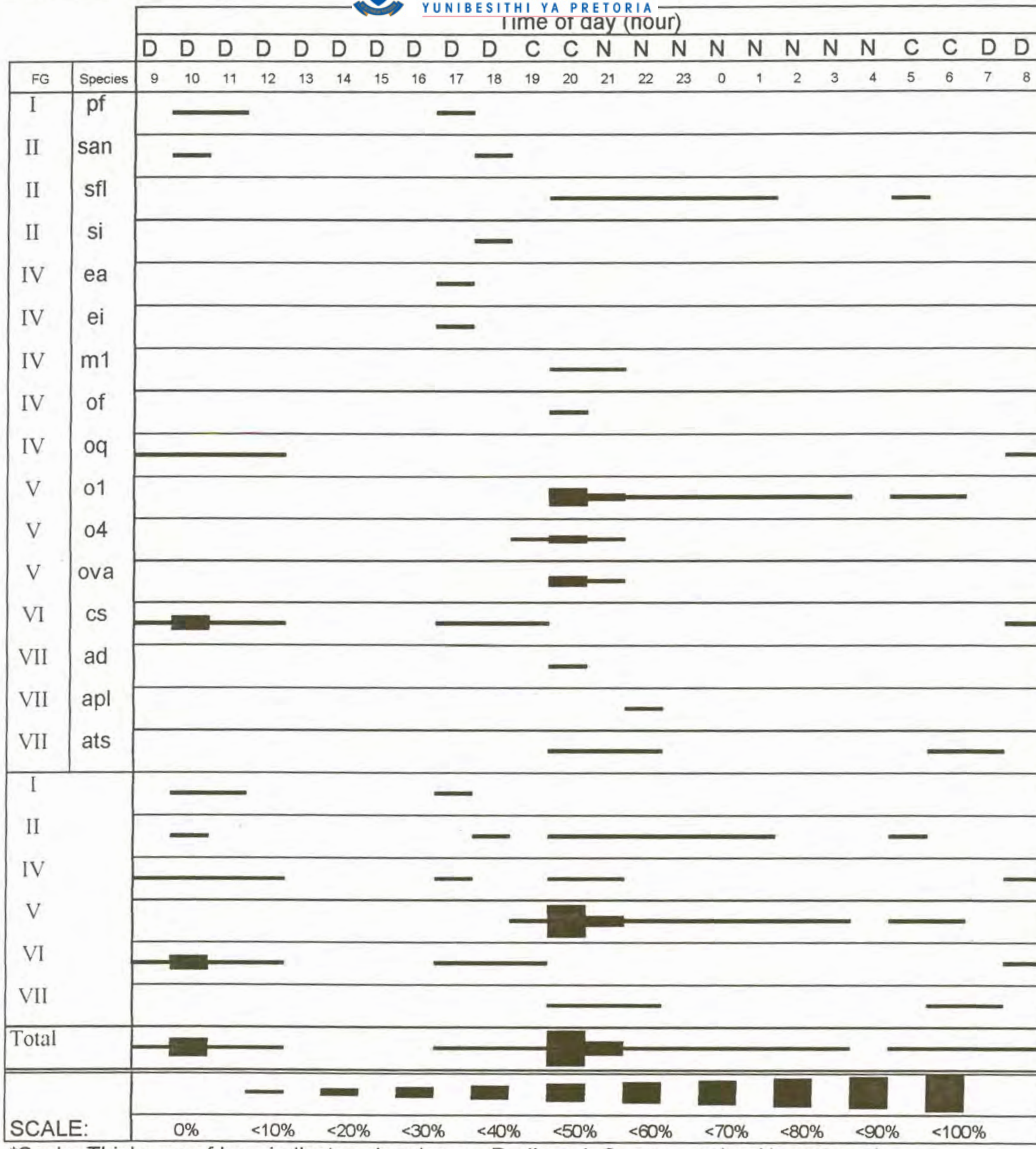
UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA



*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal
*For code of species names see Chapter 2 - Table 2.4.

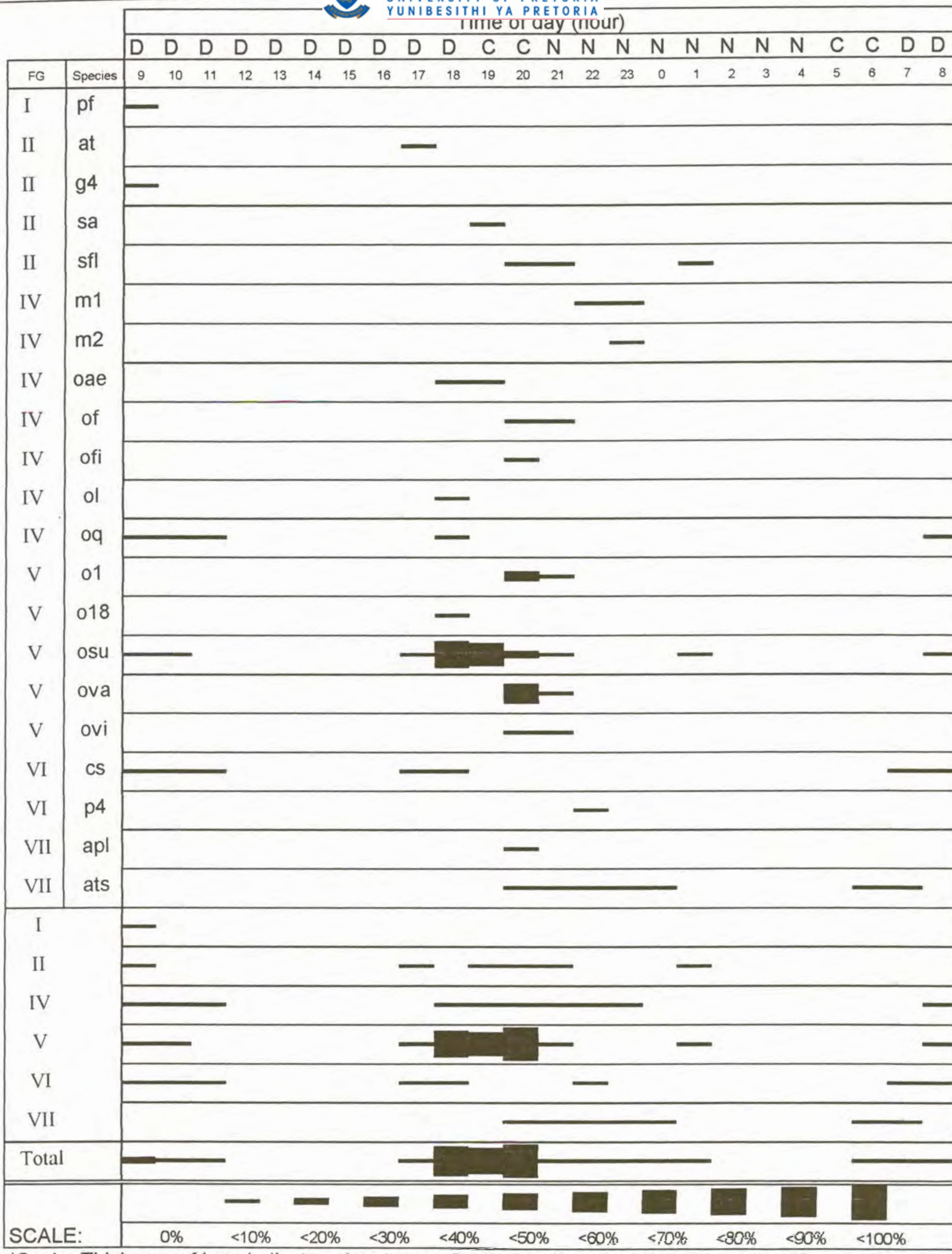
Fig. 5.6. Diel flight activity of different dung beetle species and functional groups over a 24-hour period during summer (December 1997): a) Sandveld grassveld (disturbed grassveld habitat).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA



*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).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

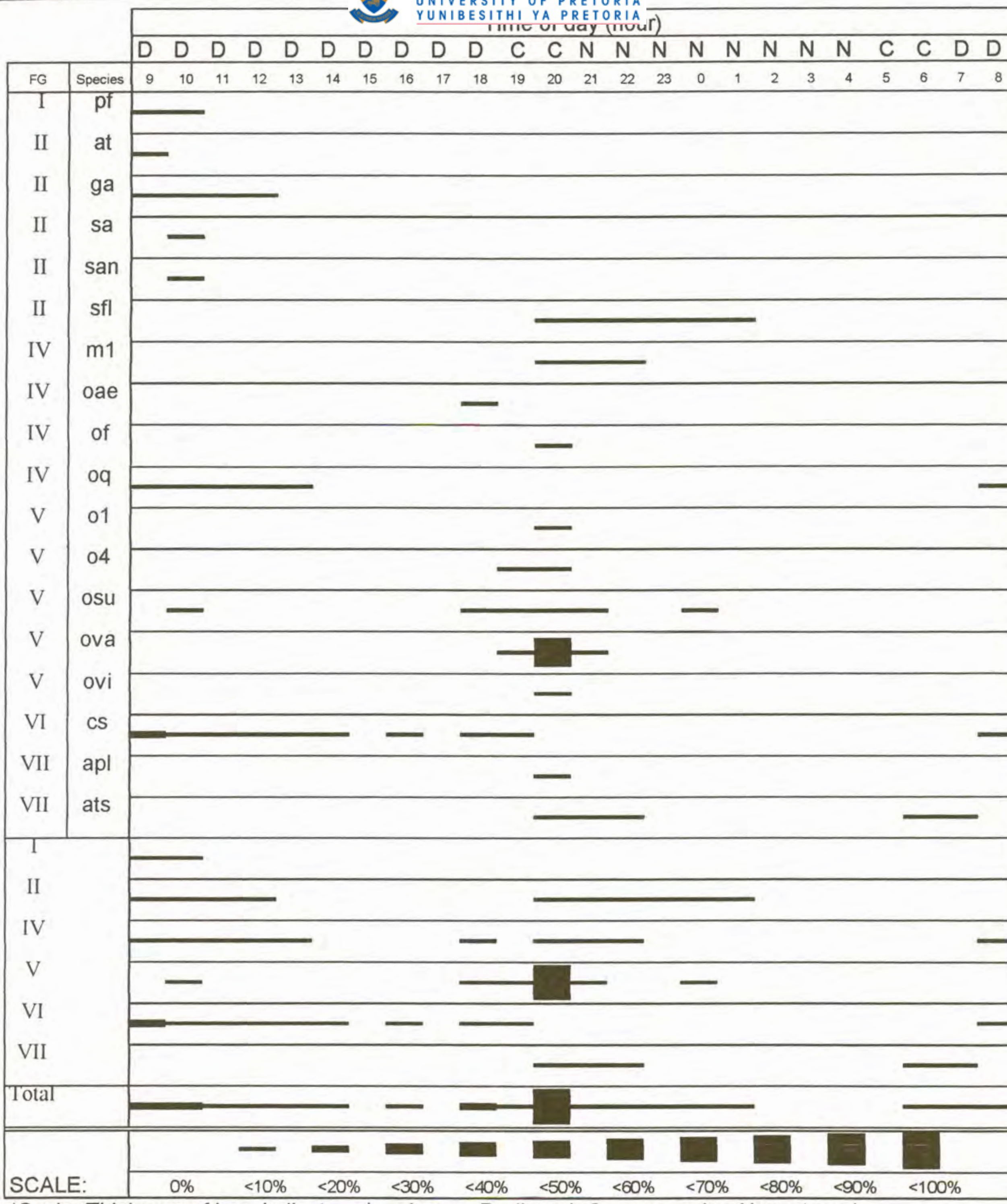


*Scale: Thickness of bars indicates abundance; D=diurnal, C=crepuscular, N=nocturnal

*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).

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA



*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).