The dung beetles of Hlane Royal National Park
– Assemblages in elephant and rhino dung –

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Summary

During the course of the present study in Hlane Royal National Park in Swaziland, 62 species of scarabaeinae, and approximately 20 species of Aphodiinae were sampled in elephant and rhino dung between November 1996 and November 1997. Most species demonstrated an activity peak at the start of the rainy season in November and a second peak near the end of the rainy season in March.

The sampled species included subtropical / tropical generalists (63%); temperate / tropical generalists (21%); and eastern climatic specialists (16%), following the climatic, biogeographical and habitat associations as defined by A.L.V. Davis (1996c & 1997a). Soil preference data was available for 55% of all species sampled in Hlane. Of the sampled species in Hlane, 43% were clay specialists, 43% were soil generalists and only 14% were sand specialists. Most species encountered were woodland and/or thicket specialists or vegetation generalists. Only a few grassland specialists were encountered.

During daylight hours, the most important dung removers per functional group (in terms of dry weight) were *Kheper subaeneus* and *Kheper nigroaenes* (FG I – large rollers); *Garreta nitens* (FG II – small rollers), *Heteronitis castelnaui* (FG IV - large slow tunnelers); *Tiniocellus spinipes* (FG V - small slow tunnelers); and *Oniticellus egrerius* (FG VII - dwellers). The small slow tunnelers (FG V) were clearly the most important in numbers of individuals (59%). In terms of weight, the large slow tunnelers (FG IV) emerged as the most important dung removers (52%). The top nocturnal/crepuscular species per functional group in elephant dung in December (in terms of dry weight) were *Anachalcos convexus* (FG I); *Heliocopris andersoni; Heliocopris neptunus* (FG III - fast tunnelers); *Onitis fulgidus* (FG IV); *Milichus apicalis* (FG V) and *Aphodiinae spec*. (FG VII). FG V also came forward as the dominant group at night in terms of number of individuals (41%), followed by FG VII (32%) and FG IV (25%). In terms of dry weight (fig. 9.), FG IV was the most important group (53%).

Kheper nigroaeneus and *Kheper subaeneus* peaked in dung that was fresh and sticky - within the first 3 hours after having been voided. *Garreta nitens* and *Allogymnopleurus thalassinus* peaked in 5-8 hour old dung, when *Kheper* populations were at their lowest. *Sisyphus costatus,* the most abundant roller species, was the last to peak in *11 hour* old dung. The first tunneling species to peak in 5 hour old dung included *Onthophagus obtusicornis* and, *Onthophagus rasipennis* along with *Heteronitis castelnaui,* a large and abundant tunneling species. *Phalops flavocinctus* and *Onthophagus nr. Pullus* were the only two species to peak in 8 hour old dung. the vast majority of species peaked in 11 hour old dung. The most abundant species active in 11 hour old dung were *Caccobius nigritulus* (more than 100 individuals per 2000g) and *Tiniocellus spinipes* with almost 300 individuals per 2000g. Other species active in 11 hour old dung included *Onthophagus nr. Sugillatus, Caccobius viridicollis, Cyptochirus ambiguus (dweller)* and *Proagoderus tersidorsis.* Although less abundant, *Drepanocerus kirbyi* also peaked in 11 hour old dung.

Introduction

The present study examines the dung beetle community associated with two wild pachyderm ungulates (White rhino and elephant) in the Hlane Royal National Park in the Swaziland lowveld. Monthly sampling and analysis conducted by the authors in 1996 and 1997 during the course of 12 months was directed towards an analysis of:

1) The functional group composition in diurnal and nocturnal dung beetle assemblages in elephant dung.

2) The temporal succession of dominant diurnal rollers, tunnelers and dwellers in aging elephant dung.

3) A seasonality study, in which dung beetle activity was monitored per species on a monthly basis over the course of 12 months and compared for elephant and rhino dung.

4) A description of the encountered dung beetle species in terms of climatic, biogeographical and habitat associations (following A.L.V. Davis, 1996c & 1997a).

Research was conducted in the Hlane Royal National Park (26 ° l5'S, 31 ° 52'E), which covers a total area of 30,000 hectares. The reserve is situated in the northeastern lowveld of Swaziland at an altitude of approx. 280m in close proximity (5-10km) to the Mozambique border. Hlane is mainly surrounded by sugarcane plantations to the north and west, and by grazing land to the south. To the east, Hlane forms a corridor with the adjacent Mlawula Nature Reserve and Lebombo escarpment (600m). Hlane is situated in the lowveld of Swaziland at 250-300m above sea level. The area is plain, apart from a fringe of rocky outcrops on the east, against the Lebombo mountains. The reserve was founded in 1964, before which it was grazing land (from which most of the wild animals, including rhino's and elephants were eradicated). In 1987, elephants were reintroduced into the Kingdom after an absence of about 90 years. Hlane is home to 22 elephants and a fair number of white rhino's. The reserve's two herds of elephants are separated into different enclosures.

Sampling was conducted in a 2km² enclosure (above) containing a herd of 14 elephants and a number of rhino. The park (and enclosure) also hosts a range of other large mammals.

Soil composition (Fig 5) in the enclosure resembles that of the rest of the reserve, consisting of a mosaic of shallow grey sand to sandy loam (25%), shallow brown or black loam to clay (50%), and smaller patches of black and red clay (25%). To the east of the study enclosure, loam and clay soils are predominant whilst sandy to sandy/loam soils predominate in the western half of the park.

Vegetation in the Hlane varies from dense pioneer bushveld thicket to open (savannah) thorn woodland. According to Gertenbach & Potgieter (1978), dominant species occur in three vegetation zones within and surrounding the research area:

1. *Spirostachys Africana – Euclea divinorum* (bushveld)

2. *Sclerocarya caffra – Bolusanthus speciosus – Acacia nigrescens* (savannah woodland)

3. *Acacia tortilis - Bolusanthus speciosus – Acacia nigrescens* (savannah woodland)

The savannah's in Hlane have to varying degrees suffered from bush/thicket encroachment over the past decades since game build-up started in 1967. Additionally, low (>6m) *Acacia nigrescens* has taken on an almost exclusive presence in large regions within Hlane. Although no major rivers run through the research area, there are areas of broadleaves along drainage lines, including *Combretum imberbe, Sclerocaria caffra* (Morula) and *Spirostachys africana*. Predominant grasses include *Themeda triandra* and *Panicum maximum*. Extensive open grasslands do not exist within the enclosure.

Climate can be characterized as mid-summer rainfall. Winter days are warm (May- August) but cold at night with temperatures sometimes falling below zero. In summer (November - March) temperatures often rise above 40°C. Annual rainfall averages at 600mm and has been recorded on a monthly bases for the purpose of this study (appendix 19). The 1996 winter was considerably drier than the 1997 winter. The summer rainfall period in 1996/97 lasted from October until March, with a dry spell for a few weeks in February.

Research area.

Method

The Elephants in Hlane tend to void their dung within three particular time slots: early morning, late afternoon and at midnight. The exact time of dung voidance was determined by observation and tracking expertise of game rangers who located the elephants and took note of the site and time at which dung was voided. When the site was located, the droppings were tagged. The heap size, structure and location were recorded. Droppings were sampled using a standard sized sealable bucket. All samples were weighed.

In order to facilitate data analysis, live content was killed using ethyl acetate. Dung was mixed with water in order to separate dung beetles from the dung (most dead beetles floated to the surface).

All dung beetles were removed from the dung and stored in alcohol until identified and counted.

For the purpose of diurnal studies, dung voided at sunrise (06:00) was sampled after 3, 5, 8 and 11hours. For the purpose of the nocturnal study, dung voided at sunset (18:00) was sampled after 5 and 11hours. Samples were analysed in terms of species (within their functional groups) and dry weight per sample, standardized to 2000g.
For the seasonality study, 2-3 samples were collected once a month at midday from rhino and elephant dung. Samples included dung voided on the same day and the previous day in order to include diurnal and nocturnal species.

The researchers doing what they do best.

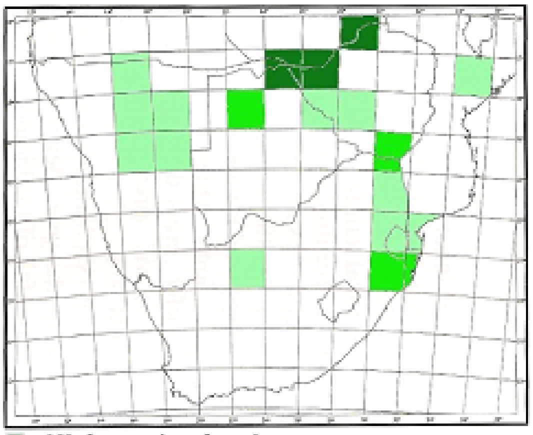
Results

A total of 62 dung beetle species were collected in elephant and rhino dung over a one year period in the Hlane Royal Game Reserve.

1. Climatic and biogeographical associations

The eastern climatic specialist group (Fig 1), was represented by a total of 10 species (16%). The largest eastern climatic specialist cluster was the game reserve cluster (4 species). The most abundant species was the nocturnal *Milichus apicalis.*

Fig. 1. Geographical species density of eastern climatic specialist cluster 5B (Game reserve group)



High species density
Medium species density
Low species density

Species representation in Hlane National Park

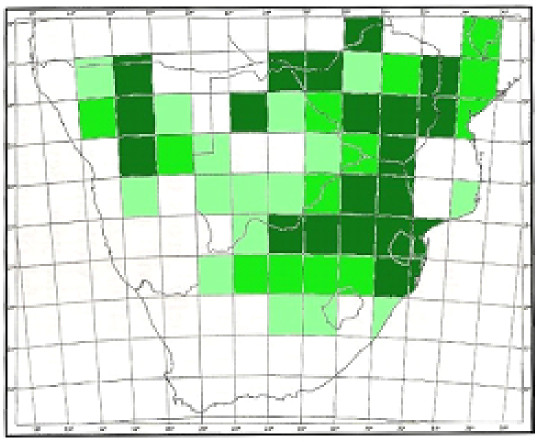
Proagoderus bicallosus
Proagoderus rectefurcatus
Milichus apicalis
Kheper cupreus
Scarabaeus deludens *
Onthophagus interstitialis * (C/G)
Catharsius philus * (C/G,OW)
Caccobius viridicollis * (C,S/G.OW)
Euoniticellus zumpti *
Drepanocerus freyi *

1) * Eastern climatic specialist species but not belonging to cluster 5B
2) Soil preference (C = clay; S = sand)
3) Vegetation preference (G = grass; OW = open woodland; t = thicket)

The remaining 6 eastern climatic specialist species fell into other clusters.

Most sampled species were subtropical/tropical generalists (39 = 63%). The largest subtropical/ tropical generalist clusters in Hlane, were the pan-mid-summer rainfall cluster (10 species, Fig 2) and the eastern mid-summer rainfall cluster (22 species, Fig 3).

Fig. 2. Geographical species density of subtropical/tropical generalist cluster 7C (Pan-mid-summer rainfall group)



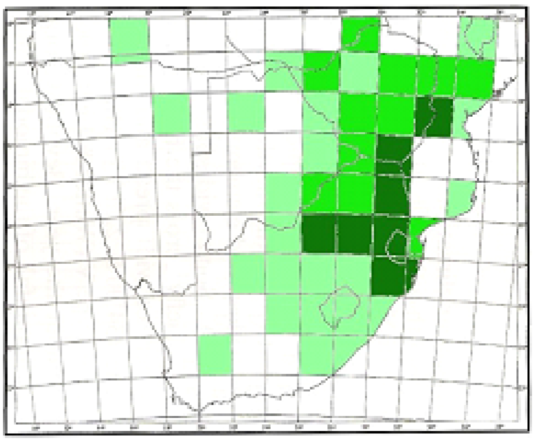
High species density
Medium species density
Low species density

Species representation in Hlane National Park

Anachalcos convexus (S,C/OW,T)
Allogymnopleurus thalassinus (S/G)
Garreta nitens (C/OW,T)
Copris elphenor (S/G,OW))
Heliocopris andersoni
Heteronitis castelnaui
Onitis uncinatus (C/OW,G)
Onthophagus vinctus (S/T,OW)
Onthophagus fimetarius (S/OW,T,G)
Onthophagus aeruginosus (S,C/OW,T)
Neosisyphus fortuitus * (S,C/OW,T)
Onthophagus pullus * (S,C/OW,G)
Onthophagus pallidipennis * (S/OW)
Onthophagus obtusicornis * (C/G,OW)
Sisyphus gazenus *
Onthophagus corniculiger *
Oniticellus egregius *

1) *Subtropical/tropical generalist species but not belonging to cluster 7C
2) Soil preference (C = clay; S = sand)
3) Vegetation preference (G = grass; OW = open woodland; t = thicket)

Fig. 3. Geographical species density of subtropical/tropical generalist cluster 7D (Eastern mid-summer rainfall group)



- High species density
- Medium species density
- Low species density

Species representation in Hlane National Park

Kheper nigroaeneus (C,S)
Kheper subaeneus (C)
Neosisyphus calcaratus
Sisyphus goryi
Sisyphus seminulum
Copris amyntor (C/OW)
Copris evanidus (C,S/G,T,OW)
Heliocopris neptunus
Onitis viridulus (C/T,G,OW)
Onitis fulgidus (C/T,OW)
Onitis picticollis
Proagoderus tersidorsis
Phalops ardea
Phalops flavocinctus (C/G,OW)
Caccobius nigritulus (S/OW,T)
Onthophagus lamelliger
Onthophagus rasipennis (C,S/OW)
Drepanocerus fastiditus
Tiniocellus spinipes (C,S/OW)
Pedaria sp.
O. (Hyalonthophagus) alcyonidis
Oniticellus formosus (C/G,OW)

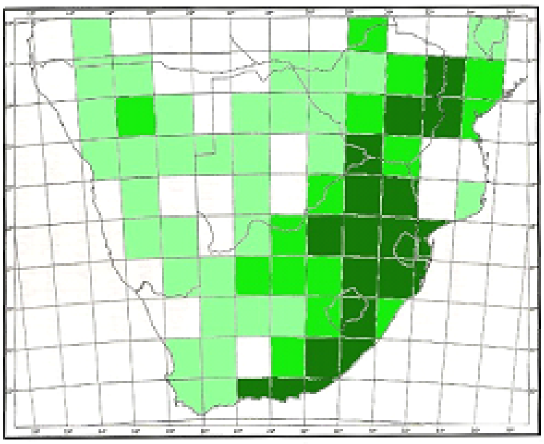
1) Soil preference (C = clay; S = sand)
2) Vegetation preference (G = grass; OW = open woodland; t = thicket)

The remaining 7 subtropical / tropical generalist species fell into other clusters. The most abundant species belonging to the pan-mid-summer rainfall cluster were *Anachalcos convexus, Garreta nitens, Allogymnopleurus thalassinus, Heteronitis castelnaui, Heliocopris andersoni, onthophagus vinctus* and *onthophagus fimetarius.*

The most abundant species belonging to the eastern mid-summer rainfall cluster were *Kheper nigroaeneus, Kheper subaeneus, Copris amyntor, Onitis viridulus, Onitis fulgidus, Onitis picticollis, Proagoderus tersidorsis, Phalops flavocinctus, Caccobius nigritulus* and *Tiniocellus spinipes.*

The temperate/tropical generalist species comprised 13 species (21%). Most of the temperate/ tropical generalist species fell into the pan southern African cluster (10 species, Fig 4).

Fig. 4. Geographical species density of temperate/tropical generalist cluster 8A (Pan southern African group)



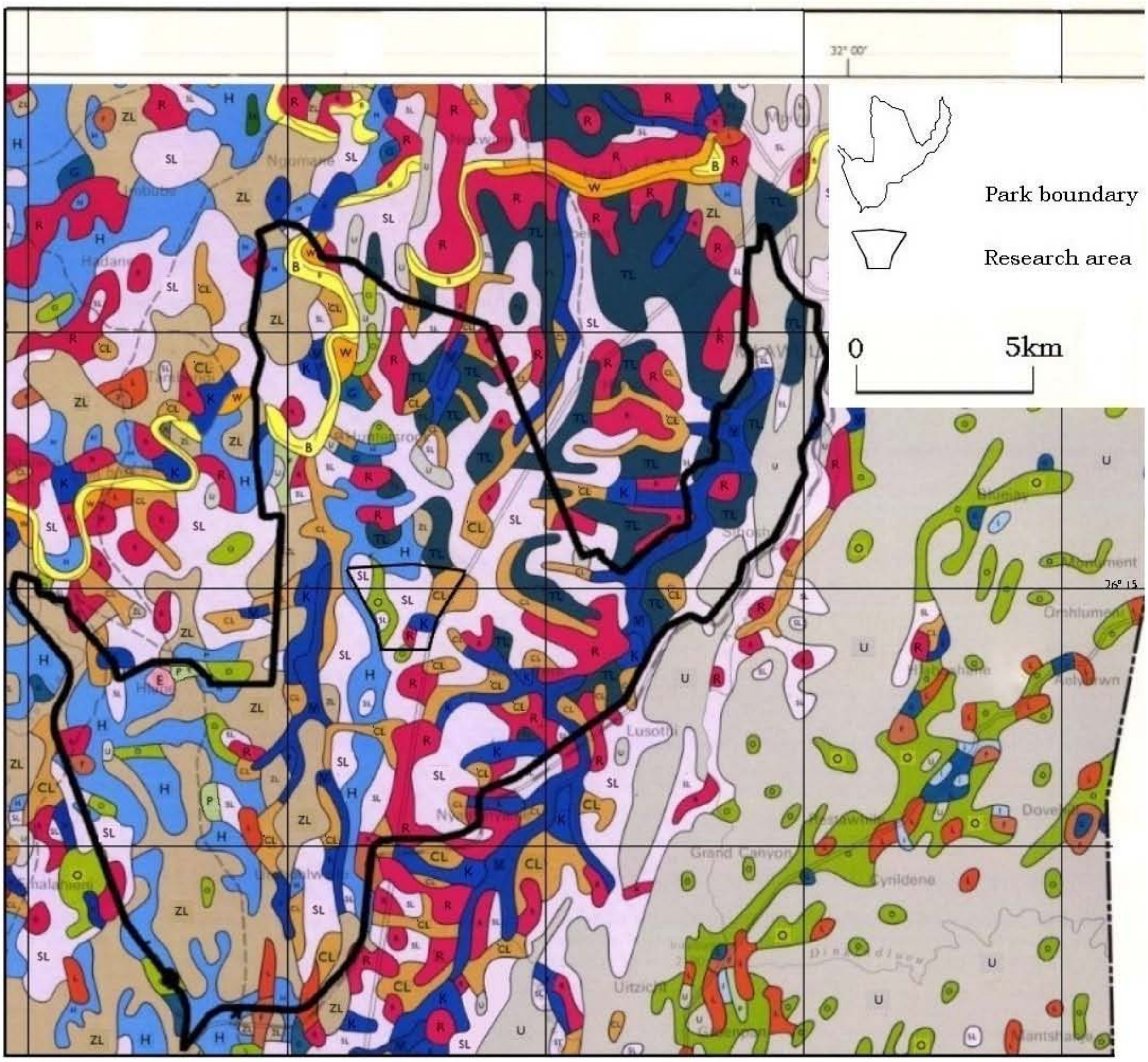
- High species density
- Medium species density
- Low species density

Species representation in Hlane National Park

Neosisyphys ruber
Onitis alexis (C,S/G,OW)
Digitonthophagus gazella C,S/G)
Cyptochirus ambiguus
Euoniticellus intermedius (C,S/G,OW)
Liatongus militaris (C/G,OW)
Onthophagus sugillatus (C,S/OW,T)
Drepanocerus kirbyi (C,S/OW,T)
Sarophorus costatus (C,S/OW,T)
Oniticellus planatus
Drepanocerus patrizii * (C,S/OW,G)
Neosisyphus muricatus *
Scarabaeus interstitialis *

1) * Temperate/tropical generalist species but not belonging to cluster 8A
2) Soil preference (C = clay; S = sand)
3) Vegetation preference (G = grass; OW = open woodland; t = thicket)

Fig 5. Soil map of Hlane National Park and research area



Predominant soil types:

SL	(Lowveld) — Shallow brown or black loam to clay: Lithosolic
H	Grey sandy loam on mottled clay pan: Pseudopodzolic
CL	(Lowveld) — Dark brown clay, neutral: Vertisolic
O	Shallow grey sand to sandy loam on hard rock: Lithosolic
K	Black clay, calcareous: Vertisolic
R	Red clay, slightly acid: Intertropical Brown Soil
TL	(Lowveld) — Dark grey clay on soft iron pan: Vertisolic
ZL	(Lowveld) — Dark grey sandy loam on clay pan: Solodized Solonetzic
U	Rock outcrops and stony ground: Raw Mineral Soil

The remaining 3 species fell into other clusters (Fig 4). The most abundant species belonging to the pan southern African cluster included *Cyptochirus ambiguus, Sarophorus costatus* and *Onthophagus sugillatus.*

2. Habitat associations

As about 75% of the enclosure (and park) consists of loam and clay soil (Fig 5), most species sampled were, as expected, either clay specialists or soil generalists (Fig 1,2,3 & 4). Sampling yielded relatively few sand specialists. Soil preference data was available for 55% of all species sampled in Hlane. Of these, 43% were clay specialists, 43% were soil generalists and only 14% were sand specialists.

Particularly abundant clay specialists included *Kheper subaeneus, Garreta nitens, H. neptunus, Liatongus militaris, Onthophagus obtusicornis, oniticellus formosus, Onthophagus interstitialis, Onitis viridulus, Onitis fulgidus, and Onitis uncinatus.* Common soil generalists included *kheper nigroaeneus, Anachalcos covexus, Neosisyphus fortuitus, Caccobius viridicolis, Onthophagus aeruginosus, Onthophagus pullus Copris evanidus, Tiniocellus spinipes, Onitis alexis, Euniticellus intermedius, Onthophagus sugillatus, Sarophorus costatus, Drepanocerus patrizii* and *Drepanocerus kirbyi.* Although less common, a few sand specialists were present in large numbers. Examples include *Onthophagus vinctus, Onthophagus fimetarius, Allogymnopleurus thalassinus* and *Caccobius nigritulus.* The presence of these species may be attributed predominantly sandy loam soils (H, ZL, Fig 5.) adjacent to the research area in the west.

Vegetation preference data was available for 52% of the species sampled in Hlane (Fig 1,2,3 & 4). Most of these were either woodland and/or thicket specialists or vegetation generalists occurring in grassland as well as woodland and dense thickets. This coincides with the vegetation in the research area, which, as mentioned varies from dense pioneer bushveld thicket to open (savannah) thorn woodland. Notable exceptions were the grassland specialist species *Allogymnopleurus thalassinus* and *Digitonthophagus gazella* which were plentiful within the study area despite the absence of open grassland within the enclosure.

3. *Diel activity*

A study was undertaken during the wet season in December, to determine the composition of the diurnal and nocturnal dung beetle communities in elephant dung samples, in terms of species (within their functional groups) and dry weight per sample, standardized to 2000g. Diel activity was determined for almost 60% of all species encountered within the research area.

3.1 Functional group composition in the month December (diurnal samples in elephant dung)

The small slow tunnelers (FG V) are clearly the most important in numbers of individuals (59%). At 27%, the dwellers (FG VII) also make up an important part of the community. At 8% and 6% respectively, the large slow tunnelers (FG IV) and small rollers (FG II) are moderately represented. In contrast, the large rollers (FG I) and fast tunnelers (FG III) appear rather insignificant in comparison to other groups (fig 6.).

When expressed in terms of dry weight (fig 7.), the importance of different functional groups in terms of dung removal is more accurately displayed. The large slow tunnelers (FG IV) emerge as the most important dung removers (52%) whereas the small slow tunnelers (FG V) now seem considerably less important. The large and small rollers (FG 1 & II) also show to be important dung removers whilst the fast tunnelers (FG III) are still minimally represented. The dwellers (FG VII), represented well in numbers, are considerably less significant in terms of weight.

Fig 6. Functional group composition (diurnal samples in elephant dung) in terms of number of individuals

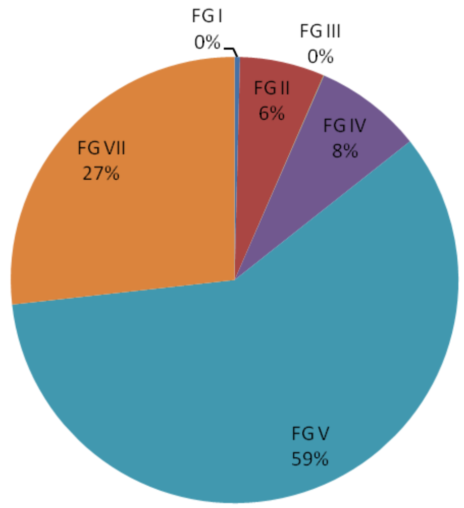
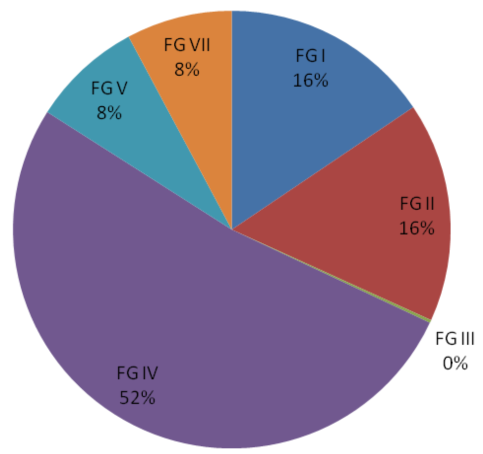


Fig 7. Functional group composition (diurnal samples in elephant dung) in terms of (dry) weight



The most important diurnal dung removers per functional group (in terms of dry weight) are *Kheper subaeneus* and *Kheper nigroaenes* (FG I); *Garreta nitens* (FG II), *Heteronitis castelnaui* (FG IV); *Tiniocellus spinipes* (FG V); and Oniticellus egrerius (FG VII). The fast-burying tunnelers (FG III) comprise principally nocturnal species, which explains their absence from diurnal sampling.

3.2 Functional group composition in the month December (nocturnal samples in elephant dung)

In the nocturnal samples, FG V once again came forward as the dominant group in terms of number of individuals (41%), followed by FG VII (32%) and FG IV (25%). FG I and II (sharp decline) were scarcely present in terms of number of individuals. FG III, completely absent from the diurnal samples is present in the nocturnal samples, albeit a minimal contribution (2%) in terms of number of individuals (fig. 8.).

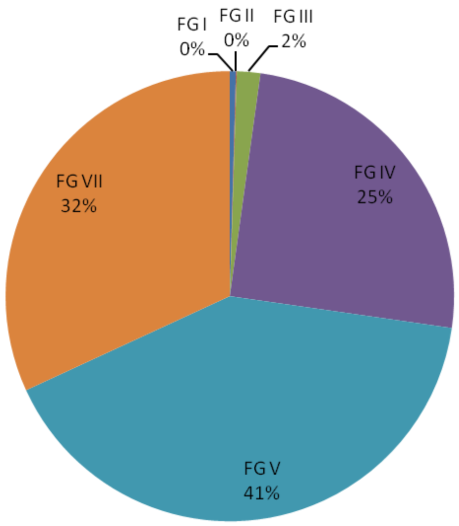


Fig 8. Functional group composition (nocturnal samples in elephant dung) in terms of number of individuals

In terms of dry weight (fig. 9.), FG IV was the most important group (53%). In sharp contrast to the diurnal samples, FG III stands second in line (26%) as most important dung remover. FG II, which showed a marked contribution in terms of weight in diurnal samples was absent in nocturnal samples. FG I remained moderately present in nocturnal samples (12%), trailed by FG V (7%). Both these groups show a very similar pattern in diurnal and nocturnal samples. FG VII contribute minimally in terms of weight and therefore arguably, also in terms of dung removal.

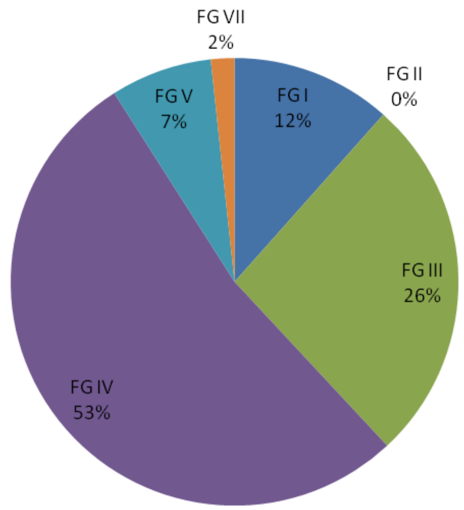


Fig 9. Functional group composition (nocturnal samples in elephant dung) in terms of (dry) weight

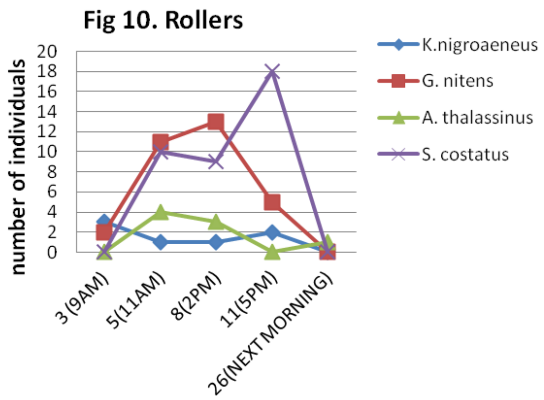
The top nocturnal species per functional group in elephant dung in December (in terms of dry weight) are *Anachalcos convexus* (FG I); *Heliocopris andersoni* (FG III); *Onitis fulgidus* (FG IV); *Milichus apicalis* (FG V) and *Aphodiinae spec.* (FG VII). The small rollers (FG II) comprise mainly diurnal species, which is why they were largely absent in the nocturnal samples. Other nocturnal species encountered in December included *Copris amyntor; Copris evanidus; Copris elphenor; Onitis uncinatus; Onitis viridulus; Onitis fulgidus; Onitis picticollis; Onitis alexis; Digitonthophagus gazella; Onthophagus interstitialis; Onthophagus lamelliger; Milichus apicalis;*

Onthophagus corniculiger; Onthophagus vinctus and *Onthophagus fimetarius.*

4. *Temporal succession*

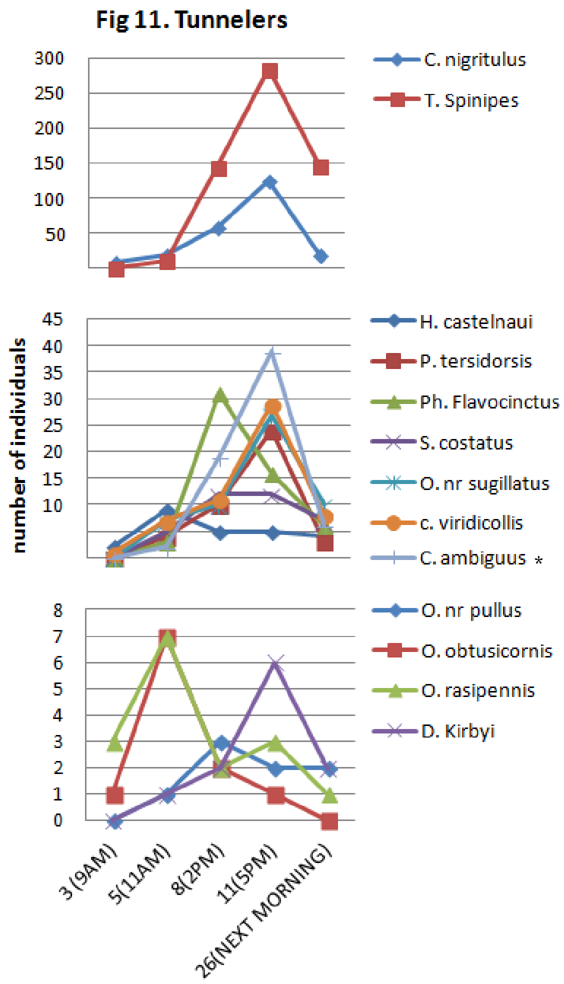
The temporal succession of key diurnal roller and tunneler species was recorded in aging elephant dung in December. For the purpose of this study, dung voided at sunrise (06:00) was sampled after 3, 5, 8 and 11hours. An additional sample was collected the following morning, after about 26 hours. Earth beneath the dung sample was also collected and analysed. The seven functional groups (following Hansky, 1990; Doube, 1994 & Davis 1996) were clustered into rollers, tunnelers and dwellers (the latter having been omitted from this study). Although dry weight may seem a more adequate measure of importance in terms of dung removal, the number of individuals were counted (and standardized to 2000g) as the sole purpose of this particular study was to examine the succession of relatively abundant species.

4.1 Temporal succession of dominant diurnal rollers in aging elephant dung (Fig. 10).



Kheper nigroaeneus and *Kheper subaeneus* peak in dung that is fresh and sticky - within the first 3 hours after having been voided. Their numbers gradually decrease as the dung dries. *Garreta nitens* and *Allogymnopleurus thalassinus* peak in 5-8 hour old dung, when *Kheper* populations are at their lowest. *Sisyphus costatus,* the most abundant roller species, was the last to peak in 11 hour old dung, when *Kheper, Garreta* and *Allogymnopleurus* populations have subsided. Numbers of rollers did not surpass an average of 18 individuals per sample, standardized to 2000g, which was significantly lower than that recorded for tunneling species.

4.2 Temporal succession of dominant diurnal tunnelers in aging elephant dung (Fig. 11).



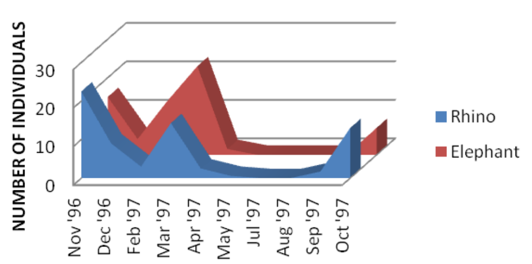
The first species to peak in 5 hour old dung include *Onthophagus obtusicornis* and, *Onthophagus rasipennis* along with *Heteronitis castelnaui,* a large tunneling species. Numbers did not surpass an average of 10 individuals per sample, standardized to 2000g. *Phalops flavocinctus* and *Onthophagus nr. Pullus* were the only two species to peak in 8 hour old dung whilst the vast majority of species peaked in 11 hour old dung. The most abundant species active in 11 hour old dung were *Caccobius nigritulus* (more than 100 individuals per 2000g) and *Tiniocellus spinipes* with almost 300 individuals per 2000g. Other species active in 11 hour old dung within the 20-40 individuals per 2000g range include *Onthophagus nr. Sugillatus, Caccobius viridicollis, Cyptochirus ambiguus (dweller)* and *Proagoderus tersidorsis.* Although less abundant, *Drepanocerus kirbyi* also peaks in 11 hour old dung.

5. *Seasonality*

Dung beetle activity was monitored per functional group on a monthly basis from November 1996 until November 1997 and compared for elephant and rhino dung. As the kleptoparasitic behaviour of many *Caccobius*, *Onthophagus* and *Pedaria* species remains unconfirmed, all species sampled in Hlane were classified as tunnelers. The functional groups generally had a bimodal distribution, with an activity peak at the start of the rainy season in November and a peak near the end of the rainy season in March. Both peaks coincide with the two heaviest downpours of the season and differ in intensity per functional group and per species. Some experience a major peak in November and a minor peak in March, whilst the opposite may be true for other species. The decrease in activity in February may be explained by the dry spell that occurred during this month. From May until the end of September, activity subsides and most species remain dormant in the soil until climatic conditions become more favourable.

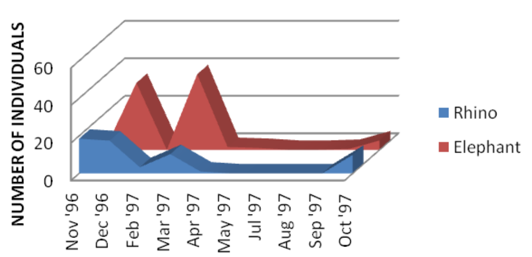
Fast tunnelling species are generally only active shortly after rainfall, whilst most other species tend to show a more gradual and sustained response to rainfall.

Fig 12. FG I (Large Rollers)



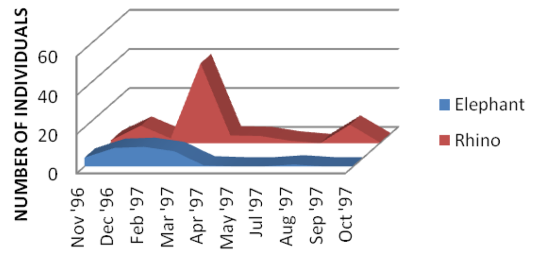
FG I, large rollers (*Kheper, Anachalcos*) peak at the start of the wet season in November (Fig. 12). Their presence in dung declines sharply in February, followed by a second activity peak in March, which seems to be more intense in Elephant dung.

Fig 13. FG II (Small Rollers)



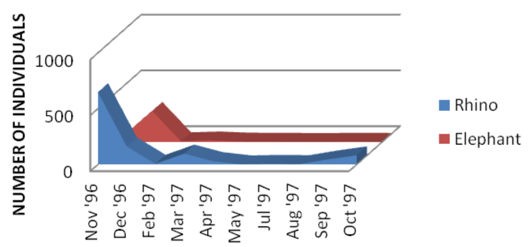
FG II, small rollers *(Garreta, Allogymnopleurus, Scarabaeus, Sisyphus, Neosisyphus)* present a similar bimodal seasonal distribution to large rollers, with a clear preference to elephant dung (Fig. 13).

Fig 14. FG III (Fast tunnelers)



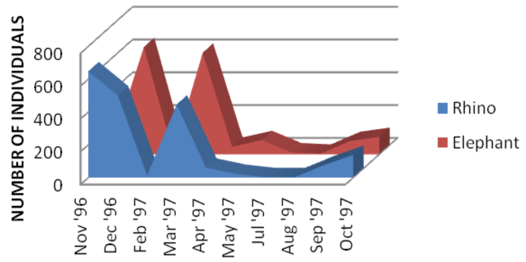
Fast tunnelers (FG III) comprise mainly nocturnal species *(Heliocopris, Catharsius, Copris)* that are only active (and present in superficial dung) immediately after rainfall, and then either return to a temporal state of dormancy or remain in brood chambers deep underground. Their rapid response to rainfall is demonstrated by a quick rise and fall in activity immediately after an early downpour in September (Fig 14). For this reason, the above graph may well have been shaped by the specific local climatic conditions that prevailed the day(s) before sampling. The differences in activity between Elephant and Rhino dung may be explained by differences in rainfall at sampling sites, rather than dung preference.

Fig 15. FG IV (Large slow tunnelers)



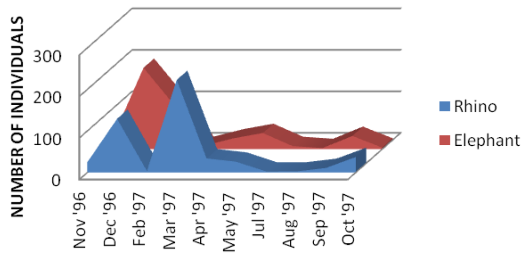
Large slow tunnelers (FG IV) comprise diurnal and nocturnal species *(Heteronitis, Onitis, Proagoderus, Phalops, some onthophagus, Cyptochirus, some Euoniticellus, Liatongus)* that peak in activity in November and December (Fig 15). *Proagoderus tersidorsis* and *Onthophagus interstitialis* account for a major portion of this peak. A second, minor peak occurs in March, albeit shadowed by exceptionally high numbers recorded during the first peak.

Fig 16. FG V (Small slow tunnelers)



FG V, small slow tunnelers (*Caccobius, Milichus, Tiniocellus, some Onthophagus, Sarophorus some Euoniticellus, Drepanocerus,*) become active at the start of the wet season in October (Fig. 16) and peak in November and December. Their presence in dung declines sharply in February, followed by a second slightly less intense activity peak in March.

Fig 17. FG VII (Dwellers)



Although the dwellers (*Oniticellus, Cytochirus, Hyalonthophagus and Aphodiinae)* seem to be more active in elephant dung at the start of the rainy season, the overall abundance of dwellers is higher in rhino dung (Fig. 17). The preference to rhino dung by dweller species may be explained by the fact that rhino's void their dung in middens with greater longevity than elephant dung. As many dwellers prefer aging dung this may explain their scarcity in elephant dung samples at the height of the dung beetle season in March.

Discussion

Approximately 800 species of dung beetles occur in Southern Africa, of which up to 150 species may be found in one locality (Scholtz and de Villiers 1983; Doube 1987). A total of 62 species were sampled over a one year period in elephant and rhino dung in the Hlane Game Reserve in Swaziland. This figure seems rather low, but the fact that only rhino and elephant dung was sampled within a relatively small enclosure (with limited variation in vegetation and soil type) needs to be taken into account. The total number of dung beetle species occurring in Hlane National Park is thus likely to be higher. Doube (1983) have demonstrated the marked effect of vegetation cover on species diversity. This may well apply to Hlane too.

Elephants and Rhino's were re-introduced into Hlane National Park after a period of absence. In this respect, Hlane is similar to Game Parks in KwaZulu-Natal such as the Ithala and Hluhluwe-Umfolozi Game Reserves. In the early 90's, *Heliocopris* species were relatively rare in the Natal reserves. Large bodied *H. andersoni* and *H. Neptunus* were common in Hlane National Park during the time of this study in 1996 and 1997 – 10 years after elephants were re-introduced into the reserve and more than 30 years after rhino were returned to the area. The long presence of rhino and adaptability of these species to other dung types (bovine) may explain the abundance of the *Heliocopris* species in Hlane (Fig. 18).

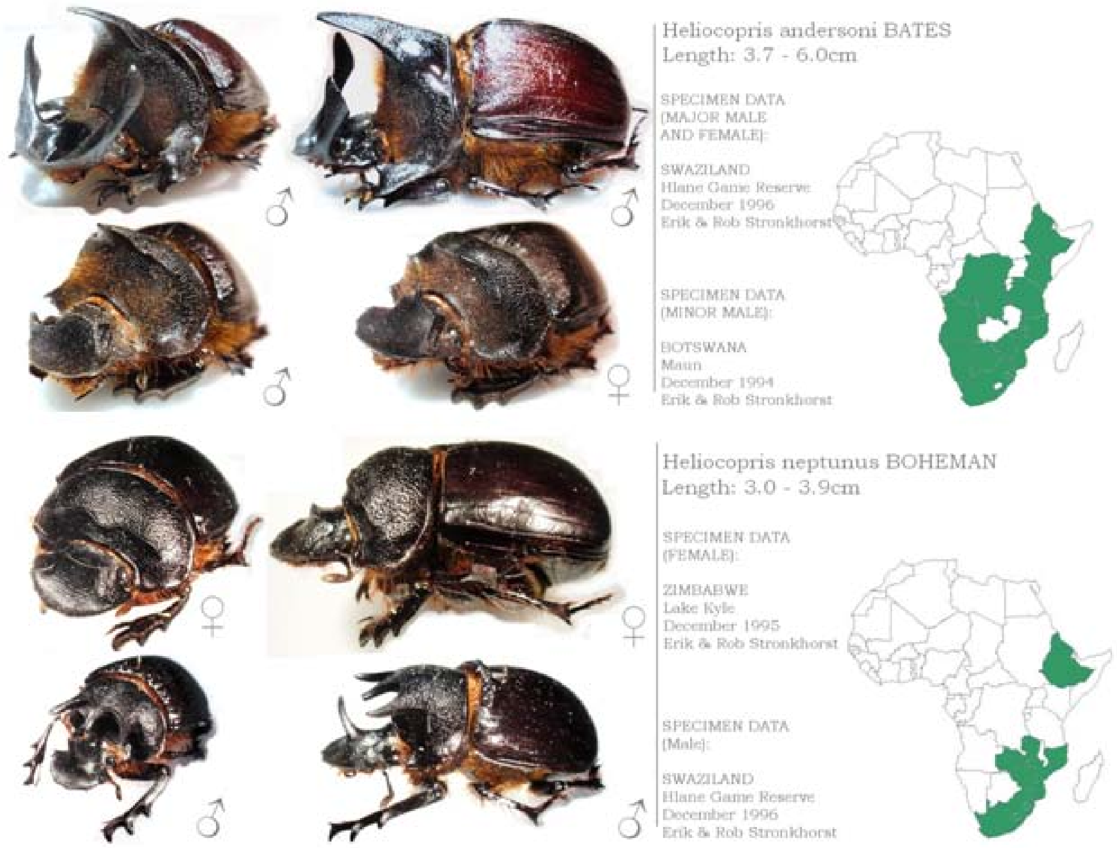
A five year study in the Hluhluwe-Umfolozi Game Reserve demonstrated the considerable influence of short term weather changes (rainfall and temperature) on dung beetle activity. The sharp fall in activity during the dry spell in February during the time of this study falls in line with these observations. In the Hluhluwe-Umfolozi Game Reserve, FG IV (large slow tunnelers) and FG V (small slow tunnelers) are well represented in clay-loam soils, whereas FG I (large rollers), FG II (small rollers) and FG III (fast tunnelers) are relatively unimportant (Hanski & Cambefort 1991). The Hlane study demonstrated FG IV (large slow tunnelers) to be the most important diurnal and nocturnal group when expressed in dry weight. As 75% of the soils in the study area (elephant enclosure) are clay-loam, this finding (as expected) coincides with the Hluhluwe-Umfolozi study. However, FG I and FG II followed as 2nd and 3rd most dominant during the day and FG I and FG III followed as 2nd and 3rd most dominant during the night. Hlane elephants only occur in a small enclosure with clay-loam soils and not in adjacent (sandy) regions. This may have led to the abundance of FG I (*Kheper,* *Anachalcos*), FG II (*Garreta, Allogymnopleurus, Neosyphus, Sisyphus*) and FG III (*Copris, Heliocopris*), despite the clear preference of some species to sandy soils. Dung type and availability therefore seems to be a stronger pull factor than soil and vegetation type.

When expressed in terms of number of individuals, FG IV, FG V and FG VII (dwellers) are the most abundant in Hlane, but this should not be considered as a measure of importance in terms of dung removal.

Succession continued for longer or shorter periods of time, depending on the size of the dung heap sampled, the exact location and disturbance by predators (such as the monitor lizard, which was often observed feeding on dung beetles in Hlane). Within the research area, the dung beetle community was richest in terms of numbers of individuals in 23-29h old dung, with an average 1152 individuals per 2000g, after which activity subsided due to resource depletion.

In terms of dry weight, the dung beetle community was richest in fresher, 4-5 hour old dung (17046mg per 2000g), slowly declining as time progresses.

Fig 18. H. andersoni and H. neptunus were common within the elephant enclosure in Hlane Royal National Park. No other Heliocopris species were encountered within the enclosure.



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APPENDIX 1. FG I/II 12/96 TEMPORAL SUCCESSION IN ELEPHANT DUNG (NUMBER OF INDIVIDUALS PER 2000G)

SAMPLE	11	16	44	46	47	8	14	18	36	37	40	13	6	35	38	41	42	43	45	7	12	39	17	TOTAL
TME PASSED	3h	3h10'	4h	5h20'	5h30'	7h	7h	7h15	7h45'	7h45'	8h	10h20'	10h20'	11h15'	11h15'	11h30'	11h30'	23h	23h	25h	25h	29h30'	29h40'	
FG I (Large Rollers)																								
K. nigroaeneus	4	2	2	0	0	1	0	0	0	2	0	6	0	0	0	0	3	0	0	0	0	0	0	20
K. subaeneus	0	2	1	2	2	0	0	0	0	2	2	0	0	0	0	0	0	0	1	0	4	0	0	16
A. convexus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
FG II (Small Rollers)																								
S. interstitialis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
A. thalassinus	0	0	0	7	4	1	0	0	2	10	2	0	0	0	0	0	0	0	1	0	0	2	0	29
G. nitens	0	3	12	5	16	4	7	6	0	47	12	14	9	0	0	0	6	0	1	0	1	0	0	143
N. calcaratus	0	0	1	0	0	0	0	2	0	15	2	0	0	4	8	0	24	2	2	0	0	0	0	60
N. fortuitus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
N. ruber	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	5
S. gazenus	14	0	5	0	1	0	2	2	0	7	3	0	0	0	5	0	9	0	7	0	1	2	0	58
S. goryi	0	0	1	0	0	0	0	2	0	2	0	0	0	4	0	0	11	0	0	0	0	0	0	20
S. costatus	0	0	30	0	0	4	8	40	0	0	0	54	40	0	0	0	14	0	0	0	0	0	0	190
TOTAL																								
FG I	4	4	3	2	2	1	0	0	0	4	2	6	0	0	0	0	3	0	1	0	4	0	2	38
FG II	14	3	50	12	22	9	17	52	2	81	19	68	49	12	13	0	64	2	11	0	2	6	0	508

APPENDIX 2. FG III/IV 12/96 TEMPORAL SUCCESSION IN ELEPHANT DUNG (NUMBER OF INDIVIDUALS PER 2000G)

SAMPLE	11	16	44	46	47	8	14	18	36	37	40	13	6	35	38	41	42	43	45	7	12	39	17	TOTAL
TME PASSED	3h	3h10'	4h	5h20'	5h30'	7h	7h	7h15	7h45'	7h45'	8h	10h20'	10h20'	11h15'	11h15'	11h30'	11h30'	23h	23h	25h	25h	29h30'	29h40'	
FG III (Fast tunnelers)																								
H. andersoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	**4**
H. neptunus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
C. philus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
C. amyntor	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	**8**
C. evanidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
C. elphenor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
FG IV (Large slow tunnelers)																								
H. castalnaui	3	1	5	13	10	3	0	17	4	5	3	6	9	4	0	8	6	11	5	2	0	5	1	**121**
O. uncinatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
O. viridulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	2	**13**
O. fulgidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	6	0	0	**24**
O. picticollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	3	0	5	**13**
O. alexis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**2**
P. tersidorsis	0	0	9	2	1	0	2	36	0	21	2	78	25	0	12	0	31	0	0	16	0	0	3	**238**
P. bicallosus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
P. rectefurcatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
P. ardea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
P. flavocinctus	0	0	1	4	5	6	16	8	52	48	56	20	3	39	25	0	11	4	9	5	0	2	16	**330**
D. gazella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	0	4	1	**12**
O. interstitialis	1	0	0	2	2	0	0	0	0	2	0	0	0	0	0	0	0	0	32	16	17	0	13	**85**
E. intermedius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**
L. militaris	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
TOTAL																								
FG III	**3**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**8**	**12**
FG IV	**4**	**1**	**15**	**21**	**18**	**9**	**19**	**61**	**56**	**78**	**61**	**104**	**37**	**43**	**37**	**8**	**48**	**15**	**48**	**81**	**26**	**11**	**41**	**842**

APPENDIX 3. FG III/IV 12/96 TEMPORAL SUCCESSION IN ELEPHANT DUNG (NUMBER OF INDIVIDUALS PER 2000G)																							
SAMPLE	11	16	44	46	47	8	14	18	36	37	40	13	6	35	38	41	42	43	45	7	12	39	17	TOTAL
TME PASSED	3h	3h10'	4h	5h20'	5h30'	7h	7h	7h15	7h45'	7h45'	8h	10h20'	10h20'	11h15'	11h15'	11h30'	11h30'	23h	23h	25h	25h	29h30'	29h40'	
FG V (Small slow tunnelers)																							
C. nigritulus	5	13	49	7	6	26	16	19	16	191	78	106	12	13	82	0	534	11	82	0	7	18	0	1291
C. viridicollis	0	1	16	1	4	11	8	13	4	19	10	16	34	18	10	0	94	2	29	0	4	7	3	304
O. nr. sugillatus	0	0	6	6	10	5	2	21	2	17	10	30	18	40	31	0	43	13	17	1	9	13	5	299
O. lamelliger	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	4
O. corniculiger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
O. vinctus	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	5	12
O. fimetarius	0	0	1	1	15	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	1	22
O. aeruginosus	0	0	19	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	24
O. nr. pullus	0	0	0	1	2	2	0	0	6	7	5	2	0	0	2	0	9	9	2	1	1	0	0	49
O. pallidipennis	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3
O. obtusicornis	1	1	17	1	3	0	0	6	0	7	0	4	3	0	0	0	0	2	0	0	0	0	0	45
O. rasipennis	3	3	20	2	0	1	2	2	4	0	0	16	0	0	2	0	0	2	1	0	0	0	0	58
Onthophagus spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2		3	0	0	0	0	0	0	5
D. fastiditus	0	0	0	0	0	0	0	2	0	2	2	2	0	0	0	0	3	0	0	0	0	0	0	11
D. kirbyi	0	0	1	0	1	0	0	6	0	2	5	2	0	0	12	0	20	0	7	0	3	0	0	59
D. freyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	0	0	0	0	0	8
D. patrizii	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	4
E. zumpti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
M. apicalis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	16	1	24	16	62
T. spinipes	1	0	17	5	13	15	19	25	140	508	162	28	80	631	480	0	483	331	343	6	11	135	53	3486
S. costatus	0	0	0	3	11	5	1	6	0	30	27	0	6	27	19	0	17	0	20	2	0	9	10	193
Pedaria spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
																							0
FG VII (Dwellers)																							0
O. egrerius	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	1	5	0	1	11
O. formosus	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
O. planatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. alcyon	0	0	0	0	1	1	0	0	4	7	2	0	0	4	0	0	0	0	1	0	0	0	0	20
C. ambiguus	0	0	5	1	0	0	1	10	0	92	12	4	12	4	78	0	137	13	15	2	0	4	1	391
Aphodiinae spec.	11	32	1	147	874	7	9	21	94	147	75	18	0	249	25	0	40	548	1285	98	73	2343	850	6947
TOTAL																							
FG V	11	18	147	30	65	65	48	102	172	783	299	208	153	737	640	0	1215	372	506	32	39	210	93	5945
FG VII	11	32	6	148	875	8	10	33	100	248	89	22	12	257	103	0	177	561	1301	101	78	2347	852	7371

APPENDIX 4. FG I/II 12/96 TEMPORAL SUCCESSION IN ELEPHANT DUNG (DRY WEIGHT PER 2000G)

SAMPLE	11	16	44	46	47	8	14	18	36	37	40	13	6	35	38	41	42	43	45	7	12	39	17	TOTAL
TME PASSED	3h	3h10'	4h	5h20'	5h30'	7h	7h	7h15	7h45'	7h45'	8h	10h20'	10h20'	11h15'	11h15'	11h30'	11h30'	23h	23h	25h	25h	29h30'	29h40'	
FG I (Large Rollers)																								
K. nigroaeneus	5000	2500	2500	0	0	1250	0	0	0	2500	0	7500	0	0	0	0	3750	0	0	0	0	0	0	**25000**
K. subaeneus	0	2710	1355	2710	2710	0	0	0	0	2710	2710	0	0	0	0	0	0	0	1355	0	5420	0	0	**21680**
A. convexus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2360	**2360**
FG II (Small Rollers)																								
S. interstitialis	0	0	75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**75**
A. thalassinus	0	0	0	645	375	80	0	0	210	850	180	0	0	0	0	0	0	0	90	0	0	340	0	**2770**
G. nitens	0	825	3300	1375	4400	1100	1925	1650	0	12925	3300	3850	2475	0	0	0	1650	0	275	0	275	0	0	**39325**
N. calcaratus	0	0	15	0	0	0	0	26	0	215	30	0	0	60	64	0	252	40	26	0	0	0	0	**728**
N. fortuitus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	106	0	**106**
N. ruber	0	0	0	0	15	0	0	0	0	0	0	0	0	60	0	0	0	0	0	0	0	0	0	**75**
S. gazenus	140	0	50	0	10	0	20	20	0	70	30	0	0	0	50	0	90	0	70	0	10	20	0	**580**
S. goryi	0	0	5	0	0	0	0	10	0	10	0	0	0	20	0	0	55	0	0	0	0	0	0	**100**
S. costatus	0	0	90	0	0	12	24	134	0	0	0	162	120	0	0	0	42	0	0	0	0	0	0	**584**
TOTAL																								
FG I	5000	5210	3855	2710	2710	1250	0	0	0	5210	2710	7500	0	0	0	0	3750	0	1355	0	5420	0	2360	49040
FG II	140	825	3535	2020	4800	1192	1969	1840	210	14070	3540	4012	2595	140	114	0	2089	40	461	0	285	466	0	44343

APPENDIX 5. FG III/IV 12/96 TEMPORAL SUCCESSION IN ELEPHANT DUNG (DRY WEIGHT PER 2000G)

SAMPLE	11	16	44	46	47	8	14	18	36	37	40	13	6	35	38	41	42	43	45	7	12	39	17	TOTAL
TME PASSED	3h	3h10'	4h	5h20'	5h30'	7h	7h	7h15	7h45'	7h45'	8h	10h20'	10h20'	11h15'	11h15'	11h30'	11h30'	23h	23h	25h	25h	29h30'	29h40'	
FG III (Fast tunnelers)																								
H. andersoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12350	**12350**
H. neptunus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
C. philus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
C. amyntor	540	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	130	0	0	545	**1215**
C. evanidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
C. elphenor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
FG IV (Large slow tunnelers)																								
H. castalnaui	2895	965	4825	12545	9650	2895	0	16405	3860	4825	2895	5790	8685	3860	0	7720	5790	10615	4825	1930	0	4825	965	**116765**
O. uncinatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
O. viridulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2035	0	0	370	**2405**
O. fulgidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5520	1740	0	0	**7260**
O. picticollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	650	390	0	650	**1690**
O. alexis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	400	0	0	0	**400**
P. tersidorsis	0	0	1170	260	130	0	260	4680	0	2730	260	10140	3250	0	1560	0	4030	0	0	2080	0	0	390	**30940**
P. bicallosus	0	0	0	0	0	0	143	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**143**
P. rectefurcatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
P. ardea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
P. flavocinctus	0	0	33	144	191	234	588	276	1930	1755	2059	760	99	1489	980	0	363	146	335	189	0	66	559	**12196**
D. gazella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80	200	0	160	40	**480**
O. interstitialis	25	0	0	50	50	0	0	0	0	50	0	0	0	0	0	0	0	0	800	400	425	0	325	**2125**
E. intermedius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	**15**
L. militaris	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	**30**
TOTAL																								
FG III	**540**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**130**	**0**	**0**	**12895**	**13565**
FG IV	**2920**	**965**	**6028**	**12999**	**10021**	**3129**	**991**	**21361**	**5790**	**9390**	**5214**	**16690**	**12034**	**5349**	**2540**	**7720**	**10183**	**10761**	**6040**	**13419**	**2555**	**5051**	**3299**	**174449**

APPENDIX 6. FG V/VII 12/96 TEMPORAL SUCCESSION IN ELEPHANT DUNG (DRY WEIGHT PER 2000G)

SAMPLE	11	16	44	46	47	8	14	18	36	37	40	13	6	35	38	41	42	43	45	7	12	39	17	TOTAL
TME PASSED	3h	3h10'	4h	5h20'	5h30'	7h	7h	7h15	7h45'	7h45'	8h	10h20'	10h20'	11h15'	11h15'	11h30'	11h30'	23h	23h	25h	25h	29h30'	29h40'	
FG V (Small slow tunnelers)																								
C. nigritulus	5	13	49	7	6	26	16	19	16	191	78	106	12	13	82	0	534	11	82	0	7	18	0	1291
C. viridicollis	0	1	16	1	4	11	8	13	4	19	10	16	34	18	10	0	94	2	29	0	4	7	3	304
O. nr. sugillatus	0	0	6	6	10	5	2	21	2	17	10	30	18	40	31	0	43	13	17	1	9	13	5	299
O. lamelliger	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	12
O. corniculiger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
O. vinctus	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0	25	60
O. fimetarius	0	0	5	5	75	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	5	110
O. aeruginosus	0	0	95	0	0	0	0	10	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	120
O. nr. pullus	0	0	0	1	2	2	0	0	6	7	5	2	0	0	2	0	9	9	2	1	1	0	0	49
O. pallidipennis	0	0	5	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	15
O. obtusicornis	10	10	170	10	30	0	0	60	0	70	0	40	30	0	0	0	0	20	0	0	0	0	0	450
O. rasipennis	3	3	20	2	0	1	2	2	4	0	0	16	0	0	2	0	0	2	1	0	0	0	0	58
Onthophagus spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2		3	0	0	0	0	0	0	5
D. fastiditus	0	0	0	0	0	0	0	2	0	2	2	2	0	0	0	0	3	0	0	0	0	0	0	11
D. kirbyi	0	0	1	0	1	0	0	6	0	2	5	2	0	0	12	0	20	0	7	0	3	0	0	59
D. freyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	4
D. patrizii	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	12
E. zumpti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
M. apicalis	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	160	10	240	160	615
T. spinipes	5	0	85	25	65	75	95	125	700	2540	810	140	400	3155	2400	0	2415	1655	1715	30	55	675	265	17430
S. costatus	0	0	0	105	385	175	35	210	0	1050	945	0	210	945	665	0	595	0	700	70	0	315	350	6755
Pedaria spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	5
FG VII (Dwellers)																								
O. egrerius	0	0	0	0	0	0	0	130	0	130	0	0	0	0	0	0	0	0	0	65	325	0	65	715
O. formosus	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
O. planatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. alcyon	0	0	0	0	20	20	0	0	80	140	40	0	0	80	0	0	0	0	20	0	0	0	0	400
C. ambiguus	0	0	250	50	0	0	50	500	0	4600	600	200	600	200	3900	0	6850	650	750	100	0	200	50	19550
Aphodiinae spec.	29	24	1	130	797	5	5	12	120	129	61	81	0	169	26	0	32	545	1280	321	571	2376	873	7587
TOTAL																								
FG V	26	27	452	182	578	295	158	468	732	3898	1865	364	704	4203	3206	0	3734	1713	2593	297	98	1272	813	27678
FG VII	29	24	251	180	817	25	55	642	220	4999	701	281	600	449	3926	0	6882	1195	2050	486	896	2576	988	28272

APPENDIX 7. FG I/II 12/96 NIGHT SAMPLES							
TEMPORAL SUCCESSION IN ELEPHANT DUNG (NUMBER OF INDIVIDUALS PER 2000G)							
SAMPLE	53	54	55	56	57	52	TOTAL
TME PASSED	5h15'	5h15'	5h30'	5h30'	5h30'	11h30'	
FG I (Large Rollers)							
K. nigroaeneus	0	0	0	0	1	0	1
K. subaeneus	0	0	0	0	0	0	0
A. convexus	7	2	0	2	2	0	13
FG II (Small Rollers)							
S. interstitialis	0	0	0	0	0	0	0
A. thalassinus	0	0	0	0	0	0	0
G. nitens	0	0	0	0	0	0	0
N. calcaratus	0	0	0	0	0	0	0
N. fortuitus	0	0	0	0	0	0	0
N. ruber	0	0	0	0	0	0	0
S. gazenus	0	0	0	0	0	0	0
S. goryi	0	0	0	0	0	2	2
S. costatus	0	0	0	0	0	0	0
TOTAL							
FG I	7	2	0	2	3	0	14
FG II	0	0	0	0	0	2	2

APPENDIX 8. FG I/II 12/96 NIGHT SAMPLES							
TEMPORAL SUCCESSION IN ELEPHANT DUNG (DRY WEIGHT PER 2000G)							
SAMPLE	53	54	55	56	57	52	TOTAL
TME PASSED	5h15'	5h15'	5h30'	5h30'	5h30'	11h30'	
FG I (Large Rollers)							
K. nigroaeneus	0	0	0	0	1250	0	1250
K. subaeneus	0	0	0	0	0	0	0
A. convexus	8260	2360	0	2360	2360	0	15340
FG II (Small Rollers)							
S. interstitialis	0	0	0	0	0	0	0
A. thalassinus	0	0	0	0	0	0	0
G. nitens	0	0	0	0	0	0	0
N. calcaratus	0	0	0	0	0	0	0
N. fortuitus	0	0	0	0	0	0	0
N. ruber	0	0	0	0	0	0	0
S. gazenus	0	0	0	0	0	0	0
S. goryi	0	0	0	0	0	10	10
S. costatus	0	0	0	0	0	0	0
TOTAL							
FG I	8260	2360	0	2360	3610	0	16590
FG II	0	0	0	0	0	10	10

APPENDIX 9. FG III/IV 12/96 NIGHT SAMPLES							
TEMPORAL SUCCESSION IN ELEPHANT DUNG (NUMBER OF INDIVIDUALS PER 2000G)							
SAMPLE	53	54	55	56	57	52	TOTAL
TME PASSED	5h15'	5h15'	5h30'	5h30'	5h30'	11h30'	
FG III (Fast tunnelers)							
H. andersoni	3	0	2	1	1	1	8
H. neptunus	0	0	0	0	0	0	0
C. philus	0	0	0	0	0	0	0
C. amyntor	8	4	2	12	5	3	34
C. evanidus	2	1	0	0	5	3	11
C. elphenor	0	0	2	0	0	0	2
FG IV (Large slow tunnelers)							
H. castalnaui	0	0	2	0	0	12	14
O. uncinatus	2	1	0	0	1	0	4
O. viridulus	5	8	3	1	1	0	18
O. fulgidus	7	52	38	21	4	0	122
O. picticollis	2	9	7	2	18	0	38
O. alexis	0	0	0	0	3	0	3
P. tersidorsis	0	0	0	0	0	0	0
P. bicallosus	0	0	0	0	0	0	0
P. rectefurcatus	0	0	0	0	0	0	0
P. ardea	0	0	0	0	0	0	0
P. flavocinctus	0	0	0	0	0	0	0
D. gazella	0	0	0	0	8	1	9
O. interstitialis	23	215	90	36	230	10	604
E. intermedius	0	0	0	0	0	0	0
L. militaris	0	0	0	0	0	0	0
TOTAL							
FG III	13	5	6	13	11	7	55
FG IV	39	285	140	60	265	23	812

APPENDIX 10. FG III/IV 12/96 NIGHT SAMPLES							
TEMPORAL SUCCESSION IN ELEPHANT DUNG (DRY WEIGHT PER 2000G)							
SAMPLE	53	54	55	56	57	52	TOTAL
TME PASSED	5h15'	5h15'	5h30'	5h30'	5h30'	11h30'	
FG III (Fast tunnelers)							
H. andersoni	13740	0	7430	2460	3715	4580	31925
H. neptunus	0	0	0	0	0	0	0
C. philus	0	0	0	0	0	0	0
C. amyntor	1165	420	160	1810	675	465	4695
C. evanidus	130	65	0	0	325	195	715
C. elphenor	0	0	780	0	0	0	780
FG IV (Large slow tunnelers)							
H. castalnaui	0	0	1930	0	0	11580	13510
O. uncinatus	540	270	0	0	270	0	1080
O. viridulus	925	1680	555	185	185	0	3530
O. fulgidus	2205	15330	11520	6615	1260	0	36930
O. picticollis	260	1170	1020	260	2340	0	5050
O. alexis	0	0	0	0	435	0	435
P. tersidorsis	0	0	0	0	0	0	0
P. bicallosus	0	0	0	0	0	0	0
P. rectefurcatus	0	0	0	0	0	0	0
P. ardea	0	0	0	0	0	0	0
P. flavocinctus	0	0	0	0	0	0	0
D. gazella	0	0	0	0	320	40	360
O. interstitialis	575	5375	2250	900	5750	250	15100
E. intermedius	0	0	0	0	0	0	0
L. militaris	0	0	0	0	0	0	0
TOTAL							
FG III	15035	485	8370	4270	4715	5240	38115
FG IV	4505	23825	17275	7960	10560	11870	75995

APPENDIX 11. FG V/VII 12/96 NIGHT SAMPLES							
TEMPORAL SUCCESSION IN ELEPHANT DUNG (NUMBER OF INDIVIDUALS PER 2000G)							
SAMPLE	53	54	55	56	57	52	TOTAL
TME PASSED	5h15'	5h15'	5h30'	5h30'	5h30'	11h30'	
FG V (Small slow tunnelers)							
C. nigritulus	0	4	0	1	3	1	9
C. viridicollis	0	0	0	0	0	1	1
O. nr. sugillatus	3	0	0	0	6	2	11
O. lamelliger	6	38	12	3	24	0	83
O. corniculiger	0	2	2	0	2	0	6
O. vinctus	52	28	0	3	43	0	126
O. fimetarius	14	84	43	32	70	1	244
O. aeruginosus	2	0	0	0	0	0	2
O. interstitialis	7	0	0	0	0	0	7
O. nr. pullus	0	0	0	0	0	0	0
O. pallidipennis	0	0	0	0	0	0	0
O. obtusicornis	0	0	0	0	0	0	0
O. rasipennis	0	1	0	2	1	0	4
Onthophagus spec.	0	0	0	0	0	0	0
D. fastiditus	0	0	0	0	0	0	0
D. kirbyi	0	0	0	0	0	0	0
D. freyi	0	0	0	0	0	0	0
D. patrizii	0	0	0	0	0	0	0
E. zumpti	0	0	0	0	0	0	0
M. apicalis	62	231	153	82	300	0	828
T. spinipes	0	0	0	0	0	0	0
S. costatus	0	0	0	0	0	0	0
Pedaria spec.	0	0	0	0	1	2	3
FG VII (Dwellers)							
O. egrerius	0	0	0	0	0	0	0
O. formosus	0	0	0	0	0	0	0
O. planatus	0	0	0	0	0	0	0
H. alcyon	0	0	0	0	0	0	0
C. ambiguus	0	0	0	0	0	0	0
Aphodiinae spec.	115	174	25	24	323	371	1032
TOTAL							
FG V	146	388	210	123	450	7	1324
FG VII	115	174	25	24	323	371	1032

APPENDIX 12. FG V/VII 12/96 NIGHT SAMPLES							
TEMPORAL SUCCESSION IN ELEPHANT DUNG (DRY WEIGHT PER 2000G)							
SAMPLE	53	54	55	56	57	52	TOTAL
TME PASSED	5h15'	5h15'	5h30'	5h30'	5h30'	11h30'	
FG V (Small slow tunnelers)							
C. nigritulus	0	4	0	1	3	1	9
C. viridicollis	0	0	0	0	0	1	1
O. nr. sugillatus	3	0	0	0	6	2	11
O. lamelliger	18	114	36	9	72	0	249
O. corniculiger	0	20	20	0	20	0	60
O. vinctus	260	140	0	15	215	0	630
O. fimetarius	70	420	215	160	350	5	1220
O. aeruginosus	10	0	0	0	0	0	10
O. interstitialis	35	0	0	0	0	0	35
O. nr. pullus	0	0	0	0	0	0	0
O. pallidipennis	0	0	0	0	0	0	0
O. obtusicornis	0	0	0	0	0	0	0
O. rasipennis	0	1	0	2	1	0	4
Onthophagus spec.	0	0	0	0	0	0	0
D. fastiditus	0	0	0	0	0	0	0
D. kirbyi	0	0	0	0	0	0	0
D. freyi	0	0	0	0	0	0	0
D. patrizii	0	0	0	0	0	0	0
E. zumpti	0	0	0	0	0	0	0
M. apicalis	620	2310	1530	820	2990	0	8270
T. spinipes	0	0	0	0	0	0	0
S. costatus	0	0	0	0	0	0	0
Pedaria spec.	0	0	0	0	5	10	15
FG VII (Dwellers)							
O. egrerius	0	0	0	0	0	0	0
O. formosus	0	0	0	0	0	0	0
O. planatus	0	0	0	0	0	0	0
H. alcyon	0	0	0	0	0	0	0
C. ambiguus	0	0	0	0	0	0	0
Aphodiinae spec.	222	612	460	24	783	341	2442
TOTAL							
FG V	1016	3009	1801	1007	3662	19	10514
FG VII	222	612	460	24	783	341	2442

APPENDIX 13. FG I/II SEASONALITY											
NUMBER OF INDIVIDUALS PER 2000G ELEPHANT DUNG											
DATE	Nov '96	DEC '96	FEB '97	MAR '97	APR '97	MAY '97	JUL '97	AUG '97	SEP '97	OCT '97	TOTAL
FG I (Large Rollers)											
K. nigroaeneus	3	1,1	4	9	0,5	0	0	0	0	4	21,6
K. subaeneus	12	0,4	8	14	1	0	0	0	0	3	38,4
A. convexus	0	2,6	2	0	0	0	0	0	0	0	4,6
FG II (Small Rollers)											
S. interstitialis	0	0	0	0	0	0	0	0	0	0	0
A. thalassinus	0	1,6	0	0	0	0	0	0	0	0	1,6
G. nitens	1,5	9,5	0	3,5	0	0	0	0	0	2	16,5
N. calcaratus	0	5,1	0	2	0	0	0	0	0	0	7,1
N. fortuitus	0	0,3	0	0	0	0	0	0	0	0	0,3
N. ruber	0	0,4	0	0	0	0	0	0	0	0	0,4
S. gazenus	0	2,5	0	3,5	0	0	0	0	0	1	7
S. goryi	0	1,7	0	1,8	0	0	0	0	0	0	3,5
S. costatus	0	14,6	0	30	1,5	1	0	0	0,5	2	49,6
TOTAL											
FG I	15	4,1	14	23	1,5	0	0	0	0	7	64,6
FG II	1,5	35,7	0	40,8	1,5	1	0	0	0,5	5	86

APPENDIX 14. FG I/II SEASONALITY											
NUMBER OF INDIVIDUALS PER 2000G RHINO DUNG											
DATE	Nov '96	DEC '96	FEB '97	MAR '97	APR '97	MAY '97	JUL '97	AUG '97	SEP '97	OCT '97	TOTAL
FG I (Large Rollers)											
K. nigroaeneus	5	0,5	1	2,3	0	0,3	0	0	0,7	7,3	17,1
K. subaeneus	17,5	7,5	2	12	2,5	0,3	0	0	0,7	4,7	47,2
A. convexus	0	1	0	0	0	0	0	0	0,3	1	2,3
FG II (Small Rollers)											
S. interstitialis	0	0	0	0	0	0	0	0	0	0	0
A. thalassinus	1	0	0	0,25	0	0	0	0	0	0	1,25
G. nitens	10,5	13	3,3	4,75	0,5	0	0	0	0	3,3	35,35
N. calcaratus	0	3,5	0	0	0,5	0	0	0	0	0,3	4,3
N. fortuitus	1	0	0	0	0	0	0	0	0	0	1
N. ruber	0	0	0	0	0	0	0	0	0	0	0
S. gazenus	4	1	0	0,5	0	0	0	0	0	0	5,5
S. goryi	1	0	0	0,5	0	0	0	0	0	0	1,5
S. costatus	1	0	0	4,3	0	0	0	0	0	6,3	11,6
TOTAL											
FG I	22,5	9	3	14,3	2,5	0,6	0	0	1,7	13	66,6
FG II	18,5	17,5	3,3	10,3	1	0	0	0	0	9,9	60,5

APPENDIX 15. FG III/IV SEASONALITY											
NUMBER OF INDIVIDUALS PER 2000G ELEPHANT DUNG											
DATE	Nov '96	DEC '96	FEB '97	MAR '97	APR '97	MAY '97	JUL '97	AUG '97	SEP '97	OCT '97	TOTAL
FG III (Fast tunnelers)											
H. andersoni	0,5	1,4	0	0,5	0	0	0	0	0	0	**2,4**
H. neptunus	0	0	0	0	0	0	0	0	0	0	**0**
C. philus	0	0	0	0,3	0	0	0	0	0	0	**0,3**
C. amyntor	4	6,1	10	7	0	0	0	1	0	0	**28,1**
C. evanidus	0	1,6	0	0	0,5	0	0	0	0	0	**2,1**
C. elphenor	0	0,4	0	0	0	0	0	0	0	0	**0,4**
FG IV (Large slow tunnelers)											
H. castalnaui	1	5,2	6	0	1,5	0	0	0	0	0	**13,7**
O. uncinatus	0	0,8	0	0	0	0	0	0	0	0	**0,8**
O. viridulus	0	3,6	0	0	0,5	0	0	0	0	0	**4,1**
O. fulgidus	0	24,4	0	0	0	0	0	0	0	0	**24,4**
O. picticollis	0	7,6	0	0	0,5	0	0	0	0	0	**8,1**
O. alexis	0	0,6	0	0	0	0	0	0	0	0	**0,6**
P. tersidorsis	41	18,8	0	5,3	0	0	0	0	0	0	**65,1**
P. bicallosus	0	0,1	0	0	0	0	0	0	0	0	**0,1**
P. rectefurcatus	0	0	0	0	0	0	0	0	0	0	**0**
P. ardea	0,5	0	0	0	0	0	0	0	0	0	**0,5**
P. flavocinctus	3	25,9	0	1,5	0	0	0	0	0	0	**30,4**
D. gazella	0,5	1,6	0	0	0	0	0	0	0	0	**2,1**
O. interstitialis	9,5	188,8	0	0	0,5	0,3	0	0	0,5	0	**199,6**
E. intermedius	0	0,2	0	6	0	1	0	0	0,5	0	**7,7**
L. militaris	0	0,2	0	0	0	0	0	0	0	0	**0,2**
TOTAL											
FG III	4,5	9,5	10	7,8	0,5	0	0	1	0	0	33,3
FG IV	55,5	277,8	6	12,8	3	1,3	0	0	1	0	357,4

APPENDIX 16. FG III/IV SEASONALITY										
NUMBER OF INDIVIDUALS PER 2000G RHINO DUNG										
DATE	Nov '96	DEC '96	FEB '97	MAR '97	APR '97	MAY '97	JUL '97	AUG '97	SEP '97	OCT '97	TOTAL
FG III (Fast tunnelers)											
H. andersoni	0	0	0	0,5	1,5	1	0	0	0	0	**3**
H. neptunus	0	0	0	0	0,5	0,3	0	0	0	0	**0,8**
C. philus	0	0	0	0	0	0	0	0	0	0	**0**
C. amyntor	1,5	8	2	38	2	2,4	1,3	0	7,5	0,5	**63,2**
C. evanidus	0	0	0	1,5	0	0	0	0	0	0	**1,5**
C. elphenor	0	1	0,5	1	0	0	0	0	2	0	**4,5**
FG IV (Large slow tunnelers)											
H. castalnaui	2	3,5	2,6	4,7	2	0	0	0	0	0	**14,8**
O. uncinatus	0,5	0	0	0	0	0	0	0	0	0	**0,5**
O. viridulus	0,5	0	0	3	7,5	0	0,3	0	1	6,5	**18,8**
O. fulgidus	0	0	0	6	5,5	0	0	0	0	0	**11,5**
O. picticollis	0	0	3,5	13,5	5	0	0	0	0	4,5	**26,5**
O. alexis	0	0	0	4	0	0	0	0	0	0,5	**4,5**
P. tersidorsis	321	96,5	0	24	7	0	0	0	1	1,3	**450,8**
P. bicallosus	1,5	1	0	0	0	0	0	0	0	0	**2,5**
P. rectefurcatus	0,5	0	0	0	0	0	0	0	0	0	**0,5**
P. ardea	1	0,5	0	0	0	0	0	0	0	0	**1,5**
P. flavocinctus	87,5	57	0	0,5	0	0	0	0	0	0,3	**145,3**
D. gazella	4,5	1	0	26,5	0	0	0	0	6	3,5	**41,5**
O. interstitialis	229	1	0	14	2,5	0,3	4,7	2,5	37,5	64,5	**356**
E. intermedius	0	1	0	0,8	0	0	0	0	0	0,3	**2,1**
L. militaris	0	0,5	0	0,3	0	0	0	0	0	0	**0,8**
TOTAL											
FG III	1,5	9	2,5	41	4	3,7	1,3	0	9,5	0,5	73
FG IV	648	162	6,1	97,3	29,5	0,3	5	2,5	45,5	81,4	1077,6

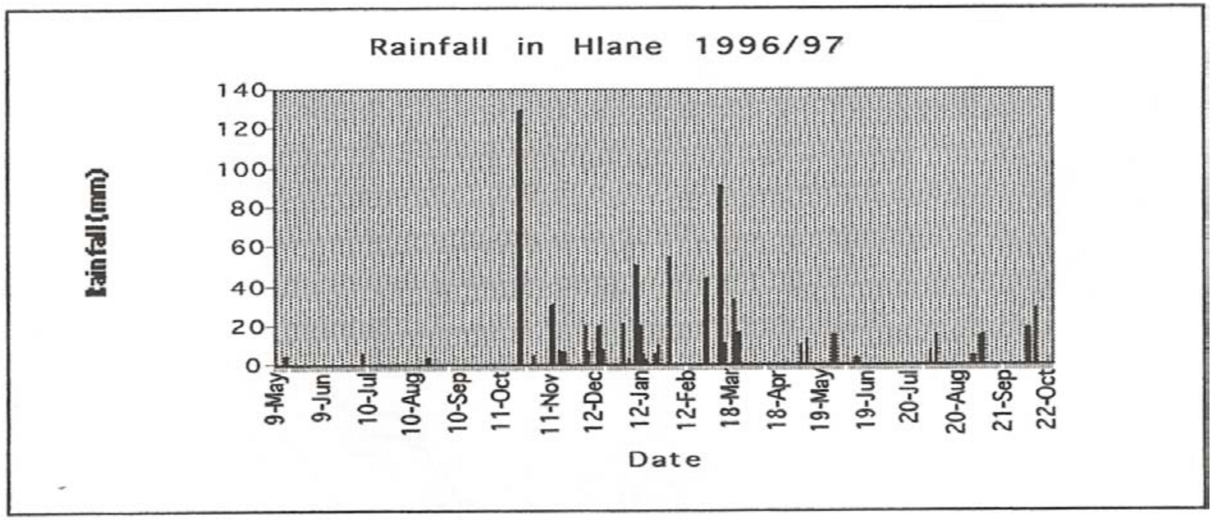
APPENDIX 17. FG V & VII SEASONALITY											
NUMBER OF INDIVIDUALS PER 2000G ELEPHANT DUNG											
DATE	**Nov '96**	**DEC '96**	**FEB '97**	**MAR '97**	**APR '97**	**MAY '97**	**JUL '97**	**AUG '97**	**SEP '97**	**OCT '97**	**TOTAL**
FG V (Small slow tunnelers)											
C. nigritulus	33	99,4	8	112,5	5	5	0	0	1	37	300,9
C. viridicollis	0	19,8	0	140,3	10,5	5,5	0	0	3	1	180,1
O. nr. sugillatus	37,5	19,9	0	22	2,5	11	1,5	0	11,5	12	117,9
O. lamelliger	0	12,1	0	0	0,5	2	0	0	0	0	14,6
O. corniculiger	0	1,2	0	0	0	0	0	0	0	0	1,2
O. vinctus	2	25,2	0	0	0	4	0	0	0	0	31,2
O. fimetarius	0	48,6	0	0	0	0	0	0	0	0	48,6
O. aeruginosus	0	0,5	0	4,3	0,5	33	0	0	0	1	39,3
O. interstitialis	0	1,4	0	0	0	2	0	0	0	0	3,4
O. nr. pullus	1	3	0	5,8	3	1,5	0	0	1,5	4	19,8
O. pallidipennis	0,5	0,2	0	1	0	0	0	0	0	0	1,7
O. obtusicornis	1	1,8	0	3,3	0	0	0	0	3,5	2	11,6
O. rasipennis	0,5	2,5	0	116,5	0	0	0	0	0	31	150,5
Onthophagus spec.	0	0,5	0	0	0	0	0	0	0	0	0,5
D. fastiditus	0	1	0	0	0,5	0	1,5	0	0	0	3
D. kirbyi	0	4,3	0	0,5	0	1	4,5	1	2	1	14,3
D. freyi	0	0,5	0	1	2,5	0	4,5	0,6	3	0	12,1
D. patrizii	0	0,4	0	0	0	0	0	0	0	0	0,4
E. zumpti	0	0	0	0,5	0,5	0	0	0	0	0	1
M. apicalis	1	165,6	0	0	0	4	0	0	0	0	170,6
T. spinipes	7	233,7	0	211,3	20,5	17,5	0	1,7	51,5	14	557,2
S. costatus	14,5	12,5	0	1	0	0	0	0	3,5	2	33,5
Pedaria spec.	0	0,2	0	0	0	0	0	0	0	0	0,2
FG VII (Dwellers)											
O. egrerius	0	1,2	0	0	0	0	0	0	0	0	1,2
O. formosus	0	0,2	0	0	0	0	0	0	0	0	0,2
O. planatus	0	0	0	0	0	0	0	0	0	0	0
H. alcyon	0	1,6	0	1	0	0	0	0	0	0	2,6
C. ambiguus	3	31,8	2	0,5	5,5	2	0	0	0,5	0	45,3
Aphodiinae spec.	29,5	161,3	107	6,3	21,5	37	7,5	2,7	31,5	4	408,3
TOTAL											
FG V	98	654,3	8	620	46	86,5	12	3,3	80,5	105	1713,6
FG VII	32,5	196,1	109	7,8	27	39	7,5	2,7	32	4	457,6

APPENDIX 18. FG V & VII SEASONALITY

NUMBER OF INDIVIDUALS PER 2000G RHINO DUNG

DATE	Nov '96	DEC '96	FEB '97	MAR '97	APR '97	MAY '97	JUL '97	AUG '97	SEP '97	OCT '97	TOTAL
FG V (Small slow tunnelers)											
C. nigritulus	143,5	56,5	5,6	107,8	12,5	3	0	0	3,3	39,7	371,9
C. viridicollis	0	89	1,3	153,8	6	0,3	0	0	0	8,7	259,1
O. nr. sugillatus	123	17	0	5,3	1,5	0,3	0,7	0	1,7	15	164,5
O. lamelliger	0	0	0	6	0,5	0	0	0	0	0	6,5
O. corniculiger	8,5	2	0	0	0	0	0	0	0	0	10,5
O. vinctus	88,5	0	0	5	3	0	0	0,5	5,5	6,5	109
O. fimetarius	0	1	0	0,8	0,5	0	0	0	0	2	4,3
O. aeruginosus	0	0	0	0,3	0	4	0	0	0,7	0,3	5,3
O. interstitialis	0	0	0	0	0	0	0	0	0	0	0
O. nr. pullus	1	2	0	2	2	1,7	0	0	0,3	1,7	10,7
O. pallidipennis	0	0	0	0	0	0	0	0	0	0	0
O. obtusicornis	0	0	0	0	0	0,3	0	0	0	0	0,3
O. rasipennis	5,5	0,5	1	0,5	0	0	0	0	0	0	7,5
Onthophagus spec.	0	0	0	0,8	0	0	0	0	0	0	0,8
D. fastiditus	0	2,5	0	0,5	0	0	0	0	1	0	4
D. kirbyi	2	7	0,3	3	2	0,7	0	0,5	1,3	2,7	19,5
D. freyi	0	0,5	0	2	5,5	1	0,6	0,5	4,3	5	19,4
D. patrizii	0	0	0	0	0	0	0	0	0	0	0
E. zumpti	0	1	0	1,5	2,5	0	0	0	0	0,3	5,3
M. apicalis	59	7	0	21	1,5	0,3	0	0	6,5	7,5	102,8
T. spinipes	139	271	4,3	128,3	23	8,3	1,3	0,5	24,7	23	623,4
S. costatus	78	44	0	7,5	0	0	0	0	26,3	25,7	181,5
Pedaria spec.	0,5	1	0	9,5	0	0	0	0	0	0	11
FG VII (Dwellers)											
O. egrerius	0	0,5	0	0,3	0	0	0	0	0	0	0,8
O. formosus	0	0	0	0	0	0	0	0	0	0	0
O. planatus	0	1,5	0	0,8	0,3	0	0,7	0	0	0,3	3,6
H. alcyon	0,5	0,5	0	0	0	0	0	0	0	0,3	1,3
C. ambiguus	12,5	38,5	0,3	19,8	9,5	6	0,7	0,5	2	4	93,8
Aphodiinae spec.	11,5	88,5	2,3	179,3	24	22,6	1	2	9	32,8	373
TOTAL											
FG V	648,5	502	12,5	455,6	60,5	19,9	2,6	2	75,6	138,1	1917,3
FG VII	24,5	129,5	2,6	200,2	33,8	28,6	2,4	2,5	11	37,4	472,5

Appendix 19.


Rainfall in Hlane 1996/97
140
120
100
80
60
40
20
0
Rainfall (mm)
9-May
9-Jun
10-Jul
10-Aug
10-Sep
11-Oct
11-Nov
12-Dec
12-Jan
12-Feb
18-Mar
18-Apr
19-May
19-Jun
20-Jul
20-Aug
21-Sep
22-Oct
Date