An annotated checklist of dung-associated beetles of the Savanna Ecosystem Project study area, Nylsvley

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PREFACE

The Savanna Ecosystem Project of the National Programme for Environmental Sciences is one of several national scientific programmes administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The Savanna Ecosystem Project being carried out at Nylsvley is a joint undertaking of more than fifty scientists from the Department of Agriculture, the Transvaal Provincial Administration, the CSIR, the Transvaal Museum, and eight universities. As far as possible, participating laboratories finance their own research within the project. The shared facilities at the study area and the research of participating universities and museums are financed from a central fund administered by the National Committee for Environmental Sciences and contributed largely by the Department of Environment Affairs.

The research programme of the Savanna Ecosystem Project has been divided into three phases - Phase I (mid-1974 to mid-1976) - a pilot study of the Nylsvley study area, in particular the description and quantification of structural features of the ecosystem, Phase II (mid-1976 to 1979) - studies in the key components and processes including the development of mathematical models, and Phase III (1979 to 1984) - extension to other sites and the study of management strategies for the optimal utilization of Burkea savanna ecosystems.

The present report forms part of the description and quantification of the structural features of the ecosystem, focusing on the species richness, relative abundance, impact and seasonality of coprophagous and saprophagous beetles (Coleoptera).

ACKNOWLEDGEMENTS

I extend my sincere thanks to Drs P Basilewsky, S Endrödi, M Mroczkowsky and R zur Strassen, and Messrs Y Cambefort, C Scholtz and J Therond who have offered their knowledge and helped generously by identifying the large, and often monotonous amount of material sent to them; to Mrs W Breytenbach and Mrs E Labuschagne who helped with the collecting and processing of the material, and to Mr M Smit for permission to work on his farm.

ABSTRACT

A study of the composition, biology and impact of the arthropod fauna associated with dung and other decaying matter was carried out on the Nylsvley Nature Reserve and on a neighbouring farm from June 1975 to July 1976. A total of 100 638 specimens of dung- and carrion beetles was collected. In the families Scarabaeidae, Trogidae and Dermestidae 78 species have so far been identified, all but five of which have been named. The presence of further, as yet unidentified, species among this material is likely to increase the list of known species substantially. The geographic distribution, habitat and food preferences, and seasonal activity of the 78 identified species are given.

SAMEVATTING

'n Studie van die samestelling, biologie en impak van die geleedpotige fauna wat met mis en ander verrottende materiaal geassosieer word, is vanaf Junie 1975 tot Julie 1976 op die Nylsvley Natuurreservaat en 'n aangrensende plaas uitgevoer. 'n Totaal van 100 638 voorbeelde van miskruiers en aaskewers is bymekaargemaak. In die families Scarabaeidae, Trogidae en Dermestidae, is 78 spesies reeds tot dusver geïdentifiseer, waarvan almal behalwe vyf benoem is. Die teenwoordigheid van verdere, nog ongeïdentifiseerde spesies onder hierdie materiaal sal waarskynlik die lys van bekende spesies aansienlik opstoot. Die geografiese verspreiding, habitat en voedselvoorkeure en seisoenale aktiwiteit van die 78 geïdentifiseerde spesies word aangegee.

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INTRODUCTION

As an end-product of digestive processes in animals, excreta comprises a mass of partially digested and undigested food material which varies widely in chemical composition, consistency, moisture content, size, shape and mass. This unique and discrete resource is exploited by plants, such as fungi, and by a variety of invertebrates, including large groups of beetles. Some groups, namely the subfamilies Scarabaeinae and Aphodiinae of the Scarabaeidae, are exclusively or almost entirely specialized dung feeders. Others, such as the Sphaeridiinae of the family Hydrophilidae, are specialized predators on dung feeders.

An expanding diversity of animals has resulted in an expanding diversity of species utilizing animal excreta. In Africa particularly, with the world's most numerous and diverse large ungulate fauna, diversification among coprophagous beetles has been extensive. The extent of this is demonstrated by the number of species in the coprophagous genera Onthophagus and Aphodius which are amongst the largest genera in the animal kingdom. This diversification involves specialization on different kinds and ages of dung, to habitat, and to climate. Further specialization has taken place in the way a single dung pile is used and involves vertical stratification, feeding method and breeding chamber construction.

During the period June 1975 to July 1976 the composition, biology and impact of arthropod dung users were studied on and around the Nylsvley Provincial Nature Reserve in the northern Transvaal as part of the South African Savanna Ecosystem Project. Detailed results are given in Endrödy-Younga (1982). The present report comprises a checklist of the more important species of dung-associated beetles in the families Scarabaeidae, Trogidae and Dermestidae. For each species, summarized information is given (when known) on the geographic distribution, habitat preferences, apparent food preferences and seasonal activity.

STUDY AREA

The study was carried out at the Savanna Ecosystem Project study site on the Nylsvley Provincial Nature Reserve (24°29'S, 28°42'E) and on an adjacent farm, Blindefontein (Smit's farm). The study area consists of a sandy plateau underlain by sandstones and conglomerates of the Waterberg System. These outcrop in the central study area as a low hill, Maroelakop (1 140 m asl). From the plateau the land surface drops gently downwards to the bottomlands of the Nyl River floodplain (1 080 m asl) consisting of compacted loams and clays. The surrounding landscape is gently undulating with low hills.

The climate has been summarized by Anon (1975), and Huntley and Morris (1978). The area is semi-arid with three distinct seasons: a hot, dry season from August to October (mean daily maximum temperature ($\bar{T}_{max}$)

27,6° C; mean daily minimum temperature ($\bar{T}_{min}$) 8,6° C), a hot, wet season from November to April ($\bar{T}_{max}$ 29,2° C, $\bar{T}_{min}$ 14,5° C) and a cool, dry season from May to July ($\bar{T}_{max}$ 22,3° C, $\bar{T}_{min}$ 2,6° C). Mean annual rainfall is 630 mm, falling mainly from November to April and mean annual temperature is 18,6° C.

The soils and vegetation of the reserve have been classified and mapped by Harmse (1977) and Coetzee et al (1976) respectively. The soils on the plateau are derived from Waterberg sandstone and are generally sandy and highly leached. They support a deciduous broadleafed savanna woodland which has been classified as Eragrostis pallens-Burkea africana tree savanna with Burkea africana and Terminalia sericea the dominant trees, Ochna pulchra and Grewia flavescens the dominant shrubs and Eragrostis pallens the dominant grass. Interspersed in the woodland are patches of leptophyllous thorntree savanna on what are believed to be sites of African villages abandoned at least 50 years ago. The sandy soils are more compacted and richer in certain minerals, such as P, K and Ca, than are the soils underlying the adjacent Burkea-dominated savanna (Harmse 1977). The dominant plants are the trees Acacia tortilis, A nilotica and Dichrostachys cinerea, and the grass Eragrostis lehmanniana. On the shallow lithosols of Maroelakop and surrounding outcrops there is a broadleafed tree savanna with Diplorhynchus condylocarpon the dominant tree and Barleria bremekampii the dominant shrub.

Between the sandy plateau and the Nyl River there is an expanse of seasonally flooded grassland ("turf vlei") underlain by vertic clays derived from basalt. The dominant plants are the grasses Setaria woodii, Dicanthium papillosum and Aristida bipartita, and the sedge Scirpus dregeanus. Adjacent to the Nyl river there are compacted loams and calcerous clays derived from alluvium on which grows an extensive leptophyllous tree and grass savanna. The dominant trees are Acacia spp (particularly A tortilis, A karroo and A mellifera), Ziziphus mucronata, Rhus pyroides and Boscia foetida. The shrubs Carissa bispinosa and Euclea undulata are prominent on termitaria while the grass Sporobolus ioclados and the forb Ocimum canum are characteristic species of the herbaceous stratus in open seasonally flooded plains in this woodland.

Huntley (1977) has suggested that the Acacia-dominated savanna is related biogeographically to the arid savannas of south-western Africa, while the broadleafed Burkea-dominated savanna of the plateau is related to the mesic and moist broadleafed savannas of central Africa. As such, the Nylsvley area represents a tension zone between these two major savanna types. The biogeographic affinities of the flora and fauna are correspondingly mixed.

METHODS

A detailed description of the collection techniques and apparatus is given in Endrödy-Younga (1982) and only a brief summary is given here.

Faunal monitoring

The composition of the dung-associated beetle fauna was studied partly from samples collected during specific experiments (see below) and partly from material obtained during check-sampling at other times.

Site selection of dung-associated beetles

Sets of baited groundtraps were operated continuously at four different sites representing some of the different biotopes of the Nylsvley area: in open secondary grassland with scattered Dichrostachys cinerea and Acacia tortilis bushes (Smit's farm); in the grasslands of turf vlei; and at two sites in the deciduous broadleafed savanna of the SASEP study area: one near the weather station in typical Burkea africana woodland with an extensive shrub layer, the other in a more open variation of Burkea woodland at the base of Maroelakop, where there is a virtual absence of shrubs in the understorey.

Food selection of dung-associated beetles

The site selection experiments were carried out with four different baits: human faeces, rotten meat, fermenting banana and cattle dung. These baits represent a range of food types: omnivore faeces, carcass, fermenting fruit and herbivore dung respectively. The baits were placed in cups in plastic buckets filled with ethylene glycol. The mouth of the bucket was set level with the ground. Collections were made, and the traps rebaited, fortnightly throughout the year.

Dung removal

Five replicates, each of one litre quantity of fresh cattle dung, were placed out monthly in secondary grassland on Smit's farm. Beetles attracted to the dung were trapped in aluminium trenches sunk into the ground around the trap. The traps were cleared daily for the first three days and the efficiency of the beetles in removing the dung was expressed as the percentage of the original one-litre volume removed.

Seasonal changes in beetle activity

The results of the above experiments were analysed monthly to establish seasonal fluctuations in the activity of adults of each species.

Effect of ageing of dung on insect activity

A number of dung pads were set out each month under mesh covers. One set of pads was exposed immediately. At 24-hour intervals thereafter a further set of pads was exposed. The beetles attracted to these pads were collected the day after the pads were exposed, thereby giving some indication of the tolerance of the different species and groups to desiccating dung.

These aspects of the biology of each species are summarized in the annotated checklist that follows. Detailed results and comparisons are given in Endrödy-Younga (1982).

MATERIAL AND IDENTIFICATION

The dung-beetle experiments at Nylsvley have resulted in the collection of 100 638 specimens of dung- and carrion beetles (primarily Scarabaeidae, Trogidae and Dermestidae). Parasitic and other dung-associated groups (Carabidae, Histeridae, Hydrophilidae, Staphylinidae and Cleridae) are not considered in this report. All samples were analysed at the Transvaal Museum. Numbers of easily recognizable species were recorded and the specimens then discarded. All other specimens were mounted and individually coded on their labels as to which replicate from a particular experiment the specimen was collected. In this way the bulk of the material was identified before the help of specialists was requested.

Identification of material has been provided by:

Dr P Basilewsky, Tervuren: Carabidae
Mr Y Cambefort, Paris: Scarabaeidae
Dr S Endrödi, Budapest: Scarabaeidae, Aphodiinae
Dr M Mroczkowsky, Warsaw: Dermestidae
Dr C H Scholtz, Pretoria: Trogidae
Mr J Therond, Nimes: Histeridae
Dr R zur Strassen, Frankfurt: Scarabaeidae, Scarabaeini

The identification of Tenebrionidae and Nitidulidae is being carried out by the author. The identification of large numbers of Hydrophilidae, Staphylinidae, Corynetidae, Cicindelidae etc is still outstanding.

All material, both identified and unidentified, is housed in the Transvaal Museum. Duplicate study collections were made for the SASEP Research Station, Nylsvley, and for the National Collection of Insects, Pretoria.

BIOGEOGRAPHICAL AND ECOLOGICAL NOTES

An analysis of the geographical distribution of species in the subfamily Scarabaeinae in the Nylsvley fauna shows that the majority of species are widely distributed across southern Africa and the savanna zones of eastern and south-eastern Africa, with a few species occurring more widely through North Africa, the Middle East and even as far as India (Endrödy-Younga 1982). Species characteristic of humid tropical environments were not found. On the other hand a number of species were collected which are representative of the south-west arid fauna of the Kalahari and South West Africa. This illustrates clearly the

biogeographically transitional characteristics of the dung-beetle fauna of the Nylsvley area with only one species, Onthophagus pilosus, being endemic to the Transvaal.

The two savanna sites (the weather station and Maroelakop) provided the largest amount of material in terms of both species and specimens. While the spectrum of species recorded from the two sites was virtually identical, the relative abundance of certain species differed markedly between the two sites, indicating an unexpected degree of sensitivity of these species to slight differences in environmental conditions at these sites. The exact cause of these differences needs further investigation.

The composition of the fauna at the secondary grassland site on Smit's farm was considerably poorer in both numbers of species and individuals. However, a number of psammophilous species usually associated with more arid regions was collected at this site. The vlei grassland site had the poorest beetle assemblage of all the sites. This may be due to the unsuitability of the heavy clay soils as a substrate in which to excavate breeding chambers, since the soils are alternately waterlogged during the wet season and hard and compacted during the dry season.

A wide range of food preferences and degrees of dietary specialization were exhibited by the dung-beetles. Many species were attracted only to herbivore dung. Other species, while exhibiting a marked preference for herbivore dung, were also attracted occasionally to alternative food sources, especially omnivore excreta. Generally though, feeders on herbivore dung were not attracted to either decaying meat or fermenting fruit. Substantial overlap was recorded in the array of species exploiting omnivore faeces and decaying meat, with no species specializing on either food source. This suggests that some of the volatile compounds found in decaying meat are also present in omnivore faeces. Some of these volatiles may also occur in fermenting fruit since surprisingly large numbers of species selecting omnivore excreta and decaying meat were also found on fermenting fruit.

The dung-beetle fauna of Nylsvley is active primarily during the summer months. Almost no activity was recorded during months of low rainfall and low temperature. Only a few species had population peaks during the dry season, usually immediately before or just after the rain season, or both. There was no similarity in the numbers of generations or periods of activity among congeneric species, suggesting that these differences must have an ecological rather than a phylogenetic basis.

The removal of dung by beetles was found to be extremely dependent on the season. Substantial quantities of dung were removed during the period September to April, with a peak in December-January. On naturally-deposited pads the removal is nearly total between November and April, whereas between May and September there is little or no removal. However, the attractiveness of dung varied with age. Generally, dung-rollers were attracted most during the first two days, this attraction declining rapidly from the third day onwards. On the other hand, some Oniticellini species, which excavate the interior of a dung pad, were more attracted once the pad had undergone some initial

desiccation. The attractiveness of dung of different ages is dependent more on the physical consistency of the pad than on any other character affected by desiccation. For example, the attractiveness persisted longest during humid weather. However, a desiccated dung pad moistened subsequently by rain would not regain much of its attractiveness.

The flying activity of dung-beetles and therefore dung removal rate is strongly influenced by the prevailing weather, and can be brought to a standstill by a stormy, rainy cold spell, or reduced markedly by an out-of-season dry spell. If the period of unfavourable weather persists for less than three days, the rate of removal will be hardly affected. However, if unfavourable weather continues for longer than this, dung pads will remain unworked by beetles even during the rain months.

CHECKLIST

Family: SCARABAEIDAE

Subfamily: SCARABAEINAE

Tribe: Scarabaeini

This tribe provides all telecoprids or dung-rollers.

1. Pachylomera femoralis Kirby 1828. (Figure 1).

A widely distributed species through the tropical and subtropical savanna zones of the African continent. At Nylsvley it was equally common in the wooded and open areas. Due to its relatively high numbers, and particularly to its body size and biomass, this is probably the most important species in dung removal in the area. It showed no definite preference for dung, faeces or meat, but was not collected on fermenting fruit.

On cattle dung it usually acts as a paracoprid, preparing its breeding site under or immediately adjacent to the dung pad. If too many individuals attack the same pad, some of them will roll a loose lump of dung some metres from the pad.
Sample size: 1 633 specimens.
Active: mid-October to early June, peaks in mid-December and March.

2. Pachylomera opaca Lansberge 1874.

This species was described from a single specimen from Ngami, Botswana and was not found again until the 1970's in the Kalahari Gemsbok Park. At Nylsvley a large number (109 specimens) was collected, exclusively on the open secondary grassland. The species is thus an important ecological indicator of the grassland biota present in the area. Being

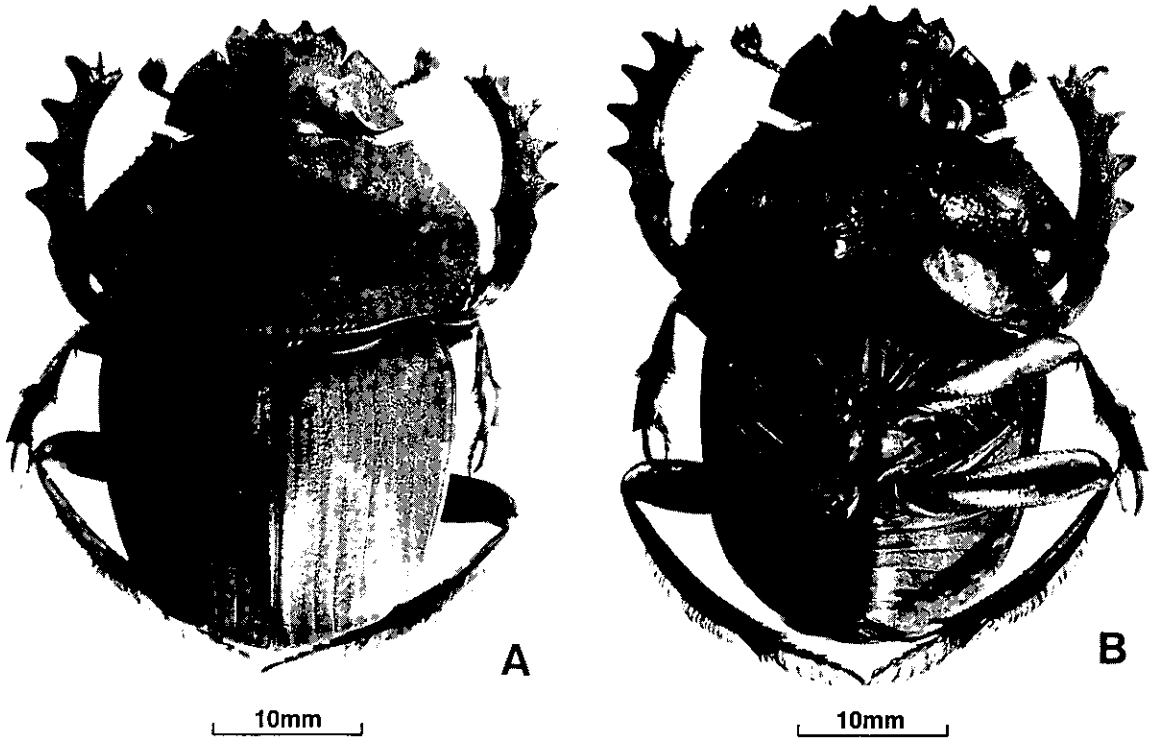

FIGURE 1. Pachylomera femoralis A: dorsal view; B: ventral view

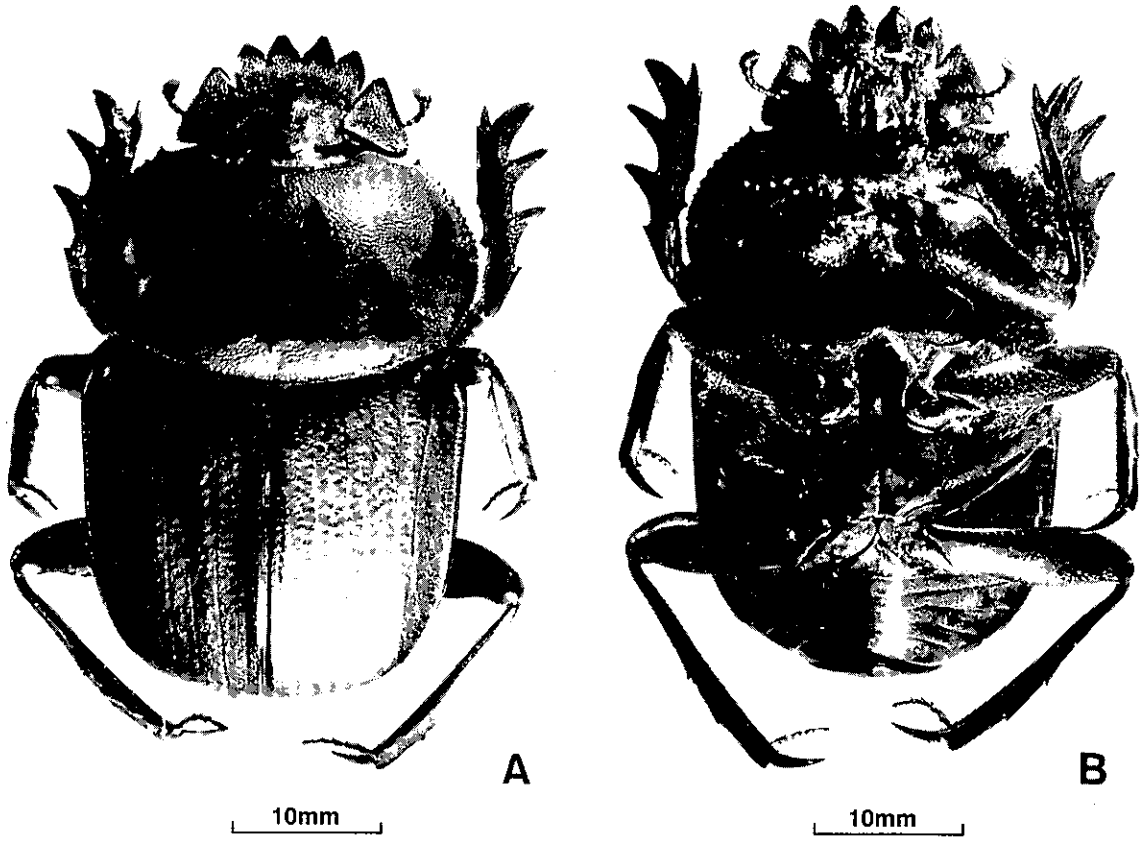

FIGURE 2. Kheper lamarcki A: dorsal view; B: ventral view

exclusively a dung feeder with a comparatively large biomass (approximately 0,9 g dry mass), it might be of importance in dung removal under very specific ecological conditions.
Sample size: 109 specimens.
Active: mid-October to February, peak in early January. One specimen in April.

3. Kheper lamarcki M'Leay 1821. (Figure 2).

A species of wide distribution in the tropical and subtropical savanna areas of the Ethiopian region. It has a marked ecological tolerance, avoiding only the rain forests and deserts. Common in all environments of the study area. Showed a preference for cattle dung, and, from its biomass, (1 g dry) seems to be the second most effective agent of removal in the area. As a compulsory dung-ball roller its action is most important in the break up and dispersion of fresh pads.
Sample size: 423 specimens.
Active: mid-October to May, with a peak in January and a lesser peak in March.

4. Scarabaeus vansoni Ferreira 1958.

General distribution is unknown as it is only represented by the holotype from Kungveld, SWA. At Nylsvley it preferred the woody savanna areas, predominantly the woodland below Maroelakop; only one specimen was found in the open pasture. Its natural food preferences are unknown. The highest proportion of specimens were trapped on fermenting fruit, which is unlikely to be its natural food source. It is unimportant in dung removal and its biology is almost unknown.
Sample size: 80 specimens.
Active: November to March (about 1% in April), peaks in December and February.

5. Scarabaeus bohemani Harold 1868.

Widely distributed in southern Africa, from Botswana and Zimbabwe to the Cape. At Nylsvley it almost entirely replaced the previous species in the woody savanna at the weather station site. This pair of species is a good example of the unexpected degree of ecological sensitivity found in scarabaeids. The species was not found on cattle dung and its highest preference is for omnivore (human) faeces, and secondarily for decaying meat. Unimportant in dung removal.
Sample size: 117 specimens.
Active: October to December (1% in February), peak in December.

6. Scarabaeus flavicornis Boheman 1860. (Figure 3).

A typical member of the Kalahari fauna, only marginally penetrating adjacent areas, it is the dominant dung-roller in semi-deserts. Equally common in all sites at Nylsvley, where its abundance was unexpected.

Its importance in herbivore dung removal in the area is limited by its preference for faeces and decaying meat.
Sample size: 382 specimens.
Active: present during the whole year, peak in March and a lesser peak in December.

7. Scarabaeus goryi Castelnaud 1840.

Apparently widely distributed in the Ethiopian Region, the limits not being clearly known. It was rather sporadic in the study area, where it was found only on cattle dung. Its biological importance, at least at Nylsvley, is apparently small.
Sample size: 6 specimens.
Active: only in November. Sample is not significant.

8. Scarabaeus zambesianus Péringuey 1900.

General distribution is limited to the eastern part of southern Africa from Zimbabwe and Mocambique to the Transvaal, excluding the arid central regions. At Nylsvley it was found mainly in the woody savanna sites, feeding most frequently on faeces and decaying meat.
Sample size: 528 specimens.
Active: November to March (1% in late October), peak in December and February.

9. Gymnopleurus aenescens Wiedemann 1821.

A southern African species which at Nylsvley occurred predominantly in the woody savanna sites. It was not found on cattle dung at all. Prefers faeces and, to a lesser degree, decaying meat.
Sample size: 274 specimens.
Active: October to February (0,5% in September), peak in December.

10. Gymnopleurus humanus M'Leay 1821.

A southern African species which was very common in the woody savanna sites, particulary the woodland below Maroelakop. It occurred sporadically in open areas. This species shows the highest preference for decaying meat and almost entirely avoids cattle dung as a food source.
Sample size: 419 specimens.
Active: November to April (1% in June), peak in February with a lesser peak in November.

11. Gymnopleurus ignitus Klug 1855.

This species occurs in the central, eastern and southern parts of sub-Saharan Africa except in desert regions. At Nylsvley it was

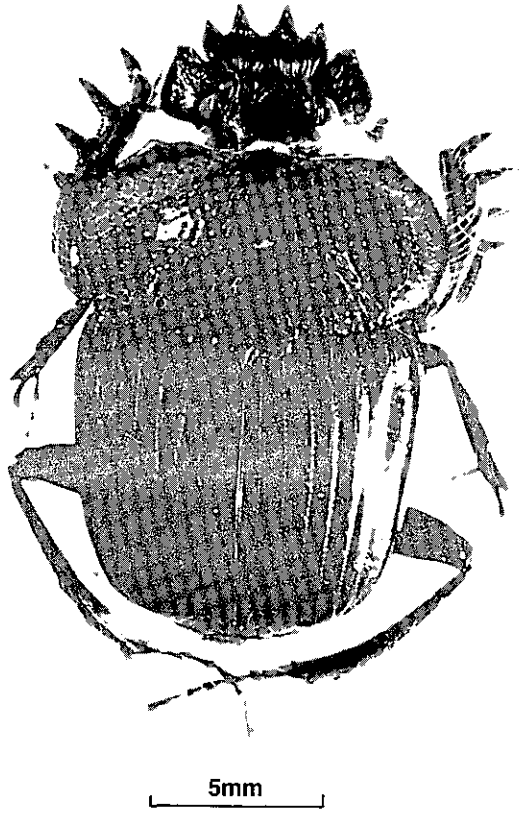

FIGURE 3. Scarabaeus flavicornis

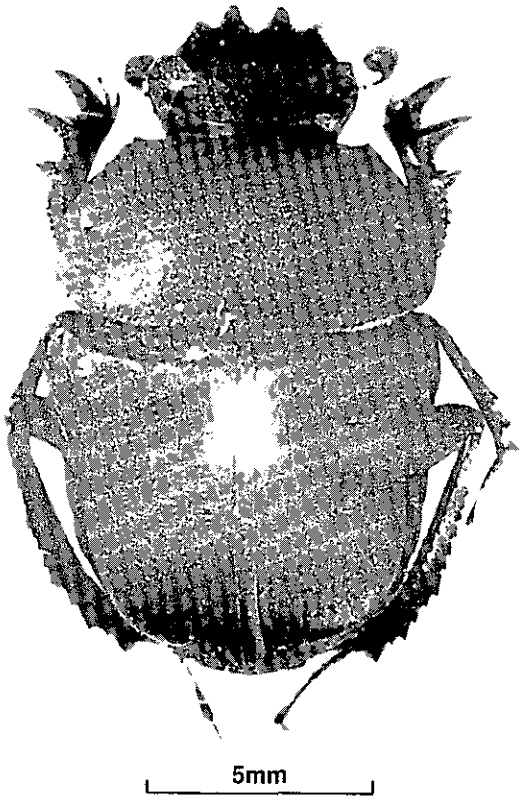

FIGURE 4. Allogymnopleurus thalassinus

FIGURE 5. Garreta nitens

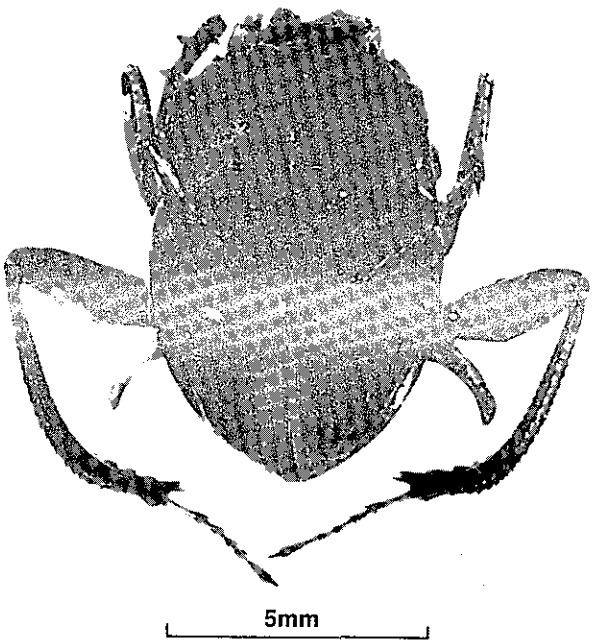

FIGURE 6. Sisyphus rubrus

restricted to the woody savanna areas and showed a definite preference for decaying meat and faeces; it was not found on cattle dung.
Sample size: 27 specimens.
Active: November and December, peak in December.

12. Gymnopleurus virens Erichson 1843.

A species with a similar general distribution to G ignitus. Only one specimen was trapped on faeces at the weather station site.
Sample size: 1 specimen.
Active: mid-November.

13. Allogymnopleurus thalassinus Klug 1855. (Figure 4).

Occurring in eastern and southern Africa, this is one of the most common and important species associated with cattle dung at Nylsvley. It was most abundant in the open sites but was also common in the woody savanna areas. As a predominantly dung feeder and dung-ball roller it plays a leading role in the break up and dispersion of fresh pads. Its second choice in food is decaying meat. There is only one other species (Copris obesus) with a similar habit.
Sample size: 3 191 specimens.
Active: December to March (1% in November, 2% in April), peak in December.

14. Garreta nitens Olivier 1789. (Figure 5).

Common in the whole Ethiopian Region except in deserts and rainforests, this species is rather scarce in the Nylsvley area. It was collected on cattle dung at open sites in the woody savannas. It is a typical dung-roller, being among the first species flying onto fresh dung. Due to its relatively low population, this species has a limited importance in the area.
Sample size: 12 specimens.
Active: November to February, peak in January.

15. Sisyphus caffer Boheman 1857.

16. Sisyphus goryi Harold 1859.

Though this group is composed of two or more species it shows marked differences to Sisyphus rubrus in many respects. These species, in contrast to S rubrus, showed a very definite preference to the woody savanna habitat, and were particularly abundant at the Maroelakop site. Their very low ranking as cattle-dung feeders is due to their habitat preferences rather than to their food preferences. They were often observed in large numbers during the monitoring of species active on cattle dung. They are obligatory dung-ball rollers.
Sample size: 1 012 specimens.
Active: September to June, peak in December and March (more than one species?)

17. Sisyphus rubrus Paschalidis 1974. (Figure 6).

This recently-described species is of major importance in dung removal, especially in the Nylsvley area. It was equally common in the open and woody areas, but in contrast to the previous group of species was virtually never attracted to faeces or decaying meat. As an obligatory dung-ball roller, it is highly active in breaking up and dispersing fresh dung pads. As it is a telecoprid it is less affected by the dessication of the dung than other dung-rolling species.
Sample size: 421 specimens.
Active: October to April (0,1% in August, 1% in May), peak in March.

Tribe: Canthonini

Species belonging to this tribe are not cattle-dung feeders. They are commonly found to be active on faeces of omnivores.

18. Anachalcos convexus Boheman 1857. (Figure 7).

Occurring in East and South-East Africa, this species avoids deserts and is most common in the relatively humid areas. At Nylsvley it was almost entirely absent from the open sites and showed a preference for the woody savanna type present below Maroelakop, indicating rather precise habitat requirements. Its highest food preference was for decaying meat and it was occasionally found on naturally occurring carcasses. This might indicate that its second choice, faeces, is not a natural preference.
Sample size: 2 949 specimens.
Active: October to March (0,1% in August, 0,5% in April), peaks in November and February.

19. Odontoloma sp

A small and rather rare species with a distinct preference for the woody savanna environment. Although preferring meat and faeces in test baits, its comparatively high capture rate in unbaited traps suggests that neither of them represent its natural preference.
Sample size: 36 specimens.
Active: October to February and April to June, peaks in January and June.

Tribe: Coprini

This tribe includes most of the potential paracoprids, though some species do not follow this pattern (Pedaria).

20. Pedaria rohani Boucmont 1922.

This is the only species of the genus Pedaria so far identified in the Nylsvley samples. The genus was represented in all environments and

showed only moderate preferences between faeces, cattle dung and meat. It is likely however, that at a specific level, differences in both habitat and food preference occur. On dung pads these species usually inhabit the dung/soil interface, and fly onto pads that have undergone initial dessication. Due to their low population size these species are unlikely to be very important in the ecosystem.
Sample size: 134 specimens.
Active: October to April, peak in November-December.

21. Heliocopris atropos Boheman 1860.

22. Heliocopris japetus Klug 1855. (Figure 8).

Both species were found in the samples in unexpectedly small numbers. In spot checks and faunal monitoring collections they were also found to be rather rare, though they are frequently observed flying to lights at night at Nylsvley. Both specimens of H atropos were collected on dung; H japetus was likewise found in dung, and also on faeces and even fermenting fruit.
Sample size: H atropos 2 specimens; H japetus 6 specimens.

FIGURE 7. Anachalcos convexus

FIGURE 8. Heliocopris japetus

23. Catharsius melancholicus Boheman 1860.

A species with a restricted distribution, predominantly in the semi-arid Kalahari. Only one specimen was collected at the meteorological station site in an unbaited trap.
Sample size: 1 specimen.

24. Catharsius pandion Harold 1877.

Restricted to the eastern side of the African continent from eastern Zaire to South Africa, this species apparently prefers the more humid savanna regions. At Nylsvley it showed a definite preference for woody savanna. Food preference: decaying meat and faeces; it was not collected on cattle dung.
Sample size: 143 specimens.
Active: October to March (1% in April), peak in December.

25. Catharsius tricornutus De Geer 1778. (Figure 9).

Inhabiting most of the sub-Saharan part of the Ethiopian Region, this species is less common in west Africa, and most common in southern Africa. At Nylsvley it occurred equally commonly in the wooded and open savannas. It preferred cattle dung and human faeces and was found only occasionally on decaying meat. Its breeding chambers are prepared in deep tunnels under the dung pad. Due to its biomass and quantity of dung utilized, this species is an important agent in dung removal.
Sample size: 172 specimens.
Active: present all year round with lowest populations in August and October (1% each), and a peak from April to June.

26. Copris elphenor Klug 1855. (Figure 10).

Present over the whole sub-Saharan part of the Ethiopian Region. This species was present in all environments at Nylsvley. The species showed a very definite preference for cattle dung, occasionally visiting human faeces. It was seldom attracted to decaying meat. Its populations are apparently not particularly high, but as a medium-sized digger it is potentially important in dung removal.
Sample size: 82 specimens.
Active: October to April, peak in January with a minor peak in April.

27. Copris fallaciosus Gillet 1907.

Occurs throughout East and southern Africa. A few specimens were collected at each site except the floodplain. It apparently is exclusively a dung feeder. Due to its small numbers, it is of limited importance at Nylsvley.
Sample size: 6 specimens.
Active: September to January.

28. Copris inhalatus Quedenfeld 1884.

A southern African species found at Nylsvley in small numbers in both the wooded and open savannas, predominantly on dung and only occasionally on faeces. It is therefore of limited importance at Nylsvley.
Sample size: 18 specimens.
Active: November-December and March-April.

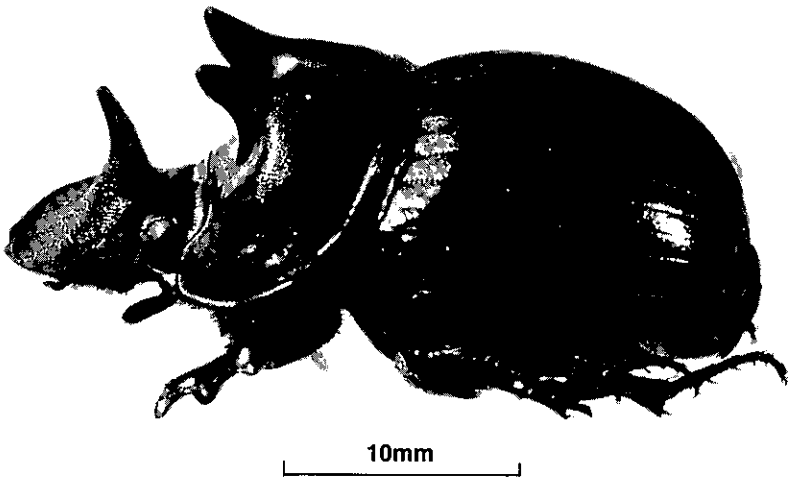

FIGURE 9. Catharsius tricornutus

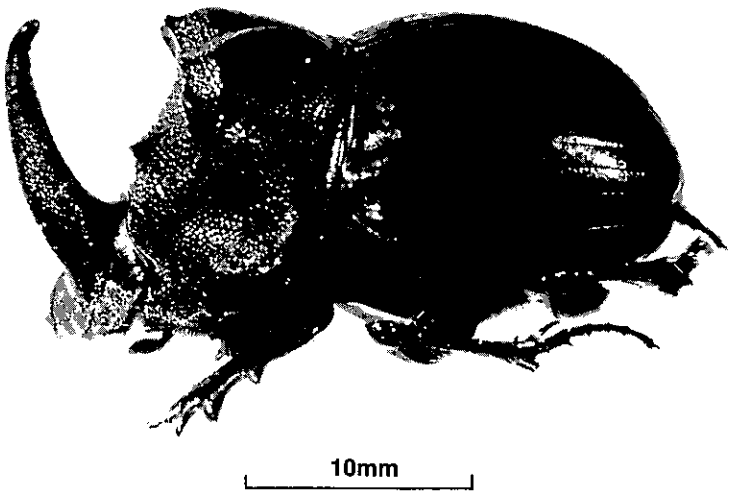

FIGURE 10. Copris elphenor

29. Copris mesacanthus Harold 1878.

This species is known from East and southern Africa. Eight specimens were collected at Nylsvley from cattle dung during faunal monitoring. Since it never occurred at the numerous dung samples in open pasture, this species appears to be restricted to woody savannas. It shows a definite preference for cattle dung.
Sample size: 8 specimens.
Active: February (sample not conclusive in this respect).

30. Copris (?) obesus Boheman 1857.

An easily recognisable but distinctive species which has not positively been identified but which is thought to be Copris obesus, occurs in the Nylsvley fauna. C obesus is known from East and southern Africa, and at Nylsvley individuals which may be attributable to this species inhabited both woody and open savannas. The species showed a marked preference for cattle dung though it was also found on faeces and very occasionally on decaying meat. Due to its high abundance and reasonably large body size this species is, as a paracoprid, one of the important species in dung removal.
Sample size: 1 235 specimens.
Active: November to May (less than 0,5% in September, October and June). The species has two definite peaks in November-December, and in March-April. At the beginning of the second peak a predominance of immature specimens was observed.

31. Metacatharsius latifrons Harold 1868. (Figure 11).

This southern African species occurred equally in both open and wooded savannas at Nylsvley. In the experiments this species was found exclusively on cattle dung, though faunal monitoring samples showed high preference for faeces.
Sample size: 44 specimens.
Active: December to April, peak in April.

32. Metacatharsius pumilionis Wallace 1881.

A collection of 175 small Metacatharsius specimens comprising several species has been made. Only two of them have so far been identified, both as M pumilionis, a species only found in the Kalahari and the Transvaal. M pumilionis was collected at the weather station site in November, one specimen on faeces, and the other in a trap of decaying meat. Food preferences are not clear though cattle dung appears to be strongly avoided. No firm conclusions can be drawn until the whole collection has been identified.

Tribe: Onitini

All species belonging to this tribe prepare their breeding chambers at the end of long tunnels under the dung pad. In many areas species of the tribe play leading roles in dung removal. At Nylsvley in the open grassland, where most of the dung experiments were carried out, species of this tribe occurred at unexpectedly low frequencies at dung. The faunal monitoring samples show that Onitis species have a greater preference for wooded savanna.

33. Chironitis scabrosus Fabricius 1776.

This southern African species is apparently rare at Nylsvley and has been found only on dung.
Sample size: 6 specimens.
Active: Collected during the dry season only; April, May and September.

34. Onitis alexis Klug 1835. (Figure 12).

35. Onitis caffer Boheman 1857.

36. Onitis fulgidus Klug 1855.

37. Onitis uncinatus Klug 1855.

Few specimens of these species have been identified from the unexpectedly small amount of material yielded by the experiments. Even though the genus is treated as an undivided unit in the discussion in Endrödy-Younga (1982), it did not rate highly in any of the habitat or food preference rankings. The genus, as a whole, showed a high preference for dung and faeces versus meat, but specific preferences for cattle dung (62%) and faeces (31%) cannot be properly estimated until the specimens have been identified to species level.
Sample size: 81 specimens.
Active: September to May. Specific differences are expected.

Tribe: Oniticellini

Members of this tribe are found usually in the dung and dung/soil interface or in breeding chambers in the soil under the pad.

38. Drepanocerus fastiditus Peringuey 1900.

The relative abundance of this species, and at least two more unidentified ones has yet to be determined. Drepanocerus fastiditus is certainly more common than D patrizii, but its numbers are likely to be much lower than those of D laticollis. It was active in the interface of dung and soil with a peak in the autumn.

39. Drepanocerus laticollis Fahraeus 1857.

Occurring in East and southern Africa, this is the dominant species of the genus. It was common throughout Nylsvley. Faunal monitoring figures suggest an even higher abundance of this species in the wooded savanna than in the open grassland, where it was the second most abundant species. Exclusively a dung feeder, it was active both in dung pads and in the interface between dung and soil. It preferred dung pads after initial dessication. Due to its high abundance and high selectivity D laticollis is an important agent in dung removal.
Sample size: 2 689 specimens.
Active: Present almost the whole year round, absent in June and August (less than 0,5% in July and September). Peaks in November and in February-March.

40. Drepanocerus patrizii Boucmont 1921. (Figure 13).

An East and southern African species which is rather rare at Nylsvley. Occurred exclusively in cattle dung where it acted in the same way as D laticollis.
Sample size: 46 specimens.
Active: December to March with 3% in February and a peak in December.

41. Oniticellus formosus Chevrolat 1830. (Figure 14).

Known from most parts of the African continent this species was moderately common throughout Nylsvley where it fed exclusively on dung.
Sample size: 85 specimens.
Active: December to March with 2% in November and 1% in April. Peaks occurred in December and March.

42. Oniticellus planatus Castelnaud 1840.

Occurring in the forest and savanna regions of sub-Saharan Africa, only a few specimens of this species were collected at Nylsvley, exclusively on cattle dung.
Sample size: 14 specimens.
Active: November to March, peak in March with a lower peak in December.

43. Euoniticellus intermedius Reiche 1849. (Figure 15).

A common species of the Ethiopian region having a wide ecological amplitude: it is common in forests, savannas and also in semi-desert areas. At Nylsvley it was equally active in all communities where it was exclusively a dung feeder. In contrast to most other species of the tribe this species showed a definite preference for fresh dung with a moderate reduction in numbers from the third day onwards. Breeding chambers are found in tunnels under the pad.
Sample size: 445 specimens.
Active: Specimens were found all year round except for June, with peaks in September, December and April.

FIGURE 11. Metacatharsius latifrons

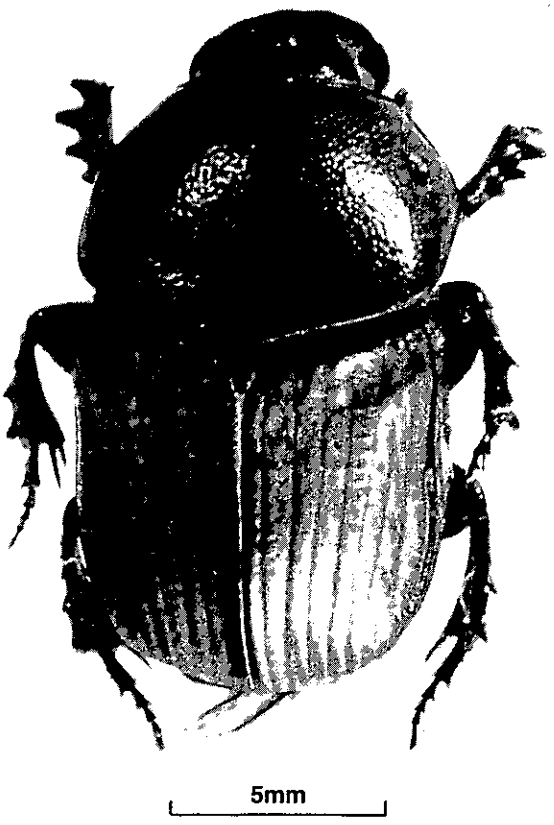

FIGURE 12. Onitis alexis

FIGURE 13. Drepanocerus patrizii

FIGURE 14. Oniticellus formosus

44. Tiniocellus spinipes Roth 1851.

A widely distributed species in Africa and apparently also in India. Only few specimens were collected during faunal monitoring in the woody biotopes of Nylsvley.
Sample size: 8 specimens.

45. Liatongus militaris Castelnaud 1840. (Figure 16).

Widely distributed in Africa with a considerable ecological amplitude, this species was common throughout Nylsvley and was exclusively a dung feeder. Due to this high selectivity and with its very high population it is one of the more important species in dung removal. Its persistent activity in dung might be due to its breeding habits.
Sample size: 1 920 specimens.
Active: September to May with less than 1% in September, October and May. Population peaks observed in November-December and February.

Tribe: Onthophagini

The tribe, which includes one of the largest genera (Onthophagus) of dung beetles, shows considerable variation in breeding habits. Probably most of the species tunnel in the soil under dung pads. Some of them are kleptoparasitic, laying their eggs in dung in breeding chambers of other species or in dung balls of dung-rollers (as observed in Onthophagus pallidipennis). Halffter and Matthews (1966) list a number of kleptoparasites from the genera Onthophagus and Caccobius. Though most of the common species at Nylsvley have been identified, a final list is likely to contain about double the number currently listed.

46. Caccobius cavatus d'Orbigny 1908.

A southern African species which occurred in moderate numbers in all biotopes at Nylsvley. Most specimens were collected from cattle dung but some were also trapped on faeces (18%), meat (9%) and fruit (2%).
Sample size: 65 specimens.
Active: November to March with a moderate population peak in January.

47. Caccobius viridicollis Fahraeus 1857.

An East and southern African species which occurred throughout at Nylsvley, almost exclusively on cattle dung.
Sample size: 135 specimens.
Active: November to March (1% February; 2% March), peaking in December.

48. Onthophagus aeruginosus Roth 1851.

Recorded from central and southern Africa. This species was most common in the woody savanna types of Nylsvley, particularly at Maroelakop. It

FIGURE 15. Euoniticellus intermedius

FIGURE 16. Liatongus militaris

FIGURE 17. Onthophagus gazella

FIGURE 18. Proagoderus saphyrinus

occurred sporadically in open grassland. This species showed a high preference for omnivore faeces (63%), less so for meat (28%) and only occasionally for dung (7%).
Sample size: 2 025 specimens, one of the most common species (fifth in rank) at Nylsvley.
Active: Present all year round, but five percent or less between February and September. Moderate peak in November.

49. Onthophagus bicavifrons d'Orbigny 1902.

An East and southern African species which was commonest in the woody savanna types at Nylsvley. It was trapped in almost equal numbers on faeces, meat and fruit. Accidental catches in unbaited traps were higher (8%) than on dung (1%).
Sample size: 535 specimens.
Active: October to June but with 1% or less in October, April, May and June. Most active from November to February, with a population peak in December and a lesser one in February.

50. Onthophagus depressus Harold 1871.

Confined to the eastern part of southern Africa, this species occurred throughout at Nylsvley, showing a high preference for the Maroelakop site. Food preferences decreased in the order: fruit - faeces - dung.
Sample size: 209 specimens.
Active: A late wet-season, early dry-season species, being most abundant from February to June, with a peak in February. It was not recorded in July, while catches from August to January comprise less than four percent of the total.

51. Onthophagus ebenus Peringuey 1888.

This species has only recently been identified from the Nylsvley fauna, so that its role in the ecosystem has not yet been evaluated.

52. Onthophagus flavolimbatus Klug 1855.

Distributed from East Africa, into the eastern parts of southern Africa, this species was present in all communities at Nylsvley. It was attracted almost exclusively to cattle dung with only 2% on faeces and 0,5% on meat. Its activity in dung is not known but it is probably a kleptoparasite.
Sample size: 260 specimens.
Active: An early rainy season species active from November to February, with 9% and 5% in January and February respectively. There was a peak in December.

53. Onthophagus gazella Fabricius 1787. (Figure 17).

Occurs widely throughout Africa, Madagascar, Arabia and India. At Nylsvley it was less common than in many other areas but nevertheless was still relatively abundant in all environments. It is exclusively a dung feeder, single catches only being made on faeces and meat. Dung is removed by tunnelling. Due to its selectivity, large body size and relative abundance, this species is potentially important in cattle-dung removal.
Sample size: 276 specimens.
Active: A wet-season species, active from October to April, with 2% and 1% in March and April respectively. Two definite population peaks occur in October and in February respectively.

54. Onthophagus leucopygus Harold 1867.

Known only from South Africa, O leucopygus was found in all communities at Nylsvley where it was predominantly a dung feeder with less attraction to faeces (18%), meat (15%) and fruit (1%).
Sample size: 484 specimens.
Active: September to June, with single records from September and October and 5 in March. Two distinct population peaks were recorded in December and in April.

55. Onthophagus obtusicornis Fahraeus 1857.

A southern African species occurring predominantly in woody savanna at Nylsvley. It is definitely not a dung feeder although during faunal monitoring occasional specimens were collected on cattle dung. Shows a similar preference for faeces (40%) and meat (37%). One of the most common (ranking third) Scarabaeids at Nylsvley.
Sample size: 3 113 specimens.
Active: October to July; abundant in November-December and May. A distinct population peak (44%) in December and a moderate peak (12%) in May.

56. Onthophagus pallidipennis Fahraeus 1857.

Confined to southern Africa this species was present in all communities at Nylsvley. It preferred dung (87%) and faeces (13%). It was observed to be kleptoparasitic on dung balls being prepared or being rolled by other species.
Sample size: 39 specimens.
Active: November and December with single recordings in February and April. A population peak was observed in November.

57. Onthophagus pilosus Fahraeus 1857.

This species is known only from the Transvaal. At Nylsvley it inhabited the woody communities almost exclusively; only a few specimens were

recorded from the open grassland and from the floodplain. No specimen was found on cattle dung. The rate of trapping on all other baits (including the unbaited controls) was fairly even, though highest preference was shown for fermenting fruit. Little is known of its biology.
Sample size: 885 specimens.
Active: October to June, with two definite population peaks in December and in May.

58. Onthophagus quadraticeps Harold 1867.

This species has been recorded from the Kalahari and the Transvaal. At Nylsvley it was present in all communities, and showed a high preference for dung; faeces (7%) and meat (5%) were less preferred.
Sample size: 266 specimens.
Active: November to May.

59. Onthophagus quadrinodosus Fahraeus 1857.

Occurs in southern Africa, possibly only in the northern parts. At Nylsvley it showed a distinct preference for the woody savanna though it was rather rare. It favoured dung but was also trapped on faeces.
Sample size: 74 specimens.
Active: A predominantly late summer-autumn season species occurring mainly from February to June (4% in December) with a peak in May.

60. Onthophagus signatus Fahraeus 1857.

Recorded only from South Africa, this species was common at Nylsvley in all communities. It is predominantly a dung feeder, only 10% being found on faeces. Its action on dung is unknown.
Sample size: 627 specimens.
Active: October to April. There is a peak in November and a possibly insignificant population increase in April.

61. Onthophagus variegatus Fabricius 1798.

A widespread species in Africa and India occurring at Nylsvley in all communities with a possible preference for open grassland. It is predominantly a dung feeder with a few records on faeces and meat. Due to its selectivity and abundance it might play a significant role in cattle dung removal.
Sample size: 1 076 specimens.
Active: This species was more abundant during the rainy season occurring from October to April with one percent or less in August and May. There were two distinct population peaks, in October and in April, and a third minor peak in February.

62. Onthophagus vinctus Erichson 1843.

Widespread in Africa south of the Sahara, O vinctus is common in all communities at Nylsvley, predominantly on dung but also on faeces (19%) and meat (3%). This species was the commonest dung specialist species of Onthophagus at Nylsvley where it seems to be an active dung remover.
Sample size: 1 391 specimens.
Active: Present throughout the year but appears to be most active in the dry season, lowest population (1%) occurring in January and population peaks in September (42%) and in April (48%).

63. Onthophagus carbonarius Klug 1855.

Found throughout Nylsvley, this species is clearly coprophagous but does not feed on cattle dung. No specimens were found on dung or in unbaited traps, and only 1% was collected from fruit. Food preferences: omnivore faeces 64%, meat 35%.
Sample size: 369 specimens.
Active: all year except August. Abundant in November-December and in May with two definite population peaks in December and May.

64. Onthophagus trinodosus Fahraeus 1857.

Only found in the woody savanna. Showed a definite preference for meat (70%) and secondarily for faeces (30%). Probably a feeder on omnivore faeces.
Sample size: 46 specimens.
Active: November to April with a definite peak in December.

Four further Onthophagus species are listed here. These species were easily recognizable in the samples, but have not yet been identified to species level. As they are strictly absent from dung samples, the usual source of Onthophagus collections, they are not represented in the collections of the Transvaal Museum and the Australian Dung-beetle Project; some of them might be new species.

65. Onthophagus sp 1.

Present in all communities at Nylsvley with preference for the woody savanna at the weather station site. It is definitely not a dung feeder. It was attracted to fruit and faeces in nearly equal numbers (38%, 36%) and was found at a similar frequency on meat and in unbaited traps (13%, 12%).
Sample size: 407 specimens.
Active: November to April with moderate peaks in the named months.

66. Onthophagus sp 2.

Found in all communities at Nylsvley. It was not found on dung. The highest preference was shown for fruit (64%) with meat (21%) and faeces (14%) being much less preferred.
Sample size: 14 specimens.
Active: sporadically between October and June.

67. Onthophagus sp 3.

This species was only found in the secondary grassland. Most specimens were found in unbaited traps (62%, the highest recorded rate), indicating a food source completely different from the baits used.
Sample size: 26 specimens.
Active: found in July (7%), February (86%) and May (7%).

68. Onthophagus sp 4.

This species showed a preference for the woody communities, especially the Maroelakop site. It was attracted to all baits except cattle dung and was found in surprisingly large numbers in unbaited traps.
Sample size: 154 specimens.
Active: October to May; abundant from November to March with a distinct population peak in December.

69. Proagoderus saphyrinus Fahraeus 1857. (Figure 18).

A southern African species which at Nylsvley occurred predominantly in woody savanna but was also common in the open grassland. This was the most abundant scarabaeid species. It is presumably a feeder on omnivore faeces as it was often seen in large numbers on baboon faeces and very occasionally on cattle dung. In the experiments it was attracted most frequently to meat (55%) and to faeces (35%).
Sample size: 39 419 specimens.
Active: Found in all months except for August, with a population peak in November-December and a slight increase in March. In June to October, 1% or less.

70. Phallops boschas Klug 1855.

Occurs throughout central, East and southern Africa. One specimen was collected on cattle dung in the open grassland site in mid-December.

71. Phallops flavocinctus Klug 1855.

This species occurs in East and southern Africa. One specimen was collected from cattle dung on the open pasture in January.

72. Phallops smaragdinus Harold 1875.

Occurs from East to southern Africa. Only two specimens were collected with P flavocinctus on cattle dung on open pasture in January.

73. Phallops wittei Harold 1867. (Figure 19).

Only recorded from the Kalahari, South Africa and South West Africa, this species was found in all communities at Nylsvley. It seems to be exclusive to herbivore dung as no specimen was collected on other baits. In South West Africa this species has been found on horse and elephant dung.
Sample size: 314 specimens.
Active: October to April, the highest population occurring from November to January. There was a distinct population peak in January. A slight increase in March was probably not significant.

Subfamily: APHODIINAE

12 082 specimens belonging to the subfamily were collected. Many species are represented in this material which is presently being identified. The component species vary considerably in seasonality and to some extent in feeding and breeding habits. Some features, which will be even more apparent when studied at specific level, are worth mentioning.
The genus Aphodius Illiger 1798, together with Colobopterus, seems to prefer cattle dung among the baits tested. The occasional catches observed on all other baits represented 0,6% on faeces, 0,1% on meat and only 0,05% on fruit. Most of the specimens attracted to baits other than cattle dung probably represent either a few specialized species, or species with a wide tolerance of alternative foods.

74. Aphodius guineensis Klug 1835. (Figure 20).

This easily recognisable, common and comparatively large species of the genus is considerably larger (9 mg), than the calculated average dry mass (2 mg) of the other species within the genus. It will be evaluated in a later publication together with some 30 as yet unidentified species of the genus.

75. Colobopterus maculicollis Reiche 1847. (Figure 21).

Probably the only species representing Colobopterus at Nylsvley. Generally distributed throughout the Ethiopian Region, this species occurred commonly in all communities in the study area. It is exclusively a dung feeder, only 0,2% of the specimens being found on faeces. Colobopterus species build their breeding chambers in the soil;

FIGURE 19. Phallops wittei

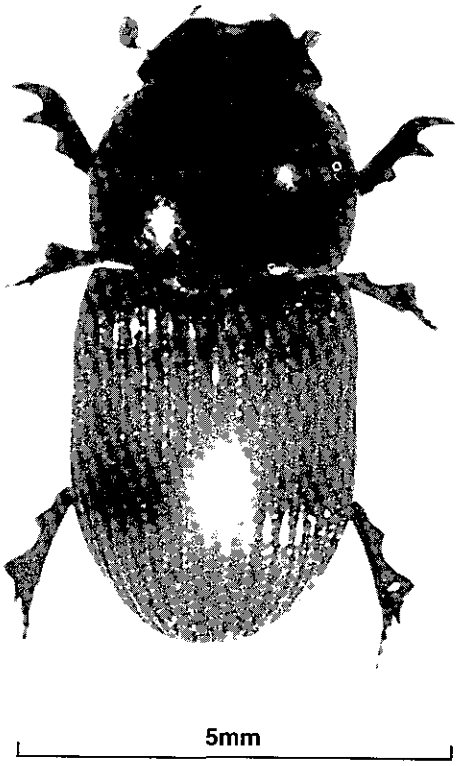

FIGURE 20. Aphodius guineensis

FIGURE 21. Colobopterus maculicollis

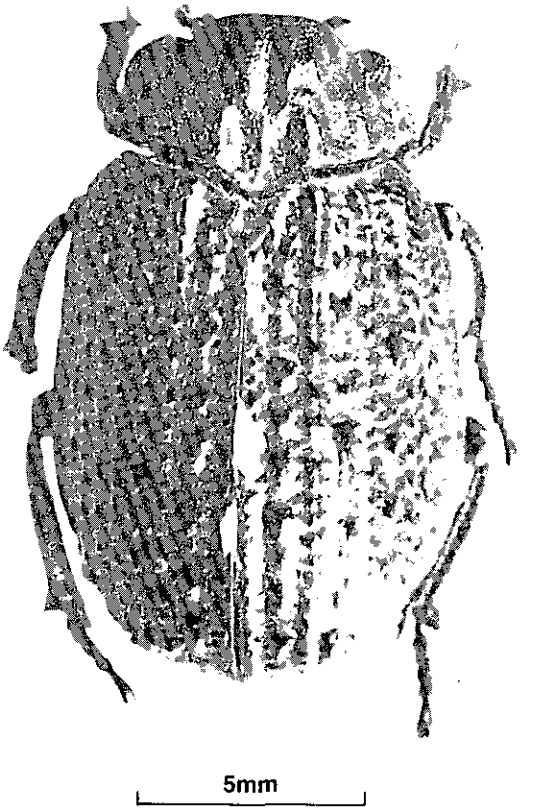

FIGURE 22. Trox squalidus

thus they are certainly active dung removers. Due to their selectivity, breeding habits and abundance, the genus plays an important role in dung removal.
Sample size: 661 specimens.
Active: August to May. Populations were higher between November and March, with a moderate population peak in November and a distinct one in February. The species becomes dominant in the late rainy season (February-March 56%).

Family: TROGIDAE

The members of this family are generally carcass feeders though some species, which feed on organic litter, are known also from bird nests and mammal burrows.

76. Trox melancholicus Fahraeus 1857.

77. Trox squalidus Olivier 1789. (Figure 22).

These are the largest carrion beetles in southern Africa, and so are important agents of carcass removal. They are markedly more common in woody savanna than in open grassland on Nylsvley, where 59% were found on meat and 32% on faeces. No specimen was found on cattle dung. Their role is however limited by their short period of activity.
Sample size: 266 specimens.
Active: October to April, with high activity only in November-December. The single population peak in November demonstrates a single generation in a year.

Family: DERMESTIDAE

The genus Dermestes Linnaeus 1758, belonging to the family known as skin beetles, comprises species which are carrion feeders. They breed on desiccating carcasses but adults are also often observed feeding on dead insects etc.

78. Dermestes maculatus De Geer 1774.

This species was represented in all communities at Nylsvley and showed a high preference (64%) for meat, but was also trapped on fruit (19%) and faeces (17%). It is an important agent in carrion reduction.
Sample size: 1 396 specimens.
Active: September to November with 1% in July and 3% in January. There is a single population peak in October-November. In contrast to Trox spp, D maculatus is typically active in the early rain season.

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