AN ECOLOGICAL INVESTIGATION OF THE INSECTS ASSOCIATED WITH EXPOSED CARCASSES IN THE NORTHERN KRUGER NATIONAL PARK : A STUDY OF POPULATIONS AND COMMUNITIES

BY

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PREFACE

The ecological work described in this thesis was carried out in the northern Kruger National Park from January 1979 to November 1984 under the supervision of Dr Raymond M. Miller, Department of Entomology, University of Natal, Pietermaritzburg.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

ACKNOWLEDGEMENTS

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ABSTRACT

Extensive seasonal collections along with absolute counts of all the arthropods attracted to medium- and large mammal carcasses resulted in the most complete record of carrion-fauna in Africa to date. The abundance of these species and their seasonal, successional, and diel patterns of carcass-attendance are discussed. More than 98% of species were insects and their presence at the carcass habitat could be classified as obligate, opportunistic, or incidental. A recognisable community of carrion-associated arthropods consistently attracted to the carcass habitat is described, comprising sarcophages, coprophages, keratophages, detritivores, predators and parasites. The interactions and functional ecology of these arthropods is described.

The blow-flies *Chrysomyia albiceps* (Wd.) and *C. marginalis* (Wd.) were found to be pivotal or key species due to the impact of their larvae on carcass decomposition and their influence on other members of the community. In view of the importance of these blow-flies, their abundance, and the potential role of the adults as dispersal agents of

disease organisms, studies were performed to clarify the population dynamics of the two species. The biology and ecology of the immature stages is discussed, including such aspects as the availability of mammal carcasses for oviposition and larval development, and mortality of larvae in the digestive tracts of vultures.

By feeding a radioactive isotope of phosphorous (p^{32}) to a reared population of adult flies, the dispersal and flight ranges, habitat preferences and population densities of both blow-fly species were studied. The seasonal abundance of C. albiceps, C. marginalis, and Lucilia spp. was monitored by monthly trapping at three sites in the study area. Further studies using radioactively-marked blood in a carcass under natural conditions revealed that the distribution of fly-specks deposited by blow-flies is largely dependent upon vegetational structure in the immediate vicinity of the carcass, and the majority of such droplets occurred near the carcass between one and three metres above ground. A distinction in fly-specks was made between vomit droplets, faecal droplets, and the newly termed discard droplets. The feeding behaviour of C. albiceps and C. marginalis is discussed with reference to the transmission of anthrax in the northern K.N.P.

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CHAPTER 1

GENERAL INTRODUCTION

The Kruger National Park (K.N.P.) lies in the north-east corner of the Transvaal, Republic of South Africa, and covers an area of 1 948 528 hectares (Pienaar et al. 1983). It is bordered on three sides by natural geographical barriers: to the north are the Limpopo and Luvuvhu Rivers, to the south the Crocodile River and the entire eastern limit is formed by the Lebombo mountain range. The western boundary, however, is an arbitrarily drawn line through vast lowveld plains and cutting across traditional migration routes of such animals as blue wildebeest (Whyte pers. comm.). Partial enclosure of the K.N.P. between 1959 and 1975 with an elephant-resistant fence created a somewhat unnatural system which necessitated some artificial manipulation and management of the wildlife in the area (Braack 1983). Watering-points in the form of dams and windmills were established so that animals no longer needed to migrate across the western boundary to the Drakensberg foothills for water, and a culling programme was instituted in 1966 to reduce the unnaturally rapid increase in elephant and buffalo populations which stemmed from their inability to migrate into areas adjoining the K.N.P. In general however, the K.N.P. is large enough and sufficiently diverse to allow it to function by itself and establish its own dynamic equilibrium dependent upon reigning natural conditions. These natural conditions include periodic droughts, floods, disease outbreaks, and the present National Parks Board policy is to allow such events to proceed with no human intervention (De Vos pers. comm.). There are exceptions, however, such as the highly virulent anthrax epizootics which result in unacceptably high mortalities. Anthrax is a fatally infectious disease caused by Bacillus anthracis that can be contracted by all mammalian species, causing death by a toxin produced by the bacteria (Choquette & Broughton 1981).

The first recorded anthrax outbreak in the K.N.P. occurred in 1959 (Pienaar 1960), but records from rangers' diaries describing unusual fatalities amongst animals and providing details of the appearance of the animals indicate that undiagnosed outbreaks have occurred earlier this century (De Vos 1973a). During the 1960 epizootic a total of 1 054 medium-sized to large mammals, the majority being herbivores, were found to have died of anthrax (Pienaar 1961). This was followed by other major epizootics in 1962 and 1970, with several small outbreaks in the intervening period (De Vos 1973a). All anthrax mortalities occurred in the Northern District of the K.N.P., and it has been established that the Pafuri areas is an endemic region for the disease, from whence it spreads to adjoining area (De Vos 1973a). The Northern District of the K.N.P., in particular the extreme northern areas adjoining and including Pafuri, is unfortunately also the preferred habitat of such rare K.N.P. species as roan antelope (Hippotragus equinus), eland (Taurotragus oryx) and nyala (Tragelaphus angasi). Of the roan antelope at least 83 of an estimated population of 250 died during the four anthrax outbreaks mentioned above. The disease therefore presents a very serious threat to the continued existence of such rare species and has led to active intervention by Parks Board staff to minimise the threat. Suppressive measures have included incineration of carcasses, burning of blocks of land where the outbreak was particularly severe, treatment of contaminated waterholes either with disinfectant or by burning after drainage, or closing of such watering-points if alternate uncontaminated water was available in the vicinity (Pienaar 1960). To safeguard the vulnerable roan antelope population, a method was developed to immunise a substantial proportion of these animals on an annual basis using disposable projectile syringes containing anthrax vaccine (De Vos et al. 1973). A research programme led by the Assistant Head of Research and Information, Dr. V. de Vos, was instituted in the early 1970's to study the dynamics of the disease and is still in progress.

National Parks Board staff involved with sanitation measures during anthrax outbreaks and in the anthrax research programme became aware at an early stage (see Chapter 7) that blow-flies and vultures were the most important agents in the dispersal and maintenance of an epidemic (Pienaar 1961, De Vos 1973b). Carcasses of animals having died of anthrax typically have blood exuding from the body orifices and even tick bite-sites, and the blood does not readily coagulate (Choquette & Broughton 1981). Thousands of blow-flies are attracted to these carcasses (Pienaar 1961, De Vos, 1973b) where they then imbibe contaminated blood and later deposit infective discard- or faecal droplets via the anus and occasionally vomit-drops via the mouth on surrounding vegetation. The contaminated leaves may then be consumed by herbivores, thus perpetuating the disease.

In the latter half of 1977 I requested permission from the National Parks Board Research Section to conduct a study on the insects at impala carcasses for a B.Sc. Honours thesis. Dr. V. de Vos, heading the research team, was keen to gain information regarding carrion insects, and permission was granted. From the results of the study, the Parks Board concluded that they would support continuation of a study on carrion insects because of its direct relevance to the anthrax research programme. This dissertation relates the findings of that study.

AIMS

Although several studies had been done in South Africa on so-called "sheep blow-flies" utilising carcasses as a breeding medium, no published data was available on the overall complex of arthropod species utilising carrion in Africa, other than an account by Coe (1978) of some species at an elephant carcass in Kenya. It was decided that the first priority would be to determine (1) which species were attracted to carcasses, (2) the relative abundance of the main groups, (3) their seasonal fluctuation, and 4) the general pattern of succession of these arthropods. Attention would then be focussed on two species of blow-flies, *Chrysomyia albiceps* and *Chrysomyia marginalis*, to learn as much as possible about their population dynamics. This would provide the Parks Board with some perspectives on the diversity, abundance and effectiveness of arthropods as scavengers on carrion. It would also provide much-needed information on the biology of blow-flies which could then be combined with other data gained in the anthrax research programme to elucidate aetiological and epizootilogical aspects of the disease.

LITERATURE REVIEW

There is a daunting array of published papers dealing with specific insect species utilising carrion, and blow-fly research especially has given rise to a considerable volume of literature ranging from the delightful behavioural accounts by Fabre (1913) to the highly sophisticated experiments by Dethier (1976) on the physiology of feeding. The findings of the authors of the more specialised papers will be referred to later in appropriate sections where they are relevant, but for present purposes I have restricted the discussion to those papers which deal with the carrion-attending arthropod-community as a whole.

Palaearctic

The studies by Mègnin (1894, 1898) on the necrophagous tomb fauna and the successional pattern of utilisation by component species in France appear to be accepted by authors as the classic and first thorough investigations to be performed in this field (Bornemissza 1957, Smith 1973, 1975, Nuorteva 1977). Mègnin accummulated sufficient data for use in forensic medicine so that the carcass age or time of death could be estimated by noting the stage of successional advance and growth of the arthropods at the carcass. He concluded, "I have achieved results much more positive and complete than Dr. Bergeret (who had attempted in 1850 to estimate the time of death of a child by using mites and a flesh-fly species (see Nuorteva 1977)) in his unique attempt, so much so that I have the right to propose that legal medicine can now have recourse to entomology under certain given conditions with as much certainty as to physiology and human pathology to supply to the courts in criminal cases, the elements of judgement required for the application of the law" (translated by Leclercq 1969). These studies were closely followed by similar work in Germany by Müller (1895) and Dahl (1896) (see Bornemissza 1956).

In a British study, Morley (1907) enumerated the different species of insects he encountered during observations over a ten year period at the remains of 31 animals ranging from an earthworm to a cow. He provided information regarding the abundance of many of these species and also a brief account of the habits of certain species, also making a useful but superficial distinction between beetles which (1) merely shelter beneath carrion or are attracted to it to prey on carrion-feeding insects, (2) saprophagous species, (3) those species occasionally found at carrion but more frequently at other habitats, and (4) true carrion-beetles the larvae of which subsist upon decaying vertebrate animals.

Other than a series of studies on segments of the carrion-fauna, such as those of necrophagous beetles by Walsh (1931, 1933), Kaufmann (1947), Hussey and Lane (1956), and Easton (1966), the next study on the carrion-associated invertebrate fauna as a whole was by Chapman and Sankey (1955). They recorded the arthropods attracted to three rabbit carcasses placed under differing microclimatic conditions, and constructed a food-chain showing the interrelationships between the various carrion-frequenting insects. They found that the insects were of two main groups: those scavenging on carcass material and those which parasitised or preyed upon dipterous larvae.

From 1969 onwards a spate of papers appeared, all dealing with the medico-legal aspects and forensic application of carrion-attendant insects (Leclercq 1969, Easton & Smith 1970, Smith 1973, Nuorteva 1977, Dear 1978, Erzinclioġlu 1983). They generally described the stages of decay which can be recognised in exposed carcasses, and indicated which insect species were associated with each decompositional stage. By doing so they focussed attention on the pattern of succession or sequential manner in which the various insect species arrive at and depart from a carcass, often enabling fairly accurate estimates to be made of the time of death of the animal or person. Although dependent upon and often complicated by uncertain knowledge of the climatic conditions prevailing prior to the time of discovery of the carcass - which would influence the rates of growth of larval insects, successional advance, and decomposition of the carcass - this application of entomological knowledge has frequently assisted in the solving of crimes and was adequately documented in some of the papers mentioned above. They recognised eight waves or phases of successional use by insects which may last over a period of three years. The data they provided is only relevant to a limited area in Europe as the species composition and climatic conditions will almost certainly vary elsewhere. Smith (1975) also gave an account of the invertebrate species attracted to a dead fox in England and provided two diagrams illustrating the pattern of succession displayed by these organisms. As in all the other studies mentioned, the vast majority of invertebrates recorded belong to the class Insecta.

Using small rodent carcasses in England, Putman (1978c) made pitfall collections of attendant arthropods as part of a larger study on the mechanics of the decay process in small mammal carcasses in temperate areas (Putman 1977, 1978a, 1978b). He exposed carcasses in all the different seasons and found that very few arthropods visited carrion in winter and spring. His observations showed that of these arthropods, few groups were positively associated with the carcass and of these only a few were actually involved in removal of carrion material and therefore assisting in carcass decomposition. He also provided a general description of the role of the main groups of arthropods occurring at carrion. In a later publication (Putman 1983) he synthesised the essential findings of previous workers and provided a broad perspective of the mechanism and some of the processes involved in the decomposition of carrion and dung.

Nearctic

The earliest published work from this region was by Motter (1898) who dealt with the fauna of buried corpses. Illingworth (1926), using the carcass of a cat in southern California, recorded a total of 32 835 insects, comprising 23 species, utilising the carcass over an eight-day period. Reed (1958) made an impressive investigation of the arthropods attracted to 43 dog carcasses in Tennessee, analysing in particular the pattern of succession, seasonal variation, and the influence of environmental factors. He referred to the conglomerate of species utilising carrion as a microcommunity, and applied the term microsere to denote successional sequence as displayed by the component species of the microcommunity. Dog carcasses were placed over a period of one year in differing vegetational and geographic conditions and recordings made of the species present, estimates of their abundance, and carcass condition. He provided an annotated list of the species encountered, and a diagram representing the probable trophic relationships of the major groups. In the diagram he recognised four trophic levels represented as (1) the carrion itself as the energy source, (2) necrophagous species, (3) omnivores, and (4) predatory species. Also of value was his compilation of a table indicating four stages of decay and the approximate duration of each, and a table depicting the successional distribution of the insect families.

A series of publications (Payne 1965, Payne & King 1968, 1969, 1970, 1972, Payne _et al_ 1968) described and listed the species involved in the decomposition of pig carcasses exposed on land, buried in soil and partially submerged in water. Payne (1965) also compared the rate of decomposition of carcasses exposed to arthropods and excluded from arthropods. This comparison revealed that when arthropods were excluded it was very difficult to divide decomposition of the carcass into well-defined stages, that such carcasses tended to retain much of their original body features but in a mummified form, and that carrion decomposed and dried very slowly.

In a study of the arthropod fauna at fowl carcasses in Massachusetts, Wasti (1972) categorised decomposition into four recognisable stages and found that the carrion fauna was made up of mainly Acarina, Coleoptera, Diptera, and Hymenoptera. He also provided a table to represent the succession pattern of the species attracted to the bird carcasses. Some of the carcasses were protected from contact with arthropods, and, as in the study by Payne (1965), he found this made it difficult to define decompositional stages and greatly decelerated the decay of such carcasses.

Johnson (1975) related the seasonal and successional variation in insect populations as found in a study on 39 small mammal carcasses in Illinois. He too found that Coleoptera, Diptera, Hymenoptera and Acarina formed the bulk of the carrion-attendant fauna, making up more than 90% of such organisms.

In a somewhat more probing study of the invertebrate and vertebrate species attracted to 40 rabbit carcasses in the Chihuahuan desert, McKinnerney (1978) divided decomposition into four stages, recorded six vertebrate and 80 invertebrate species, and presented the probable feeding roles of the various families. She went further and calculated the species diversity in each seral stage using the Shannon-Weaver index of general diversity (H'), and also the similarity between seral stages using the Sorenson index of similarity (S). She provided a figure depicting the succession pattern of the major groups of arthropods at three different study sites and speculated upon the adaptive implications of late colonisation of a carcass by burying beetles and the possible transmission of parasites from carcasses to vertebrate scavengers via carrion insects. Also working in the Chihuahuan desert, Schoenly and Reid (1983) examined the community structure of arthropads at 18 mammalian carcasses of varying mass. They found a significant positive relationship between arthropod species richness and carcass mass, and that the biomass of necrophagous taxa exceeded predator biomass in all carcass sizes.

Abell et al. (1982) monitored the incidence and succession of arthropods at decomposing turtles. The main visitors were Acarina, Coleoptera, Diptera and Hymenoptera, and they found that the soil fauna below the carcass was heavily influenced by carrion fluids draining into the ground.

Neoptropical

Only two publications were found in the literature on arthropod communities utilising carrion in South and Central America. Cornaby (1974) studied the decomposition of 4 lizard and 4 toad carcasses in contrasting dry and wet tropical forest regions in Costa Rica, and found that calliphorids, sarcophagids, formicids and scarabaeids were the most important groups in the reduction of such carcasses to the dry skin stage. As in most other carrion studies, he also provided details on rates of decay, trophic interactions, succession patterns, and an inventory of 170 arthropod species collected at the carcasses. Analysis of his results suggest a difference in the species-complexes of reducer-insects associated with toad carcasses as opposed to lizard carcasses, but he conceded that more exhaustive fieldwork was required to strengthen the evidence for resource partitioning of vertebrate carcasses by saprophagous arthropods. Also in Costa Rica, Jiron et al. (1981) observed the succession of insects at a dead dog and found that this depended upon the specific feeding preferences of the different species, interspecific competition, and the microclimate provided by the substratum.

Australian

Despite many papers on aspects of the economically important sheep blow-fly, *Lucilia cuprina*, and also other blow-flies, only two published works have emerged from Australia dealing with the entire complex of arthropods found at carrion.

Fuller (1934) was the first person who attempted ".. to study the carrion complex in Australia as an ecological unit - to discover the inter-relations and interactions of this association of insects." She did this mainly in the Canberra area over a four and a half year period, using mostly guinea pig, mouse, cat and sheep carcasses. A total of 87 insect species of 29 families were recorded as breeding in or associated with carrion, and she provided some data on feeding and other habits of most of these groups. She briefly described the decompositional stages of carrion and gave an account of the insect succession during different seasons. A substantial portion of her publication was devoted to a detailed study of intra- and interspecific competition amongst blow-fly larvae, the seasonal abundance of blow-flies, the influence of physical factors on the blow-fly population, and the effect of predators, parasites, and other insects.

Working in Perth on the western side of the continent, Bornemissza (1957) examined the succession of arthropods at guinea pig carcasses, providing excellent diagrams depicting the successional pattern and relating this to five stages of decay. He divided the arthropods into four communities described as necrophagous, saprophagous, dermatophagous and ceratophagous. Going a step further than previous workers, he examined how the various stages of decomposition affected the underlying soil and the typical fauna normally associated with it. He described how body fluids form a crust in the upper soil layer resulting in the eventual destruction of the underlying plants and soil fauna. Continuing his observations at the site for a year, he found that arthropods normally found in soil had not completely re-established themselves in the upper zone occupied by the carrion, and that subterranean forms had been more successful in re-invading the habitat than soil-surface or litter dwellers. The soil fauna referred to were mainly Collembola, Acarina, Pauropoda, Symphyla, Protura and Pseudoscorpiones.

Ethiopian (Afrotropical)

Wool production in South Africa underwent a tremendous surge in growth and importance during the early part of this century, so much so that by the late 1920's this country was the second largest producer of fine wool in the world, surpassed only by Australia (Smit 1931). The severe economic losses caused by myiasis resulted in a considerable volume of research being conducted on these and the carrion-infesting blow-flies, the most notable studies being done by Hepburn (1943a, b), Mönnig (1942), Smit (1929, 1931), Smit and Du Plessis (1927), and Ullyett (1945, 1950a, b). No publications dealing with the carrion-attendant arthropod complex as a whole appeared before the 1970's.

Coe (1978) studied the decomposition of three elephant carcasses and their associated fauna at intervals over a four-year period in the Tsavo National Park, Kenya. This represented the first attempt to clarify and describe the removal of carrion material from such a large source, and is particularly interesting as the study occurred during a period of severe drought when up to 5 900 elephant died over an 18 month period. Because of the abundance of carrion in the area, vertebrates had only minimally utilised the main study carcasses so that a good idea could be formed of the invertebrate influence and impact on decomposition. Despite the considerable volume of soft tissues available (51,5% of total mass), such material was removed within 20 days from all three elephant carcasses so that only skin, bone and negligible ligamentous tissue remained, micro-organisms and dipterous larvae being the main agents of removal. Another significant finding by Coe was that the skin of all three elephant carcasses, representing 11,6% of total body weight, was removed within 13 days after death with only the soles of the feet remaining after this period, Dermestes vulpinus being the main organism responsible. Bone persisted for a very long period despite extensive flaking and fissuring due to climatic conditions, and Coe suggested that even an estimated recycling time of 20 years for elephant skeletal remains may be too low.

As part of a study on the natural removal of ungulate carcasses and some of the adaptive features displayed by the scavengers involved, Richardson (1980) gave a broad and general description of the succession, role and impact of arthropods participating in carcass decomposition in parts of the Transvaal and southern Zimbabwe. He made only infrequent diurnal observations and divided the arthropod complex into three categories, namely blow-fly larvae, beetles, and "other arthropods".

Prins (1980) investigated the arthropods associated with decomposing organic matter in the southern and western Cape Province of South Africa, collecting as many different species as he could from beached kelp, animal droppings, dead seabirds and other small animals. By rearing the immatures of selected arthropod species he made extensive notes on the morphology of the various stages and also provided brief biological notes of a general nature. He devoted a section to the forensic aspects of animal carcasses and human cadavers, recognising eight successive waves of decompositional fauna which he classified as necrobiotic stage, saprophagous stage, two dermatophagous stages, and four keratophagous stages. His treatment of ecological aspects was very superficial, and the bulk of his work being devoted to a listing of the species encountered and morphological descriptions.

Meskin (1980) made extensive morphological studies on all the life-stages of the most common blow-flies at mainly laboratory rat carcasses in the Highland region of South Africa. He found that seven species were common breeders in such carrion, and provided keys to separate the eggs, larvae, pupae and adults of most of these species. Observations on the biology and ecology of the various flies showed that although their niches at carrion superficially appeared similar they were separated by habitat preference, seasonal succession, ecological succession and different larval feeding habits.

In a short abstract, McClain (1983) summarised her observations on the major carrion feeders at three gemsbuck carcasses in the central Namib Desert, Namibia. She classified decomposition into five stages, namely initial decay, bloat stage, advanced bloat, wet phase, and a dry phase which commenced with the departure of maggots from each carcass. An estimated 70% of carcass biomass was recycled by dipterous carrion feeders. Of interest was that she found sarcophagids to be the first to colonise the carcass, then followed by the more usual calliphorid blow-flies <u>Chrysomyia</u> <u>marginalis</u> and <u>C.</u>

albiceps. She also mentioned consequences of high desert temperatures coupled with low humidities on mortality of blow-fly larvae, stating additionally that internal carcass temperature sometimes reached 45°C which resulted in unique thermoregulatory behaviour in the maggots.

What can be concluded from this survey of the literature is that there have been relatively few truly probing studies on the total community of insects associated with carrion, and that these studies have tended to emerge from relatively confined geographic areas. Also notable is the sudden but belated surge in interest in Africa - especially South Africa - on this topic during the latter half of the 1970's, despite the considerable volume of work done on blow-flies since the 1920's (e.g. Smit 1929, Mönnig 1942, 1931, Hepburn 1943a, b, and others). This work was centred on blow-flies causing sheep-strike in South Africa, and a study of the co-inhabitants of these flies at carrion seems logical to judge the role and impact of these other insects, yet no publications resulted.

The papers mentioned in this review have in most cases served merely to confirm what Mêgnin had already indicated in 1894, that there is a general succession of insects at a carcass whereby species or groups of species are attracted in a generally predictable manner as decomposition progresses. All that subsequent publications have really done was to indicate which species are involved in the process, and how the climatic conditions existent in the particular country of study influence the duration of this period of decay. Because the successionary sequence is predictable in most cases, it is often possible to make use of this knowledge in medico-legal instances where doubt exists as to the time of death, and a number of entomologists have indeed used this as a method to assist law enforcement officials in their task (e.g. Nuorteva 1977, Prins 1980).

With such advantages as ease of study, ease of control, ready availability of carrion, and often rapid turnover of associated insect populations, it is curious that relatively little use has been made of carcasses as a substrate for general studies on the actual dynamics of animal succession, competition, or other interactive processes. Perhaps with most of the groundwork on the life-histories of many of the component species having now been completed, and many of the factors affecting their abundance been identified, such studies may gradually replace the more traditional approach.

STUDY AREA

Location and geographic features.

The area covered during the various facets of the present study extended over the entire extreme northern region of the K.N.P. which is known as the Punda Maria-Pafuri-Wambiya area. Although the southern limit is an arbitrary line, it is situated completely within the tropics between 30°52' and 31°25' East, and 22°19' and 22°47' South. The bulk of the work was performed in the Pafuri area immediately south of the Luvuvhu River with the Anthrax Research Camp as a base (Fig. 8). The study area lies wedged between three countries - the Limpopo River in the north demarcating the border with Zimbabwe, the eastern boundary represented by the Lebombo mountains with Mocambique beyond, while the Luvuvhu River north of Punda Maria marks the western border with the Republic of Venda. (Fig. 1).

The vast arid plains so typical of the northern K.N.P. form the southern part of the study area where it is known as the Hlamalala Plain and varies between 364 m and 424 m in altitude. It gives way to an extensive series of hills and outcrops concentrated mainly in the western and northern regions (Fig. 2) which reach a maximum altitude of just over 606 m in the Punda Maria area. Undulating country predominates in the north-east with a fairly broad alluvial floodplain between the Luvuvhu and Limpopo Rivers near their confluence, this being only 191 m above sea-level (Tinley 1980). To the east a somewhat unique strip of deep sand with characteristic vegetation, known as the Nwambia sandveld, juts in from parent areas in Mocambique, the altitude here varying between 474 m and 530 m (Gertenbach 1983).

The rugged outcrops and hills of the western and northern parts of the study area are composed mainly of Sandstone of the Waterberg System and Cave Sandstone of the Clarence Formation, but in the more flat parts the geological base changes to Ecca-shales of the Karoo System and basalts with extensive dolerite intrusions. This latter

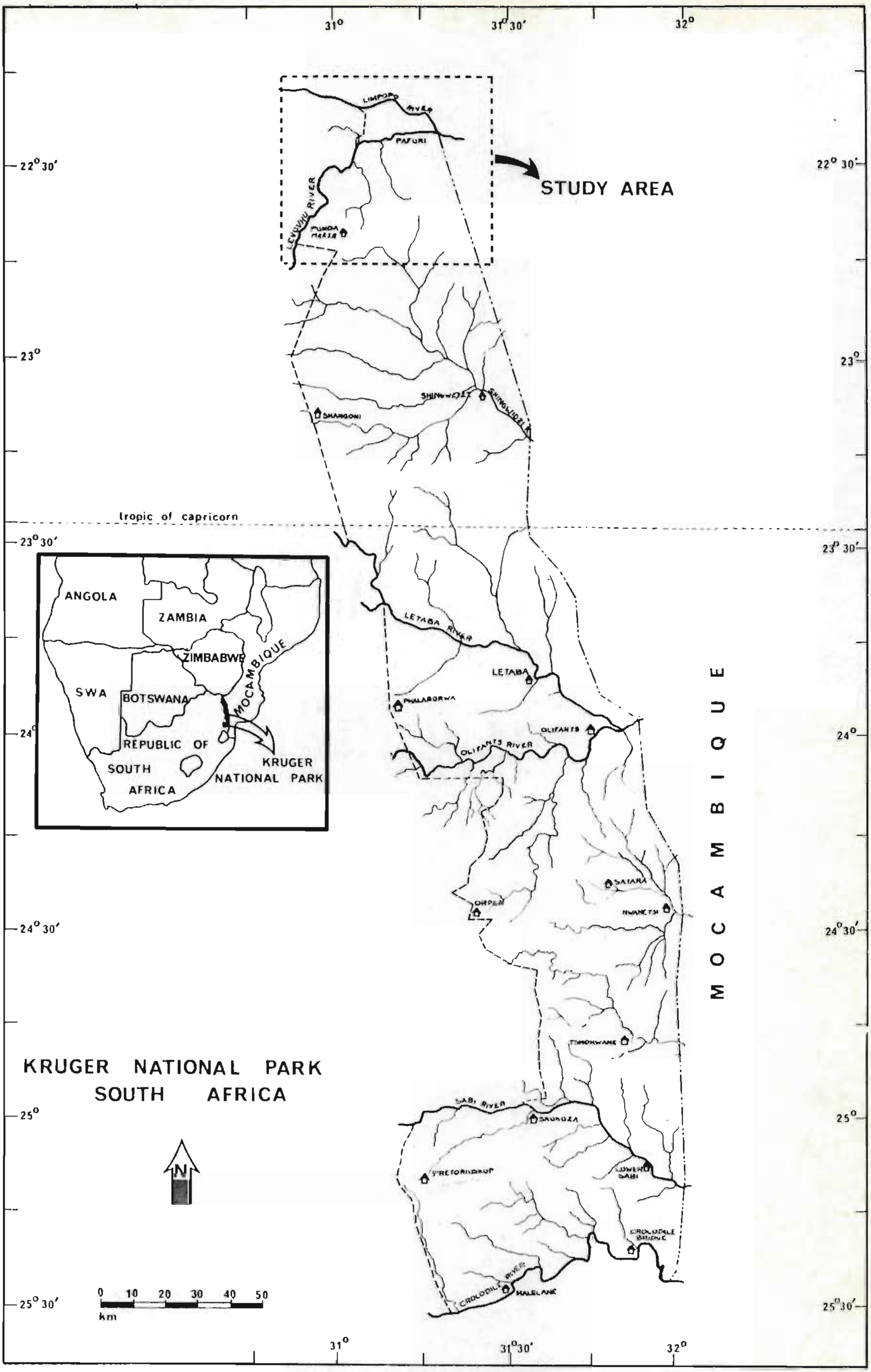


FIGURE 1 : Relative position of the study area and the Kruger National Park in Southern Africa. Study area is enlarged in Figure 2

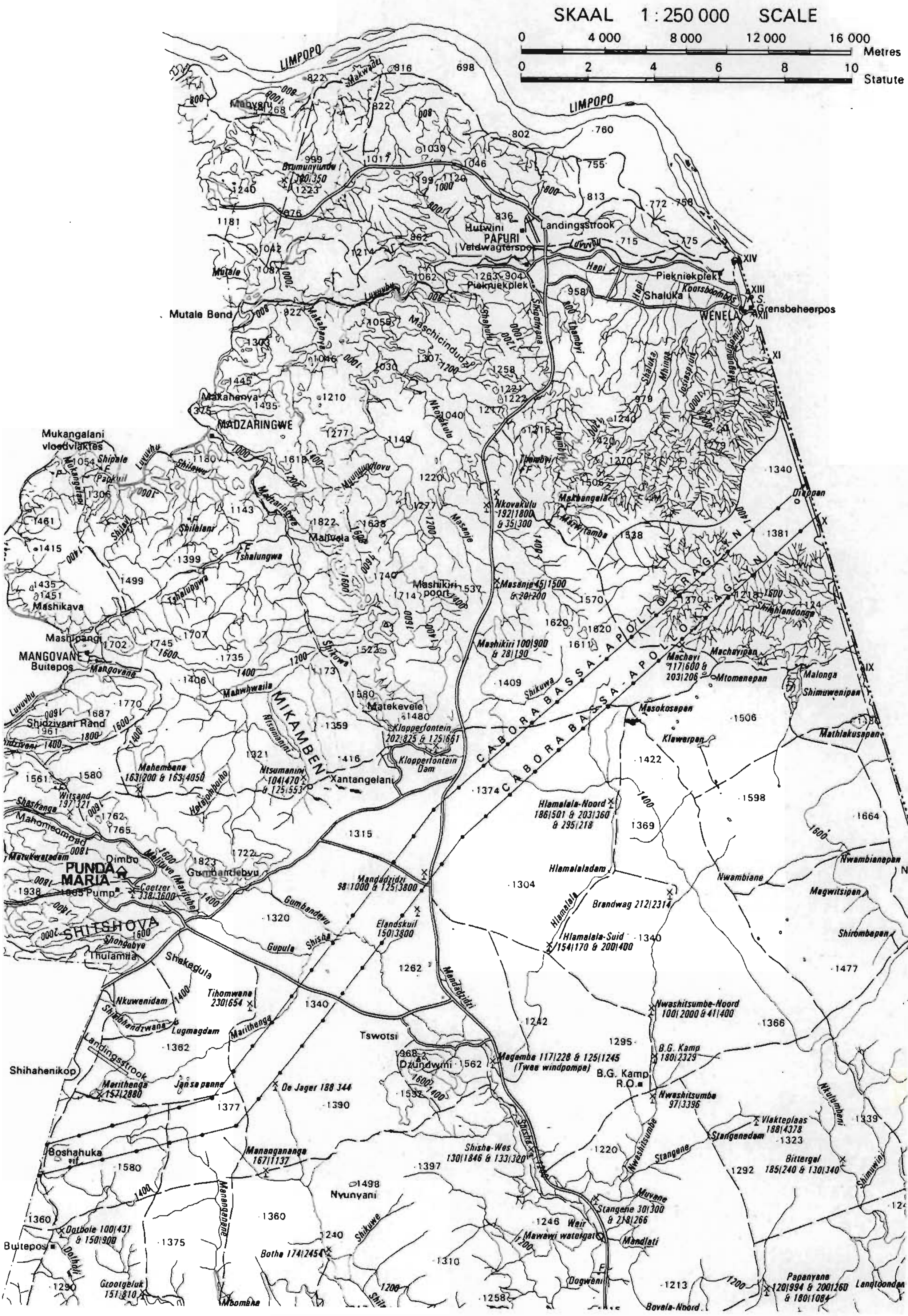


FIGURE 2: Map of the Punda Maria-Pafuri-Wambiya study area showing contours, drainage areas and other geographic features.

area is separated from the Nwambia sandveld in the extreme east by a broken strip of white sand of Quaternary origin mixed with gravel and basalt (Gertenbach 1983).

Two major rivers with their associated drainage areas pass through the area. From its junction with the K.N.P. west of Punda Maria the Luvuvhu flows in a north-easterly direction for a considerable distance before veering east to link with the south-easterly flowing Limpopo River (Fig. 2). In its more western reaches the Luvuvhu forms magnificent gorges with steep krantzes before levelling out to give rise to the eastern floodplains with rich alluvial deposits.

Important tributaries which drain part of the study area and flow into the Luvuvhu are the Shidzivane, Mangovane, Matukwala, Shipudza, Madzaringwe, Mashikiri, Nkovakulu, Thambyi and Mutale. Unlike the Luvuvhu, which generally has flowing water all year round, the Limpopo is dry during most months of the year. Like the Luvuvhu, however, it is subject to periodic floods in summer which has given rise to an extensive flat floodplain near their confluence. Large pans which at times retain water for considerable periods between these rivers include Gwalala, Mapimbi, Rietbok, Nwambi, Nyala, Dakamila, Hulukulu, Makwadzi and Spokenyolo. Other important pans further south and east include Hape, Machayi, Mathlakusa, Masokosa, Klawer, Nwambiane, Magwitsi and Shirombe. A series of fountains also provide water and these are Shipudza, Shipale, Shilalani, Tshalungwa, Malonga, Makhangela, Matukwale, Shashanga and Klopperfontein.

Climate

(a) Rainfall

Rainfall data for the Pafuri area date back to 1925 and provide an average annual figure of 438,1 mm, whereas the corresponding average annual rainfall for Punda Maria worked out over a 51 year period comes to 587,8 mm (Gertenbach 1980). A generalised map providing isohyets to show the distribution of annual rainfall in the K.N.P. is given in Figure 3. It is now well-known and widely accepted, however, that the summer rainfall areas of South Africa undergo oscilla-

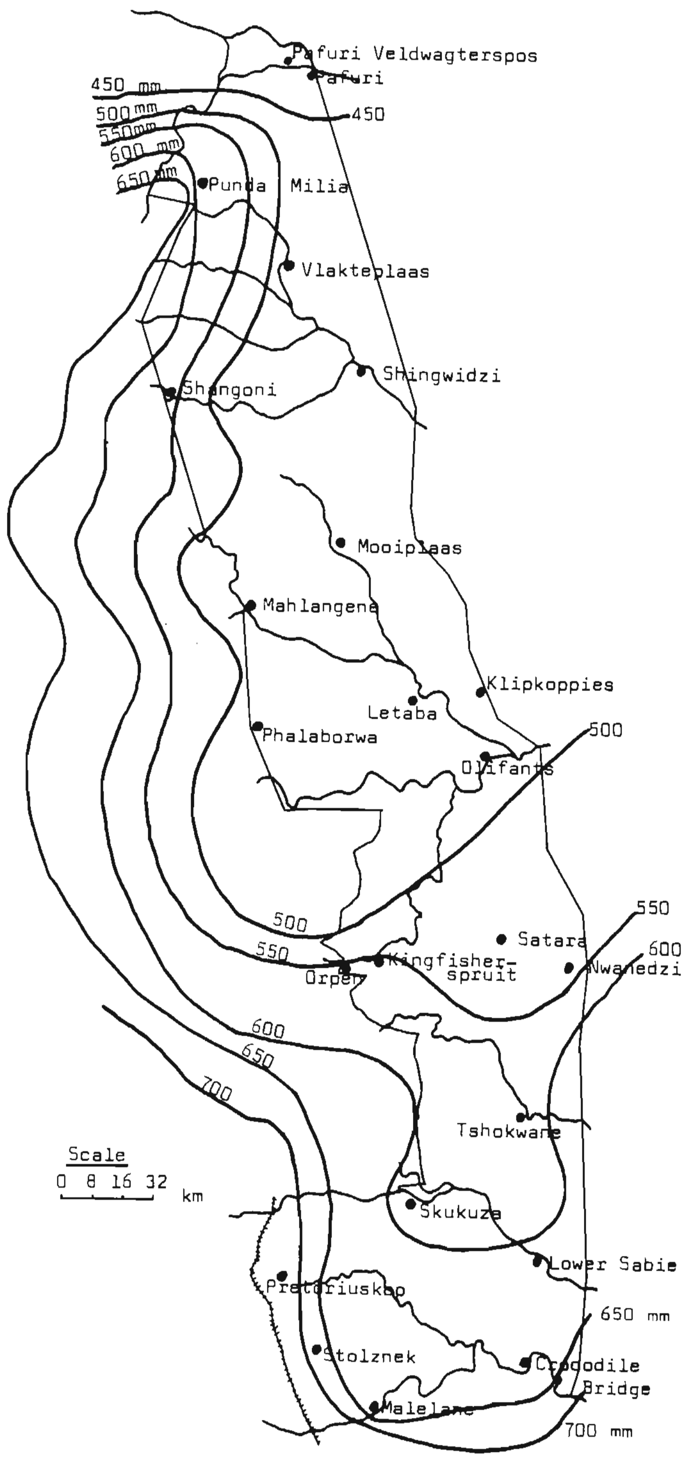


FIGURE 3: Rainfall map for the Kruger National Park (After Gertenbach 1980)

tions in which approximate 10 year periods of above average rainfall alternate with below average rainfall over a period of similar duration, giving rise to wet and dry cycles which are fairly predictable (Tyson & Dyer 1978, Vines 1984). Analyses of the available rainfall data in the Kruger Park have shown that this area is subject to the same cyclic pattern, although the phases are slightly shortened, and this is well depicted in Figure 4. The average monthly rainfall for Punda Maria and Pafuri as determined by Gertenbach (1980) are presented in Table 1. As the bulk of the fieldwork for this study was performed in the Pafuri area between January 1979 and March 1982, the monthly rainfall received during this period is shown in Figure 5. Where more detailed rainfall and other weather data are required, these will be presented in later chapters or sections where they are relevant.

Punda Maria and the Pafuri area receive the bulk of their rain between November and March, with the driest period experienced from June to August. Most of this rain occurs as thunderstorms. Pafuri is the most arid area in the K.N.P. and this is mainly due to the frequent presence of a high pressure system above the Limpopo valley and adjacent Gazaland region of Mocambique, resulting in dry conditions over south-east Zimbabwe, central Mocambique (up to the Zambezi River) and the northern Transvaal Lowveld (Tinley 1980).

(b) Temperature

Temperatures in the study area tend to be high as reflected in Table 2. The hottest months are from October to December, and although Pafuri experiences much lower absolute minimum temperatures, it tends on average to be much warmer by several degrees than Punda Maria. The Pafuri area is also subject to greater temperature fluctuations with extremes of 47,5°C in November and 0,8°C in July being recorded. The average monthly temperatures at Pafuri for the study period January 1979 to March 1982 are presented in Figure 6.

(c) Wind

Data on wind is available from records of the Mocambican

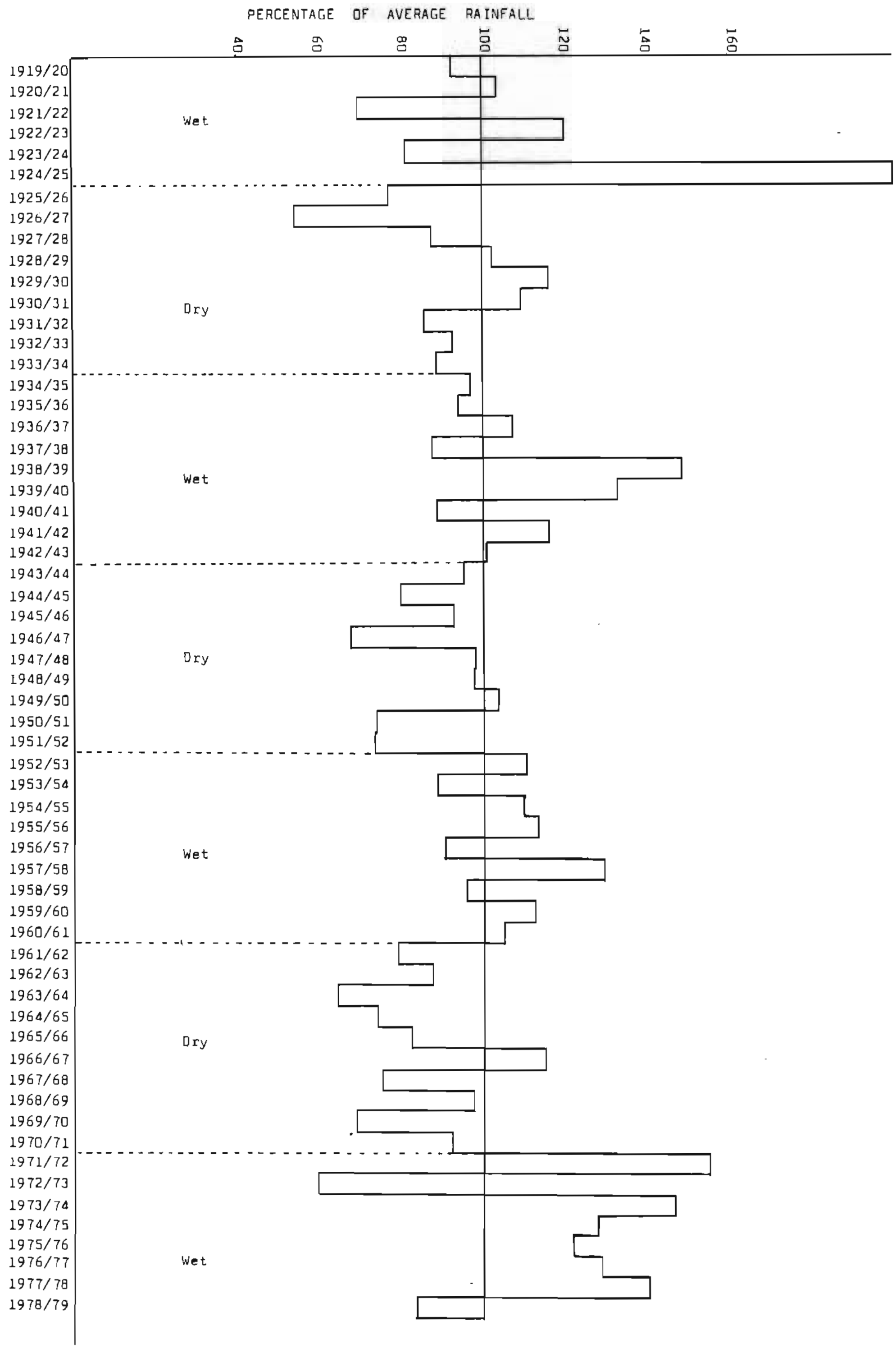


FIGURE 4: Cyclic nature of rainfall in the Kruger National Park. Rain for each year is expressed as a percentage of the long-term average rainfall for the area (After Gertenbach 1980)

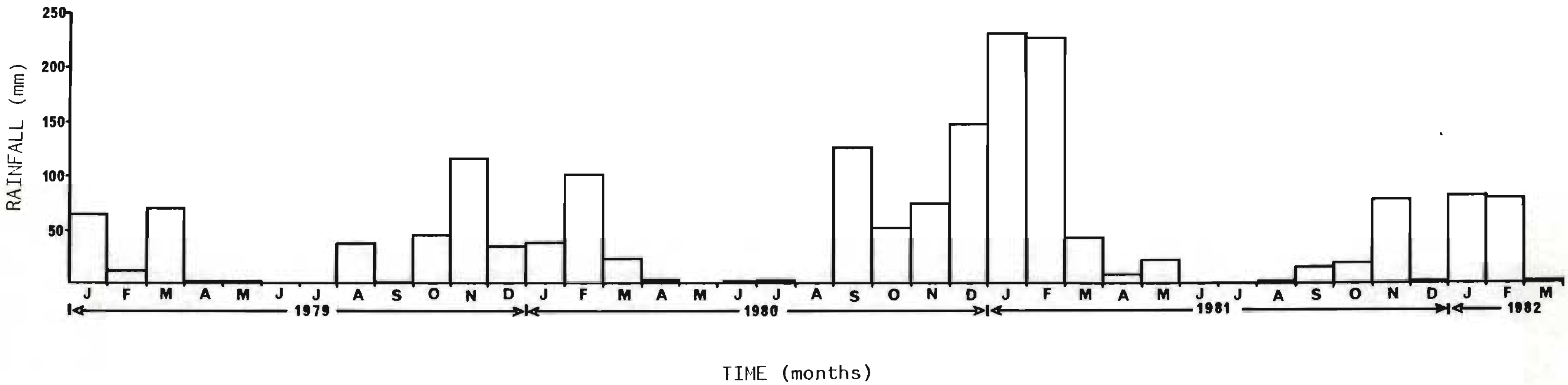


FIGURE 5: Monthly rainfall measured at Pafuri (Station 812/567) for the period January 1979 to March 1982

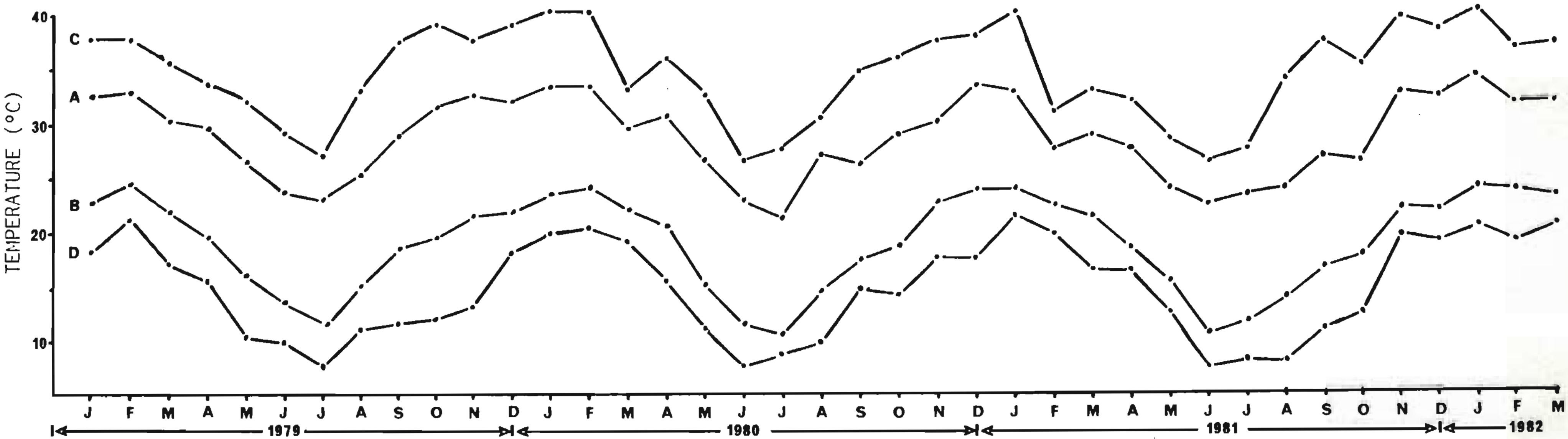


FIGURE 6: Monthly maximum and minimum temperatures for the period January 1979 to March 1982 from records of the Pafuri weather station (No. 812/567)

A = AVERAGE MONTHLY MAXIMUM TEMPERATURE

B = AVERAGE MONTHLY MINIMUM TEMPERATURE

C = ABSOLUTE MAXIMUM TEMPERATURE FOR THE MONTH

D = ABSOLUTE MINIMUM TEMPERATURE FOR THE MONTH

Pafuri weather station and is provided in Table 3. The information pertains to morning conditions at 08h00, but although wind does often tend to increase towards early afternoon, its strength very rarely exceeds a moderate breeze (11 to 16 knots, personal observation). The prevailing wind direction for the greater part of the year is south-easterly, reverting to north-easterly for most of the remaining months.

(d) Relative humidity

Average monthly figures are provided in Table 3 and more detailed data for specific periods will be provided in later sections where such information is relevant to a particular experiment.

(e) Cloud cover

The average extent of cloud-cover on a 0-10 scale for Pafuri is provided in Table 3. Again, where more extensive data are required to clarify weather conditions prevailing during a particular study, these are provided in later sections.

TABLE 1: Average rainfall for Pafuri and Punda Maria as adapted from Gertenbach (1980).

			Monthly Average											
	No. of years	Average	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Punda Maria	51	587,8	130,4	115,0	95,4	29,1	13,4	5,6	4,3	2,8	14,7	25,0	73,1	113,4
Pafuri	50	438,1	89,1	81,9	49,9	21,3	8,7	5,1	1,9	2,9	10,1	17,0	54,2	88,6

TABLE 2: Temperature data for Punda Maria and Pafuri as adapted from Van Rooyen (1978).

Month	Station	Temperature in °C computed over a 10-year period			
		Average daily max.	Average daily min.	Absolute daily max.	Absolute daily min.
January	Punda	32,0	19,9	41,1	15,0
	Pafuri	33,9	21,4	42,9	13,5
February	Punda	30,9	19,9	38,9	15,0
	Pafuri	33,8	21,7	44,0	15,5
March	Punda	30,0	18,8	38,9	13,3
	Pafuri	33,5	20,1	42,2	7,0
April	Punda	29,8	16,9	38,3	8,3
	Pafuri	32,7	17,3	40,6	10,5
May	Punda	27,1	13,6	36,1	7,8
	Pafuri	30,7	12,3	40,9	3,8
June	Punda	25,2	11,5	32,2	5,6
	Pafuri	27,7	8,9	36,3	1,2
July	Punda	25,3	11,4	32,2	5,0
	Pafuri	28,1	8,1	36,4	0,8
August	Punda	27,0	12,9	37,2	6,1
	Pafuri	30,1	10,5	39,5	1,0
September	Punda	29,3	15,1	38,9	7,8
	Pafuri	31,8	14,9	43,5	3,9
October	Punda	31,5	17,6	41,1	10,6
	Pafuri	34,4	18,9	46,7	8,7
November	Punda	31,4	18,9	40,6	11,1
	Pafuri	34,1	20,4	47,5	11,6
December	Punda	32,9	20,0	43,3	14,4
	Pafuri	34,5	21,2	43,5	14,4
Year	Punda	29,4	16,4	43,3	5,0
	Pafuri	32,1	16,3	47,5	0,8

TABLE 3: Average monthly relative humidity, wind velocity, wind direction and cloud-cover as recorded at 08h00 at Pafuri (Adapted from Van Rooyen, 1978).

	Average monthly relative humidity	Wind velocity (km/h)	Wind direction	Cloud cover (0-10 scale)
Period of observation (years)	10	3	10	5
January	65,4	9,9	SE	3,3
February	67,5	9,1	SE	2,0
March	64,2	9,1	S	1,3
April	61,9	6,5	NE	1,5
May	62,4	5,7	N	1,2
June	64,2	5,9	NW	1,6
July	60,4	6,3	NE	0,4
August	55,1	7,4	NE	1,0
September	57,7	8,1	SE	2,0
October	56,6	8,9	SE	3,6
November	59,3	10,0	SE	4,8
December	62,3	7,7	SE	5,0

Vegetation zones and mammal communities

Because of the soil diversity and varied structural features of the study area, such as hills, valleys and plains of divergent geological origins, a considerable range of distinct plant communities have established themselves on these substrates. The vegetational composition in turn determines to a large extent the distribution and abundance of mammals.

Van Rooyen (1978) made a detailed study of the plantlife of the Punda Maria-Pafuri-Wambiya area and categorised this into four major vegetation types comprising 24 communities, these being (1) diabase and hill communities, (2) mopane veld with eight communities, (3) sandveld with eight communities, and (4) six hygrophilous communities. In a more broad divisioning which combined certain of these elements, Gertenbach (1983) provided a practical grouping of nine landscapes with several subdivisions for the region covered by this study. Both authors gave descriptions of the geology, soil types, drainage areas, rainfall, and a thorough listing of the flora associated with these determining factors. For the purposes of this study, however, the more generalised description of Van Wyk (1972) is more appropriate. Where a specific part of the study required a more detailed knowledge of the vegetational cover to enable better interpretation of the influence on blow-fly behaviour, this will be provided in the appropriate section.

The following vegetation zones, as delimited by Van Wyk (1972), can be recognised and are indicated in Figure 7.

(a) Area C

Almost the entire eastern half of the K.N.P. north of the Olifants River consists of a near-homogeneous stand of mopane (Colophospermum mopane). This can be subdivided into area C1 on the basalt plains where the mopane trees are multi-stemmed and stunted so that they generally only reach one to two metres in height, although much larger specimens are common in the vicinity of streams and other well-watered areas. C2 comprises the area of junction between granite and basalt where large stands of tall mopane forest have developed, with associated

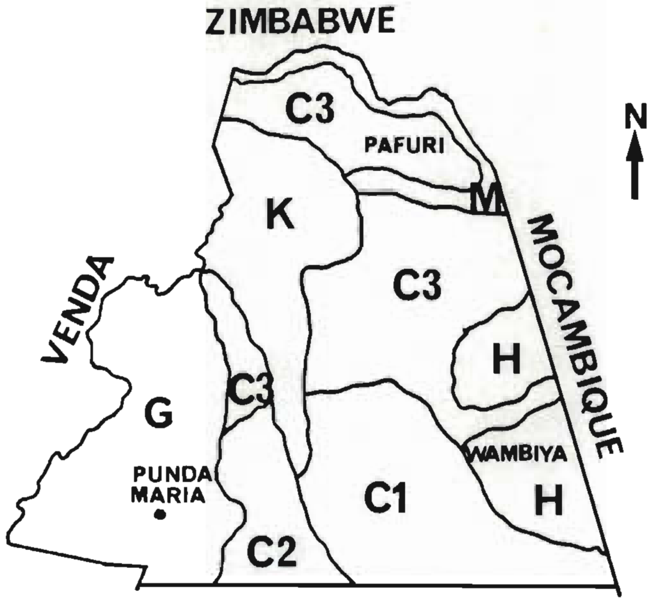


FIGURE 7: Vegetation zones of the Punda Maria-Pafuri-Wambiya study area (after Van Wyk 1972)

LEGEND

C1 = SHRUB MOPANE VELD (BASALT PLAINS)

C2 = TREE MOPANE VELD (SANDSTONE PLAINS AND ALLUVIAL SOILS)

C3 = MIXED MOPANE VELD (BASALT RIDGES)

G = PUNDA MARIA SANDVELD (SANDSTONE RIDGES)

H = WAMBIYA SANDVELD (SANDY FLATS)

K = KAROO SANDVELD (KAROO SEDIMENTS)

M = RIVERINE FOREST (ALLUVIAL SOIL)

specimens of marula (Sclerocarya birrea), leadwood (Combretum imberbe), rain tree (Lonchocarpus capassa), and Lowveld terminalia (Terminalia prunioides) which becomes the dominant species in localised stony patches. Area C1 tends to be fairly open and C2 somewhat overgrown with shrubs, while both areas have a good covering of grass. Area C3 has a more heterogeneous composition of woody species such as Lowveld terminalia, corkwood (Commiphora glandulosa), C. mollis, C. merkeri, species of Boscia, white seringa (Kirkia acuminata) and baobab trees (Adansonia digitata), while Lebombo ironwood (Androstachys johnsonii) occurs in dense concentrations on and against many of the hills and ridges. Grass cover tends to be poor in this region.

Area C1 is of considerable importance as it supports a high concentration of roan antelope, while other rare or fairly rare animals which have established themselves here are sable, eland, reedbuck, and tsessebe. Kudu, giraffe and impala are not common, but zebra, elephant and buffalo are plentiful. Carnivores such as lion, leopard, and cheetah are widely dispersed but much less frequently seen than further south in the K.N.P. Area C2 also has concentrations of buffalo and elephant, while impala and kudu are common and nyala and Sharpe's grysbok are also frequently seen. Area C3 supports a considerable number of buffalo, zebra, and elephant, while kudu and impala are common. Nyala, duiker, and steenbok are also fairly common.

(b) Area G

This is a very complex vegetational region around Punda Maria stretching west and north to the Luvuvhu River. It is a mountainous terrain with sandy well-drained soil and has a very wide range of trees of which the following are important: Xylopia odoratissima, Burkea africana (wild seringa), Hymenocardia ulmoides, Diplorrhynchus condylocarpon, Pteleopsis myrtifolia, Markhamia acuminata, Psendolachnostylis maproneifolia (kudu-berry), Entandrophragma cundatum (mountain mahogany), Albizia tanganyicensis, Securidaca longipedunculata (violet tree), and dense stands of Lebombo ironwood on many of the hills and ridges.

The grass cover is also varied and fluctuates from sparse to fairly dense. The area does not support a high concentration of larger mammals, although herds of buffalo and elephant are present, and species such as kudu, nyala, bushbuck and grey duiker are regularly seen. Lion are fairly rare.

(c) Area H

Growing on a deep layer of sand, this is a unique well-defined plant community which includes several species present only in very low numbers or nowhere else in South Africa. The area is generally referred to as the Wambiya or Nwambia Sandveld, and supports important woody species such as Xeroderris stuhlmannii, Hugonia swynnertonii, Baphia massaiensis, Pterocarpus antunesii, Drypetes mossambicensis and Cleistanthus schlechteri. In structure the zone can better be described as tall shrubveld with few of the trees attaining great height, the crowns generally only reaching between two and four metres (Gertenbach 1983).

Grass-cover in this zone is sparse over the greater area, and medium to large-sized mammals are relatively scarce. Nevertheless kudu, duiker, nyala, steenbok, Sharpe's grysbok, zebra, eland, sable antelope, buffalo and elephant do occur.

(d) Area K

A large number of rocky outcrops and cave sandstone hills occur in this region and have a characteristic associated fauna. Some of these species are Boscia angustifolia, Toddaliopsis bremekampii, Artobotrys brachypetalus, Rothmannia fischeri, Ficus smutsii, and Stadmannia oppositifolia.

Little undergrowth occurs and the grass-cover tends to be sparse although it does become dense in patches. Medium to large-sized mammals are not abundant although elephant, buffalo, impala and kudu are frequently seen. Baboons are also plentiful in localised areas.

(e) Area M

This is an hygrophilic association of plants and adjoins all the rivers and major streams as a narrow band. Made up of large trees and a dense undergrowth, the foliage is darker than that of vegetation in the more arid zones away from the stream edges so that such communities are easily recognisable even from a distance. The most noticeable and important of the component species are Ficus sycomorus (sycamore fig), Trichilia emetica (Natal mahogany), Acacia robusta (Highveld knobthorn), Acacia albida (ana tree), Adina microcephala (water matume), Diospyros mespiliformis (Transvaal ebony), and Xanthocercis zambesiaca (nyala tree). The trees reach a height of about 20 metres with a lush canopy, which together with the dense undergrowth permits very little grass growth below.

The largest concentration of nyalas in the K.N.P. occurs in this area, and it also supports in abundance such species as bushbuck, kudu, baboons, vervet monkeys, hippopotami and crocodiles. Buffalo, impala and warthogs are common visitors, together with waterbuck, duiker, bushpigs and elephant in lesser numbers. A large number of birds also concentrate in this zone, and in general it can be said to be very rich in animal life.

Annual aerial censuses are undertaken to obtain counts of population numbers for the various larger mammal species in the K.N.P. The extreme northern area, closely corresponding to the study area, is surveyed by means of a helicopter with several observers aboard, and the census totals for 1982 and 1983 are listed in Table 4.

TABLE 4: Population totals for the larger herbivores of the study area as obtained from helicopter surveys (Adapted from Joubert, 1983).

SPECIES	1982	1983
Impala	2 440	1 694
Zebra	178	144
Kudu	541	359
Giraffe	16	8
Warthog	273	64
Eland	117	68
Sable antelope	44	68
Waterbuck	90	30
Hippopotamus	225	89
Buffalo		3 585
Elephant	± 600*	± 600*

* Hall-Martin, personal communication

With regard to the population numbers recorded in Table 4, it should be mentioned that these are not absolute counts as individuals hidden in dense vegetation will of course not be visible for counting, with some species count such as warthog, being more prone to such error. So although the totals presented in the table are minimum numbers they are nevertheless also a good reflection of probable absolute numbers especially of such very visible species as elephant and buffalo. What will also be evident from examination of Table 4 is the very steep decline in population numbers from 1982 to 1983. This is attributable to the severe drought experienced in the latter half of 1982 when numerous animals died as a result of malnutrition. The totals for 1982 would therefore be a more accurate reflection of population status of the various species during the major part of the study period, and also for population numbers during more normal years over a long period.

History

Archaeological evidence, such as the abundant Stone Age implements in the Pafuri area, Bushman paintings at various sites, and stone rampart remnants at sites at Makanja and Pafuri, suggests a probable continuous human presence in the study area estimated as dating as far back as 500 000 years (Meyer pers. comm.). The human inhabitants appear to have been in low numbers with and probably well integrated in the ecology of the area with no major impact on the wildlife.

In 1931 a tourist rest camp was established and named Punda Maria (see Fig. 8). In 1960 the name was changed to Punda Milia but has recently officially reverted to the original name. Besides Punda Maria rest camp, a small base-camp along the Madzaringwe Spruit (Nyala-land Trails Camp, see Fig. 8) used by tourists on Wilderness Trails, Pafuri Rangers Quarters, and a recruiting station for the Employment Bureau of Africa at Pafuri, the only other locations of permanent human habitation in the study area at present are the old Pafuri Border Control Post on the S.A./Mocambique border, and a small army base near the Limpopo/Luvuvhu confluence.

The alarming anthrax epizootics during 1959 and 1960, followed by others in 1962 and 1970, resulted in considerable attention being focussed on the disease. A large elephant-resistant enclosure was constructed at Nwashitsumbe in 1966 for establishment of a breeding herd of roan antelope and research on their population dynamics. A field laboratory with animal pens, known as the Anthrax Camp, was erected at Pafuri during 1971/1972 for anthrax research. This was used as base-camp for the present study (see Fig. 2) and is still used for anthrax research.

In 1969 the land between the Luvuvhu and Limpopo Rivers was incorporated into the Kruger National Park by exchanging this from the Department of Bantu Administration and Development for a stretch of land south of Punda Maria on the western boundary. The Luvuvhu/ Limpopo ground was only proclaimed as National Park on the 28th April 1976, while the land south of Punda Maria was deproclaimed simultaneously. The Bantu inhabitants between the Luvuvhu and Limpopo were relocated to areas outside the K.N.P. in August 1969 (Van Rooyen 1978).

According to Mr. H. Mockford (pers. comm.) the number of these native inhabitants never exceeded about 250 during his memory, but Mr. D. Marais (pers. comm.), also closely associated with this area

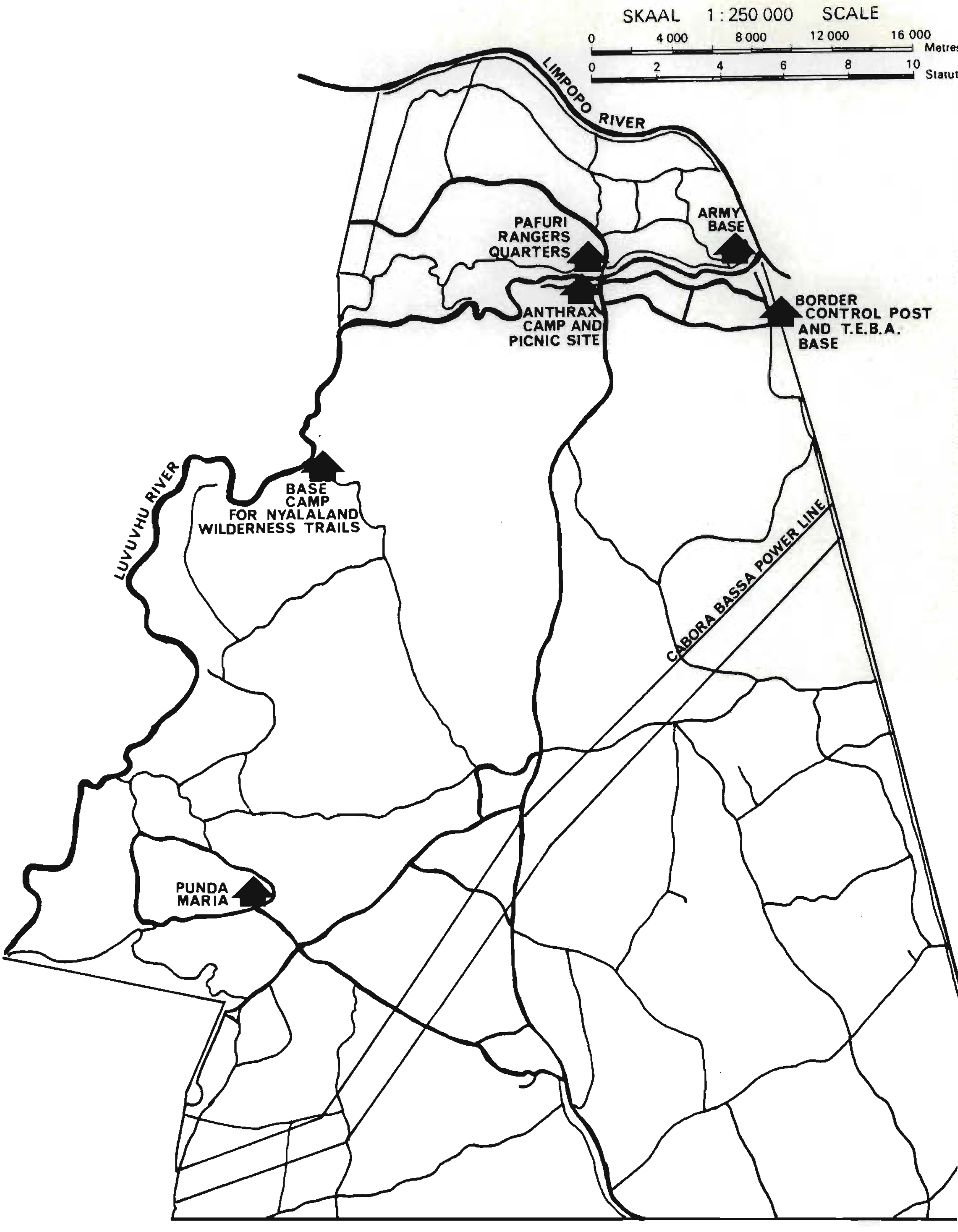


FIGURE 8: Map of the Punda Maria-Pafuri-Wambiya study area showing roads and sites of human habitation

for a lengthy period, placed an upper limit of 500 inhabitants. No bridge existed over the Luvuvhu River prior to the erection of a military bridge (Bailey Bridge) in 1973, so that the only access to the north bank of the Luvuvhu prior to that date was via Bobomene Drift (immediately east of the Thambyi Spruit) when the level of the river was low. In October 1975 a tarred-road construction programme was commenced to link Pafuri with Punda Maria and areas further south, and this was completed in December 1976. It included a high-level bridge for permanent access over the Luvuvhu River (Van Rooyen 1978). The study area is therefore very sparsely populated by humans, and their influence has been minimal, making the area ideal for studying natural populations.

CHAPTER 2

CARCASS DECOMPOSITION

Although the present study focusses on the insects attendant at carrion it is nevertheless desirable to gain some knowledge of the dynamics and progression of decomposition for a better perspective of the breakdown of carcass components and its possible influence on attending insects. A general discussion of post-mortem changes found in mammal carcasses is therefore given below, followed by a more pertinent examination of the physical changes after death as exibited by the study animals. Unless otherwise stated the information is derived from Simpson (1965, 1979).

The accounts of some of the post-mortem changes presented below show that they (or the factors bringing about that change) mostly occur independent of each other and at varying rates. So variable are these factors that experienced highly qualified persons have been misled by using only a few obvious changes and estimating on the basis of this evidence that several days or as much as a week had passed since death, when in fact only a few hours had passed.

Similarly, it is my experience that many of the staff in the K.N.P., including the Rangers, consistently overestimate the time elapsed since death of an animal, and that they may state a carcass to be several weeks old when in fact less than a week had elapsed. This overestimation, sometimes gross, occurs most frequently under summer conditions when carcass decomposition is very rapid.

DEATH AND SUBSEQUENT CHANGES IN THE CARCASS

Disregarding the complications which arise in the definition of death in humans and experimental animals where individual vital organs may be kept alive and functioning by artificial means, somatic death can be said to have taken place when the following three factors are established: loss of electroencephalogram rhythms, cessation of respiration, and cessation of circulation.

Many organ systems, however, remain functioning for a variable period of time after loss of the three symptoms of death. The various tissues, cells, and enzyme systems therefore do not all cease functioning immediately or simultaneously.

Loss of body heat

One of the first changes manifested after death is a cooling of the body until it reaches the temperature of the surrounding environment. The rate of heat loss can be determined and this has long been used especially in medico-legal situations to estimate the time at which death occurred. To be accurate, however, the temperature of the body at the time of death must be known in addition to the rate of heat loss. It is often not correct to assume that at the time of death an animal had a temperature the same as its living conspecifics as several factors such as asphyxiation, a fat or air embolism or certain other vascular conditions affecting the thermal control centres of the brain may alter normal body temperature. A number of factors influence the rate of temperature decrease, some of these being:

(i) the temperature differential between the body and its environment - in general the greater the difference in temperature the faster the rate of cooling.

(ii) the size of the animal - young animals have a greater surface area relative to mass so that a greater area for heat loss is available.

(iii) obese animals will tend to lose heat less rapidly than their leaner conspecifics as fat is a poor conductor of heat;

(iv) in humans, the extent of clothing worn on the body may influence the rate of cooling, whereas in other mammals the thickness of the fur will play a role.

Changes in the skin

Circulation ceases with death so that the supply of fresh blood to the peripheral areas is cut off. The skin becomes unreactive and loses elasticity.

Changes in the eye

The eye and its component structures undergoes many changes, some of these being:

(i) loss of corneal reflex.

(ii) clouding of cornea.

(iii) flaccidity of the eyeball, where the eyeballs subside into the orbital fossae.

(iv) size of the pupil, which will change as the muscles of the iris lose "tone", causing the iris to settle into a position of equilibrium.

(v) changes in the retinal blood vessels, which take on a segmented appearance soon after death and retain this appearance for about an hour, after which the vessels contract to an extent that they are difficult to observe.

(vi) chemical changes in the vitreous humour, such as a steady rise in potassium levels, which nevertheless exhibit too wide a range to be useful for determining time-lapse since death.

Post-mortem lividity or hypostasis

With cessation of circulation fluid blood will sink to the lowest parts in accordance with gravity. As the red blood corpuscles are heavier they settle first and therefore impart a red colour to those areas affected by lividity. Pressure points (such as objects pressing against the body where it has fallen) and areas of constriction (such as a stiff collar or rope around an animal) will prevent lividity from developing at these sites. Lividity or hypostasis should not be confused with a bruise which it may resemble. Lividity may persist for some time after death but disappears when haemolysis sets in. Putrefactive gases also disperses this blood.

Fibrinolysis

In cases where "shock" or "collapse" is present before death, the blood may remain fluid for longer than normal. This appears to be brought about by release of fibrinolysin due to some non-specific general reaction to injury. The fibrinolysin prevents blood clotting by adhering to the clot as it is formed, moving into solution again when the clot lyses.

Chemical changes

The post-mortem changes examined thus far are all influenced by various environmental factors so that it is generally difficult, or impossible, to establish the rate at which such change occurred, so that estimation of the time of death is generally fraught with uncertainties.

Investigations into the changing levels of cerebrospinal phosphates, potassium, lactic acid, non-protein nitrogen, several amino acids, the ascorbic acid and potassium in the vitreous humour of the eye, potassium and urea levels in the blood, indicated that although the change is often closely correlated with lapse in time, it is generally subject to so many variable factors or offers so wide a range as to be too inaccurate and unsatisfactory (Evans 1963, Simpson 1965).

Muscle changes

With the exception of the relatively infrequent occurrence of cadaveric spasm, whereby a part, or the entire body, is instantly stiffened at the moment of death, the muscles usually relax and soften after death. Joints are easily flexible.

Voluntary muscle may retain the power of contractility for an hour or so after death. The cells remain alive and can be stimulated into contraction mechanically or electrically. This stage soon passes however, giving way to one of the most obvious of post-mortem changes: cadaveric rigidity or rigor mortis. The muscles become rigid and remain in this position for a variable length of time, thereafter relaxing, never to regain the power of contraction. From this stage, depending on environmental conditions, the muscles may putrefy, mummify, or form adipocere.

Rigor mortis commences when the muscles have lost their power of irritability, i.e. with death of the component cells, usually within two hours of somatic death. All the muscles, both voluntary and involuntary, experience a shortening and stiffening of the fibres. Rigor mortis depends to a great extent on the amount of waste metabolites present in the muscles at the time of death, so that the onset and disappearance varies amongst other things according to how active the animal was in the immediate period prior to death, the state of health of the animal, and also on environmental temperature.

The muscles of the face, neck and trunk are usually the first to stiffen, followed by those of the limbs. Relaxing of these muscles, with the passing of rigor mortis, takes place in the same order.

Putrefaction

Following the onset of rigor mortis, the next change to affect the carcass is putrefaction. This is caused partly by autolysis due to enzymes already present in the cells, but mainly from the invasion of bacteria, protozoa, fungi, and insects, many of which produce proteolytic, lipolytic, and carbohydrate-reducing enzymes resulting in the formation of substances such as amines and amino acids like leucin and tyrosin, aromatic substances such as indol and skatol, and a number of acids such as formic, acetic, butyric, valerianic, palmitic, lactic, succinic, and oxalic.

Aerobic bacteria such as species of Pseudomonas, Achromobacter, Streptococcus, Bacillus and Micrococcus, invade the lungs and surface areas causing bad odour, ill-taste, and slime, with an estimated 3-5 x 10^7 bacteria per 1 cm² of meat surface usually present when surface slime and smell become evident. Species of Lactobacillus, Serratia, Pseudomonas, Micrococcus, Flavobacterium and Chromobacterium cause discolouration of meat while Photobacterium cause luminescence. The most important bacteria contributing to putrefaction are the anaerobic forms, generally species of Clostridium (Noble & Naidoo 1979).

Assuming the animal to remain undisturbed after death (i.e. not scavenged by hyenas, vultures, etc., or otherwise mutilated), the first organisms of putrefaction to invade the body are anaerobic bacteria moving in from the bowel into the blood vessels and from there throughout the body. Airborne bacteria add to the putrefaction process, but are overshadowed by the anaerobic intestinal forms. The organs closest to the bowel therefore are first to be affected by putrefaction, and the normal sequence in which putrefaction affects the various body parts are:

(i) intestines, stomach, liver blood, heart blood and circulation, heart muscle.

(ii) Air passages, lungs, liver.

(iii) Brain and cord.

(v) Voluntary muscles.

(vi) Uterus, Prostate.

Putrefactive bacteria moving from the intestines into the blood vessels rapidly cause haemolysis of the blood resulting in the formation of hydrogen sulphide bubbles (H_2S) and a green discolouration of parts of the skin due to S-methaemoglobin. As the bacteria spread the body bloats extensively due to the production of gases such as hydrogen sulphide, ammonia, phosphorelated hydrogen, mercaptans, carbon dioxide and methane.

Of the gases produced during decomposition, carbon dioxide is one of the first to be liberated and results from oxidation and fermentation processes initiated by micro-organisms (Prins 1980). Carbon dioxide is the major pathway of gaseous carbon release from a carcass and Putman (1978) measured the carbon release from carrion and used this as an index of overall metabolic activity of decomposer fauna within carrion. He found that in carcasses of laboratory mice with only bacteria present the rate of CO_2 release steadied to 15-20 microlitres per gramme dry weight of carcass per hour. With blow-fly larvae present the respiratory release of CO_2 increased to a maximum of 260-270 microlitres CO_2 per g. dry wt. carcass per hour. The total amount of CO_2 evolved from the carcass remained the same however.

Production of hydrogen sulphide appears to be brought about by the breakdown of organic sulphur compounds such as the mercaptans or sulphydryl groups of amino acids, whereas ammonia is liberated during deamination of amino acids resulting from the breakdown of proteins under anaerobic conditions (Prins 1980). Putrescine and cadaverine, which are produced by decarboxylation of other amino acids, together with related products, methyl mercaptan, and hydrogen sulphide, are amongst others responsible for the foetid odours of the carcass (Prins 1980).

Gas production is usually considerable so that a great deal of pressure is exerted in the body, having effects which include:

(i) post-mortem bleeding and an emptying of the heart,

(ii) shifting of lividity (hypostasis) as blood is forced to other areas,

(iii) bloating of the body such that the features become grossly distorted,

(iv) stomach contents may be pushed up through the mouth, rectal contents through the anus, urine from the bladder, and in some cases the foetus may be forced out of the uterus by the buildup of internal gaseous pressure,

(v) submerged bodies rise to the surface and float on water.

With continuing putrefaction the tissues become soft, liquefy, and bloating passes off.

Due to the main cause of putrefaction being the presence and action of bacteria and other organisms, the entire process is subject to considerable variation in its time of onset, degree of severity, and time of disappearance. Many factors will influence putrefaction, mainly in the way they promote or retard the multiplication or activity of bacteria and other small organisms. Some of these are:

(i) air temperature - warm temperatures promote bacterial activity and growth, whereas cool temperatures are detrimental. Freezing stops bacterial activity, as does very high temperatures.

(ii) extent of available moisture - which is generally more than ample in normal mammalian tissue, except in hair, bone, and teeth, for bacterial needs.

(iii) amount of covering material - clothing or covering material may keep the body warm when environmental temperature is low, thus aiding putrefactive organisms.

(iv) the condition of the body - obese bodies tend to have the initial putrefactive stages accelerated, dehydrated bodies slow it down, whereas animals dying from acute diseases normally putrefy faster than those resulting from chronic diseases.

(v) submersion in water - which will affect putrefaction at a rate depending on the organic content of the water, its temperature, its rate of flow, and salinity. Generally water is below atmospheric temperature so that the main effect of immersion in water is to slow down the rate of putrefaction.

(vi) burial under soil - which among other factors will depend also on the intervening period between death and burial, depth the body is placed, type of soil, and temperature of the soil. In general, bodies are usually buried fairly deep and this will slow down the rate of putrefaction due to the cooler environment.

The formation of adipocere

When a body is placed in a damp or wet environment, unsaturated body fats may undergo hydrogenation over a period of several weeks to change into adipocere, so-called as it has properties between those of fat and wax. This substance appears expanded compared to its original state, is white, stiff, and has a displeasing odour. In cool temperate areas this process may require several months, but may form within three weeks in subtropical climates.

Mummification

In hot dry areas, such as in arid deserts, the body of an animal may become dehydrated rather rapidly after death, resulting in little or no increase of bacteria or other putrefactive organisms. Mummification results unless removed by scavengers.

Carrion utilisation by arthropods

If carcasses lie exposed for long enough in conditions where the ambient temperature is not too close to freezing point, blow-flies and other insects will arrive to utilize the carcass. As will be seen clearly in the discussion on insects attendant at carcasses in the K.N.P., such insects generally have specific requirements or preferences and arrive at the carcass in a sequential or successional pattern.

Because of the relative predictability of this successional pattern of carrion usage, it is often possible to use the particular combination of insect species present at a carcass as an aid to determine time elapsed since death (Nuorteva 1977, Erzinclioglu 1983).

Blow-fly larvae are usually first to make significant use of the decomposing material, excreting digestive enzymes which soften and liquefy the muscles and other soft tissues. They greatly accelerate the rate of putrefaction by dispersing bacteria throughout the carcass by their wriggling and tunnelling actions (Fuller 1934).

Although Putman (1978b) found that during winter and spring in England only microorganisms were present and after 85 days as little as 3% of available carrion material had been removed, he also found that carcasses were rapidly colonised by blowfly larvae in summer and autumn so that after 7-8 days nothing remained but bones and hair. Payne (1965) compared the rates of decay of baby pigs exposed and unexposed to arthropod attack, and here the efficient and important role of insects as consumers of carrion was equally clearly revealed. In the much warmer climate of the K.N.P., blow-fly larvae were easily capable of reducing a medium-sized mammal such as an impala or even kudu to skin and bone within a matter of five days in summer (Braack 1981) or under two weeks in winter without any assistance from vertebrate scavengers (pers. obs.). Other insects, such as dermestids, trogids, clerids, tineids and scarabaeids were also present in warm weather and soon removed carcass remains such as skin, fatty deposits, rumen-contents and some keratinous material (e.g. bovid horns) so that only bare bone and hair remained.

Putman (1977) described experiments which reveal that blow-fly larvae consume in excess of 80% of available carrion material. The extraordinary efficiency of food use by these larvae was also shown in the same paper by his finding that each larva consumed the approximate equivalence of 186,18 $\pm$ 70,81 calories, which when compared to the mean weight of a larva ready to enter the pupal stage converted to its calorific equivalent of 147,39 clearly indicates the exceptional efficiency of these larvae to assimilate and convert consumed material into body components as growth or reserves with minimal waste. Similar results were obtained in another study by Hanski (1976a) who found that the instantaneous net production efficiency of Lucilia larvae during the intense growth phase varied between 79% and 84% (measured in joules).

DECOMPOSITION OF CARCASSES IN THE K.N.P.

The main purpose of the preceding discussion on post-mortem changes was to provide some background of these events and show the difficulty in producing a standard series of stages to describe decompositional changes as attempted in Fig. 9 and Table 5.

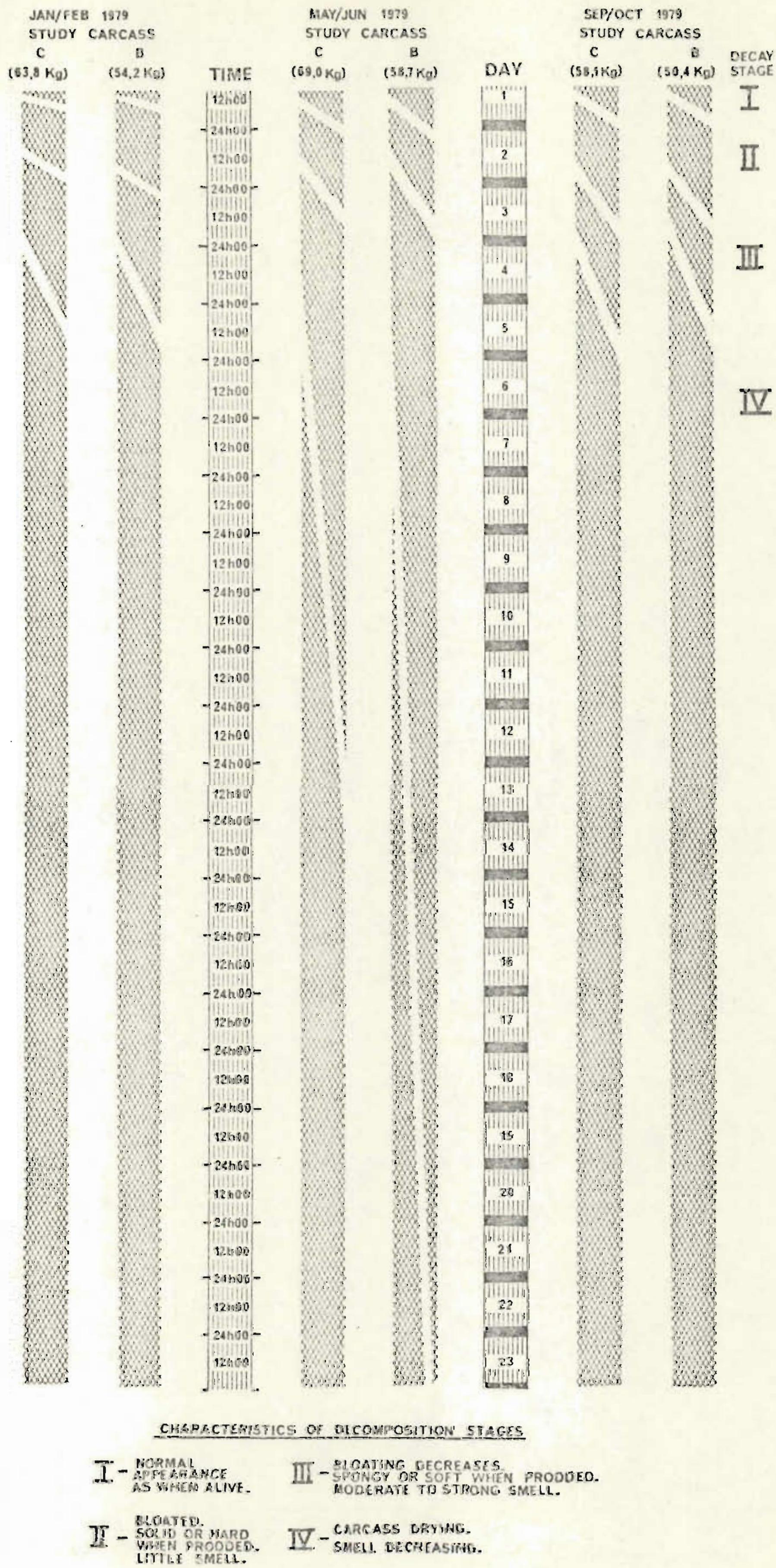


FIGURE 9: Decomposition of impala carcasses used for survey of attendant insects at Pafuri, 1979

TABLE 5: Stages of decomposition for carcasses on land as proposed by various authors

AUTHOR	STAGE 1	STAGE 2	STAGE 3	STAGE 4	STAGE 5	STAGE 6	STAGE 7	STAGE 8
MEGNIN (1894)	Bodies fresh	Decomposition commenced	Fatty acids	Caseous products	Ammoniacal fermentation Black liquefaction	Desiccation	Desiccation extreme	Debris
FULLER (1934)	Not smelling strongly	Active liquefaction and disintegration noticeable. Dipterous larvae and Coleoptera abundant	Drying of carcass with loss of smell					
BORNEMISSZA (1957)	Initial decay	Putrefaction	Black putrefaction	Butyric fermentation	Dry decay			
REED (1958)	Fresh	Bloated	Decay	Dry				
PAYNE (1970)	Fresh	Bloated	Active decay	Advanced decay	Dry	Remains		
McKINNERNEY (1978)	Fresh	Active	Advanced decay	Dry				
COE (1978)	Bloat a) Primary bloat b) Full bloat	Wet or collapse phase a) Primary collapse b) Total collapse c) Putrefaction paste	Dry					
BRAACK (present study)	Fresh	Bloat	Putrefactive	Drying				

During the peak winter months decomposition was slow due to the low night-time temperatures which decreased not only the rate at which enzyme systems - present in the cells of the decomposing animal and in the digestive fluids exuded by bacteria and insects - operate, but also the general activity of bacteria, other micro-organisms, and insects at the carcass. In summer, however, decomposition proceeded extremely rapidly.

In Table 5 I condensed carcass decomposition in the K.N.P. into four fairly distinct stages corresponding to those used in a previous study at the same site (Braack 1981). The classification is not intended to reflect any underlying biological distinctness characterizing each stage, the purpose being merely to facilitate description of the appearance of the carcass by a human observer as decay progresses. It should be emphasized that decomposition is a continuous uninterrupted process with no clearly defined or easily demarcated stages, so that each of the stages I suggest - and those given by other authors in Table 5 - have somewhat arbitrarily designated beginnings and ends. Nevertheless it is a workable classification based on the more obvious physically manifested changes associated with decomposition, and is easy to apply in the field.

Richardson (1980) judged the normal classification such as "fresh", "bloat", and "dry" given by most carrion-workers as superficial. Instead he proposed a system which categorised carcasses as "fresh", which had three further subdivisions (i) with soft tissues, skin and bone, (ii) with skin and bone, (iii) only bone; "maggots", which signified that stage when blow-fly larvae were present and also had the same three subdivisions as above; and "dry" which had only two subdivisions (i) dry skin and bone and (ii) dry bone. This classification must unfortunately be regarded as equally superficial. The stages of decomposition as advanced by most carrion-workers are based on a combination of the physical appearance of the carcass and the accelerating influence which arthropods have on the rate of decay. Richardson did exactly the same using vertebrates instead of arthropods and differed only in degree. His classification was more gross and structured in such a way that it is not as useful for carcass-age estimation as that advanced by the systems he rejected. The essential difference arises due to a variation in approach: Richardsons method is better for indicating the extent of carcass-remains, whereas the methods in Table 5 are better for indicating carcass age.

In the generally hot climate of the K.N.P., combined with the numerous insects normally attendant at carcasses, decomposition proceeds with such rapidity that the stages suggested by the authors listed in Table 5 are either completely obscured, ill-defined, or overlap so considerably that in many cases it is impractical and confusing to attempt using their systems.

Decomposition of impala carcasses used for insect collections during 1979.

Figure 9 represents in diagrammatic form the decomposition of caged impala carcasses used for the study on species composition, abundance, and successional pattern of attendant insects. Observations of carcass-condition were made hourly for the first four hours after death, thereafter every six hours for the first 13 days, and finally every 12 hours up to and including Day 23. Field-notes were taken at each visit, and Figure 9 is derived from these observations. Figure 9 may be considered as representative of the decomposition of most medium-sized mammal carcasses lying undiscovered or only partially consumed by vertebrate scavengers in the K.N.P. The portion portraying the decomposition of carcass B during May/June has an unusually extended Stage 3 due to a muscle remnant in the neck which in theory kept the carcass in Stage 3. Carcass B should thus be viewed as a theoretical complication and for practical purposes Carcass C would be more representative of decomposition in early winter.

Description of decompositional changes

STAGE 1 (Fresh) refers to the period from death to disappearance of the normal external features displayed by the animal in life. Bloating is the main initial factor responsible for distortion of these features. As within other ruminants the bacteria and protozoa continue their digestive activities in the rumen after death, resulting in the production of considerable amounts of gas which causes bloating of the abdomen within an hour or two of somatic death, both in summer and winter. There is no distinct smell or obvious sign of rigor mortis, the limbs being easily manipulated and the body muscles having the normal tone as in life, not hard due to the rigidity of rigor.

In all the carcasses examined it was found that, irrespective of the time of year, within four hours of death the carcass was so distorted by bloating that it could no longer be described as life-like in appearance. That season of year should not play a great role in this initial stage of post-mortem change is logical as the body temperature is still high so that the activity of micro-organisms and enzyme systems can continue unimpeded.

STAGE 2 (Bloat) describes the carcass now grossly swollen by gases from bacterial activity, together with rigid muscles from rigor mortis. A slight smell, the first sign of advancing putrefaction, is also evident. Of these features of Stage 2, bloating is the first to appear, evident within an hour or two after somatic death irrespective of season. This is followed by the onset of rigor mortis, a gradual stiffening of the muscle fibres until fully contracted, making the muscles solid and hard when prodded. Rigor was detectable within 4 hours of death in all seasons. The end of Stage 2 is signalled when the carcass is unmistakeably soft, combined with a moderate smell.

Average daily temperature significantly influenced the duration of this stage, hastening the onset of putrefaction in summer but slowing it in winter. During monitoring of impala carcass decomposition in 1979, I found in January/February that Stage 2 persisted approximately 34-40 hours after death, while in May/June the cold temperatures at night extended the stage to 46-52 hours after death.

STAGE 3 (Putrefactive) refers to the stage of obvious putrefaction of the carcass, characterized by a moderate to bad smell and a softness or sponginess of the body due to liquefaction of the constituent tissues.

Putrefaction of impala carcasses at Pafuri was found to be very rapid during the warmer months, brought about by the combined action of autolysis, bacteria, and numerous blow-fly larvae releasing digestive enzymes to cause a speedy breakdown of soft tissues. In addition to bringing about liquefaction this also resulted in the production of foul smelling gases, often in prodigious amounts so that

PLATE 1: Stages of decay of impala carcass

a) Fresh. Less than one hour after death. No distortion of external physical appearance.

b) Bloat. Distortion of features. Rigor mortis present. Muscles hard when prodded. Little or no smell.

c) Putrefactive. Rigor mortis passed. Muscles soft when prodded. Smell bad. Maximum maggot activity.

d) Dry. All soft tissues (except skin) consumed. Maggots departed. Little smell.

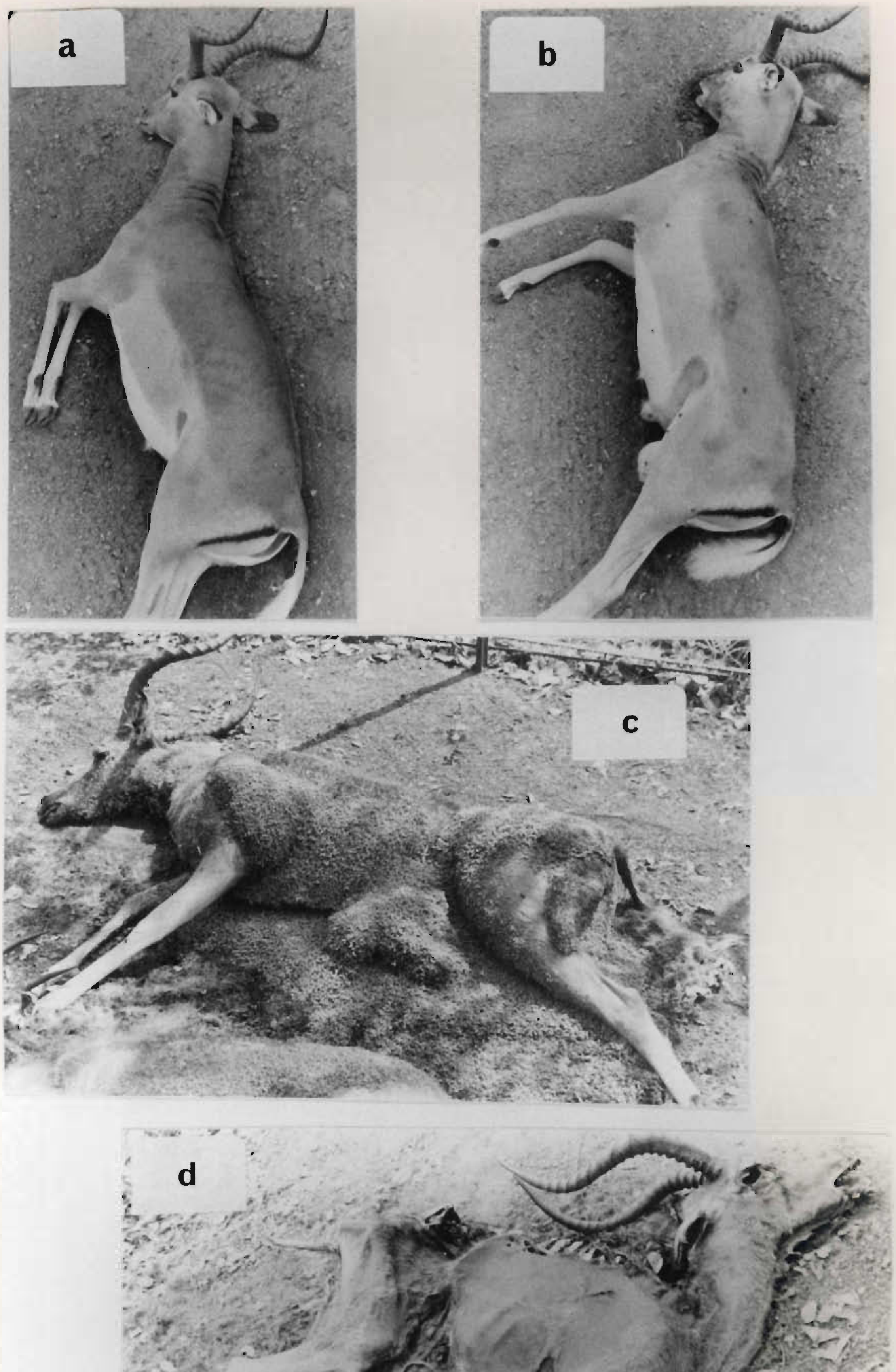


PLATE 1

at times these gases are visible as wafts.

As seen in Figure 9, Stage 3 at the impala carcasses generally commenced between 24 and 34 hours after death, beginning earlier during the warmer months than the winter months. Stage 3 continues until all the soft tissues, excluding parts of the skin, have been drained away by liquefaction or consumed by insects, chiefly blow-fly larvae. Again this occurs faster in the warmer months but is prolonged in winter when the low temperatures at night severely inhibit bacterial and maggot activity. In general Stage 3 was found to have decreased considerably by between 94 and 268 hours after death. In Figure 9, for decomposition in May/June, Carcass B is shown as remaining in Stage 3 until Day 23; this is an unfortunate theoretical complication as some flesh remained in the neck region so that, applying the characters of Stage 3 strictly, this stage had not passed. The flesh was examined at 10h00 Day 24, 554 hours after death, and had a soapy half-jelled consistency, pale red in colour, with a distinct odour.

STAGE 4 (Drying) was closely correlated with maggot activity. Blow-fly larvae had entered the carcass and consumed tissues rapidly so that deflation and collapse of the carcass resulted. A simultaneous general decrease in smell and a gradual drying of the carcass occurred. The rate of drying and reduction of odour increased rapidly when the maggots had stripped the carcass of soft tissues and departed for pupariation. Stage 4 can be considered as being fully established when the carcass has collapsed entirely, consists essentially of skin and bone, and has a decreased smell when compared with Stage 3.

Temperature and pH fluctuation within decomposing impala

To gain some concept of the range of temperature and pH values associated with carrion decomposition it was decided to monitor these parameters using a recently killed impala. An impala ram (47,3 kg) was shot (head-shot, minimal damage) near study site "C" (Fig. 11) at Pafuri at 07h20 on the 23rd February 1981. Temperature and pH values were immediately recorded in the following manner. Rectal temperature was taken using a -10 to +110°C thermometer inserted via the anus for a distance of 7 cm; abdominal temperature with a similar thermometer pushed in through a 1 cm incision immediately below the rib-cage on the right-hand side of the body to a depth of 10 cm, these depths ensuring reliable appropriate readings for the longest possible period independent of solar influence and maggot activity. Ambient temperature was obtained from a whirling psychrometer used for determination of atmospheric relative humidity at the same time, which was read at 10 cm above ground.

pH was determined with a portable Digital Data System model 800 pH meter designed to read directly from a moist surface, with a range of 0 to 13,99 pH and a repeatability of 0,01 pH, and included a temperature compensation facility. The pH-meter probe was inserted in a 2cm deep incision made into the right-hand side of the rump. After transfer to the enclosure at site "C" (Fig. 11) the thermometers were re-inserted and left in place for the duration of the experiment. Insect visitation and utilisation proceeded as normal, and temperature and pH readings were taken at intervals as indicated in Fig. 10.

The results are graphically represented in Figure 10. The pH-meter probe accidentally broke during the Day 4 12h00 reading so that pH values are not available from that time. By 06h00 Day 7 all blow-fly larvae had left the carcass, no soft tissues were available, the carcass-remains were rapidly drying, and carcass temperatures had reached a plateau of even fluctuation slightly above ambient temperature, so the experiment was discontinued.

From examination of Figure 10 certain trends could be established for temperature and pH fluctuations as decomposition progressed. Temperatures in the rectal and abdominal areas followed a similar sigmoidal curve which was independent of ambient temperature until 24h00 Day 4, after which outside temperature had an increasing influence on carcass temperature. From a body temperature of 39°C immediately after death, both rectal and abdominal temperatures gradually decreased to a minimum at 08h00 Day 2. From here on temperature rose steadily due to the combined activity of bacteria and blow-fly larvae which had gained entry into the abdominal cavity after digesting the skin at the soil/carcass interface. Due to this dissolving of the abdominal wall ambient temperature had some initial influence on internal abdominal temperature, but with the rapid growth and increase in activity of the maggots the abdominal and rectal temperature rose steeply. By the end of Day 4 the maggots had attained maximum size, nearly all the soft

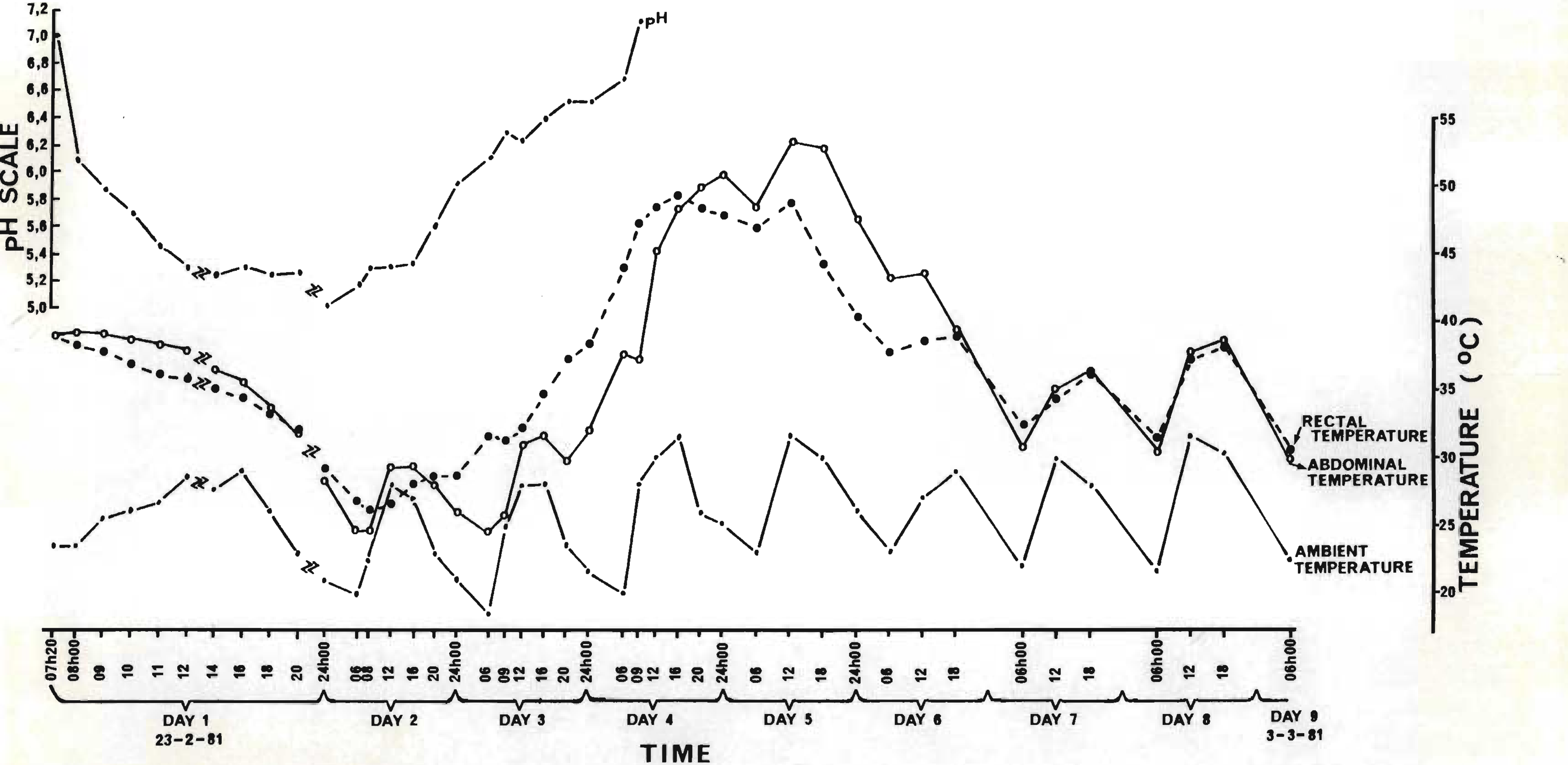


FIGURE 10: Temperature and pH values for a decomposing impala carcass, Pafuri, February 1981

tissues had been consumed, and competition between these larvae for food and space was at its greatest so that the frenzied activity in the confined carcass interior resulted in a maximum recorded temperature of 53,3°C in the abdominal cavity. Larval migration from the carcass caused a rapid drop in temperature until all the maggots had departed and all that remained was the skeleton with a dome of skin on the dorsal surface.

From an initial pH value of 7,0, autolysis and other cell-changes brought about an increase in acid-levels until a minimum pH value of 5,03 was recorded at 24h00 Day 1. Further changes in cellular contents combined with increasing bacterial and maggot influence raised the pH to a value of 7,14 at 09h00 Day 4, after which no further recordings could be made due to a broken probe. For reasons indicated below, the experiment was not repeated and no opportunity thus presented to determine pH values in the final stages of decay.

As a parameter for estimation of carcass-age, temperature was found to be too dependent upon blow-fly larval activity and not an intrinsic feature which could be monitored independent of external influence. Similarly, no correlation could be found between carcass temperature or pH and the timing of arrival and departures of insects. Useful information which did emerge, however, was the ability of blow-fly larvae to withstand high levels of acidity and temperature.

AVAILABILITY OF CARCASSES FOR ARTHROPOD UTILISATION

Upon questioning of Kruger Park field-staff at commencement of this project the overwhelming response was that unscavenged carcasses were exceptionally rare and that dead animals were soon stripped of soft tissues by vultures, hyaenas, and jackals. This presented an anomalous situation as observations at deliberately-placed carcasses, blow-fly trap-catches, and from determinations of blow-fly population densities (see Chapter 6), revealed that the K.N.P. supported a large population of carrion-breeding Chrysomyia albiceps and C. marginalis blow-flies, yet the general opinion of staff intimated that there were insufficient carcasses to give rise to this population. It was therefore decided to place a series of impala carcasses under varying densities of vegetational cover to determine how long these carcasses remained available for exploitation by arthropods before being consumed by vertebrate scavengers.

Impala carcasses were used because of the relative abundance of these animals. All the impala were adult males and shot in the head using a 0.222 calibre rifle. The carcasses were placed in position as soon as possible, always between 07h00 en 09h00 in the morning, and were securely tied to a sturdy tree using thick wire doubled several times to prevent scavengers removing the carcass from the site. Two metres generally separated each carcass from the tree. Two categories of vegetational habitat were used, these being riverine forest and open woodland. The riverine forest was represented by tall (15 metres and more) Ficus sycamorus (Sycomore fig), Xanthocercis zambesiaca (Nyala tree), Diospyros mespiliformis (Jackalberry), and others with dense spreading canopies which disrupt visibility of carcasses from vultures flying overhead. Riverine forest adjoins the Luvuvhu river at Pafuri as a swath varying in width from about 30 m up to 200 m along each bank. The open woodland was represented by predominantly Colophospermum mopane (Mopane tree) roughly 5 km east, west and south of Hape pan with Terminalia prunioides (Purple-pod terminalia), Adansonia digitata (Baobab) and species of Acacia, Boscia and Commiphora interspersed. Carcasses in this open woodland were generally easily visible from above.

All the carcasses were placed in locations where impala had previously been observed feeding or walking along paths to water. The carcasses were therefore not in unnatural situations for the species. Care was also taken not to have more than one carcass out at any time so that the potential for discovery of a particular carcass was not diminished by having scavengers concentrated at another carcass. The results of this monitoring programme are provided in Table 6.

TABLE 6 : Impala carcasses placed under varying vegetational cover to monitor rate of scavenging by vertebrates

Date carcass placed	Site of carcass placement		Approximate time elapsed until all soft tissues (excl. skin) removed	Main agents of soft tissue removal
	Riverine Forest	Open Woodland		
13/2/79		1	36 hrs	Vultures/Hyaena
2/6/79		1	9 hrs	Vultures
6/10/79		1	11 hrs	Vultures
19/1/80	1		72 hrs	Maggots/Crocodi
1/2/80		1	65 hrs	Maggots/Hyaenas
26/2/80		1	14 hrs	Hyaenas
6/10/80	1		65 hrs	Crocodile
17/1/80		1	8 hrs	Vultures
28/1/81	1		40 hrs	Crocodile
16/2/81	1		38 hrs	Hyaena
20/2/82	1		42 hrs	Hyaena
22/9182	1		64 hrs	Hyaena
27/9/82		1	75 hrs	Vultures
23/1/83	1		39 hrs	Crocodile
25/1/83		1	12 hrs	Hyaena
25/8/83	1		14 hrs	Lion?
27/8/83		1	14 hrs	Hyaena
27/2/84		1	5 hrs	Vultures
26/3/84	1		38 hrs	Crocodile
15/4/84	1		12 hrs	Hyaenas
Total	10	10		

The results provided in Table 6 should only be taken as a rough approximation of the availability of carcasses to blow-fly larvae.

As will become clear from observations presented in the remaining pages of this chapter, the extent of scavenging noted at naturally-occurring carcasses encountered during field-work suggested that Table 6 does represent a fair approximation of carcass-availability in riverine environments. In open woodland, however, carcasses of medium-sized mammals (up to kudu) rarely provided opportunity for blow-fly larval development.

Table 6 shows that carcasses on average lasted about 42,4 hours in riverine forest before all soft-tissues were removed, whereas in open woodland the corresponding period was only 24,9 hours. These figures are also a fair reflection of "discovery time" i.e. time elapsed from carcass placement until vertebrates first discover the carcass; once discovered these carcasses were very rapidly stripped of all soft tissues within a few hours so that only skin and bones remained, except for small amounts of soft tissue in the lower limbs and inside the cranium.

Crocodiles and hyaenas were the main agents responsible for consuming carcasses under riverine conditions, with no vultures present at any of these carcasses. Crocodiles moved up to 150 metres across land to reach a carcass and in all cases snapped the wire and dragged the carcasses back into the river.

In open woodland vultures and hyaenas were the main agents responsible for rapidly consuming carcasses. Removal of carcasses was generally much more rapid than the average 24,9 hours calculated for all ten carcasses placed in open woodland, the average figure being distorted by two unusually long discovery periods (65 hrs on 1/2/80 and 75 hrs on 27/9/82). Both these carcasses had been deliberately placed in the shade of a Terminalia prunioides and Albizzia anthelminthica tree, respectively, partially but not completely concealed from above.

The fact that no carcass remained undiscovered indefinitely did not mean that blow-flies were unable to utilise these carcasses. In all cases blow-fly adults arrived as normal (see Chapter 3) to feed on blood and other carcass fluids, laid eggs, and larval development progressed despite intermittent disruption or disturbance by tawny eagles, jackals or bushpigs. When vultures, hyaenas or crocodiles arrived and consumed all soft tissues before the larvae had grown to a size large enough for sufficient nutrient reserves to have been accumulated for pupation, such larvae wandered in search of carcass remnants and if unsuccessful, died. Experiments showed that in summer larvae of C. marginalis voluntarily departed from a carcass after as little as 72 hours after oviposition (See Fig. 100) and C. albiceps shortly after (Fig. 99). These were voluntary departures from a carcass, and in Chapter 5 it is shown that underfed larvae successfully pupariate and give rise to reproductively viable adults. Even the average 42,4 hours that carcasses lasted in riverine forest was insufficient for larvae of C. marginalis and C. albiceps to reach a growth-stage allowing successful pupation. Of the carcasses listed in Table 6, however, one in riverine forest (19/1/80, 72 hrs) remained undiscovered by vertebrates sufficiently long for development of the full quota of maggots (see Chapt. 5) that would normally develop at undisturbed, fenced-off carcasses (pers. obs.). Very little soft tissues remained on the carcass as the blow-fly larvae had consumed an estimated (visual inspection only) 95% of such soft tissues so that eventual removal of the carcass by crocodiles did not prevent the successful pupariation, pupation and adult emergence of blow-flies. One other carcass (6/10/80, 65 hrs) remained sufficiently long for a few thousand C. marginalis larvae to establish sufficient reserves to ensure continued development after carcass removal. Cold night-time ambient temperatures resulted in lengthy egg-incubation and also first larval stage development so that insufficient time was available for the majority of C. marginalis and C. albiceps larvae to make adequate use of carcass resources (see Chapter 5 for development rates).

Contrary to expectations, carcasses placed in open woodland also allowed the development of the full complement of larvae at one carcass (1/2/80, 65 hrs) before the carcass was removed by hyaenas, and one other carcass (27/9/82, 75 hrs) remained sufficiently long for successful pupation of a small proportion of C. marginalis larvae.

Of the carcasses which remained on land (i.e. excluding those taken by crocodiles) after being fed on by vertebrate scavengers, all had extensive portions of skin remaining, at least some shreds of sinew, ligamentous tissue and some muscle tissue in the lower parts of the limbs, and fatty deposits on the bones and skin. These remains were utilised by dermestids, clerids, trogids and other beetles discussed in Chapter 3, and also by piophilids and other flies. The skulls were also intact in all carcasses and larvae (up to 50) of C. marginalis were frequently found inside the cranial cavity.

Observations in May and June 1980 at 20 buffalo carcasses left uncut in open woodland near Mahembane windmill north-east of Punda Maria by the K.N.P. culling team due to the presence of foot and mouth disease, 33 uncut buffalo during the same month left individually or in small groups in the Pafuri area also due to foot and mouth disease, an elephant dead due to a severely injured leg at Klopperfontein (north-east of Punda Maria) in April 1980, an elephant shot and minimally utilised by poachers in March 1983 in the Shilahlandonga spruit, and five elephants, two rhino, seven buffalo and three giraffe carcasses found individually elsewhere in the K.N.P., revealed that large numbers of blow-fly larvae completed their development at such carcasses, and that more than one million larvae may be present at an elephant carcass (Chapt. 5). At carcasses of large mammals shot by poachers, vultures and other scavengers such as marabou storks, bush-pigs and jackals were unable to gain entry into the carcasses until hyaenas had chewed holes through the thick skin. In many of these large carcasses sufficient soft tissues remained - generally in the neck, lower limbs and often the rump - for a week or longer so that large numbers (tens of thousands) of larvae of both C. albiceps and C. marginalis were able to complete their development. Fifteen buffalo carcasses lying individually in the Pafuri area and two in the Lower Sabie area (outside study area, southern KNP) were exclusively utilised by blow-fly larvae which completely consumed all the soft tissues after gaining entry to the carcass by digesting away the skin at the soil/carcass interface.

Observations of naturally-occurring carcasses

In 1980 I requested game-rangers throughout the K.N.P. to indicate on questionnaires all carcasses encountered and to provide relevant data such as date, time elapsed since death, species of animal, locality, cause of death, amount of soft tissues remaining and appearance of carcass. During an eight-month period from early July

1980 to end February 1981, Ranger Flip Nel noted 61 medium and large carcasses in the Pafuri section (between the Luvuvhu and Limpopo rivers and the area east of the tarred road from the Luvuvhu to Klopperfontein) all of which were naturally-occurring deaths due to predation, injuries, illness, or age. The species composition and number of carcasses are indicated in Table 7.

TABLE 7 : Number of naturally-occurring carcasses found in the Pafuri area between 1st July 1980 to 23rd February 1981. (As reported by Senior Ranger P.J. Nel)

Species of carcass	Number of carcasses
Impala	17
Bushbuck	11
Warthog	7
Kudu	6
Nyala	5
Buffalo	3
Grey Duiker	3
Wild dog	2
Hippopotamus	2
Steenbuck	2
Reedbuck	1
Bushpig	1
Lion	1
TOTAL	61

On the carcasses listed in Table 7, 10 carcasses had been lying in the bush for 3 days or longer and had considerable quantities of soft tissues remaining (5 were untouched by vertebrate scavengers). Two of these were hippopotami. Although hippo carcasses do occasionally support hundreds of thousands of blow-fly larvae which successfully emerge as adults (personal observations at four hippo carcasses) the majority are generally in deep water too far from the river edge for post-feeding 3rd stage blow-fly larvae to reach pupariation sites (see Chapt. 5) so that these larvae drown. Only eight (13,1%) of the 61 naturally-occurring carcasses were therefore utilisable by blow-fly larvae. These were three buffalo, two wild dogs, and one each of nyala, bushbuck and bushpig. My own observations in the Pafuri area during the duration of this project indicate this (13,1%) to be a realistic estimate for that area. It is also likely that it should be regarded rather as a conservatively low estimate as almost without exception field-staff are led to carcasses by vultures circling overhead and dropping down to the carcass, although in a few cases carcasses are encountered unintentionally. Aside from the relatively few large carcasses where large numbers of blow-flies regularly breed, the experimental carcasses as indicated in Table 6 also reveal that large numbers of larvae utilise occasional medium-sized mammal carcasses which remain undiscovered by vertebrates for some time. Humans are therefore also unlikely to find these carcasses, so that the number of carcasses, especially those which could be utilised by blow-flies, indicated in Table 7 is likely to be an underestimate.

In his study on the removal of ungulate carcasses in the Transvaal and southern Zimbabwe, Richardson (1980) found that due to competition by vertebrate scavengers, blow-fly larvae were only able to develop in 15 of 89 carcasses observed (16,85%). He stated that arthropod competition with vertebrates was less severe on farms than in nature reserves, so that they consumed more carrion on farms. Blow-fly maggots, for example, were found to consume 20% of carcass soft tissues on farms, but only 1,9% on nature reserves. He went on to say, however, that "in this study all carcasses were placed or found in sites accessible to vultures and carnivores. However, many carcasses, particularly smaller ones, may be inaccessible to vertebrate scavengers and the arthropod scavengers in the Transvaal probably play their greatest role in the decomposition of these carcasses" (page 101).

At virtually all medium- and large-sized carcasses scavenged by vultures, hyaenas, jackals and other vertebrates in the present study, some remnants of skin, ligamentous tissue and fatty deposits were available for utilisation by carrion-insects such as dermestid, clerid and trogid beetles, and at carcasses such as those of elephant literally hundreds of thousands of dermestid larvae were present inside the abdominal cavity during the later stages of decay. It became obvious early in this project that sufficient resources were available for the coleopterous component of the carrion-community, but doubt existed as to the availability of soft-tissues especially for species such as blow-flies.

The findings as presented in the preceding pages show that up to 20% of naturally-occurring carcasses in the Pafuri area may at times remain available for a period long enough for blow-fly larvae to complete their development, and that large carcasses, especially such as giraffe, buffalo and elephant, often present nutrients in the form of soft tissues for long periods of time.

It should be noted however, that development periods for blow-fly larvae in winter are approximately double that in summer (Chapt. 5) so that in winter such larvae generally only develop in soft tissue remaining available for six days or longer. Only larger carcasses (giraffe, buffalo etc) normally present such a resource for so long a period, so that, together with a reduced ovipositional response in female C. albiceps and C. marginalis (Chapt. 5), the populations of these two species of blow-flies is considerably lower in winter than in summer. This trend is well reflected in the discussion on blow-fly seasonal abundance in Chapter 6.

CHAPTER 3

THE ARTHROPODS ASSOCIATED WITH CARCASSES

Priority objectives of the present study included investigations to determine the species composition, abundance, and periods of peak attendance of the main groups of arthropods associated with carrion. These investigations were centred in the Pafuri area due to its being the focal endemic region in which anthrax occurred and from whence it spread. A knowledge of the invertebrates attracted to dead animals would assist in determining potential avenues of disease dispersal, and further studies could then be encouraged on groups of invertebrates which were likely agents of transmission. As this study progressed it became clear that blow-flies were the only group to have a potentially important role in dispersal of infective material from a carcass in a manner which may result in other animals acquiring the disease-organisms.

MATERIALS AND METHODS

For the purposes of this monitoring programme it was decided to use impala carcasses as an attractant due to the availability of these animals in the K.N.P. Observations at carcasses of a wide range of other species have shown this to be a prudent selection as the attendant insect-complex remains unchanged in species composition, and to a very large extent even in the proportionate abundance of each species, whether using hares or elephant as study substrate. The number of insects present at an impala carcass at any given time was also such that the dominant species were sufficiently numerous not to allow statistical error or disruption of a pattern of insect attendance due to random fluctuation of numbers as can be expected at very small carcasses. Insects were not too numerous so that two persons were able to cope with collection of these insects.

To assess the species composition, abundance, and succession of insects at carcasses in a continuous manner it was necessary to exclude spotted hyaenas (Crocuta crocuta) and other scavengers by fencing off the impala carcasses. The results obtained from this survey under 'ideal' conditions could then be compared with the insects and their visitational patterns at naturally occurring carcasses whenever opportunity arose. From species examinations and observations at more than 500 carcasses of medium to large mammals encountered in the field, the species composition, relative abundance, visitation pattern and successional sequence of insects as determined from the study carcasses was equally applicable to carcasses under natural conditions.

Three rectangular wire enclosures (approximate dimensions: 2m x 3m x 2m) were constructed (see Figure 11) using large mesh fencing wire (diameter ca. 8 cm). The upper layers of fencing were folded over to prevent vultures from entering, and all three enclosures had the bottom segment of fencing on one side untied but hooked to a tree to serve as entrance.

For each survey period, three full-grown male impala in prime condition were shot (head shots, minimal damage) early in the morning of Day 1 and place in their respective enclosures by 08h00.

To simulate natural conditions to some extent, such as scavenging, each carcass was given one 45 cm longitudinal and one 30 cm transverse incision ventrally on the abdomen at 12h30 on Day 1, these being the only mutilations besides the bullet hole in the head.

The three carcasses were treated in different ways so as to derive maximum benefit. At Carcass B only beetles and other insects reluctant to fly were collected. It was placed on a doubled-up fencing-wire platform (1m x 0,75m) so that the carcass could be lifted to facilitate collection of insects from below. The apertures of the platform were such as to allow insects unobstructed access to and from the carcass. Collection of insects was done by hand, 'pooters' and forceps and at no time were less than two people present. Insects were not only taken from the carcass itself but also within a radius of one metre. Dry-cell torches and two fluorescent lights powered by a 12 volt battery were used for night collecting. Flies were not collected at this carcass, although notes were taken of the physical condition of the carcass, insects other than those collected, weather and general observations.

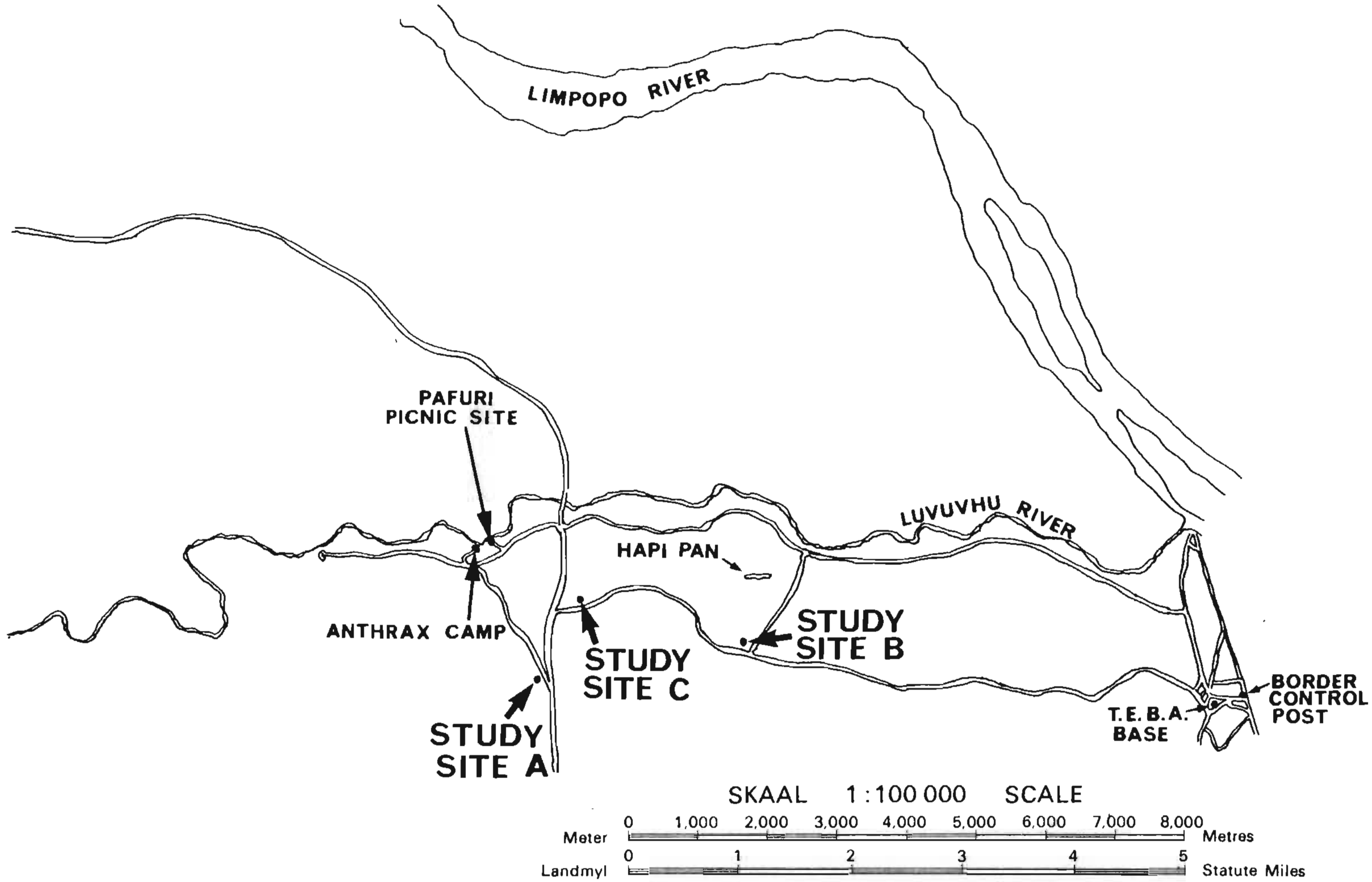


FIGURE 11: Map of the Pafuri area to show the relative position of the three study sites used for the survey of carrion-insects during 1979

Diptera and other readily flying insects were caught at Carcass C using a large, tent-like, very fine mesh net (dimensions: length = 2,20m; breadth = 1,27m; height = 1,23m; and mesh diameter = 0,25mm). The net tapered to a central point where detachable bags were affixed. Night collection at this carcass was done by making minimal use of torches until the net had been dropped, since light soon attracted flies settled on vegetation in the area. Notes were also taken at this carcass at each collection period.

The third impala, Carcass A, was used as a control carcass where collections of insects were made once every five days to determine the effect of regular collection on the insect populations at the other two carcasses and the possible effect on the rate of decomposition. The impact of constant collections of insects was found to be minimal due to the rapid rate of recruitment and interchange of insects arriving and departing all the while, and carcass decomposition was not influenced.

Collections of insects were made every six hours up to Day 13 inclusive, thereafter every 12 hours due to the low number of insects present. Collections generally required about one hour (30 minutes at each carcass), so that arrival at Carcass C was timed for 30 minutes before the stipulated hour, Carcass B being attended to during the last half-hour.

As two of the aims of the project were to determine which insect species visit carcasses and their numbers, it was decided to do absolute counts of the insects at each carcass (excluding larval stages). This had the advantage that species present only in low numbers would not be overlooked and the number of individuals per species would be reflected more accurately.

The method of handpicking insects at Carcass B served well, but on a few occasions some beetle species were so numerous that it was not possible to do a total collection. This necessitated an estimation of the percentage remaining after 30 minutes of collecting, which was then incorporated as a correction factor.

Representative specimens of all the arthropods encountered

MAX.TEMP.	32,0	34,5	34,0	37,0	38,0	37,0	38,0	37,5	32,0	25,0	27,0	29,5	32,0	34,0	34,0	35,0	33,5	30,0	29,0	30,5	32,0	31,0	32,0
MIN. TEMP.	22,0	22,5	21,5	22,0	21,5	24,5	23,5	24,0	21,0	19,5	19,0	16,5	14,5	20,0	21,0	23,5	26,0	23,0	22,0	20,5	21,0	21,0	22,5
RAINFALL	22 mm	1 mm	–	–	–	–	–	16 mm	1,5 mm	0,5 mm	–	–	–	–	–	–	–	1 mm	0,5 mm	–	–	–	–
CLOUDCOVER	●●	◐●	○◕	○⦶	○⦶	○⦶	○●	⦶●	◐●	●●	◔●	○◑	○◔	○⦶	○⦶	○◔	○◔	◔●	◑●	○◕	○◕	○◑	◐◕
MAX. WIND VELOCITY	3	1	1	3	4	7	8	1	16	15	9	4	3	3	3	4	8	6	9	4	6	3	3
DAY	13 JAN	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	4 FEB

MAX. TEMP.	26,5	29,0	26,0	29,0	27,5	26,5	27,0	31,0	31,0	27,5	26,5	28,0	29,5	30,0	26,0	28,0	22,5	25,0	25,0	27,5	26,0	25,5	29,0
MIN. TEMP.	11,5	12,5	11,0	12,5	9,5	12,0	10,5	12,0	12,5	12,0	10,0	8,5	8,5	11,5	15,0	13,0	9,0	7,5	8,0	7,5	9,0	9,5	9,5
RAINFALL	–	–	–	–	–	–	–	–	2,0 mm	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CLOUDCOVER	○⦶	○⦶	○⦶	○○	○○	○◔	○◔	○⦶	○●	○●	○○	○○	○○	○⦶	○◕	○◕	○●	○○	○○	○○	○⦶	○◕	○○
MAX. WIND VELOCITY	1	5	2	3	1	3	6	5	8	8	4	5	2	4	9	6	5	4	3	3	5	3	4
DAY	18 MAY	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	9 JUN

MAX. TEMP.	33,0	33,5	36,0	31,0	33,0	29,5	30,5	33,0	37,0	39,5	26,5	28,0	33,0	31,5	35,0	38,0	33,0	39,0	41,0	30,0	38,0	36,0	27,5
MIN. TEMP.	15,5	12,0	12,5	17,5	20,0	18,5	15,5	19,0	15,5	15,5	15,5	21,0	22,5	21,5	20,0	21,0	21,5	23,0	22,5	21,0	21,5	21,0	13,5
RAINFALL	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CLOUDCOVER	○◑	○○	○○	○●	●●	◔●	○●	○●	○○	○◕	○◔	○●	○●	○◔	○⦶	○○	○○	○○	○◑	○⦶	○◑	○●	○●
MAX. WIND VELOCITY	1	4	11	6	4	10	9	6	14	11	14	4	15	13	12	3	5	5	15	13	1	4	8
DAY	14 SEP	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	6 OCT

TABLE 8 : Weather conditions at Pafuri during the three carrion-arthropod survey-periods undertaken in 1979.

were sent to the acknowledged specialist(s) in each group for identification, these persons being indicated in the 'Acknowledgements' section of this dissertation.

The weather conditions prevailing during the various monitoring periods are summarised in Table 8, while the times of sunrise and sunset for the first and last day of each survey period is indicated in Table 9 below.

TABLE 9 Times of sunrise and sunset for the first and last day of each carrion-insect monitoring period in 1979 (as provided by the Weather Bureau, Dept. of Transport).

	13th January	4th February	18th May	9th June	14th September	6th October
Sunrise	05h16	05h32	06h24	06h34	05h52	05h29
Sunset	18h49	18h43	17h16	17h11	17h46	17h54

RESULTS

Coleoptera, Diptera and Hymenoptera were found to be the most numerous and important of the arthropods attracted to the study carcasses. The principal members of these groups are discussed below and are followed by a more brief treatment of the insects and other arthropods which were present only in low numbers. The results are also presented in summarised form as Table 13.

ORDER: COLEOPTERA
FAMILY: HISTERIDAE

Richards and Davies (1977) stated that this is a large family of distinctive beetles ranging from very small to medium in size. They tend to be compact, very hard, and are usually black, brown or metallic blue in colour. Several genera occur in the nests of ants or termites, some beneath bark in the burrows of bark-beetles, others in decomposing plants, whereas Hister, some Saprinus, and others frequent dung and carrion where they feed on the eggs and immature stages of other insects (Balduff 1935, Summerlin *et al* 1981). The larvae are elongate with short legs, have a soft cuticle except for a well-sclerotised head-region, have prominent mandibles and most are presumed to be carnivores (Richards & Davies 1977, Summerlin *et al* 1981).

Species recorded

Twenty four species were collected and are listed in Table 13.

Biology

Using small quantities of maggot-infested fish in polythene pails, Nuorteva (1970) showed that histerids were highly effective in depleting the numbers of blow-fly larvae in parts of Finland and elsewhere in Europe, occasionally resulting in near total eradication of fly larvae at the carrion habitat. It is important to note, however, that at small quantities of meat supporting low numbers of blow-fly larvae (in the experiments of Nuorteva generally less than a thousand maggots were present per baited pail), histerids are far more able to physically reach and successfully overcome maggots than they would at a medium-sized carcass - such as impala - where tens of thousands of maggots normally congregate as a vigorously wriggling mass.

Working with the dung-frequenting, medium-sized histerid *Pachylister chinensis* on the island of Fiji, Bornemissza (1968) found that these beetles have a preferance for larger maggots as prey-items, the smaller individuals measuring less than 5 mm presumably finding it easier to escape from the beetles. Using small samples of dung (generally 100 c.c.) with a low number of dipterous larvae and histerid beetles, he found that up to 95% mortality of fly-larvae could be achieved by the beetles. By extrapolation he concluded that a mortality of between 30% and 50% could be expected for fly larvae occurring in dung pads under natural conditions. The difference in mortality is brought about as ..."It is probable that the effectiveness of *P. chinensis* would vary inversely with the size of the dung pad, and that maggot destruction might decline to 30% in the largest pads" (Bornemissza 1968).

No attempt was made to determine the percentage mortality of blow-fly larvae brought about by histerids at carcasses at Pafuri, but mortality can be expected to be far less than 30% for the same reasons as outlined above. The large number of maggots present at a carcass tend to be present in a pool with only the fringe areas exposed to predation, the inner areas being an unstable writhing area affording no secure footing for beetles which therefore avoid this region.

At the Pafuri study carcasses adults of a wide range of histerid species were commonly observed to individually attack active blow-fly maggots, soon being joined by other histerids so that closely-pressed clusters were formed. Maggots of all stages were attacked, and although those of Chrysomyia albiceps were frequently taken, the bulk of the prey is consisted of C. marginalis larvae. The cuticle was punctured and the body contents sucked until only a shrivelled skin remained, this then being discarded. Several species of histerids were seen feeding simultaneously off one prey, and they often joined with other insects feeding on maggots, generally Dermestes maculatus (Dermestidae), but also Necrobia rufipes (Cleridae), Trox spp. (Trogidae), and even with predacious larvae of C. albiceps (Calliphoridae).

Very noticeable during all the carcass-studies since the beginning of 1979 was the low numbers of Hister individuals attendant at such sites, which contrasts with the fairly high numbers frequenting an impala carcass in January 1978 (Braack 1981). Several unusual features characterised the insect-community monitored during the January 1978 study, which indicated that the high number of Hister at that time was somewhat abnormal, possibly related to the unusually heavy rains which had fallen in 1977 (Braack 1981). Based on observations at numerous carcasses during the present study, the species and numbers of insects encountered during the 1979 survey are a better indication of average conditions which can be expected at carcasses. These are presented below.

Patterns of carrion-attendance

Because of the large number of histerids and their morphological similarity, certain species were lumped together for the purpose of counting. In this way Saprinus splendens (Payk), S. rhytipterus Mars, and S. bicolor Fabr. were combined as one group, referred to as the Saprinus splendens group, whereas Chaetabraeus echinaceus (Schm), Chalcionellus amoenulus (Fahrs), C. splendidulus (Schm), Hypocacculus harmonicus (Mars), H. metallescens (Er.), Paratropus aptistrius Lew, Saprinus cupreus Er., S. intricatus Er. and S. strigil Mars were combined as another group called the Saprinus cupreus group. The Saprinus splendens group comprised mostly medium-sized histerids with a metallic blue colour, whereas the S. cupreus group were rather small beetles having a reflective black colour. Species not included in these two groups were present in low numbers and erratic in their visitation patterns.

During Jan/Febr 1979 histerid visitors to the study carcasses were relatively few (Figs. 12 & 13). As can be expected, their numbers fluctuated according to the availability of dipterous larvae which formed the bulk of their prey. From a total absence on the first day, histerid numbers increased steadily to reach a peak of 390 on Day 4 when maximum numbers and growth of maggots was attained, decreasing from Day 5 as maggots left the carcass to seek pupariation sites. A few individuals arrived on most days after the disappearance of blow-fly larvae, attracted generally to the scattered larvae of Musca, Ophyra, (Muscidae) and Piophila (Piophilidae). A total of 1 118 histerid adults were collected during the 23-day survey in Jan/Febr, representing 8,08% of all Coleoptera at Carcass B during this period.

Despite the lower number of maggots present at carcasses during winter (Chapt. 5), histerids were most abundant during May/June (Figs.14 - 19), showing that, like Dermestes maculatus, they are likely to have a preference for cooler weather. Figure 19 indicates the increasing numbers of histerids which reached a peak on Day 9, corresponding closely to the period when maximum numbers and size of blow-fly maggots was attained. Intraspecific competition especially amongst C. marginalis larvae for available food and space was intense at this stage so that large masses of maggots fell from the carcass and individuals were attacked by the beetles. Decreasing numbers of maggots, as they left the carcass to pupariate, resulted in a corresponding de-

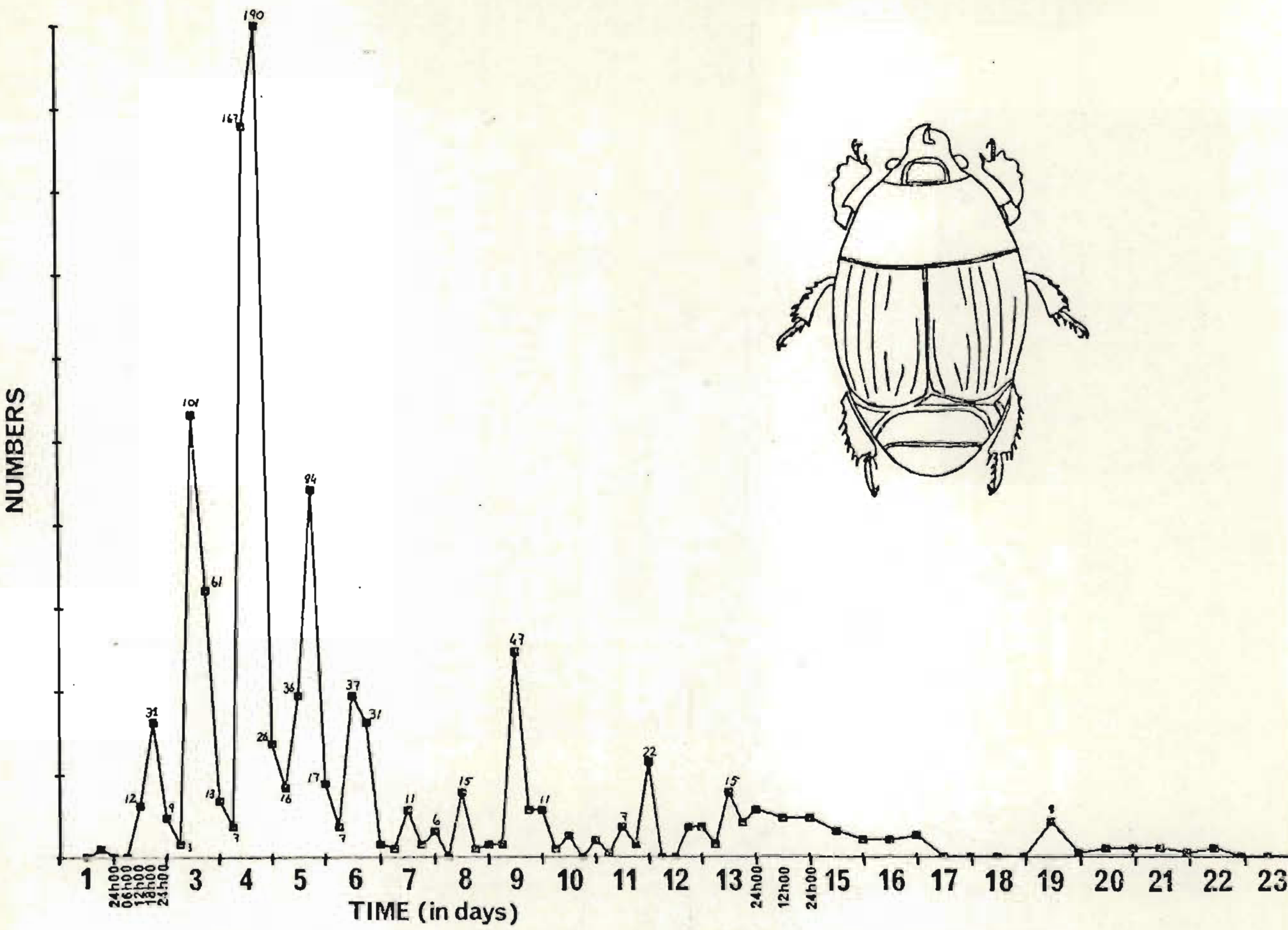


FIGURE 12: Number of all adult Histeridae present at each collection period at Carcass B, Pafuri, 13th January to 4th February 1979, to show diel activity cycle

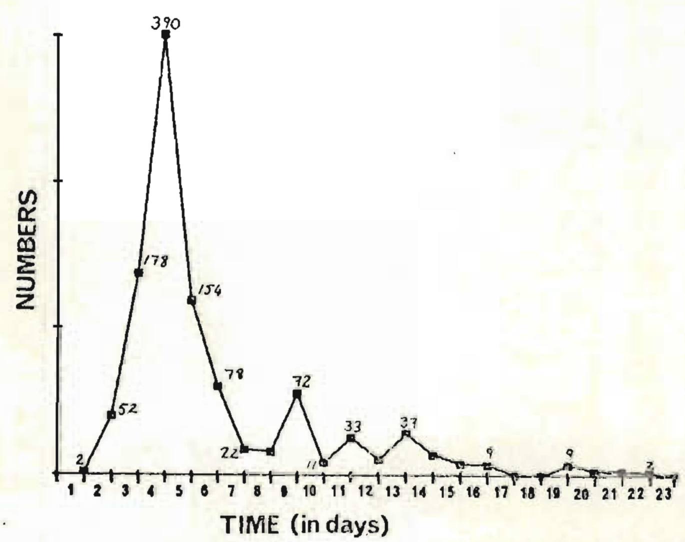


FIGURE 13: Daily totals of all adult Histeridae present at Carcass B, Pafuri, 13th January to 4th February 1979

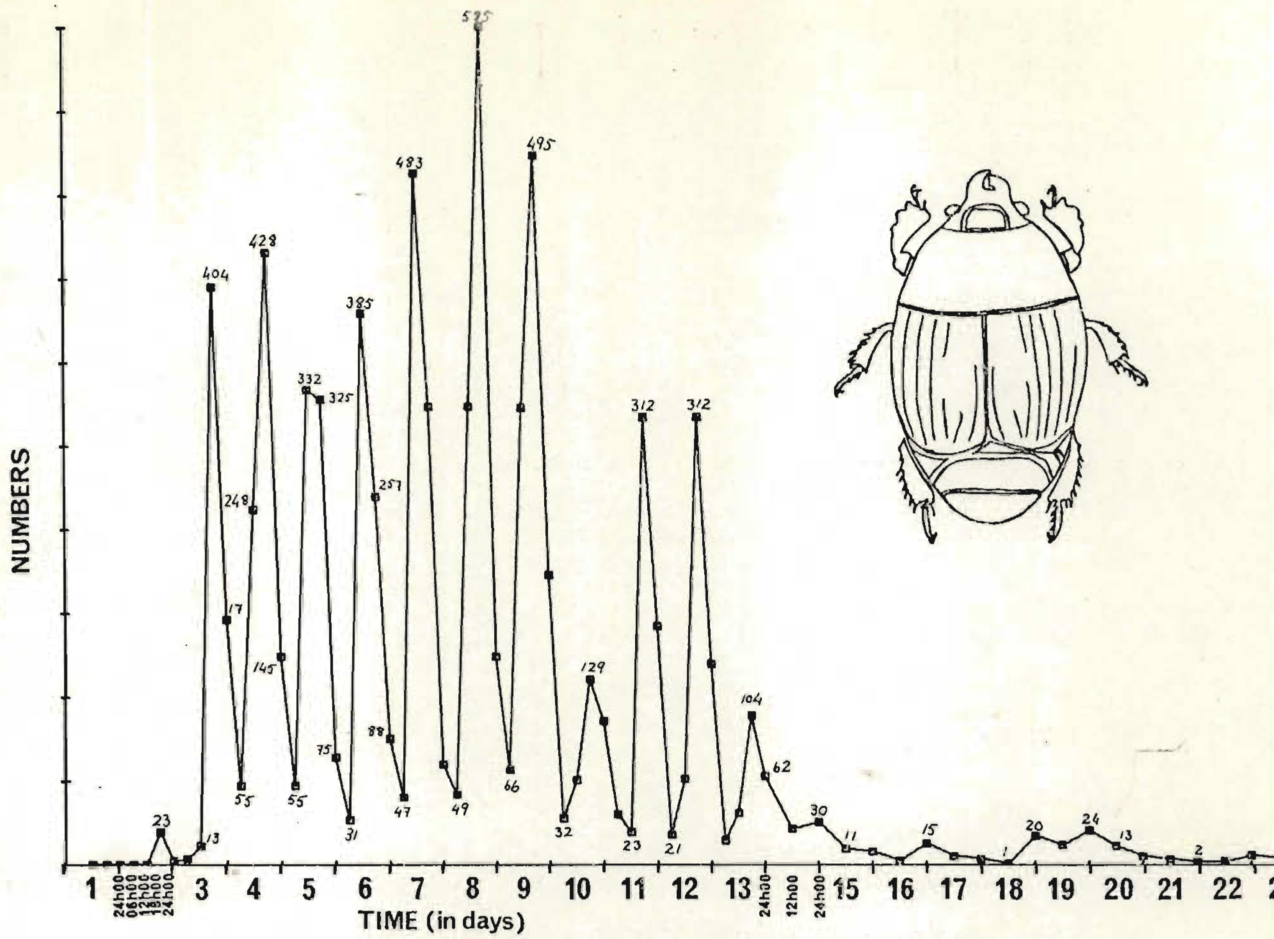


FIGURE 14: Number of adult Histeridae of the Saprinus splendens group present at each collection period at Carcass B, Pafuri, 18th May to 9th June 1979, to show diel activity cycle

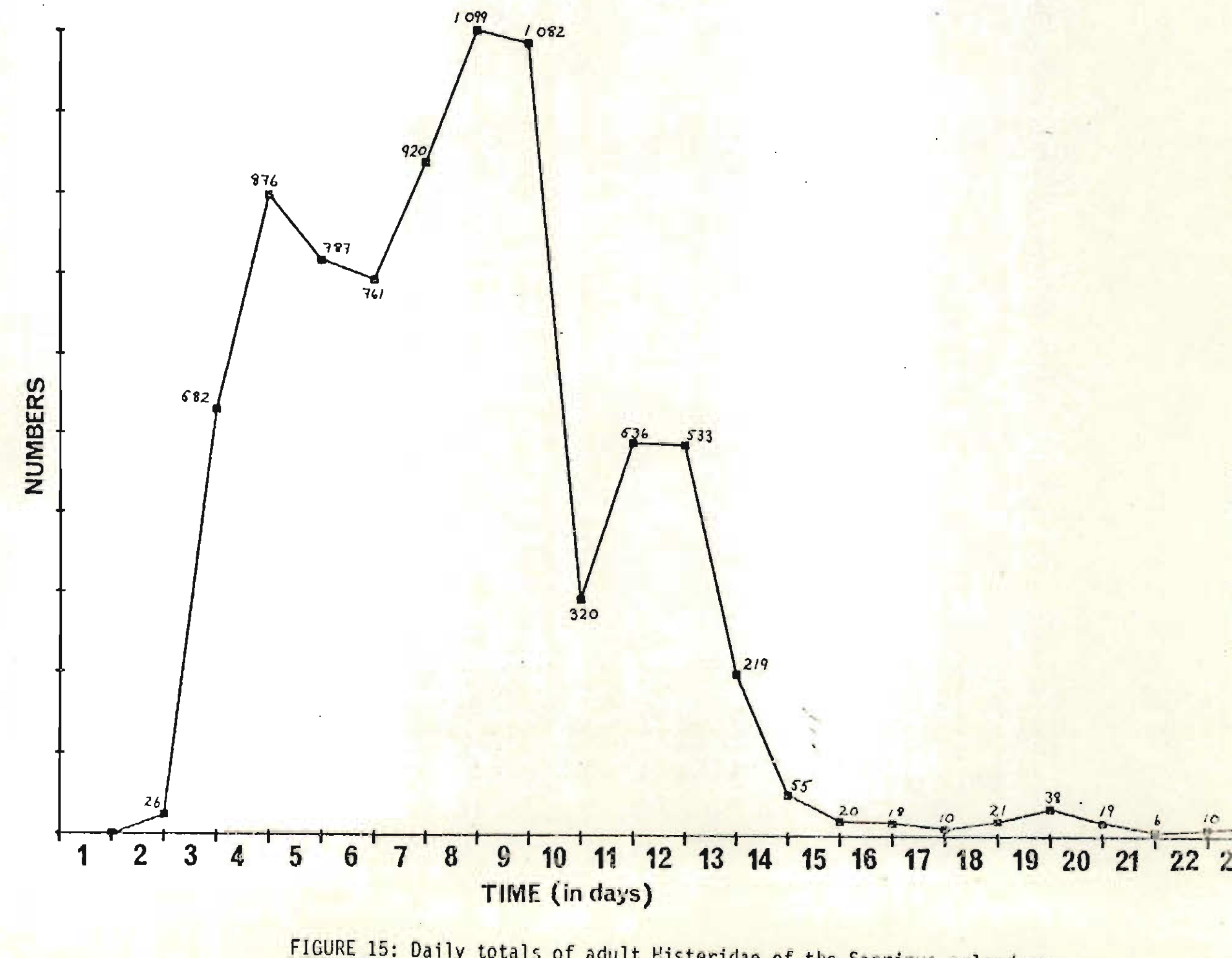


FIGURE 15: Daily totals of adult Histeridae of the Saprinus splendens-group present at Carcass B, Pafuri, 18th May to 9th June 1979

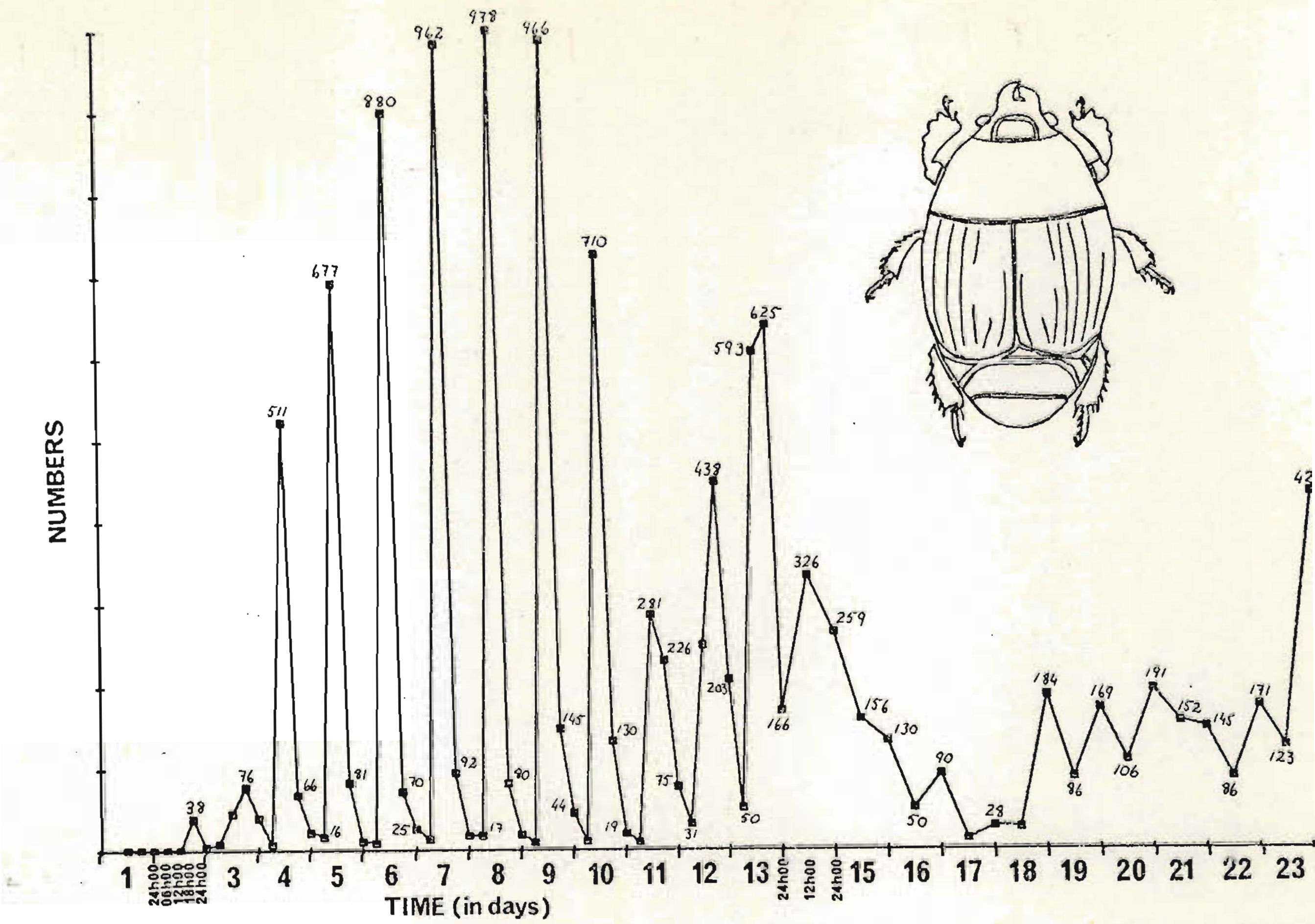


FIGURE 16: Number of Histeridae of the Saprinus cupreus-group present at Carcass B, Pafuri, 18th May to 9th June 1979, to show diel activity cycle

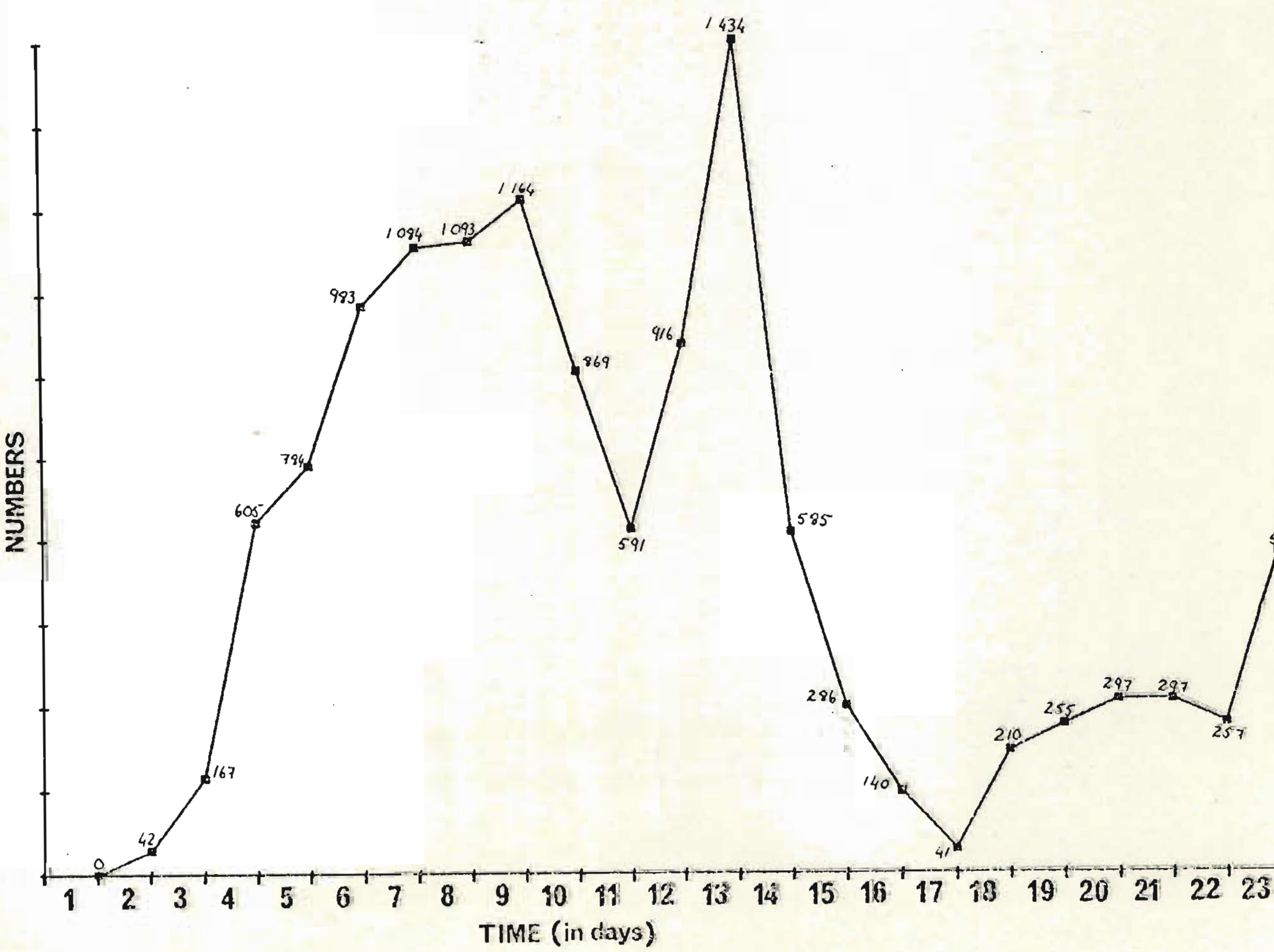


FIGURE 17: Daily totals of adult Histeridae of the Saprinus cupreus-group present at Carcass B, Pafuri, 18th May to 9th June 1979

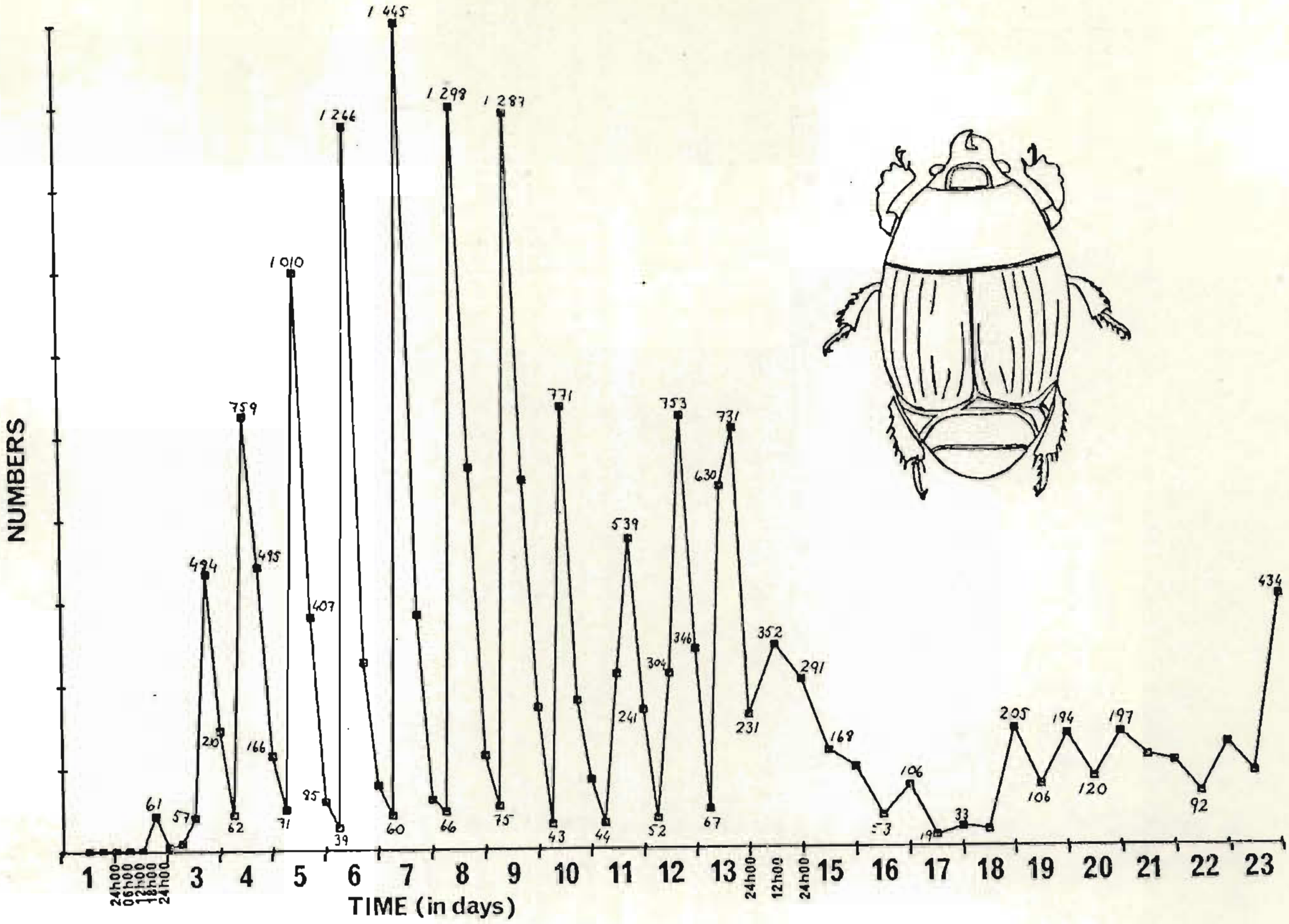
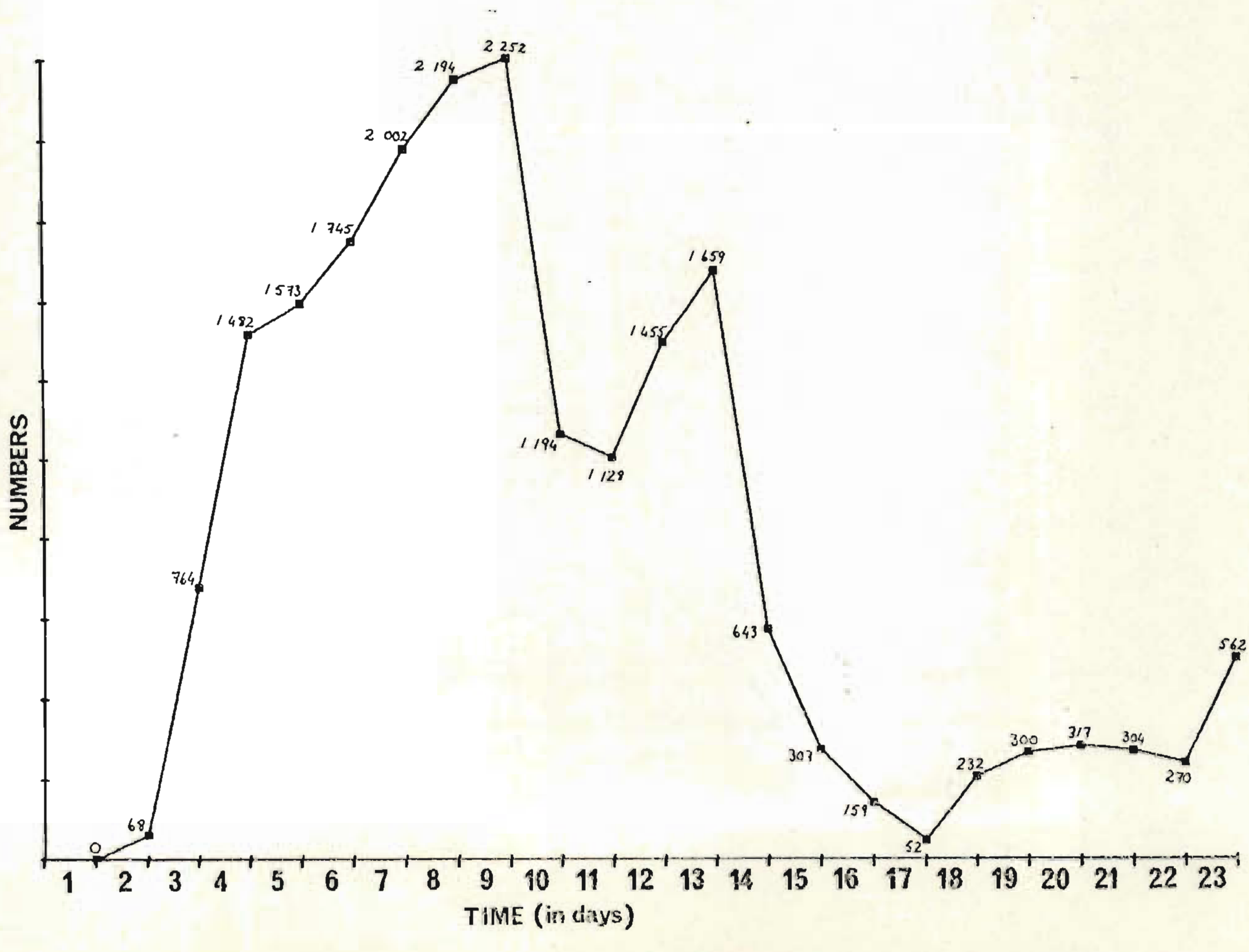


FIGURE 18 : Number of all adult Histeridae present at each collection period at Carcass B, Pafuri, 18th May to 9th June 1979, to show diel activity cycle



crease in histerid abundance. Many maggots remained at the carcass, however, so that histerid numbers remained relatively high throughout the 23-day May/June study period (Fig. 19), with a total of 20 662 being captured. This represented 83,77% of all coleopteran adults present at Carcass B. Also of interest was the very clear diel visitation pattern which these beetles displayed (Fig. 18). The early hours of morning before dawn appeared to be an inactive period with few arrivals at the carcass. Numbers increased rapidly after dawn until a peak was reached around midday, decreasing thereafter. This pattern was particularly pronounced in Saprinus cupreus Er., and is well reflected in Figure 16. Previous findings at the same site (Braack 1981) confirmed this pattern, and Tribe (1976) stated that 92% of histerids encountered at dung at Mkuzi (Zululand) were active between 05h00 and 12h00.

Figures 15 and 17 show that the initial daily increase in numbers of the S. splendens- and S. cupreus-groups followed the same general pattern, probably due to having the same larval blow-fly population as food-source. The larger beetles represented by the S. splendens-group peaked on Day 8 however, dwindling thereafter most likely due to blow-fly larvae departing for pupariation. The S. cupreus-group, representing smaller beetles sustainable by a smaller food source, peaked on Day 13 but also decreased thereafter due to a decrease in number of calliphorid larvae; finally increasing again as numbers of larvae from other families, especially Muscidae, increased (Fig. 17).

Figures 20-25 indicate a decrease in histerid abundance during Sept/Oct relative to their numbers in May/June, with a total of 3 214, forming 66,70% of all beetles present at carcass B, being captured during the 23-day survey period. The pattern of arrival of histerids at the carcass was much the same as that of May/June and Jan/Febr, with maximum numbers being present immediately prior to the departure of C. marginalis larvae from the carcass, and a visitation peak around midday within each 24-hour cycle.

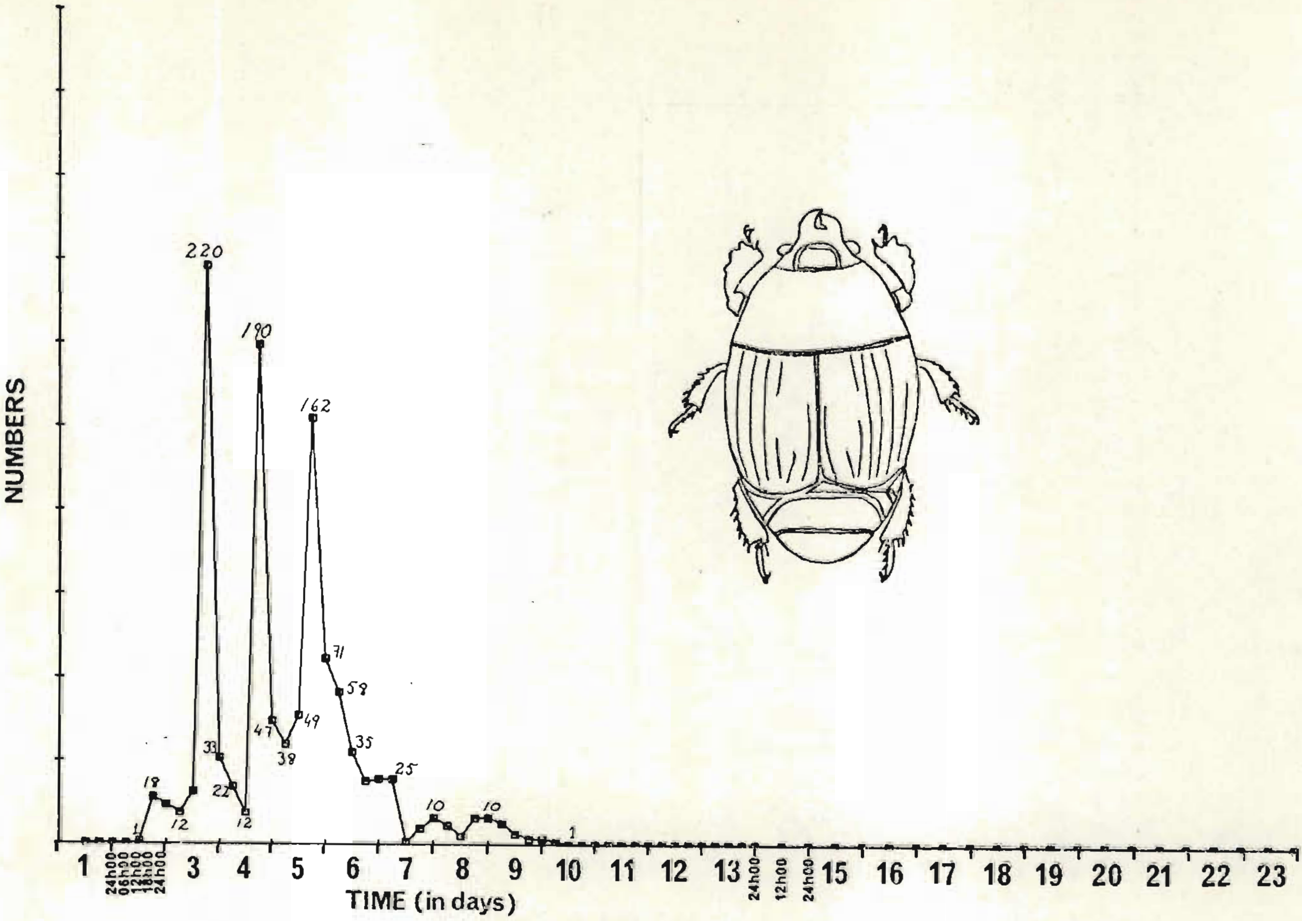


FIGURE 20: Number of adult Histeridae of the Saprinus splendens-group present at each collection period at Carcass B, Pafuri, 14th September to 6th October 1979, to show diel activity cycle

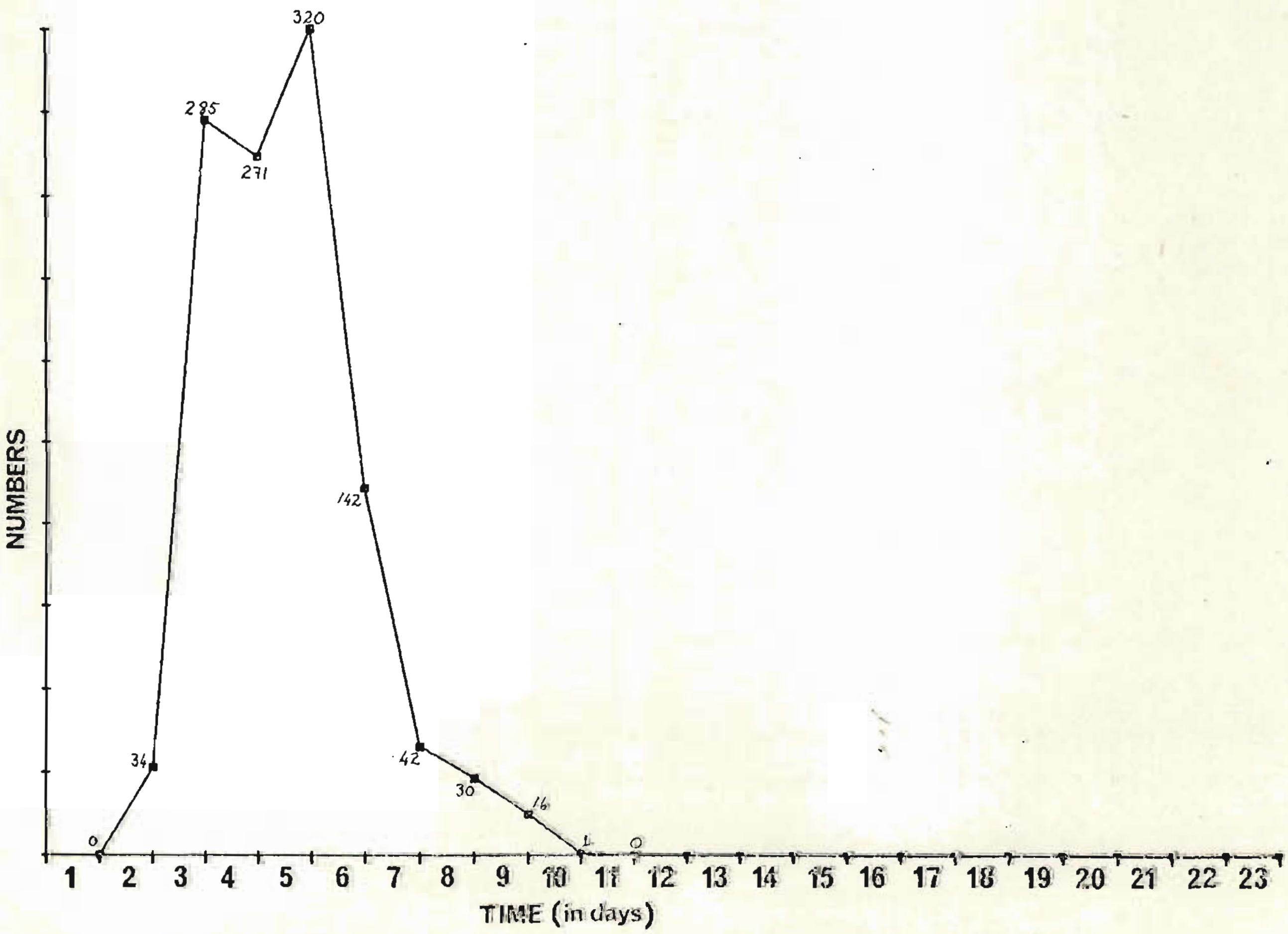


FIGURE 21: Daily totals of adult Histeridae of the Saprinus splendens-group present at Carcass B, Pafuri, 14th September to 6th October 1979

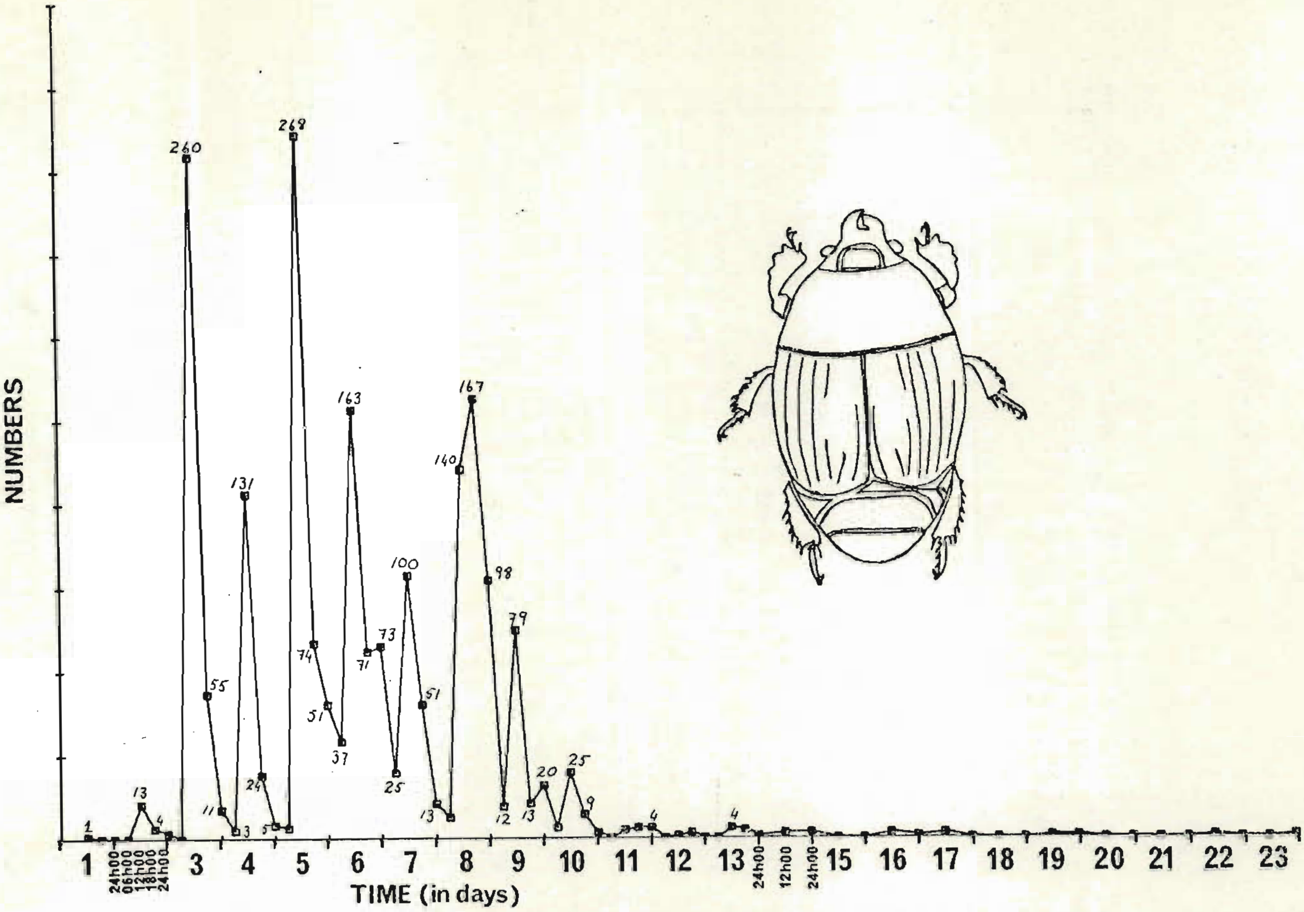


FIGURE 22: Number of adult Histeridae of the Saprinus cupreus group present at each collection period at Carcass B, Pafuri, 14th September to 6th October 1979, to show diel activity cycle

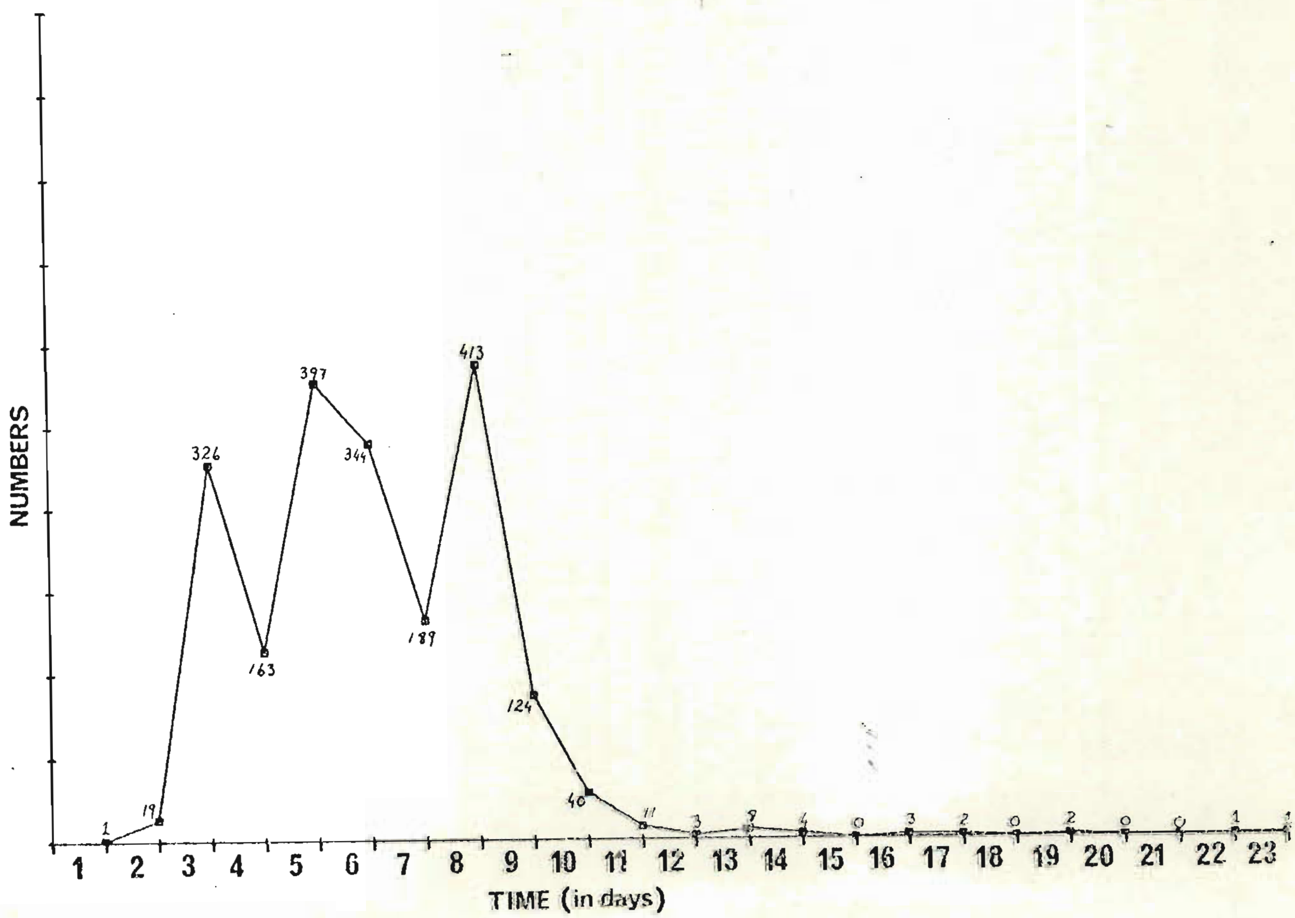


FIGURE 23: Daily totals of adult Histeridae of the Saprinus cupreus-group present at Carcass B, Pafuri, 14th September to 6th October 1979

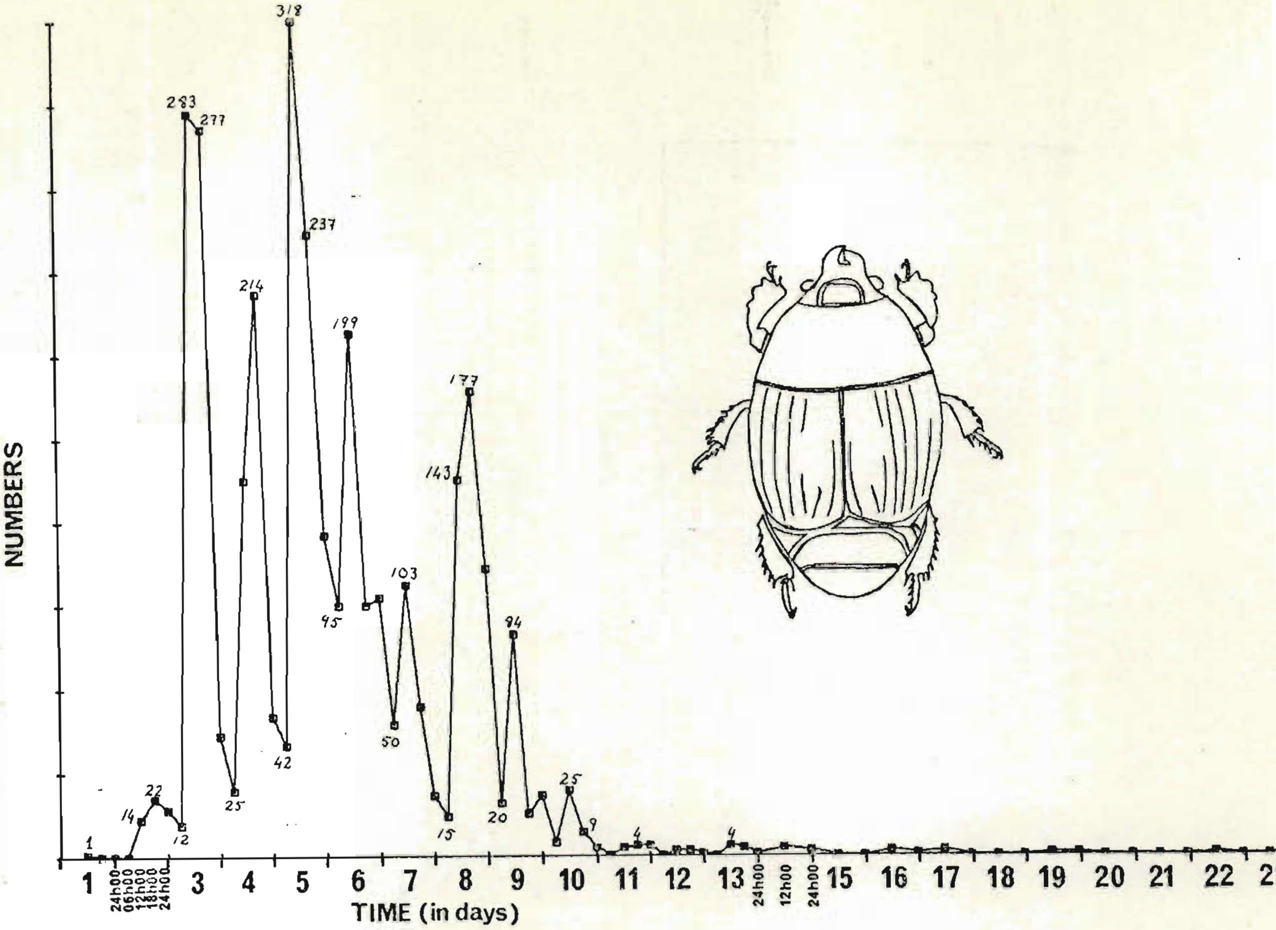


FIGURE 24: Number of all adult Histeridae present at each collection period at Carcass B, Pafuri, 14th September to 6th October 1979, to show diel activity cycle

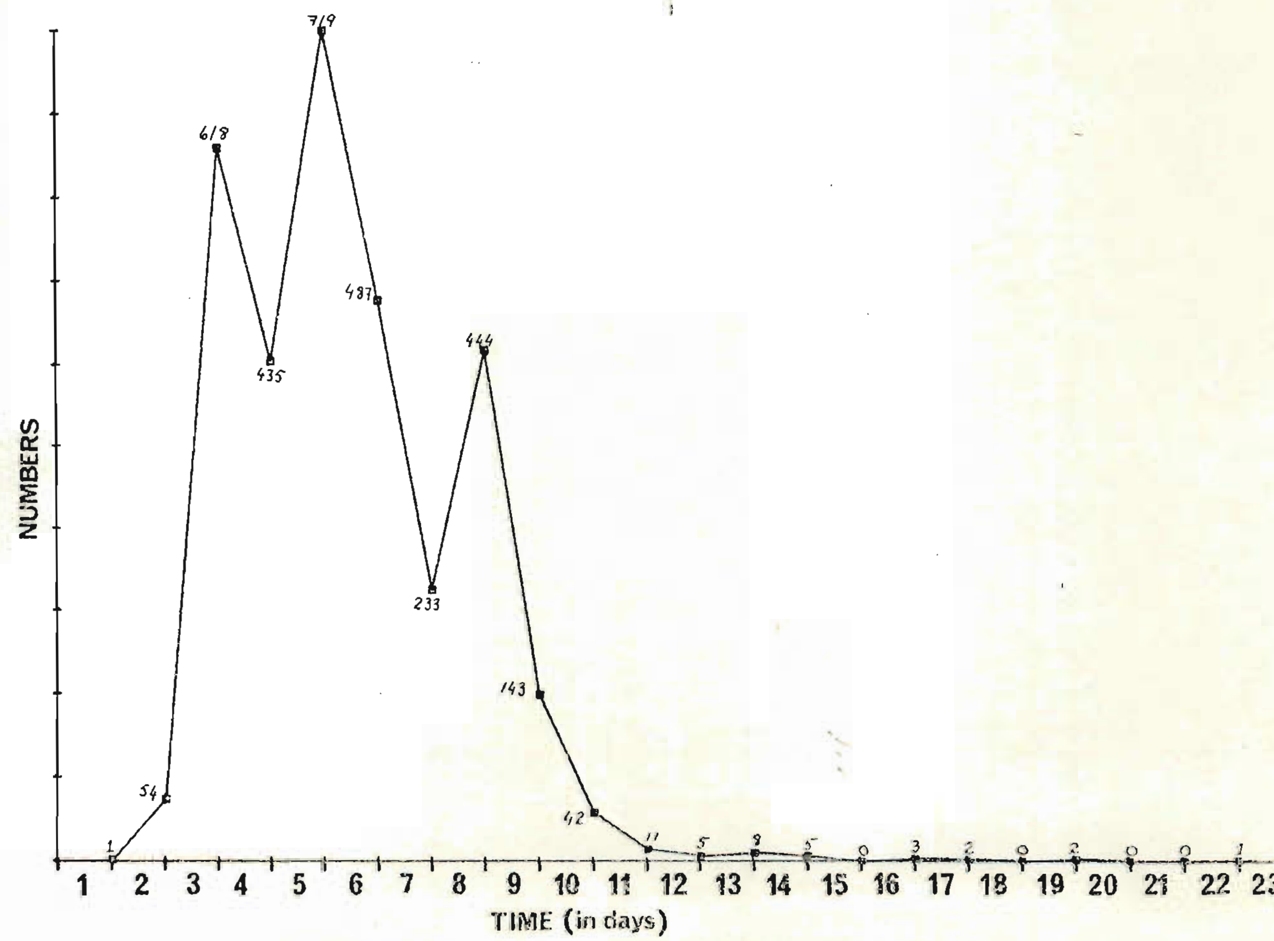


FIGURE 25: Daily totals of all adult Histeridae present at Carcass B, Pafuri, 14th September to 6th October 1979

ORDER: COLEOPTERA
FAMILY: SILPHIDAE

Most of the members of this family are large in size and feed on carrion, although some species also readily prey on other invertebrates such as snails (Balduf 1935, Richards & Davies 1977). The well-known "burying beetles" of Europe and elsewhere which bury the bodies of small vertebrates belong in this family.

Species recorded

Despite having been common at impala carcasses in the same study-enclosures in January 1978, no silphids were recorded at any of the study-carcasses in 1979. During the course of other investigations at carcasses in 1980 and 1981 however, small numbers (up to 10) of these beetles were occasionally seen. Representative specimens of these and also beetles collected previously during the 1978 study (Braack 1981) were sent away for identification and all found to be *Thanatophilus* (*Chalcosilpha*) *micans* Fabricius.

Biology

Many genera of silphids are well-known to be carrion-specialists attracted to the carcass-habitat either to feed directly on the decomposing tissues or as facultative predators, and include amongst others *Nicrophorus* (Conley 1982) as well as *Silpha* and *Necrodes* (Shubeck & Blank 1982). Balduf (1935) quoted reports of *Thanatophilis dispar* Hbst. feeding on snails. At the study-carcasses I regularly observed both adults and larvae feeding on carcass muscle-tissue, and also preying on larvae of the blow-fly *Chrysomyia marginalis*. Silphid larvae kept in large glass-jars also killed and consumed blow-fly larvae offered to them, but such larvae were always smaller than the silphid larvae themselves. Although they were offered to both adult and larval silphids, no *C. albiceps* larvae were ever attacked by these beetles. By way of contrast, *C. marginalis* larvae were often attacked within seconds of being proffered.

Patterns of carrion-attendance

The only carcass at which Thanatophilis micans was observed in abundance was at the remains of an impala in February 1981. Here silphid larvae were numerous both upon but especially below the carcass from Day 5. It is presumed that the population fluctuations of these beetles is related to rainfall as they are more abundant further south in the K.N.P. and even more so in higher rainfall areas such as Pietermaritzburg and Swellendam (pers. obs.). The Pafuri study-area falls within a region having a relatively arid climate, and the dry-cycle of rainfall which set in during the late 1970's would have further depressed the population in what may be a marginal habitat for this species.

ORDER: COLEOPTERA
FAMILY: STAPHYLINIDAE

Most of these beetles are easily recognised by the characteristically shortened elytra which conceal the large, elaborately-folded hindwings below. The family is very large and widely distributed, comprising mostly rather small, inconspicuously coloured beetles having a wide range of habits and habitat preferences (zur Strassen 1975). Many occur at decaying organic substances such as dung, carrion, vegetation; most are predacious, a large number are myrmecophilous with remarkable mimetic adaptations, and the number of termitophilous genera is also large (Voris 1934). Oviposition and associated behaviour is considered to be primitive as actual egg-laying appears to be an "incidental aside" in the general vicinity of the preferred habitat to which the female is initially attracted for the primary purpose of feeding (Voris 1934). Only a few eggs are laid, generally individually and in soil. The larvae are campodeiform and many species are known to be predacious, while some are parasitoids on the pupae of cyclorrhaphous Diptera (Richards & Davies 1977, Voris 1934). When ready to pupate, the larvae produce a cavity by wriggling and moulding the surrounding substrate,such as soil, dirt, hay, into a protective covering shelter, and then transform into the pupal stage (Voris 1934).

Species recorded

Twenty-two species in five genera were collected from the study carcasses used during the 1979 survey, these being listed in Table 13.

Biology

The vast majority of staphylinids collected from the carcass habitat at Pafuri occurred beneath the carcass or within the dung-component lying extruded alongside the carcass, making direct observation of feeding behaviour, or even food sources, impossible. All the staphylinids encountered were easily disturbed, reluctant to remain exposed in the open, and rapidly ran for crevices and other concealing positions when the carcass was even very gently turned.

Although not occurring at Pafuri, Richards and Davies (1979) stated that larvae of Aleochara bilineata and A. algarum parasitise pupae of cyclorrhaphous Diptera, and that newly hatched larvae of the first-mentioned species gnaw their way into the host puparium, thereafter undergoing hypermetamorphosis by changing from a campodeiform to an eruciform larva, with "... obvious degeneration in adaptation to a parasitic life ...". This provides some indication of the possible habits of the various Aleochara collected at carcasses at Pafuri, especially as Voris (1934) referred to the same habit of yet other species of Aleochara also invading fly puparia.

Despite examination of several hundred Chrysomyia albiceps and C. marginalis puparia (Tables 12, 19 & 20) to determine causes of pupal mortality and percentage parasitism, no staphylinid larvae or adults were found in any of the puparia. This would seem to indicate that either the species of Aleochara attending carcasses at Pafuri were not pupal parasitoids (unlikely in view of the findings of the authors mentioned above), or that they parasitised such puparia in very low numbers so that my sampling did not reveal such parasitised pupae (also unlikely in view of the number of puparia examined), or that the pupae of C. albiceps and C. marginalis were not parasitised by these staphylinids, perhaps due to the puparia being too hard to penetrate. Some support for this latter possibility was afforded in a letter by P.M. Hammond (pers. comm.) of the British Museum (Natural History) who suggested that dung is their preferred habitat, where muscid puparia and those of other smaller Diptera with softer puparia would be abundant and readily available. Prins (1980) also never found Aleochara breeding at carcasses during his studies in the southwestern Cape Province, although reproduction commonly occurred at dung-pads. This would seem to indicate a preference for dung-breeding flies as hosts.

With regard to the feeding habits of Philonthus, Voris (1934) stated that they are predators which kill and eat flies and fly larvae. Prins (1980) found Philonthus natalensis abundantly in fresh cow-dung along the Cape south-coast, and stated that the larvae and adults were predaceous on other insects and also fed on the dung fluids. With regard to Philonthus and other species of staphylinids captured at Pafuri, Hammond (pers. comm.) stated that "Philonthus, Gabronthus and Erichsonius (all Staphylinini) are predators; most of your species likely to be predators of dipterous larvae. ... Atheta (Alaeocharinae) are also predators of dipterous pupae. I doubt if any of your Staphylinidae are carrion-specialists. I have seen all the named species from other habitats, such as dung."

Patterns of carrion-attendance

During the 1979 survey staphylinids were most abundant during January and February, with a total of 625 individuals being captured (4,52% of all adult Coleoptera at Carcass B). The numbers declined so that only 110 (0,44% of all Coleoptera) were found at a similar carcass during May/June, with a further decrease to only 54 individuals (1,12% of all adult Coleoptera) recorded in Sept/Oct. Examination of Figures 26 and 27 reveal that during the Jan/Febr. survey, staphylinids had a dual period of peak visitation to the carcass habitat. At first a relatively low peak occurred between Days 2 and 4, with a greater abundance period between Days 8 and 13. A maximum number of 313 visitors was recorded on Day 9. The first period of abundance between Days 2 and 4 coincided with rumen-content being extruded from the abdomen by the activity of dung-beetles and maggots and as a consequence of bloating. The resultant odour would be a strong attractant

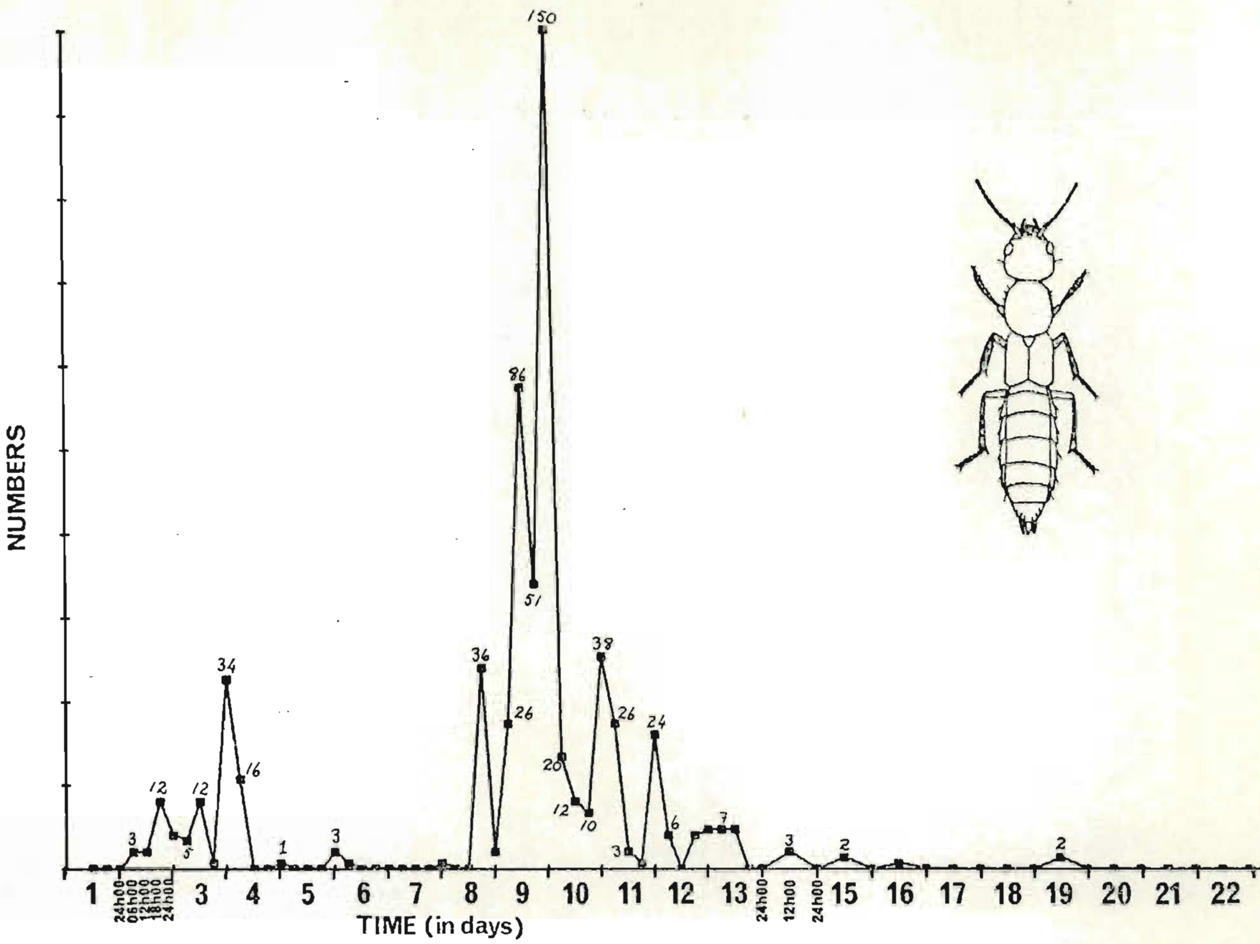


FIGURE 26: Number of all adult Staphylinidae present at each collection period at Carcass 73, Pafuri, 13th January to 4th February 1979, to show diel activity cycle

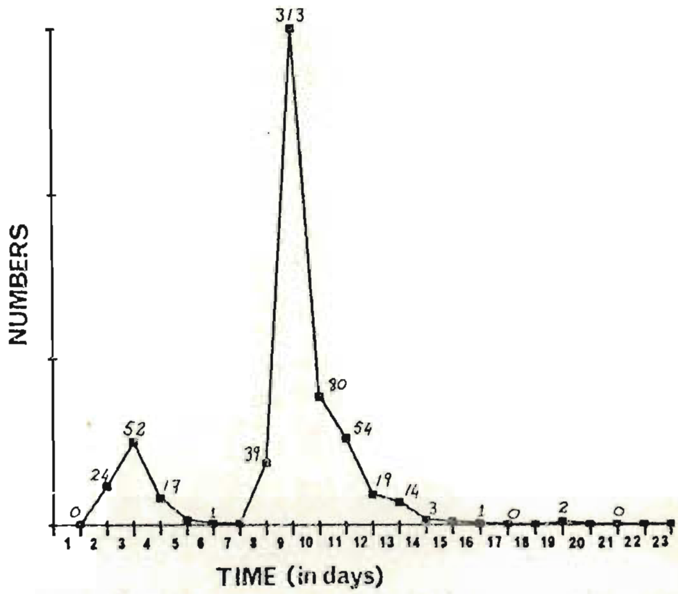


FIGURE 27: Daily totals of all adult Staphylinidae present at Carcass B, Pafuri, 13th January to 4th February 1979

for these staphylinids as dung is probably the component luring them to the carcass habitat (see earlier statement by Hammond). It also coincided with the presence at first of numerous small blow-fly larvae, and later with the availability of injured or partially eaten larger blow-fly larvae left by histerids, dermestids and clerids, which would form a source for predation and scavenging.

A downpour of rain after the noon collection on Day 8 thoroughly soaked the dry rumen-content remaining around the carcass, releasing the characteristic odours again, and would explain the sudden abundance of staphylinids at the 18h00 collection (Fig. 26). Further rain occurred on Days 9 and 10 (Table 8) which would have ensured continuous odour being given off, an odour which would not be obscured by the evolution of gases given off during the early stages of carcass decomposition as in Days 3 and 4, which presumably explains the greater abundance of staphylinids during this second peak (Fig. 26, 27). It coincided with the period of emergence of adult blow-flies from larvae which had fed at the carcass, and for the first few moments after eclosion these flies are very weak and susceptible to predation especially by ants, so that the emerging flies may also have served as an attractant for staphylinids using them as a food source.

Although somewhat erratic in their diel visition pattern, Figure 26 reveals that the staphylinids did have a preferred period of visitation and reached maximum numbers during the cooler hours between 18h00 and midnight.

Figures 28 and 29 indicate the daily totals of staphylinids arriving at the carcass habitat, and in both instances peak visitation coincided with periods of high maggot activity, when their internal wriggling actions would keep releasing odours from rumen-content they moved over or through, and the digestive fluids released by the maggots would keep such stomach contents moist. This, together with any odours from the blow-fly larvae themselves, would serve as attractant.

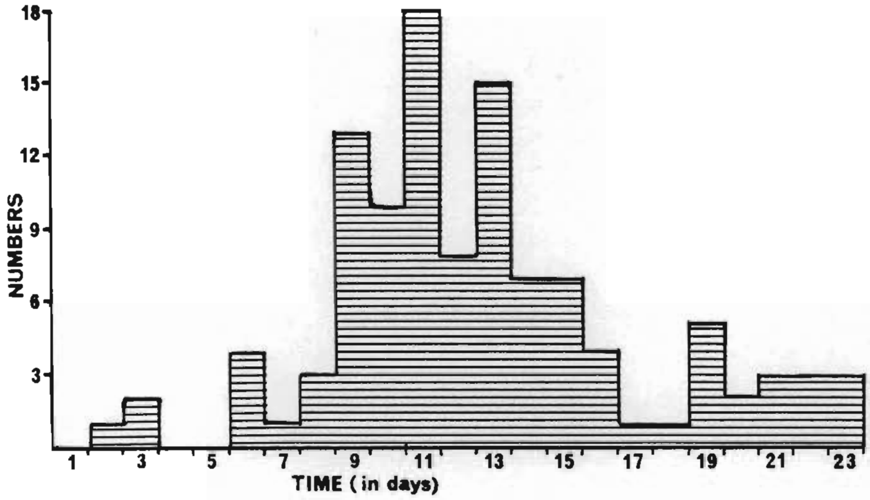
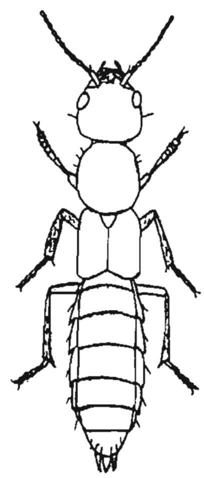


FIGURE 28: Daily totals of all adult Staphylinidae present at Carcass B, Pafuri, 18th May to 9th June 1979



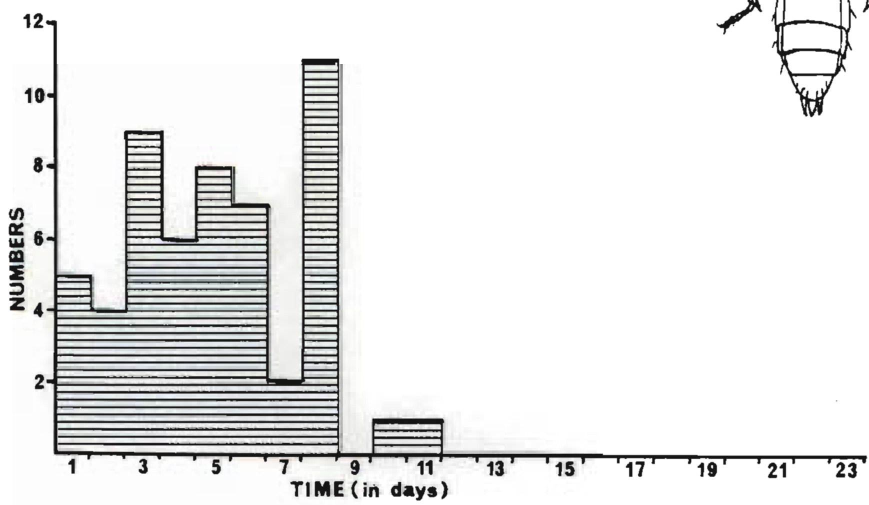


FIGURE 29: Daily totals of all adult Staphylinidae present at Carcass B, Pafuri, 19th September to 6th October 1979

ORDER: COLEOPTERA
FAMILY: TROGIDAE

Previously regarded as a subfamily of the Scarabaeidae, this group of medium-sized to fairly large beetles with a worldwide distribution has been raised to family rank in all the more recent entomological texts. The majority of species occur within the genus Trox which tend to be compact, ovoid-shaped beetles with a strongly sculptured dorsal surface, the heads are deflexed beneath the pronotum, and most species are a uniform black or reddish-brown colour (Richards & Davies 1977, Skaife *et al*. 1979, Scholtz 1980). Most are capable of flight but prefer to walk in a slow lumbering fashion, and when disturbed they hold the legs close to the body and remain motionless.

Females generally deposit their eggs in the soil beneath the food source and the larvae pass through three instars in about four weeks, after which they enter a pupal stage which usually lasts about two weeks (Scholtz 1980).

The larvae have the typical scarabaeiform shape and appearance with well-developed thoracic legs and a fossorial habit (Richards & Davies 1977).

Species recorded

Six species were collected, all belonging to the genus Trox (Table 13).

Biology

Adult and larval trogids are facultative necrophages associated with decomposing animal matter, especially carrion (Richards & Davies 1977, Scholtz 1978, Skaife *et al*.1979), but adults have also been found feeding on bat guano in caves, locust eggs, a carpet, felt hat, horsehair cushion, and some North American Trox are held to be endemic to the nests of certain birds and burrows of foxes (Scholtz 1980).

Direct interaction between Trox and other components of the carrion-insect complex at Pafuri was minimal, except for occasional instances where Trox beetles were observed feeding on larvae of all sizes of both Chrysomyia albiceps and C. marginalis. To examine the possibility of predation by Trox on insects,an activity previously unrecorded in this genus, I placed ten T. tuberosus (subsequently identified by C.H. Scholtz) in a large net-topped consol jar with ten full-grown larvae of each of C. albiceps and C. marginalis at 10h00 on 26/1/1980. By 08h00 the next morning two C. albiceps had been completely eaten and one partially consumed, while one and one half C. marginalis larvae had been consumed. The remaining maggots were uninjured. In another jar at the same time the experiment was repeated, using Trox squalidus. By 08h30 on 27/1/80 three C. albiceps and all the C. marginalis larvae had been eaten, with only small pieces of cuticle remaining. The previous afternoon I observed a T. squalidus beetle walk up to an actively wriggling C. albiceps larva, bite into the mid-dorsal region and pull away small shreds of tissue.

Although the above observations indicated that species of Trox can resort to predatory behaviour, their impact on the numbers of maggots at a carcass was negligible, partly because the period of overlap between large numbers of blow-fly larvae and trogids at the carrion habitat was short (most maggots had departed by Day 6 in summer), and also because the maggots were near full-grown and in a frenzied mass of activity concentrated on and immediately around the carcass so that the slow and lumbering Trox beetles experienced difficulty in obtaining a foothold. Observation during this period of overlap showed that such captures by trogids were few in number.

I have found Trox beetles for the most part to be general scavengers on animal tissue. They tend to dig into the soil near the food source or seek refuge below the carcass during the hottest hours of the day, coming out at other times to feed on accretions of organic tissue such as hair matted with congealed blood or other organic ooze, moist or dry muscle tissue, shreds of skin, collagenous fibres adhered to the bones, pools of semi-congealed blood soil drenched with carcass fluids, and also maggots partially eaten by histerids. I have also on several occasions found Trox feeding continuously and exclusively on the solid keratinous hooves of impala and buffalo, despite alternate food sources such as skin being available in the immediate vicinity . Although they did feed on skin this was largely left to dermestids, unless the skin was moist in which case Trox avidly joined in feeding on it. For the most part they preferred feeding on other carcass remnants directly in contact with the soil. Only rarely did they climb onto a carcass component.

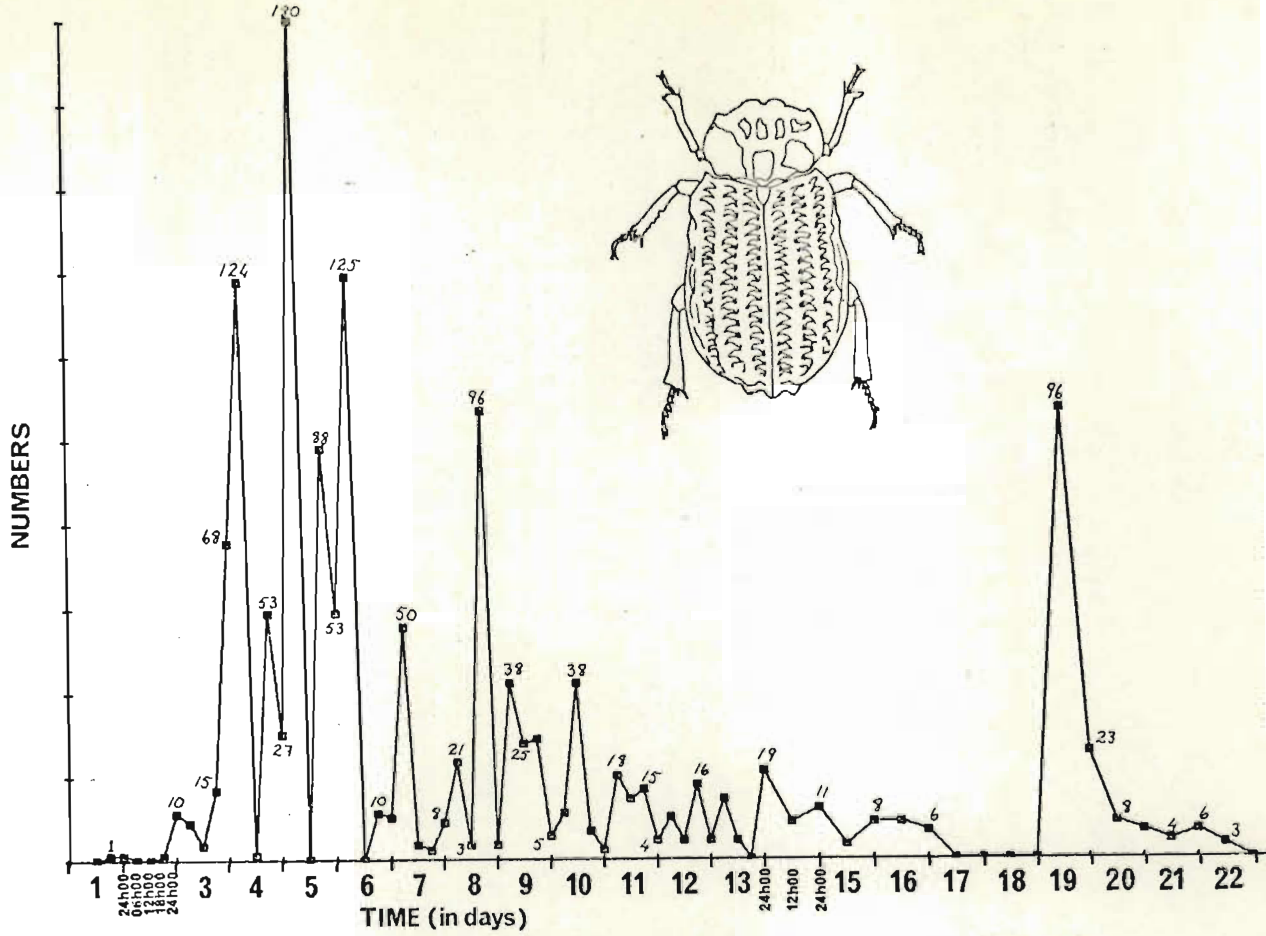
Patterns of carrion-attendance

Because such large numbers were involved at times and the great difficulty in distinguishing some of the species it was not practical to separate the species when counting, and instead they were simply recorded as Trox. They were very similar in habits, however, so that for the purposes of this study the grouping of the various species does not represent a loss of essential detail. A good indication of the relative abundances of the various species was afforded by the comments of Scholtz (pers. comm.) who, after examining a collected batch of 1 422 Trox specimens from a single impala carcass in January 1979, generalised the frequency of occurrence of the component species in the following manner:

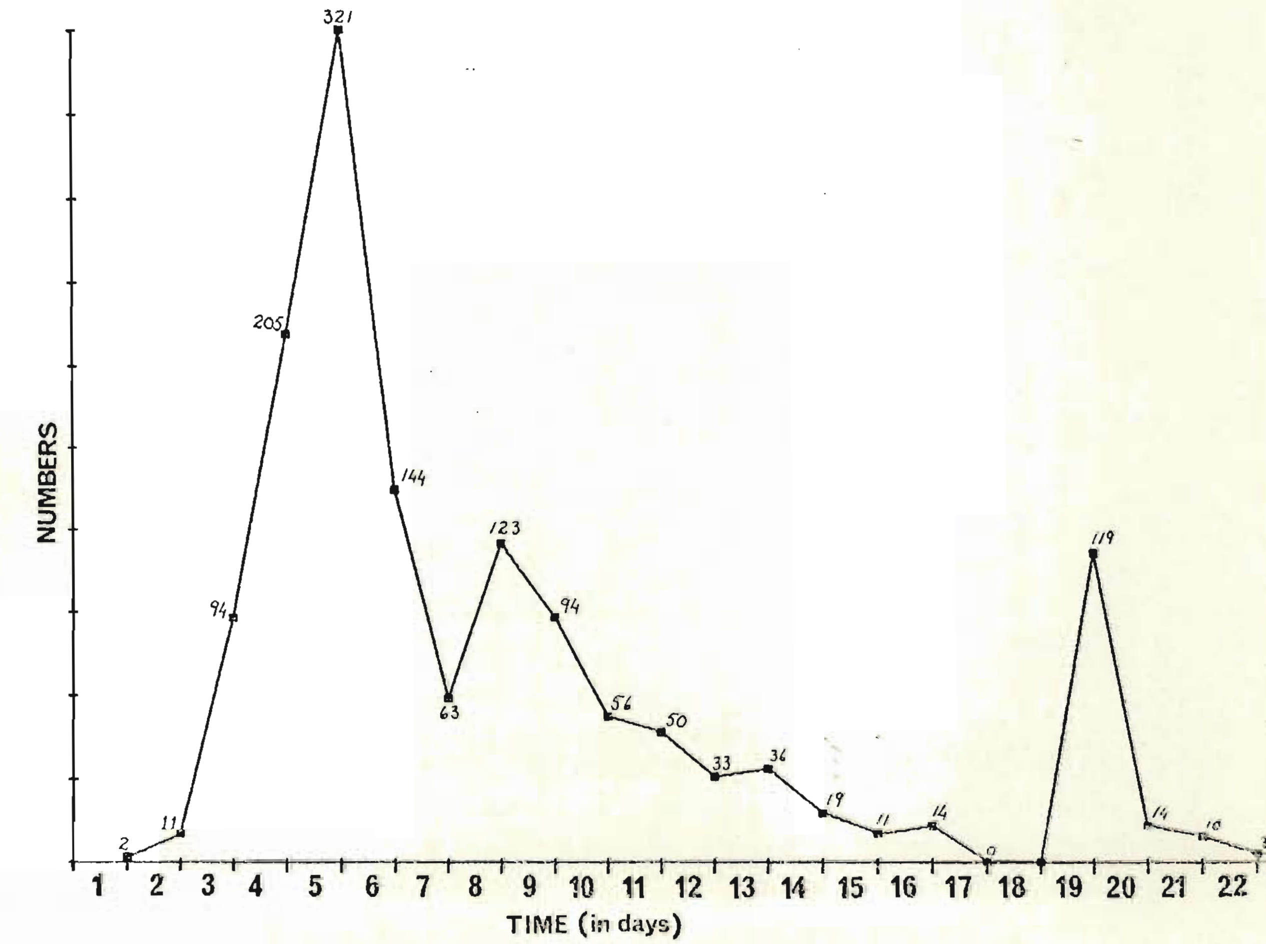
"T. squalidus : very common
T. melancholicus : very common
T. tuberosus : common
T. radula : common
T. rusticus : rare
T. mutabilis : rare"

Figures 30 to 33 show Trogids were most abundant in Jan/Febr. of 1979 but present in very low numbers during May/June and Sept/Oct. The depressed numbers present in the latter two periods were not due to possibly having exhausted the population during the preceding Jan/Febr. survey as well over a thousand Trox were again observed at each of two carcasses place in January 1980. The graphs therefore do reflect natural seasonal fluctuations in populations numbers.

Figure 30 reveals that within each 24-hour cycle the recruitment rate of Trox at the carrion habitat was high at dusk, followed by a



<u>FIGURE 30</u>: Number of all adult Trogidae present at each collection period at Carcass B, Pafuri, 13th January to 4th February 1979, to show diel activity cycle



<u>FIGURE 31</u>: Daily totals of all adult Trogidae present at Carcass B, Pafuri, 13th January to 4th February 1979

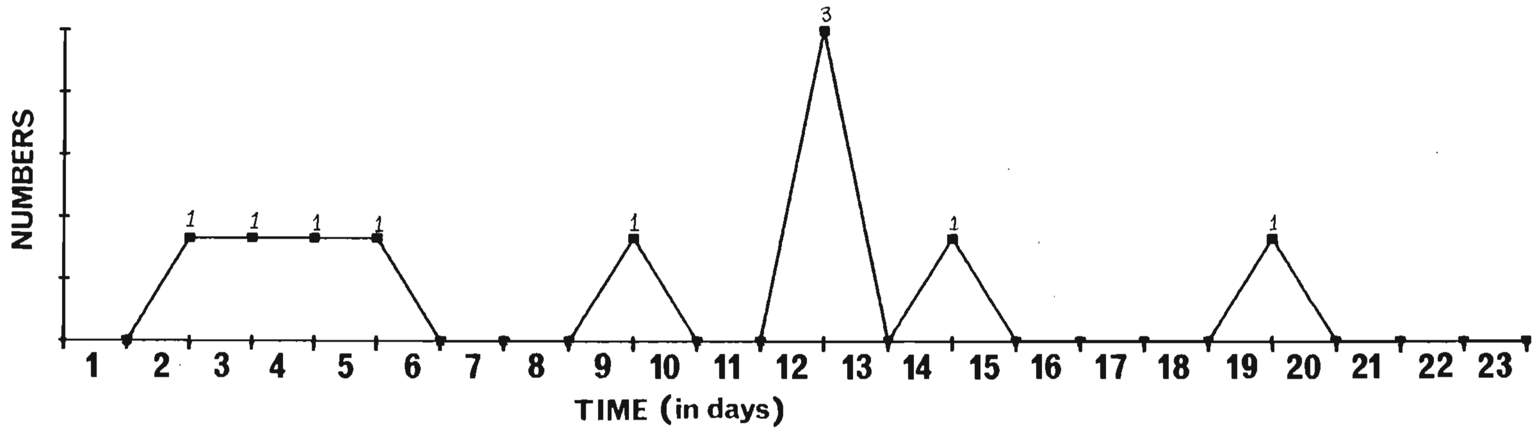


FIGURE 32: Daily totals of all adult Trogidae present at Carcass B, Pafuri, 18th May to 9th June 1979

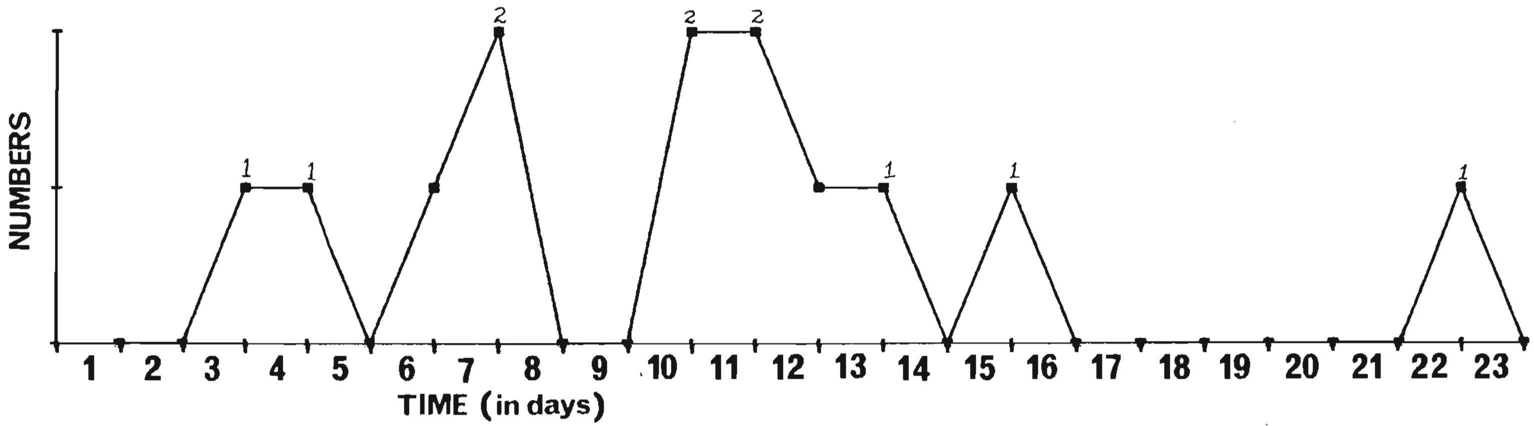


FIGURE 33: Daily totals of all adult Trogidae present at Carcass B, Pafuri, 14th September to 6th October 1979

slight slump around midnight, after which there was a very high rate of new arrivals around dawn with very little or no subsequent recruitment until well after midday. This gave the appearance of a bimodal peak with the greatest numbers arriving in the early morning and in late afternoon. The pattern was most easily discerned when comparing the numbers captured at each collection period between Days 3 and 7. Observation has shown that the peak hours for recruitment are between 05h00 and 07h00.

Scholtz (1978, 1980) stated that Trox ".... are usually among the last of the succession of insects that invade carcasses ....". Trox are most numerous in summer (Figs. 30 to 33, pers. obs.) and at such times I consistently found that the peak recruitment period for Trox occurred before Day 10 (Figs. 30 & 31, Braack 1981) but that these high numbers of early arrivals remained for several weeks at the carcass so that they were in fact abundant in the first stages of decomposition but they were not late arrivals at this habitat, at least not in large numbers. Nevertheless they do have a very extended period of attendance at the carrion habitat, beginning when blow-fly maggots are still very active at the carcass and remaining long after their departure until only bone and a few shreds of skin are left. Peak arrival and utilization of the carcass, however, corresponded roughly with the departure of blow-fly maggots when an abundance of most carcass tissue was available, but decreased steadily as the carcass dried.

An unavoidable consequence of the method used in this study to monitor the species composition and abundance of insects utilizing carrion was that because all insects were removed from the habitat at each collection period, the duration of stay and buildup of individuals at the carcass was not reflected. By using control carcasses where collections were not made as frequently, however, an added impression of the natural sequence of events could be obtained. By comparison of results it appeared that a buildup of Trox did occur and also that such a concentration of trogids acted as a stimulus in itself which attracted other Trox to the site at a rate which exceeded the recruitment which would have occurred had there not been such a concentration. This was confirmed during a short trial during Days 17 and 18 at Carcass B when trogids were deliberately not collected, and by Day 19, when normal collections were resumed, their numbers had dramatically risen in accordance with the explanation provided above. Stated simply therefore, (a) maximum arrivals occurred relatively early in the decay process but (b) the beetles remained for several weeks at the carcass so that (c) a buildup of numbers occurred meaning that (d) maximum total numbers would be found in the advanced or latter stages of decay. An additional finding was that (e) such concentrations of trogids acted as a stimulus which attracts other members of the family.

A total of 1 422 Trox were captured at impala Carcass B during the January/February 1979 survey, which constitutes 10,28% of all Coleoptera collected at this carcass during the same period.

ORDER: COLEOPTERA
FAMILY: SCARABAEIDAE

Forming part of a large superfamily which is most easily recognisable by the lamellate, clubbed structure of the antennae, the Scarabaeidae is a widely distributed group of small to very large beetles with divergent feeding habits. It comprises several subfamilies, the number ranging according to the system of classification used (Ritcher 1958), but only the Scarabaeinae and Hybosorinae are of relevance here.

Sub-family: Scarabaeinae

Generally oval or round in shape, with some 71 genera in subsaharan Africa, the majority of these beetles are coprophagous (Tribe 1976) although the adults of some species are also known to feed on carrion, decaying vegetable matter, and fungi (Ritcher 1958). Whereas the adults have membranous mandibles and only ingest the expressed liquid or colloidal components obtained when moist dung is squeezed between their mouthparts, the larvae have mandibles adapted for chewing and feed on whole dung particles (Tribe 1976).

Adult females usually lay their eggs singly in brood balls consisting of dung collected with or without the aid of a male. Such balls may be located within a dung-source (endocoprids), below a dung-source in soil (paracoprids), or well away from a dung-source but also buried in soil (telecoprids) (Tribe 1970, Weaving 1982). The larvae feed on the dung thus provisioned for them, most passing through three instars before entering the pupal stage within a self-constructed cell inside the original brood-ball or in nearby soil (Ritcher 1958). The duration of the life-cycle varies, but in general they have an expectancy of one year, the larvae and adults being capable of aestivating during dry periods for several months until suitable temperatures and rain arrives (Ritcher 1958, Tribe 1976). Rain is a very important factor determining the activity of Scarabaeinae, as it softens the soil thus allowing freshly emerged adults to burrow from their brood-balls to the surface, and permits burial of new brood-balls (Tribe 1976).

Species of Scarabaeinae recorded

A total of 46 species were collected at the decomposing impala carcasses used at Pafuri during 1979. A listing of these species is provided in Table 13.

Anachalcos convexus and especially *Onthophagus* spp. by far made up the bulk of the Scarabaeinae attendant at the impala carcasses, the remaining species being present only in low numbers and at irregular intervals. *Sarophorus costatus*, which was present in large numbers during another survey at the same site in January 1978 (Braack 1981), never again reached abundance at any of the carcasses subsequently studied.

Biological notes on Anachalcos convexus Boheman

This large (average length = 2,25 cm) telecoprid beetle occurs widespread in Africa and is considered to be a primitive member of the Scarabaeinae (Tribe 1976). Although generally regarded as being coprophilous, *Anachalcos convexus* was observed to feed preferentially on flesh, and sometimes skin, despite an ample and readily accessible supply of rumen being available in the immediate vicinity.

Confirming these observations, Coe (pers. comm.) stated that necrophagy is fairly common in many scarab species, and went on to say that "... Anachalcos is a case in point which actually burrows below carcasses in Tsavo and takes pieces of skin and flesh below ground". Tribe (1976) considered the necrophagous habit to have arisen in certain scarabs due to competition for available dung especially in forest environments where bovine dung was less plentiful than in open grassland.

Patterns of carrion-attendance of Anachalcos convexus

Anachalcos convexus occurred in fairly large numbers during January and February 1979, with a total of 1 164 individuals being collected from Carcass B during the 23-day monitoring period. This represented 15,12% of all adult Scarabaeinae collected during the corresponding period, and 8,42% of all Coleoptera. No specimens were observed during the May/June and Sept./Oct. 1979 surveys.

Figure 35 indicates that during January 1979 the number of beetles increased rapidly from Day 1 to a peak of 197 individuals on Day 3, thereafter dropping steeply as carrion-material decreased and the carcass and its immediate surrounds became increasingly covered by a dense mass of wriggling blow-fly larvae. A sharp rise occurred again on Days 8, 9 and 10, coinciding with a period of rain (Table 8). This second peak can be ascribed to drenching of the near-dry carcass-remains rendering it attractive once more to these beetles which home in on the newly generated odour. As the carcass dried again their numbers rapidly dwindled, only to be slightly elevated again by soft rain soaking the carcass on Days 18 and 19.

As can be seen from Figure 35, A. convexus had a distinct diel activity cycle. From a near-complete absence during the daylight hours, their numbers increased markedly after dusk, but decreased again so that by dawn very few were present at the carcass. Tribe (1976) found that in Zululand A. convexus had its peak activity period between 19h00 and 20h00 when average hourly temperatures were about 23°C.

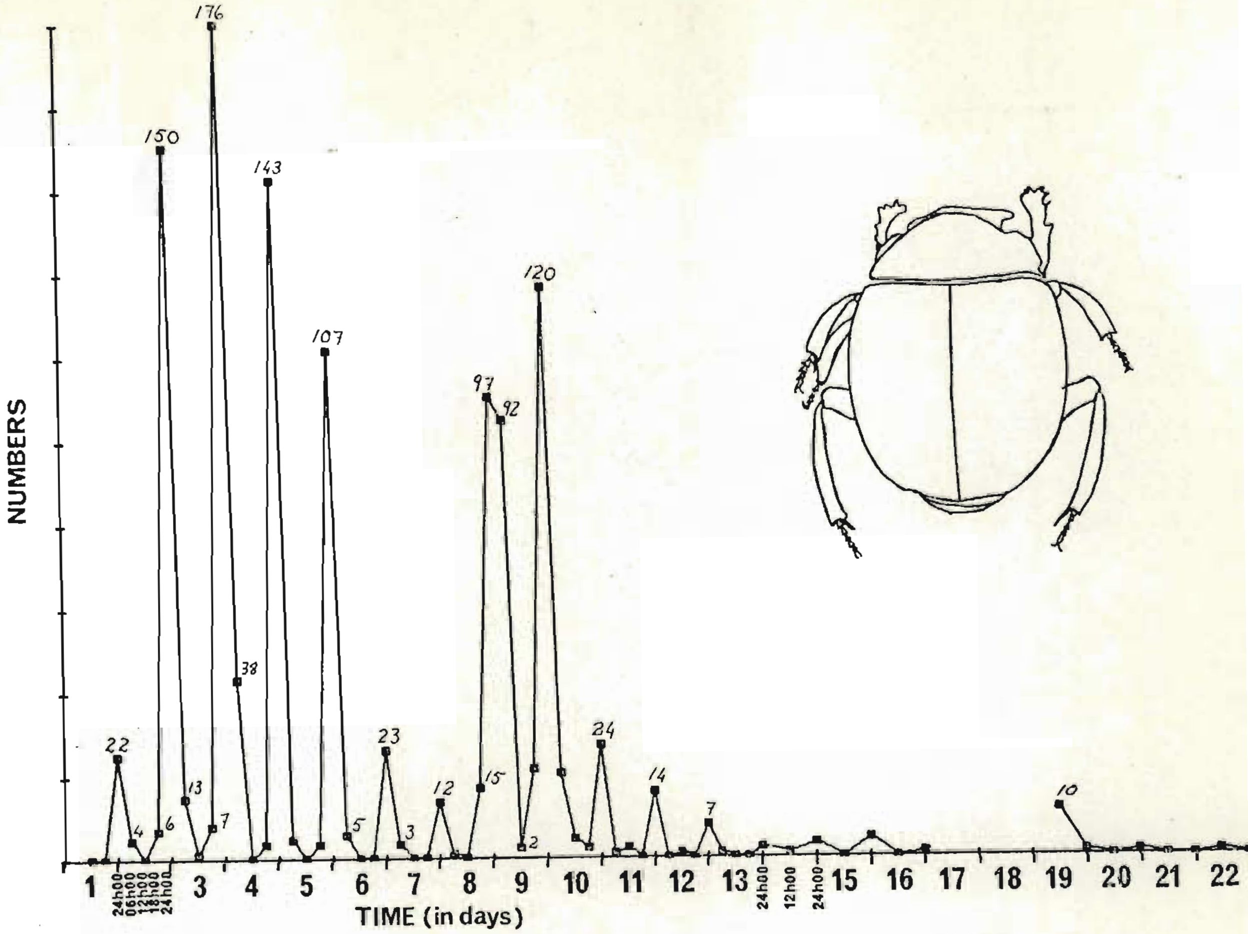


FIGURE 34: Number of adult Anachalcos convexus (Scarabaeidae) present at each collection period at Carcass B, Pafuri, 13th January to 4th February 1979, to show diel activity cycle

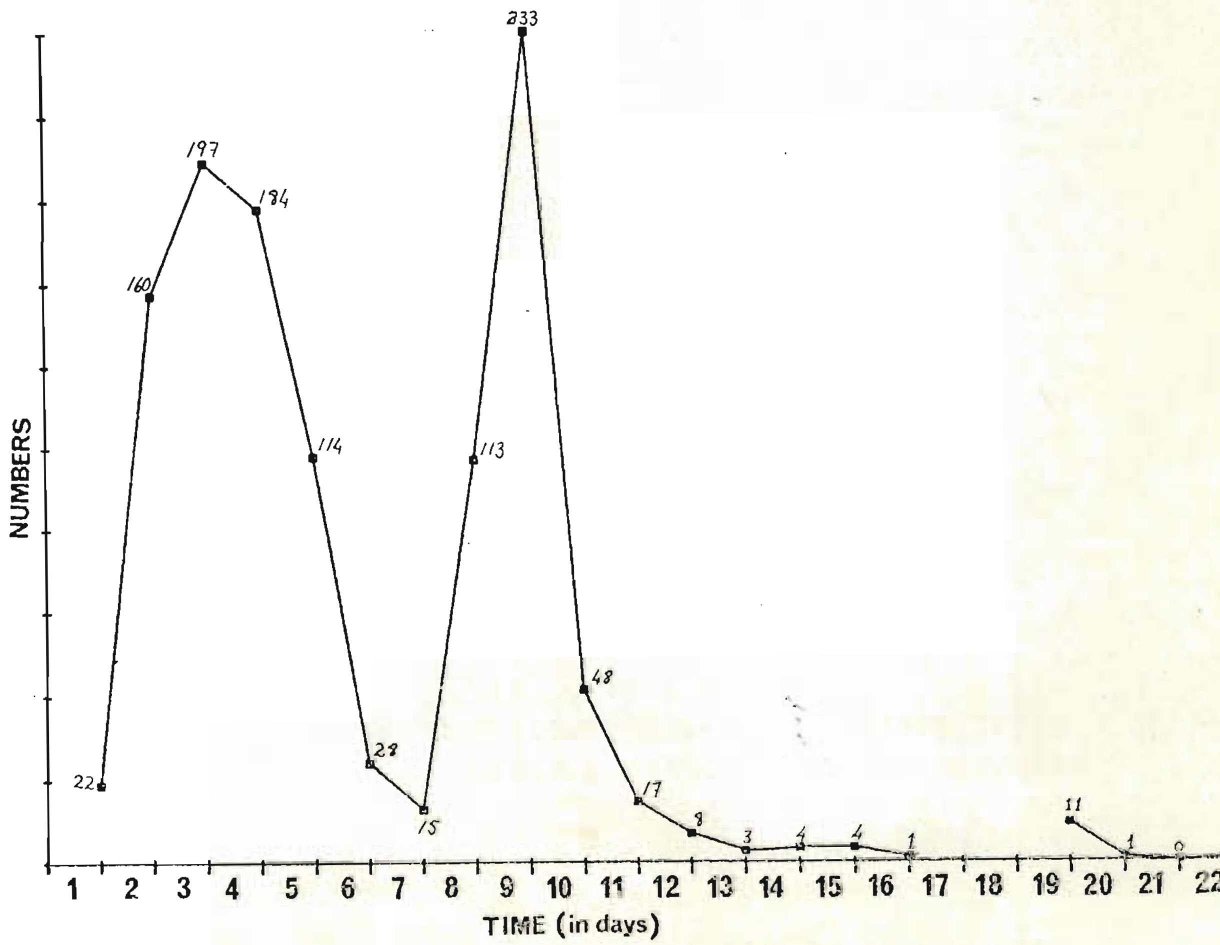


FIGURE 35: Daily totals of all adult Anachalcos convexus present at Carcass B, Pafuri, 13th January to 4th February 1979

Biological notes on Onthophagus spp.

With 914 species and 64 varieties in subsaharan Africa, this is the largest genus within the sub-family Scarabaeinae (Tribe 1976). All are paracoprid and, excluding members of the subgenus Proagoderus which were present only in very low numbers during the Pafuri survey, are mostly brown or black in colour (Tribe 1976). Fifteen species were encountered during the three survey periods in 1979, but they varied considerably in abundance. Onthophagus carbonarius, O. lamelliger and O. vinctus were by far the most numerous, but the large numbers present and the close similarity of many species prevented counts being made to determine the proportionate contribution of each species to the total numbers of all beetles present. This was also not considered necessary as they are very similar in habits so that in terms of ecological impact and for the purposes of this study all species of Onthophagus were grouped together.

Despite the large number of Onthophagus beetles present at the carcass, their impact and influence on other species at impala carcasses appears to be small. Removal of rumen material was negligible, perhaps because the texture was not suitable. Instead they fed on the abundant rumen fluids and other juices drained into the soil around the carcass. On a number of occasions I also observed several species of Onthophagus feeding on moist muscle tissue.

Patterns of carrion-attendance of Onthophagus spp.

Onthophagids were present during all three survey periods in 1979, but were most abundant in the hot weather of Jan/Febr. when a total of 5 670 adults were captured. This represents 73,65% of all Scarabaeinae and 41,0% of all adult Coleoptera captured during the 23-day survey at Carcass B. They arrived in large numbers from the first day of placement of the carcass (Fig. 37), reaching a peak on Day 2. They declined rapidly thereafter as blow-fly maggots increased in size and activity, the maggots effectively preventing the beetles from getting close to the rumen by covering almost the entire carcass and wriggling incessantly. The attractant smell of rumen-content was also disguised by the strong smell of decomposition at that stage.

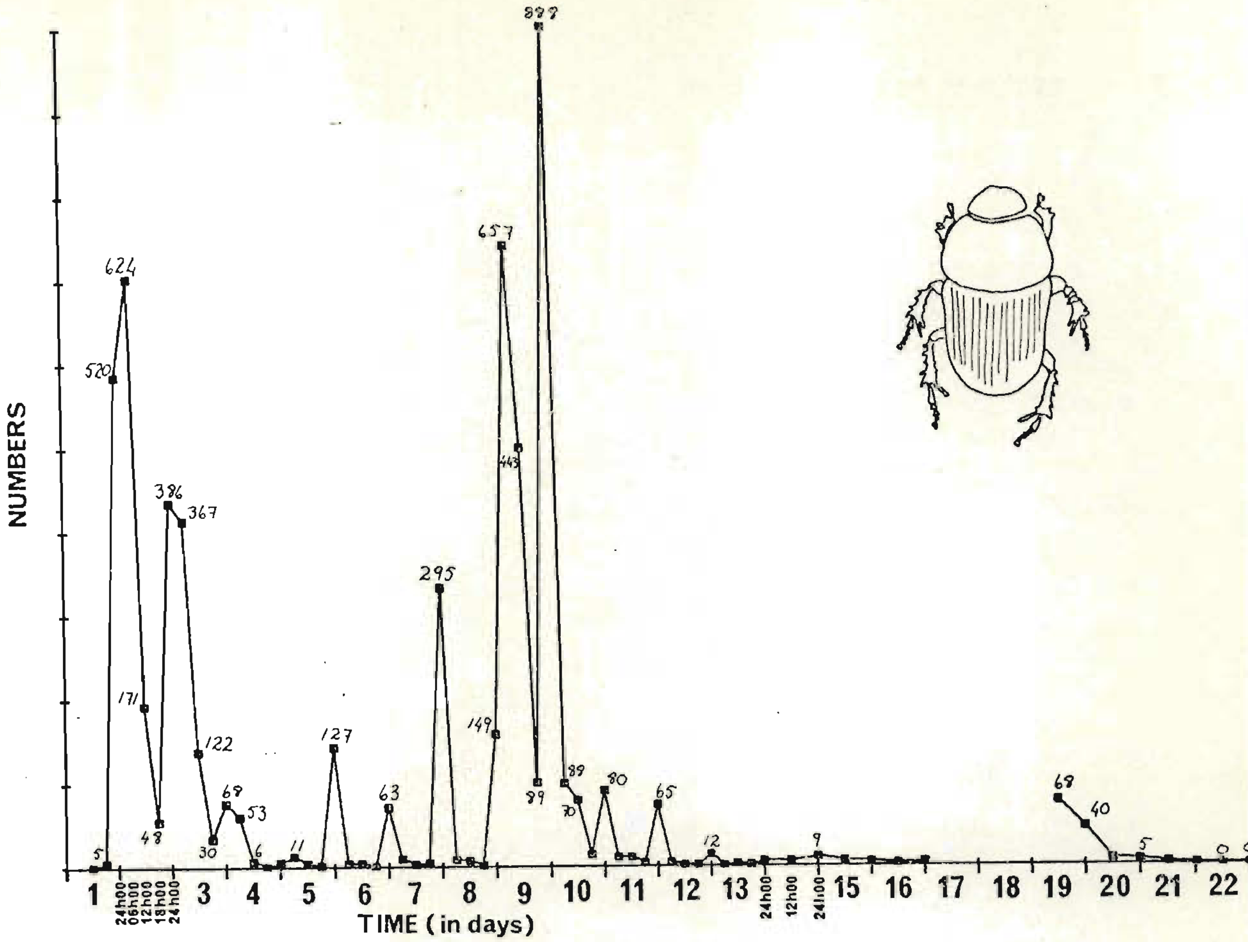


FIGURE 36: Number of all adult Onthophagus spp. (Scarabaeidae) present at each collection period at Carcass B, Pafuri, 13th January to 4th February 1979, to show diel activity cycle

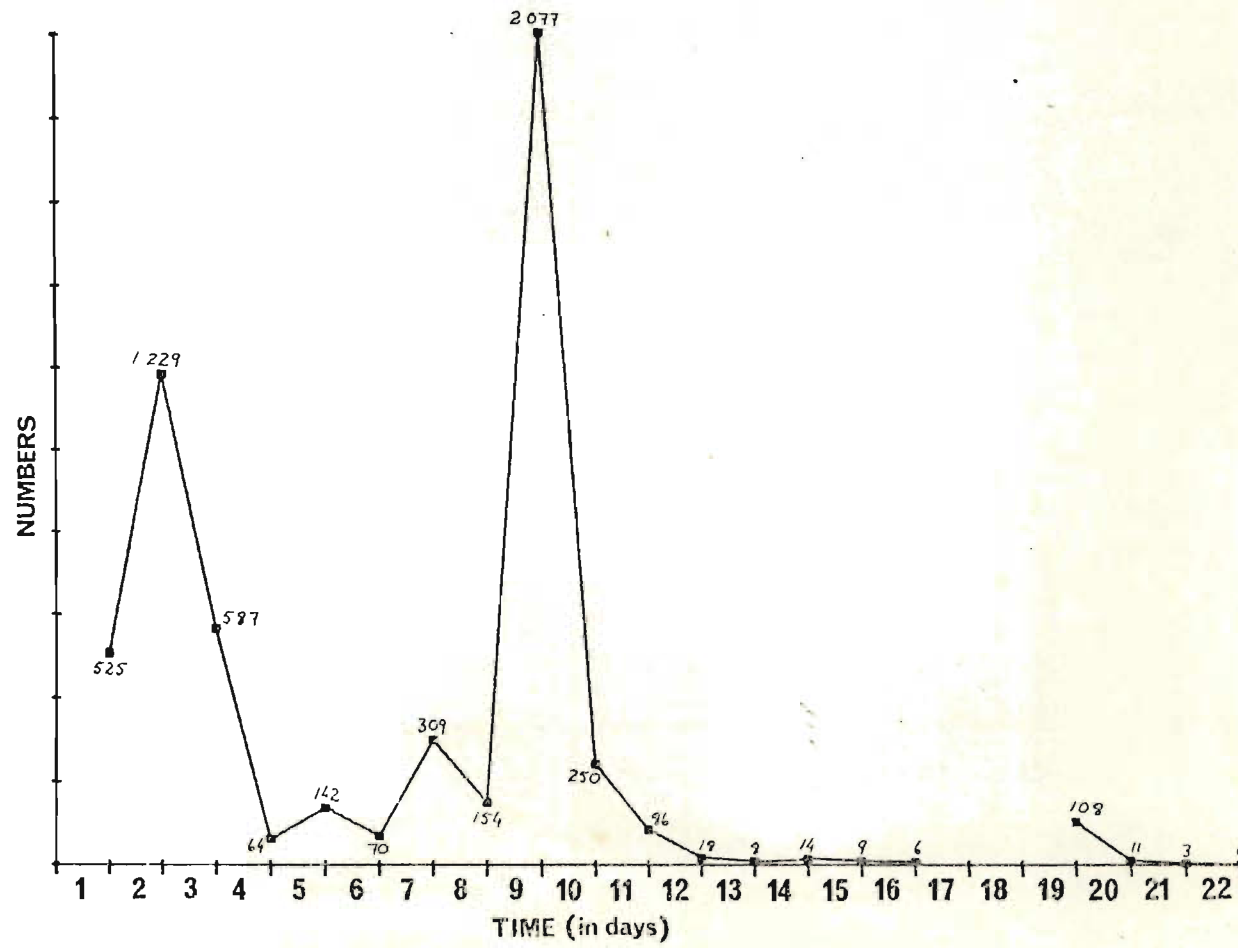


FIGURE 37: Daily totals of adult Onthophagus spp. (Scarabaeidae) present at Carcass B, Pafuri, 13th January to 4th February 1979

A massive resurgence occurred on Day 9 due to rain having soaked the dried-out carcass remains thus again releasing a strong odour of dung from rumen-content lying strewn in the vicinity of the carcass. This was a short-lived increase in numbers, however, which rapidly decreased until daily totals averaged less than ten individuals per day, with another small but temporary increase on Day 19 due to rain.

Figure 36 shows that Onthophagus had clearly discernable preference periods for activity, with low numbers of arrivals at the carcass during daylight hours and a sudden sharp increase to attain maximum numbers between 18h00 and 24h00. This agreed with previous findings (Tribe 1976, Braack 1981) indicating peak activity being attained in the early evening.

As winter approached and average daily temperatures decreased the numbers of onthophagids attendant at dung also rapidly decreased, so that during the May/June survey only 32 indididuals were captured, representing 0,13% of all beetles at Carcass B (Fig. 38). Low numbers were still present during Sept/Oct. when 51 individuals were attracted to the carcass during the 23-day survey period (1,06% of all Coleoptra) (Fig. 39).

Figures 40 to 43 depict the attendance patterns of all Scarabaeinae at the carrion habitat, but are to a large extent merely reflections of Figures 34 to 39 (diel patterns of Anachalcos and Onthophagus).

Concluding remarks on the Scarabaeinae

The important and crucial role played by dung-beetles in a system where herbivores and their dung abound is now widely recognised, mostly as a result of widespread interest in the introduction of such beetles into Australia to complement local scarabaeids which were ill-adapted to cope with dung from cattle introduced in the eighteenth century (Waterhouse 1974, Bornemissza 1976).

Dung beetles are important in controlling the number of Diptera breeding in dung as they bury much of this material. The burial of dung also increases soil fertility and soil aeration, increases soil

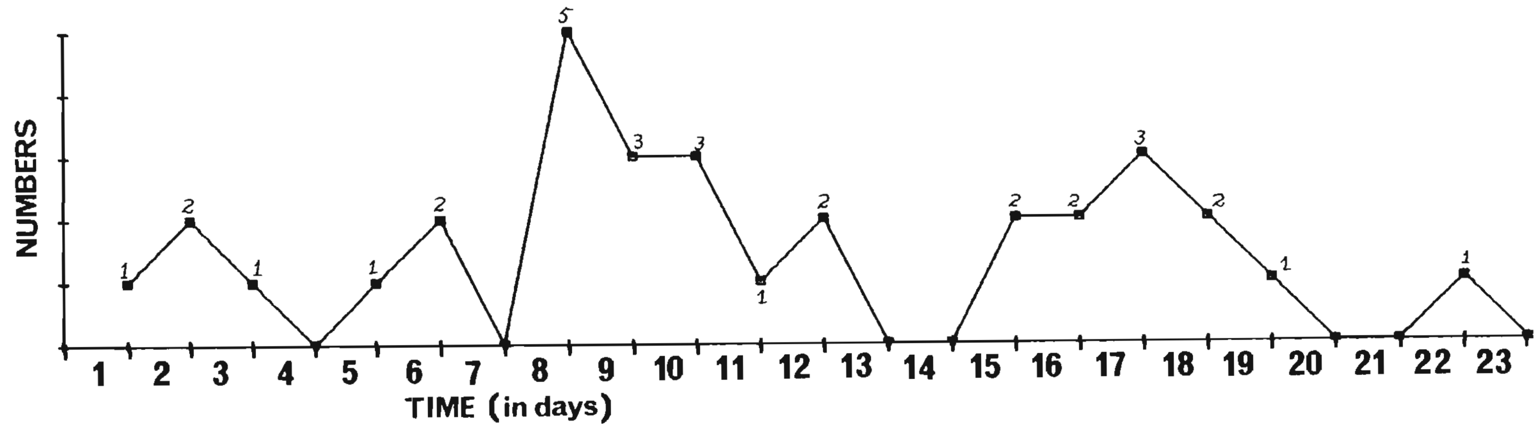


FIGURE 38: Daily totals of adult Onthophagus spp. (Scarabaeidae) present at Carcass B, Pafuri, 18th May to 9th June 1979

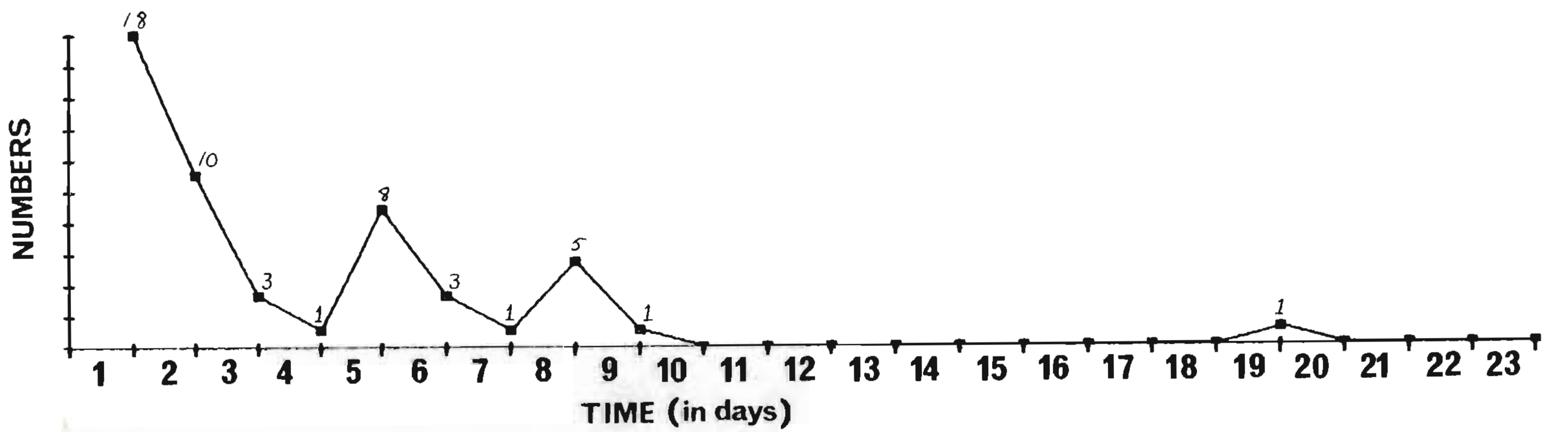
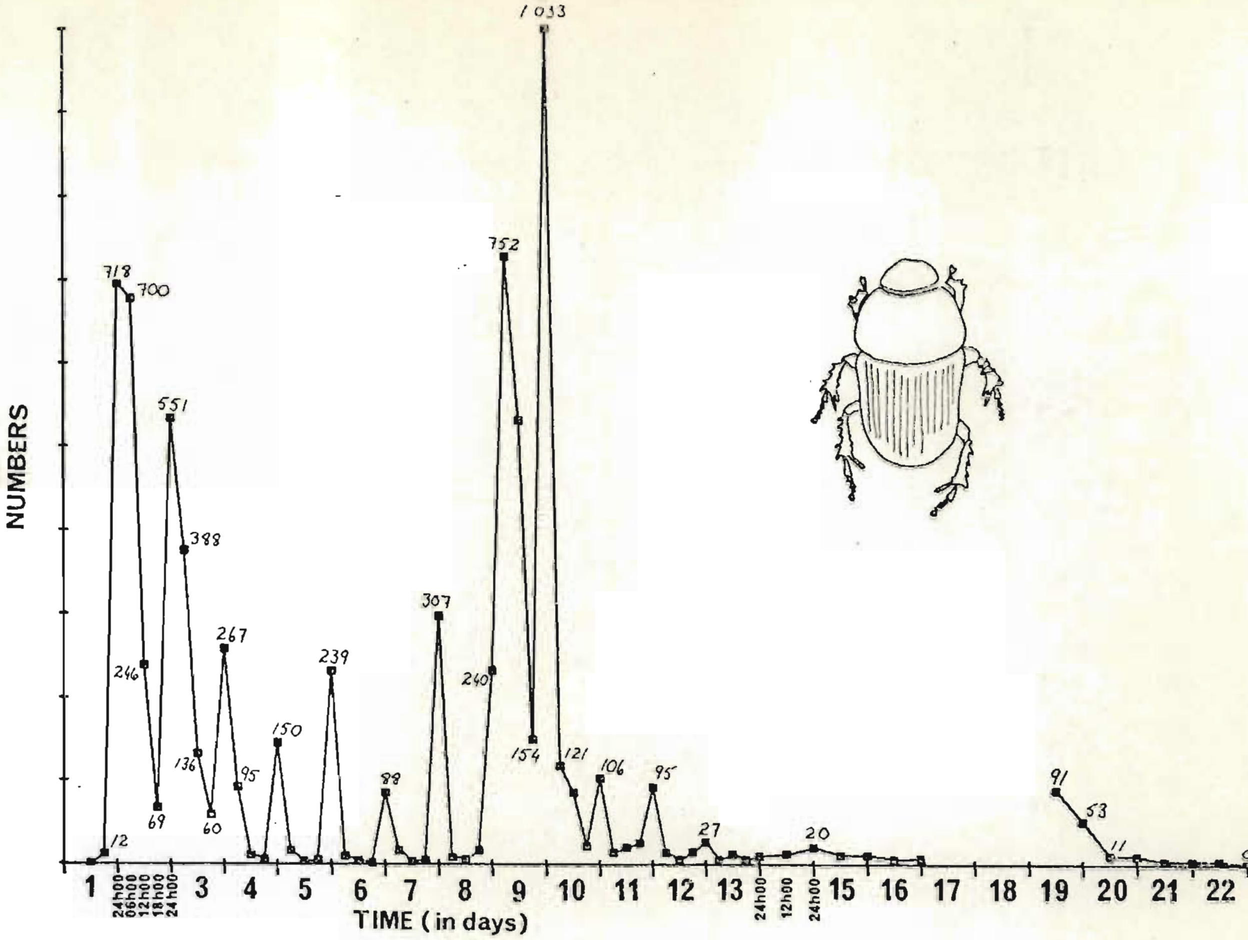
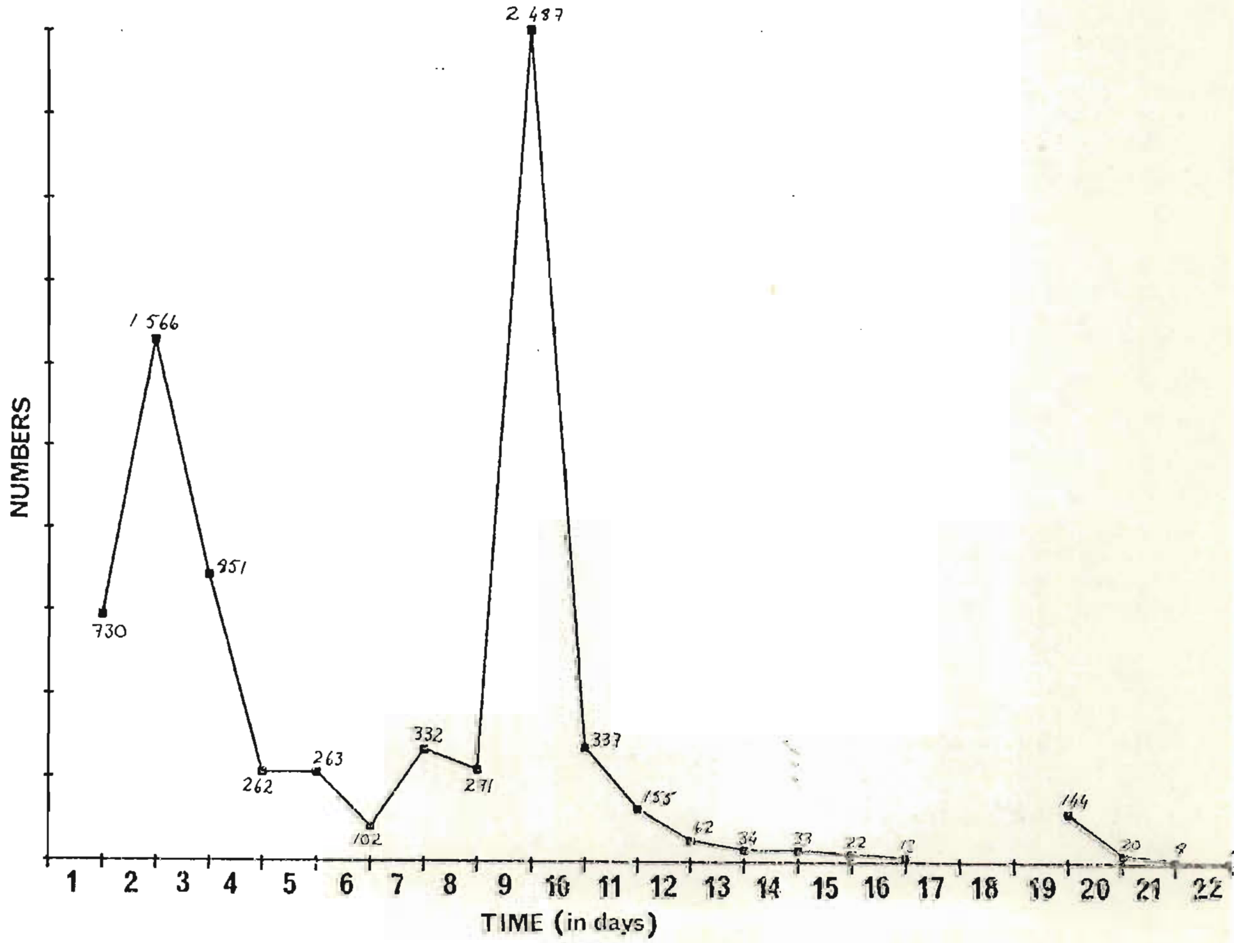


FIGURE 39: Daily totals of adult Onthophagus spp. (Scarabaeidae) present at Carcass B, Pafuri, 14th September to 6th October 1979



<u>FIGURE 40</u>: Number of all adult Scarabaeidae present at each collection period at Carcass B, Pafuri, 13th January to 4th February 1979, to show diel activity cycle



<u>FIGURE 41</u>: Daily totals of all adult Scarabaeidae present at Carcass B, Pafuri, 13th January to 4th February 1979

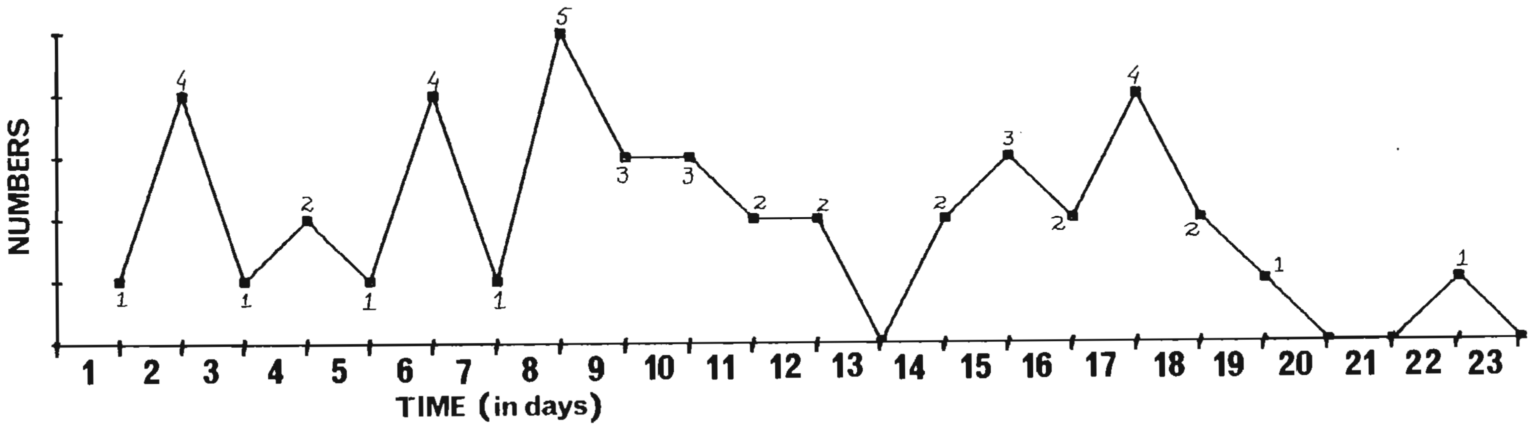


FIGURE 42: Daily totals of all adult Scarabaeidae present at Carcass B, Pafuri, 18th May to 9th June 1979

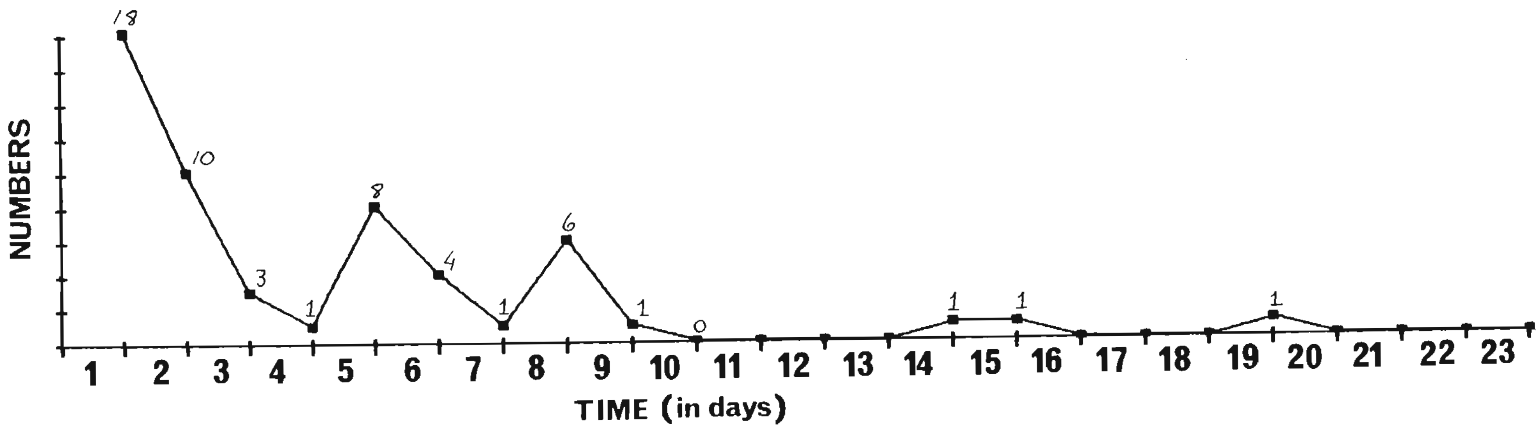


FIGURE 43: Daily totals of all adult Scarabaeidae present at Carcass B, Pafuri, 14th September to 6th October 1979

permeability to water, and reduces the number of parasitic helminths reaching pasture (Tribe 1976). In field experiments in South Africa, Fay and Doube (1983) found that telecoprids reduced the survival of flies to the adult stage from 33% to 5%, and that paracoprids reduced survival from 39% to 6%. Breeding of dung-utilising flies in the rumen-content of impala and other carcasses used during this survey of carrion-insects at Pafuri was remarkably low, indicating that dung-beetles and others were very effective in preying upon eggs and larvae of such flies as Musca and Ophyra. No attempt was made to establish the proportionate contribution of scarabaeids to this mortality of non-calliphorid flies, but the two most abundant groups of scarabaeids at the carcasses, Anachalcos and Onthophagus, did not engage in much rumen removal and spent most of their time consuming flesh and liquids, respectively. Mortality of flies breeding in rumen-content during the monitoring periods must therefore to a large extent be ascribed to other beetles such as histerids and staphylinids which are known to be effective predators (Fay & Doube 1983), and were very abundant at the carcass habitat at certain times.

Also of relevance here is the low number of Sarophorus costatus (Fahraeus) recorded during January 1979, compared to their great abundance the previous year at the same site (Braack 1981). Less than 50 individuals were collected during the 23-day survey in Jan/Febr. 1979, and their numbers remained low at all carcasses examined during the ensuing 4 years at Pafuri and elsewhere in the K.N.P. No convincing reason can be offered for this major shift in population numbers, but, as is the case with Phaeochrous madagascariensis (see next section) the drop was presumed to be correlated with climatic factors, especially rainfall. Very high rainfall and an exceptionally good supply of food for herbivores was available for several months prior to the 1978 study (Braack 1981), and this should have favourably influenced the population numbers of S. costatus. The numbers of Onthophagus present during the January 1978 study were also much higher than in January 1979, thus supporting the above reasoning. Further evidence that rainfall influences population numbers was presented during another visit to Pafuri in January and February 1980. This visit was preceded by good rains during the previous several months, and resulted in higher numbers of especially Onthophagus and, for the first time since January 1978, Phaeochrous madagascariensis.

Subfamily: Hybosorinae
Biological notes and general observations

Previously I (1978, 1981) reported on the abundance of the only member of this subfamily thus far collected at Pafuri, namely *Phaeochrous madagascariensis* Westwood. In the January 1978 study, 4 486 individuals of this species were collected at one collection period (20h00, Day 4), whereas no more than a total of 10 individuals were collected from any carcass placed during the 1979 survey at the same site. This contrast in population numbers appeared to be related to rainfall, and was supported by similar trends in the numbers of *Onthophogus* and *Sarophorus*. Good rains fell over the Pafuri area during the final quarter of 1979, and during a visit to Pafuri in January and February of 1980 the greatly increased numbers of *P. madagascariensis* was obvious, although no absolute counts were made.

Literature on the feeding habits of Hybosorinae appears non-existent. During the January 1978 survey these beetles were abundant at the study carcass from Days 3 to 6, with a peak on Day 4. The period of maximum abundance coincided with the carcass being covered with a mass of maggots and an abundance of organic-rich moisture. At the time I speculated (Braack 1978) on the pabulum of *P. madagascariensis*, stating "... whether the beetles were actively preying on the dipterous larvae or merely feeding on the juicy film surrounding each maggot, is not certain." During their period of abundance in February 1980 I had opportunity to observe these beetles more closely. They were attracted in large numbers to fresh baboon meat at night and were seen to apply their mouthparts to the fluid-layer present at certain sites on the meat, while others were observed gnawing at the muscle tissue itself.

ORDER: COLEOPTERA
FAMILY: DERMESTIDAE

With about 700 member species in this family, most are small to medium-sized beetles and are well-known to feed on animal products, especially of integumentary origin, during the adult and larval stages (Richards & Davies 1977). The so-called "museum-beetles" of the genus Anthrenus are included in this family, these being very destructive in museums as they feed on pinned insects and other display specimens whenever opportunity arises. Dermestes includes many species, some cosmopolitan or nearly so, and has several very harmful pest species which consume skin, hides and dried meat. (Saunt 1931, Hinton 1945, Richards & Davies 1977, Freeman 1980). Dermestid larvae have a dorsal coat of setae of varying lengths, often arranged in tufts (Richards & Davies 1977). The habit of keratophagous dermestids to feed on such substances is unusual in the animal kingdom, and they share the ability to digest keratin with only a very few other insects such as bird-infesting Mallophaga, the moth family Tineidae, and possibly some close relatives of this latter-mentioned group of moths (Waterhouse 1957).

Species recorded

Only one species, Dermestes maculatus Degeer, was collected from carcasses at Pafuri and elsewhere in the K.N.P.

Biology

D. maculatus is variously referred to as the Skin-, Hide-, Tallow-, or Leather-beetle. It has a very wide distribution range in mainly subtropical countries, and is an acknowledged pest in its adult and larval stages on various animal products such as skin, fur, dried meat, dog-biscuits, or almost any decomposing or dry animal matter (Hinton 1945, Busvine 1966, Binns & Pemberton 1981, Peacock pers. comm.). The species is also widely distributed in southern Africa, and I have collected specimens from dead animals throughout the Kruger National Park, near Volksrust, Ladysmith, Pietermaritzburg, Bontebok National Park (Swellendam), and Butterworth (Transkei).

Hinton (1945) gave a detailed description of the species and its life-history in various parts of the world. Thornton (1981) provided information on the rate of growth and development of a Transvaal strain under various temperature regimes. His experiments indicated an inverse relationship between developmental period and temperature, while "... the temperature preferenda of these insects seem to lie between 25 and 30°C; at 20°C and at 30°C and above there are signs of disruption of normal physiological processes with lethal effect." A summary of his main findings is provided in Table 10. He also found that the number of larval instars increased with increasing temperatures, with a mean of 5,7 instars at 20°C, increasing to 6,9 at 35°C. Temperatures of 40°C resulted in death of the larvae and inhibition of egg-laying, while pupation did not take place at or below 20°C. More eggs were laid by females at lower temperatures (20°C to 30°C, mean number of eggs laid = 1 129 to 1 464) than at 35°C when a mean of only 604 eggs were deposited.

TABLE 10: Mean duration in days of the life-stages of *Dermestes maculatus* at controlled temperatures (Adapted from Thornton 1981)

Temperature °C	Eggs	Larvae	Prepupae	Pupae	Adults	
					Males	Females
20	6,7	43,9	10	-	139	134
25	4,0	29,4	4,3	11,1	113	98
30	2,5	21,9	4,7	6,8	68	57
35	2,1	20,8	4,0	6,0	40	27
40	1,9	-	-	-	10	10

At Pafuri and elsewhere in the K.N.P., *D. maculatus* is one of the most important components of the carrion-insect complex as it is almost solely responsible for the removal of the skin and remaining dry bits of flesh and sinew after blow-fly maggots have removed the bulk of the soft tissues. The adult beetles have a preference for moist or partially dry muscle, intestine or other fleshy tissue, but will also feed on dry meat. Skin, especially when moist, is also readily eaten, as are dead insects.

During the initial stages of carcass-decay when blow-fly larvae are still present, adult beetles were often observed feeding on larvae of *Chrysomyia albiceps* and, more often, *C. marginalis* killed by histerids or other beetles. Feeding occurred individually, as tightly pressed groups of beetles, or as mixed groups comprising dermestids, histerids, and trogids. The maggot cuticle was punctured and the soft innards consumed until only a shrivelled skin remained. Unlike the larval stages, adults show no reluctance in feeding on the exterior of the carcass. Occasionally D. maculatus adults resorted to predatory behaviour, although I only observed them attacking C. marginalis larvae in the process of shrinking up to form puparia. Blow-fly puparia were also chewed to reach the soft pupae within. C. marginalis puparia lying above-ground were especially prone to such attack.

I noted the larval stages to feed mainly on skin and dried flesh, although occasionally they were also found inside blow-fly puparia where they fed on the pupae. Whether entry was gained by themselves by chewing a hole or only after other insects had first entered was not established.

If offered a choice between dry skin and dry muscle tissue, dermestid larvae preferred the latter. Such larvae were generally late in the sequence of insect-arrivals at the carcass-habitat, however, so that by the time they made their appearance most or all of the flesh had been removed. Probably because they were more susceptible to the desiccating effects of the sun, larvae tended to remain below the carcass and gnaw away at the skin from inside. On overcast days larvae would come out in large numbers and move around all over the carcass. Accumulated frass and exuviae were a common sight below old carcasses.

Larvae were highly effective in removing the skin and any remaining shreds of dried meat, and were easily able to consume the hide from a fully grown male impala within 47 days in summer, leaving only bare bone, hooves and horns.

Observations at many other carcasses showed that wet weather considerably lessened the time required for these larvae to consume the skin and whatever soft tissues remained in a carcass after blow-fly larvae departed, probably due to the rain softening the pabulum and making it easier for the larvae to feed (e.g. full-grown female impala shot 17/2/80, fenced in and used for maggot collections, heavy rains fell almost daily, carcass was stripped to bare bone and hooves by 10/3/80 = 23 days).

During the cold winter months, especially June and July, the activity of these insects was considerably decreased and it normally required several months for an average-sized impala skin to be consumed. (e.g. On 12/5/80 a full-grown impala ram was shot, placed in a fenced area, used for maggot collections, examined again on 15/10/80. Intervening period had been very dry, and about 15% of the skin remained on the carcass as a fragile parchment-like cover gnawed away from the inside, full of holes and large areas totally eaten away. Other than that only bare bones remained. At another large impala ram shot 1/7/80, placed in a fenced area and left untouched, only about 70% of the skin had been removed by demestid larvae by 15/10/80, despite there being several thousand larvae below the carcass when examined on that date. The skin had been gnawed very thin and was full of holes). Observations on at least 20 other carcasses confirmed that during warm wet weather, as generally occurs in summer, dermestids could very easily and without the aid of other organisms reduce a medium-sized carcass to bare bone, hooves and horn within 7 weeks, but that this was more than doubled during cold, dry weather. Large carcasses with thick skins, such as elephant and buffalo, were also heavily utilised by D. maculatus which is quite capable of eating through elephant skin, but it takes correspondingly longer for the larvae to consume it.

It was noted from many naturally occurring carcasses that where large animals such as buffalo died in July, the cold weather often inhibited egg-laying by adult dermestids at the carcass. By the time warmer weather arrived the dried up skin no longer presented a strong attraction to dermestid females which preferred to oviposit elsewhere at fresher carcasses. At such carcasses few dermestid larvae were usually present, sometimes less than a hundred, so that the skin often remained for a year or more, unless eaten by hyenas. This preference by both adults and larvae of D. maculatus for partially dry carcasses instead of old, very dry carcasses was clearly exhibited when offering them a choice: they all migrated to a partially dry carcass if this was placed alongside an old dry carcass.

Unlike observations made by several other investigators on the pupation habits of D. maculatus and congeneric species (Miller 1931, Morison 1931, Richards 1931, Walker 1931, Walsh 1931, Bedwell 1932) I never found D. maculatus to actively tunnel into wood prior to pupation. Between July and September 1980 I placed 20 larvae in batches of 5 in large glass Consul-jars topped with netting and containing pieces of skin, dry meat, chunks of Mopane wood (Colophospermum mopane) (a hard-wood, the most common tree in the study area), Pine (Pinus), softwood and leaves. None of the larvae tunnelled into the wood, instead they all pupated amongst the leaf-litter. Of interest here was that during the same period I kept 15 additional larvae in a similar jar but with only impala hair as food. All the larvae died having hardly fed on the hair at all.

Larvae moved away from the carcass-habitat and pupate elsewhere. On three occasions pupae were found after extensive searching: one in a crack in Mopane-bark, and twice in leaf-litter at the base of Mopane trees.

Patterns of carrion-attendance of Dermestes maculatus

Adults were common during the middle and latter stages of decomposition, whereas the larvae generally attained great abundance during the final stages. D. maculatus was present at carcasses throughout the year, but became most numerous during May and June when temperatures more closely approximated the optimum range for this species as determined by Thornton (1981).

Figures 44 to 49 indicate the pattern of arrival of these beetles at the carrion-habitat and their diel rhythms. In January 1979 dermestids first arrived at the carcass on Day 2 and rapidly built up to a peak on Days 3, 4 and 5. During May and June the number of new arrivals each day remained high from Day 3 onward to Day 15 when relatively low numbers started arriving, probably due to virtually all of the soft tissues of the carcass having been removed by blow-fly maggots at that stage. During September/October large numbers were already present by Day 2, remaining high until Day 8, new arrivals thereafter fluctuating between zero and 50 per day.

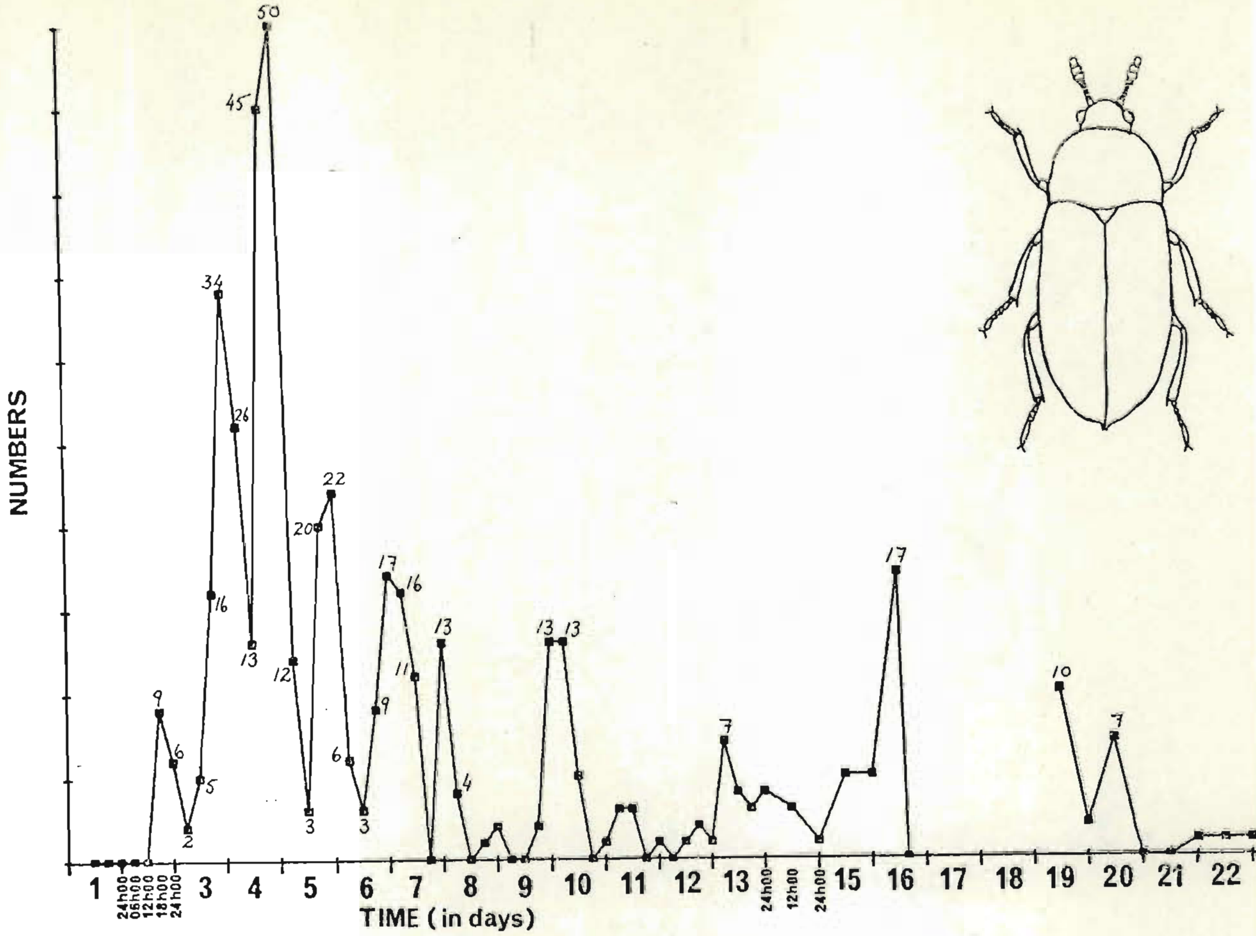


FIGURE 44: Number of adult Dermestes maculatus (Dermestidae) present at each collection period at Carcass B, Pafuri, 13th January to 4th February 1979, to show diel activity cycle

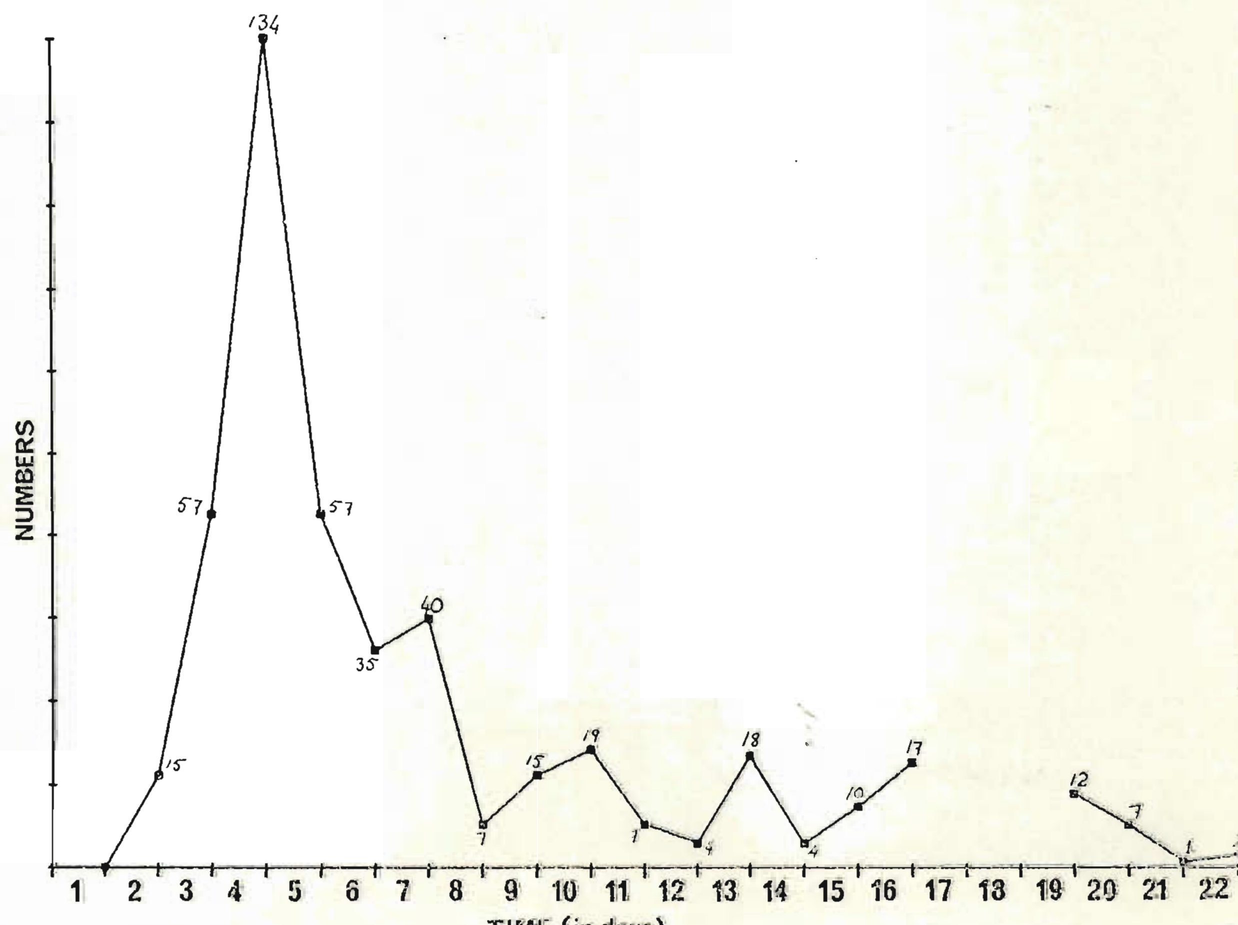


FIGURE 45: Daily totals of adult Dermestes maculatus (Dermestidae) present at Carcass B, Pafuri, 13th January to 4th February 1979

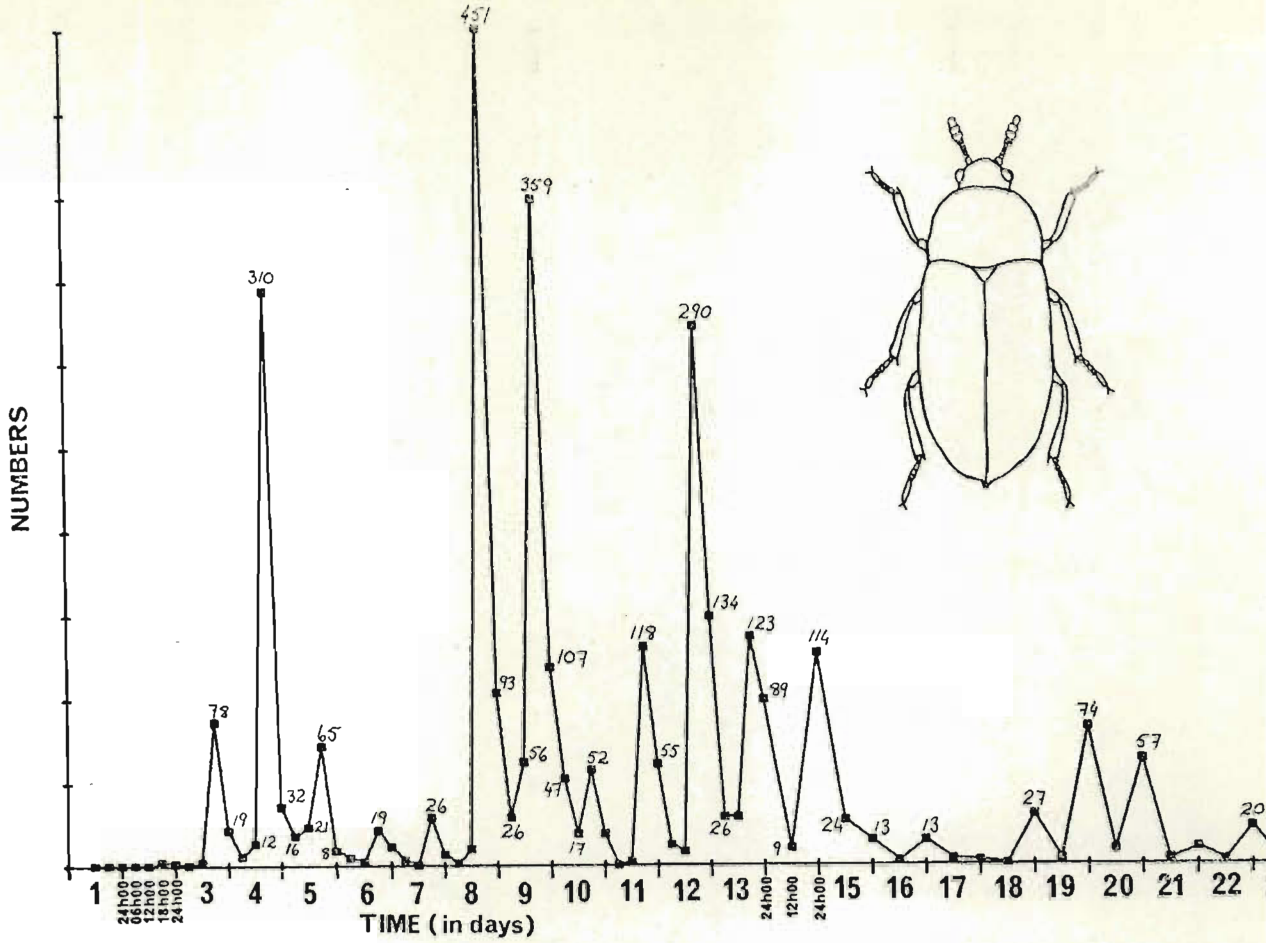


FIGURE 46: Number of adult Dermestes maculatus (Dermestidae) present at each collection period at Carcass B, Pafuri, 18th May to 9th June 1979, to show diel activity cycle

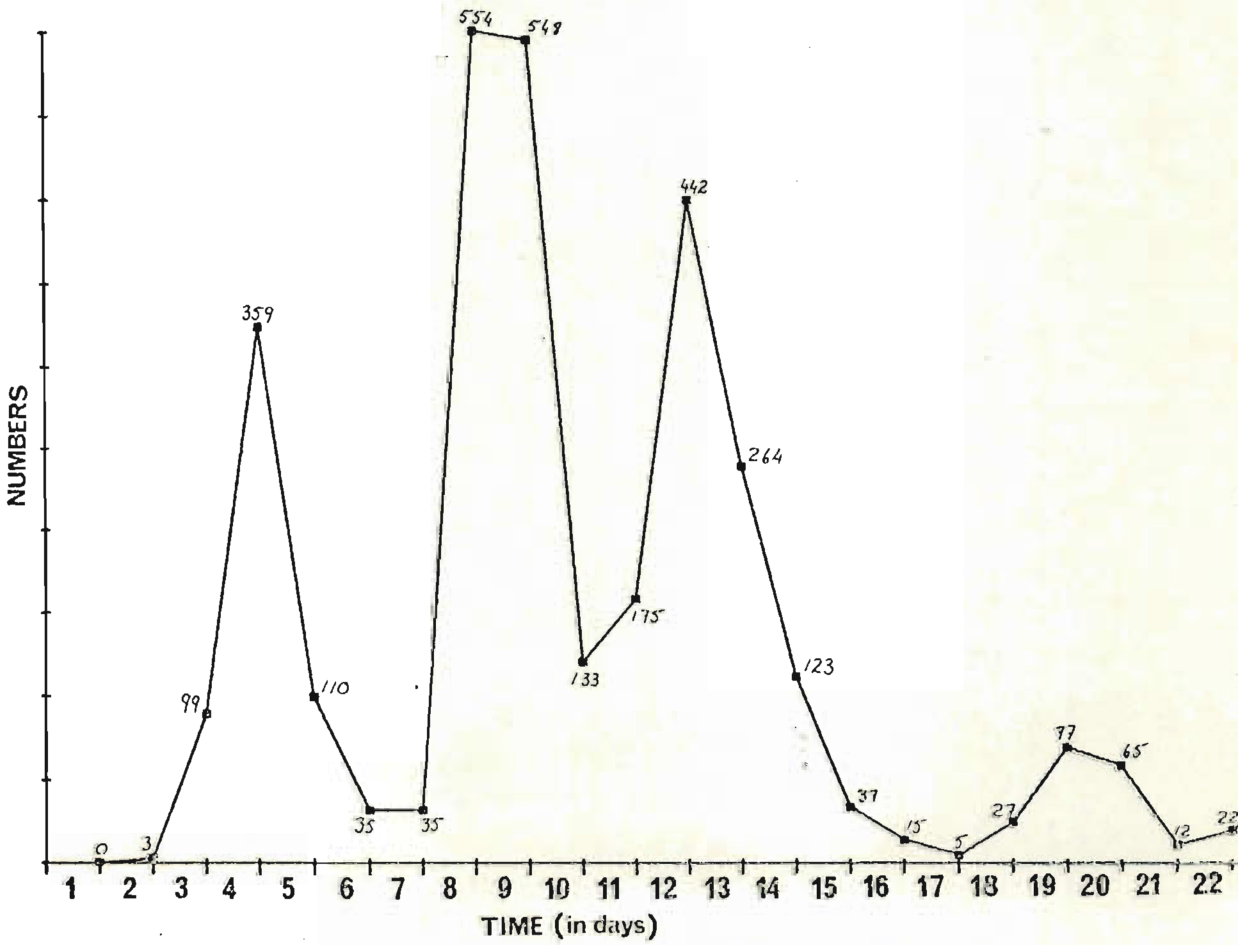


FIGURE 47: Daily totals of adult Dermestes maculatus (Dermestidae) present at Carcass B, Pafuri, 18th May to 9th June 1979

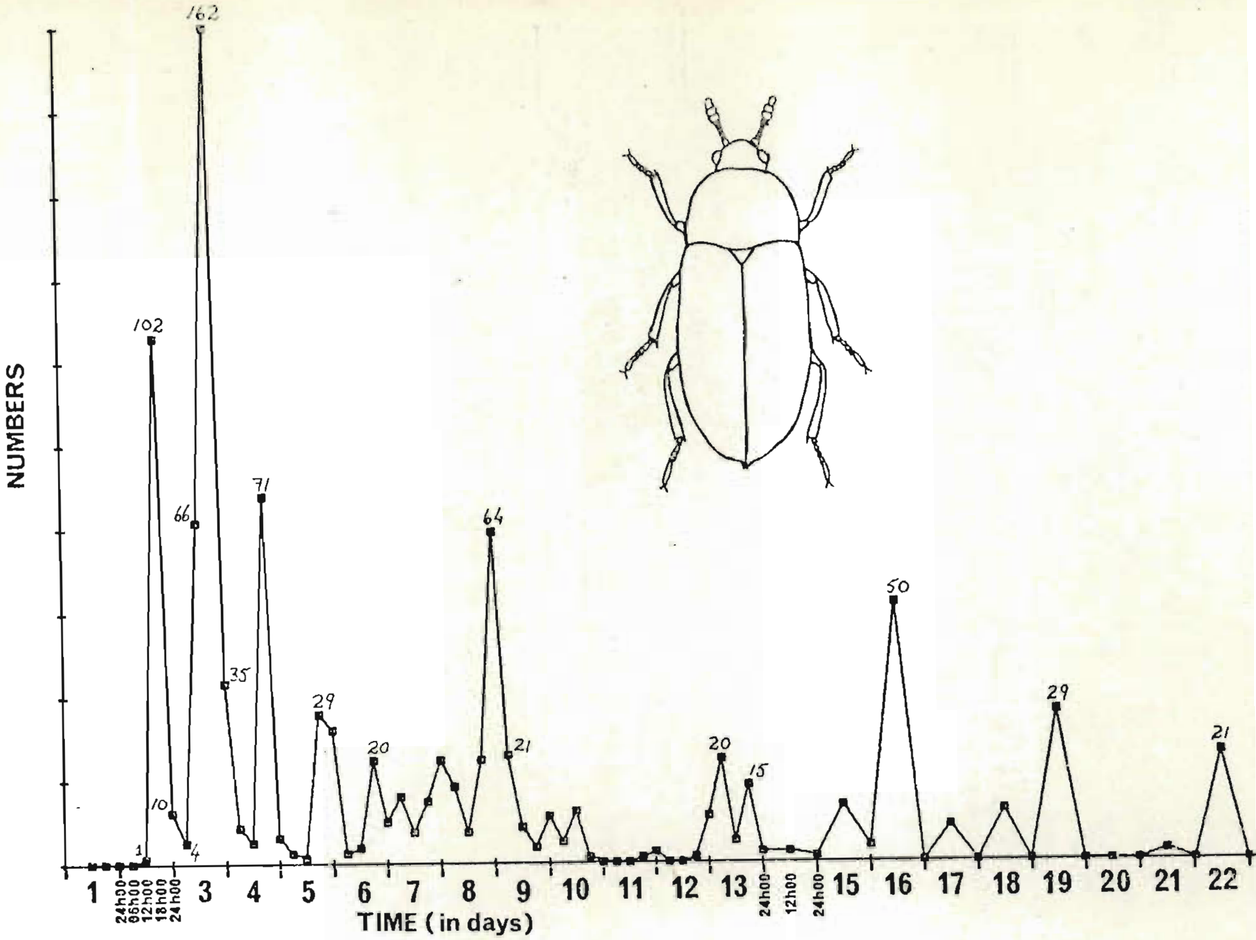


FIGURE 48: Number of adult Dermestes maculatus (Dermestidae) present at each collection period at Carcass B, Pafuri, 14th September to 6th October 1979, to show diel activity cycle

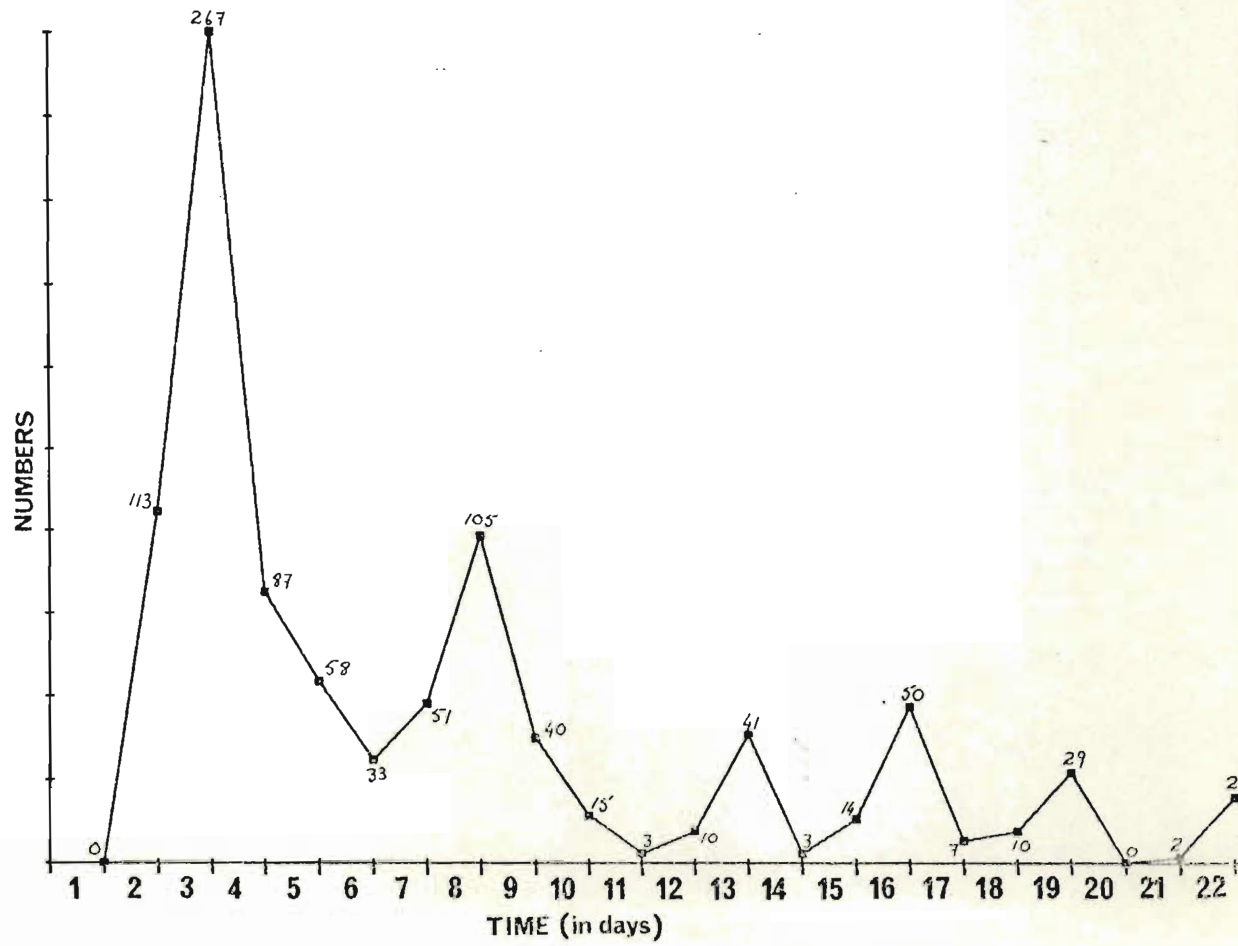


FIGURE 49: Daily totals of adult Dermestes maculatus (Dermestidae) present at Carcass B, Pafuri, 14th September to 6th October 1979

Thornton's 1981 findings showed that D. maculatus has a temperature preference ranging between 25°C and 35°C, and it was interesting to note that during the 23-day study period in Jan/Febr. 1979 only 462 adults were caught in total, 3 191 were captured during May/June when it was cooler (Table 8), and 963 during an equivalent period in Sept/Oct. The figure of 3 191 represents 12, 93% of all adult Coleoptera present at Carcass B during the May/June survey. Also interesting to note was that arrival of D. maculatus adults at the carcasses reached a peak during the evening hours - after the heat of the day but before the cold of early morning (Fig. 44, 46 & 48).

Copulation took place at the carcass and mating pairs were a common sight. During Jan/Febr. 1979 the first larvae were noticed at 18h00 on Day 12. During May/June it was on Day 9 at 12h00 and during Sept/Oct. they were first seen at 18h00 Day 6.

ORDER: COLEOPTERA
FAMILY: CLERIDAE

Comprising mainly elongate medium-sized species, this is a large, essentially tropical family which has most of its members attractively coloured. The majority of species live on vegetation where they prey heavily on wood- and bark-boring insects, the adults generally attacking adult prey whereas the larvae feed on the eggs and immature stages within the wood (Balduff 1935). Necrobia and Korynetes are well-known exceptions associated with carrion and stored meat products, where predation appears to be the exception and scavenging more the norm.

Species recorded

Besides a single individual of Phloeocopus, the only clerid species recorded at carrion was the well-known "Red-legged ham beetle", Necrobia rufipes (De Geer).

Biological notes on Necrobia rufipes

Having identified some clerid specimens I had collected at Pafuri and in the Bontebok National Park, Ginter Ekis (pers. comm.) made the following remarks in a letter regarding Necrobia rufipes (De Geer) and Necrobia ruficollis (Fabricius): "These species, along with a third N. violacea (Linnaeus) .. are cosmopolitan and differ from most clerids in that they can subsist entirely on dried protein, in reality they are omnivorous; capable of predation."

Several publications deal with the biology of Necrobia rufipes (e.g. Simmons & Ellington 1925, Papp 1959), all indicating its importance as a problem species which occasionally ruins large quantities of meat by the feeding activities of especially the immature stages. Although their pest status is derived mainly from their attacks on "long-stored hams, shoulders, and bacon", they also feed on cheese, bones, fish, drying carrion, hides, salt fish, dried egg, dried figs, copra, herring and whale guano, even Egyptian mummies (Simmons and Ellington 1925). The adults are between 3,5 to 7 mm in length, the legs and bases of the antennae are red, while the general body colour is metallic blue or sometimes green. Larvae tend to bore into meat, preferentially burrowing into fatty areas, whereas the adults usually feed at the surface. Based on studies in the United States, Simmons and Ellington (1925) provided the following data regarding the life-history of this species: Adults may live in excess of 14 months, during which period a female may deposit as many as 2 100 eggs. In warm weather (21 to 29°C) the eggs hatch in four or more days, and the larvae live through three or four instars before pupating. From egg hatching to adult emergence may take as little as 30 days, of which 13 days are spent within a cocoon. The cocoon is constructed in crevices or similar locations in darkened areas, and consists of a frothy white foam which hardens after extrusion from the mouth. The adults emerge by chewing a hole in the pupal cell. Mating occurs soon after emergence, but a pre-ovipositional period of two days appears necessary. Besides feeding on ham, cheese and similar substances, adults are also predacious, feeding especially on larvae of Piophila flies and also blow-fly maggots, and cannibalistic, readily eating eggs and larvae of their own species, as well as any injured or dead adults.

I have commonly found adult N. rufipes feeding on drying muscle or congegrating on apparently bare bone where they gnaw away at the very thin film of organic deposits on the bone surface. They spend a considerable amount of time briskly walking over the carcass, occasionally stopping to feed at exposed drying muscle tissue, and when on the ground they were commonly observed to stop and feed on C. marginalis larvae which had been killed and partially eaten by histerids or C. albiceps larvae. On several occasions I observed single adult N. rufipes approach half-grown active C. marginalis larvae, deliberately bite into them in the anterior half of the body, enlarge this hole until the maggot was quiescent, then feed on the larva for a period lasting less then one minute, and then depart. During June 1980 I kept several adult N. rufipes in net-topped Consol jars with pieces of semi-dry meat and Dermestes maculatus (Dermestidae) larvae of all sizes. During the three-week period no Dermestes larvae were killed, and the clerids appeared to survive well on the dry meat. This, together with the total lack of observations of N. rufipes feeding on D. maculatus larvae at any of the study carcasses, contradicts to some extent the findings of Papp (1959), who recorded this clerid as preying on dermestid larvae.

Although adult N. rufipes were very common, I saw less than 30 larvae during all the work with carrion. The few larvae encountered were present in the debris below carcasses, except three which were found having made cocoons within empty puparia of C. albiceps, the entrances having been sealed with the characteristic white foam used in cocoon-formation.

Patterns of carrion-attendance of Necrobia rufipes

I found N. rufipes to be present at carcasses throughout the K.N.P. at all times of the year. As indicated in Figures 51, 53 and 55, this species was most abundant during Jan/Febr. 1979 with a total of 2 572 adults captured during the 23-day monitoring period, decreasing to a total of 484 adults captured during a similar 23-day period in Sept/ Oct. 1979. These figures represent 18,6% and 10,04% of all adult Coleoptera present at Carcass B for each respective period. N. rufipes was found to be most abundant immediately after the bulk of

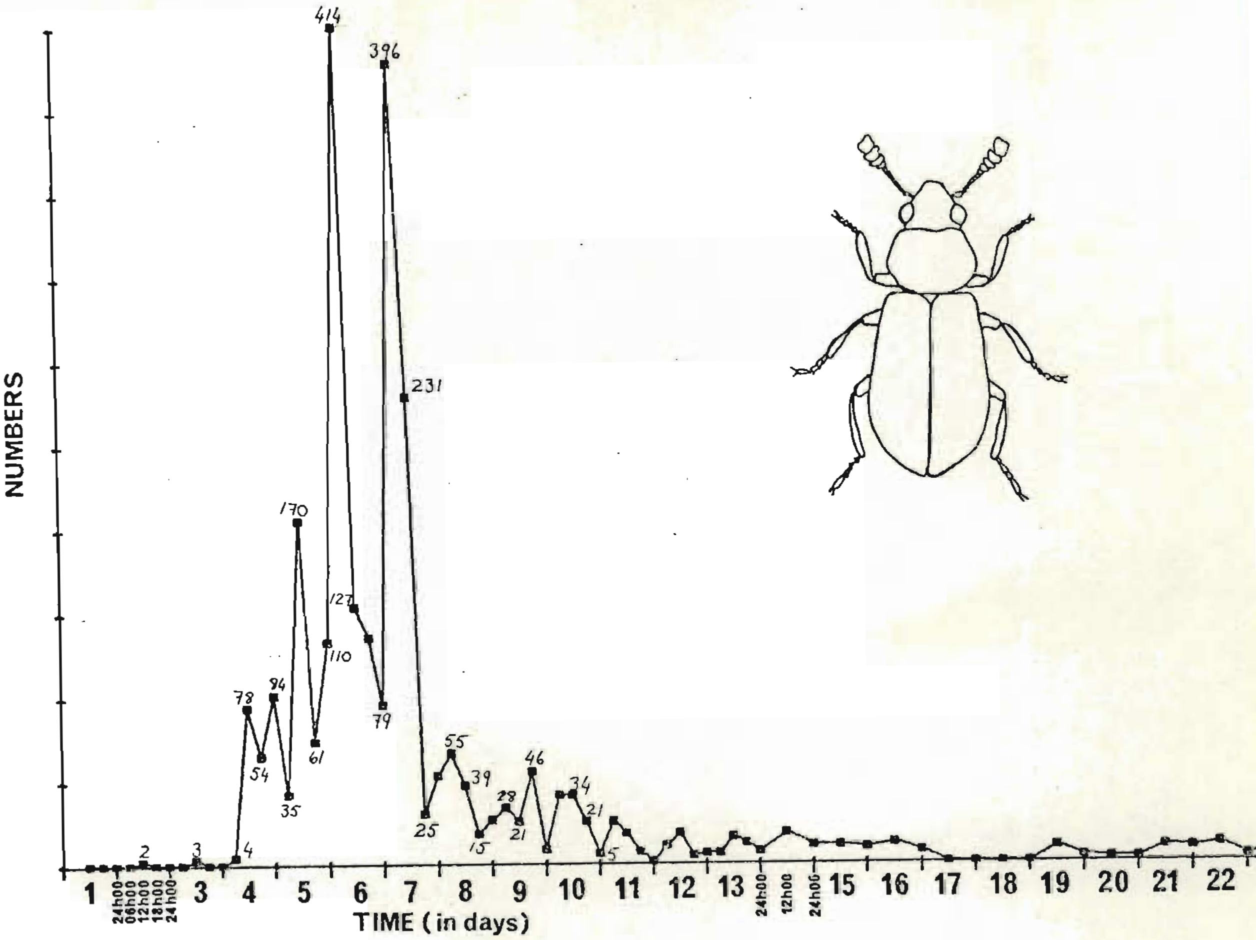


FIGURE 50: Number of adult Necrobia rufipes (Cleridae) present at each collection period at Carcass B, Pafuri, 13th January to 4th February 1979, to show diel activity cycle

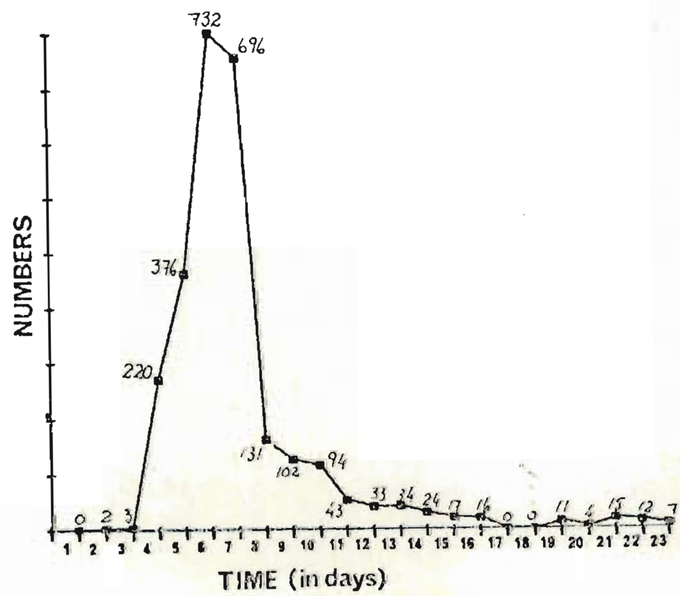


FIGURE 51: Daily totals of adult Necrobia rufipes (Cleridae) present at Carcass B, Pafuri, 13th January to 4th February 1979

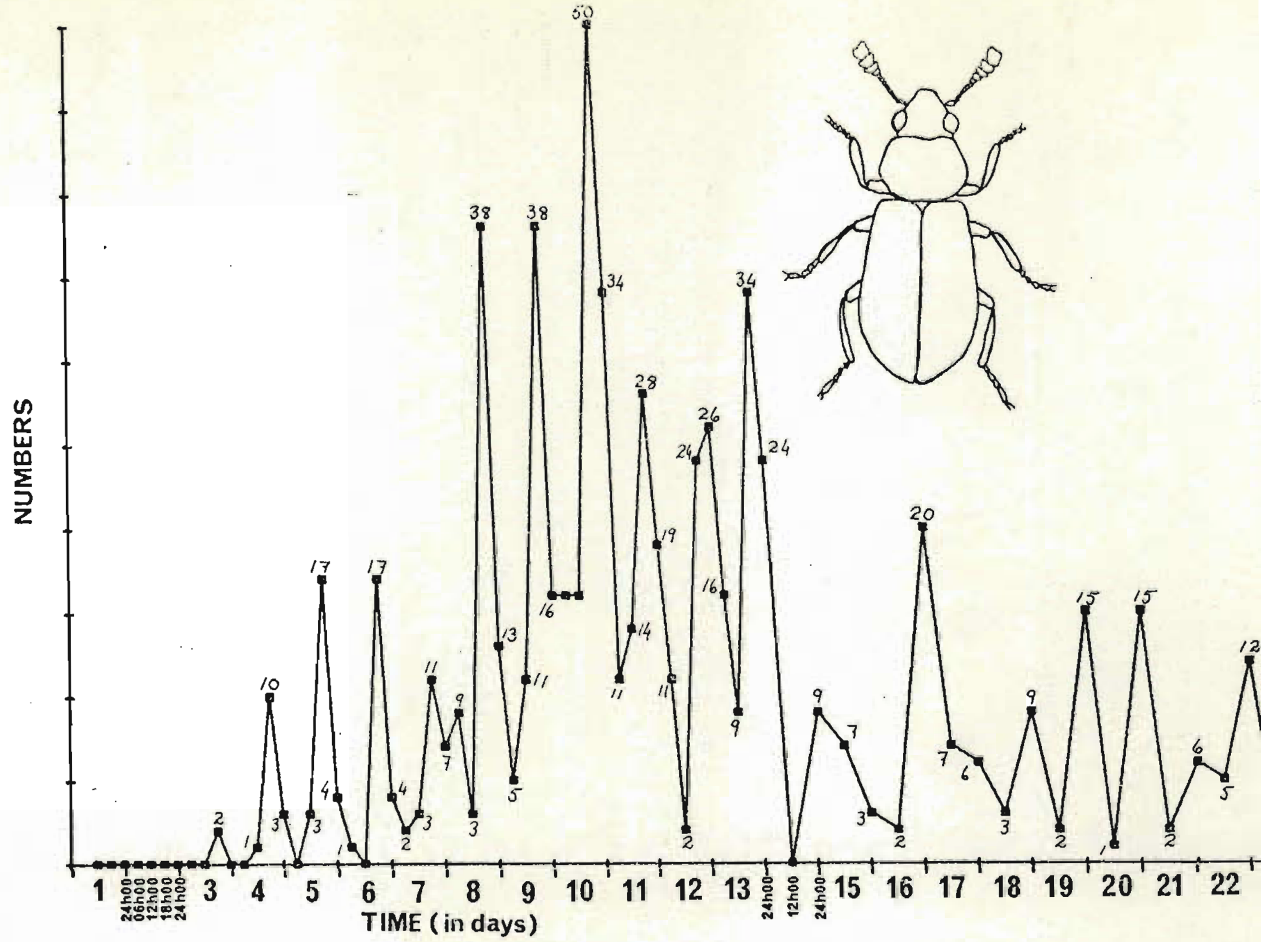


FIGURE 52: Number of adult Necrobia rufipes (Cleridae) present at each collection period at Carcass B, Pafuri, 18th May to 9th June 1979, to show diel activity cycle

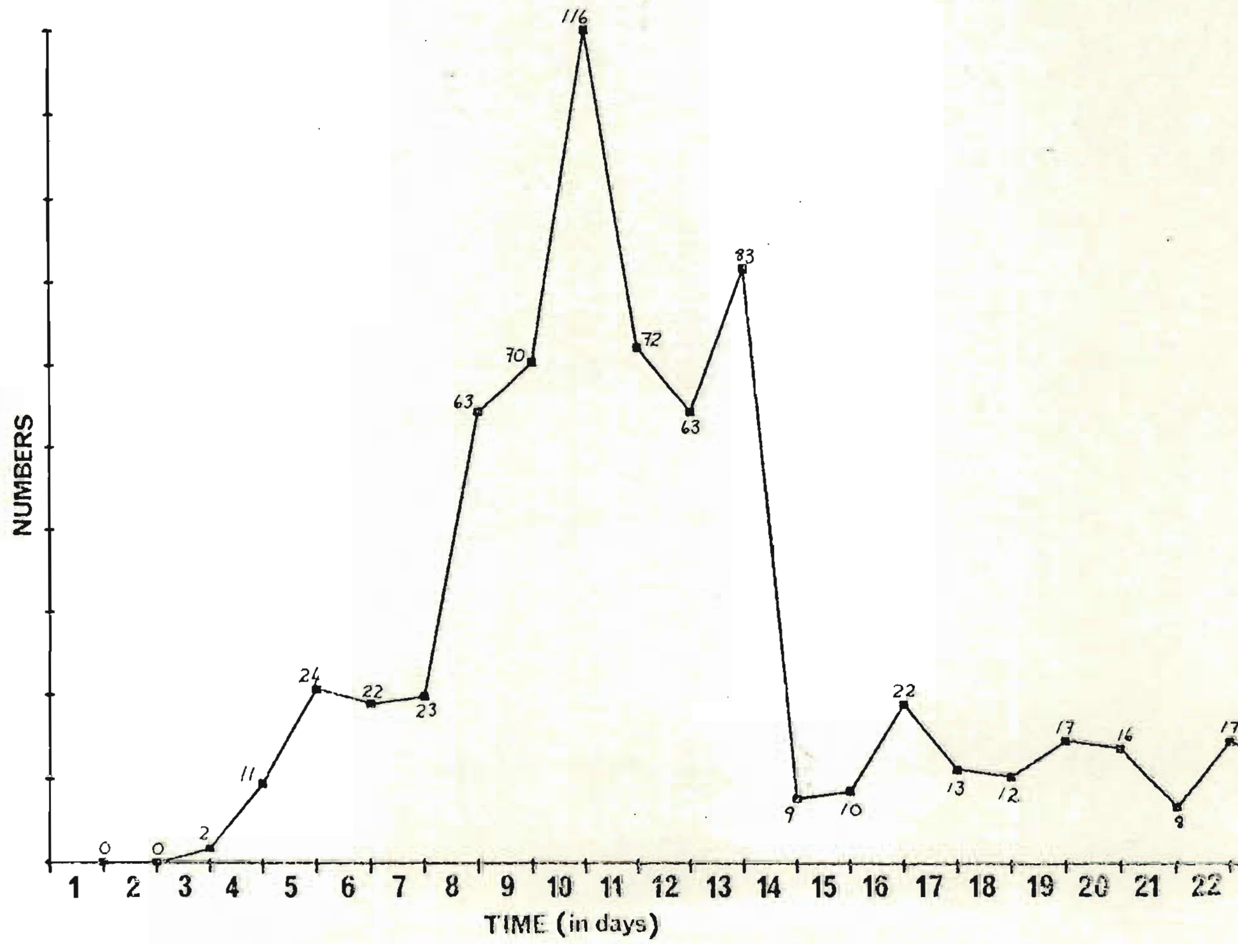


FIGURE 53: Daily totals of adult Necrobia rufipes (Cleridae) present at Carcass B, Pafuri, 18th May to 9th June 1979

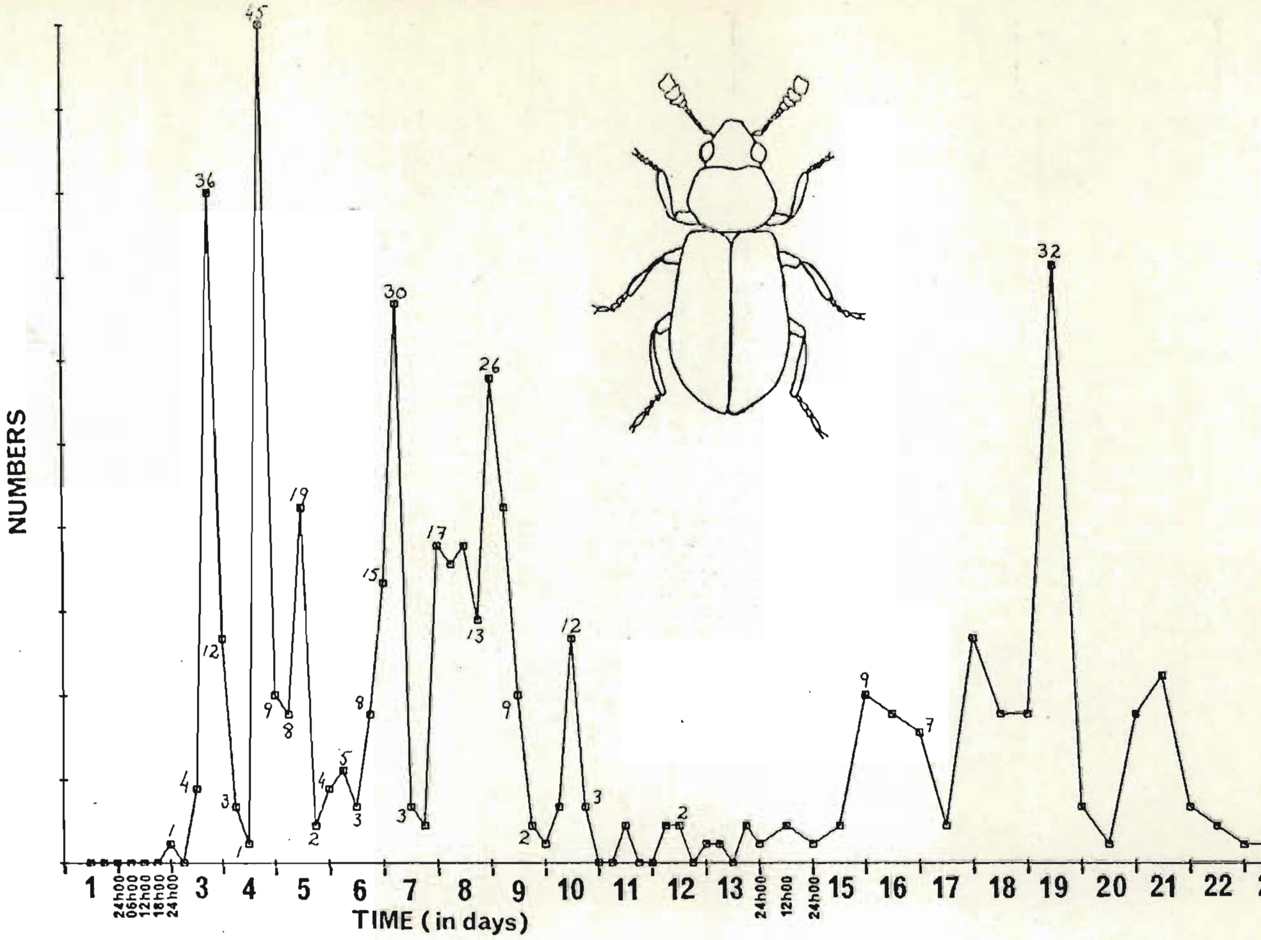


FIGURE 54: Number of adult Necrobia rufipes (Cleridae) present at each collection period at Carcass B, Pafuri, 14th September to 6th October 1979, to show diel activity cycles

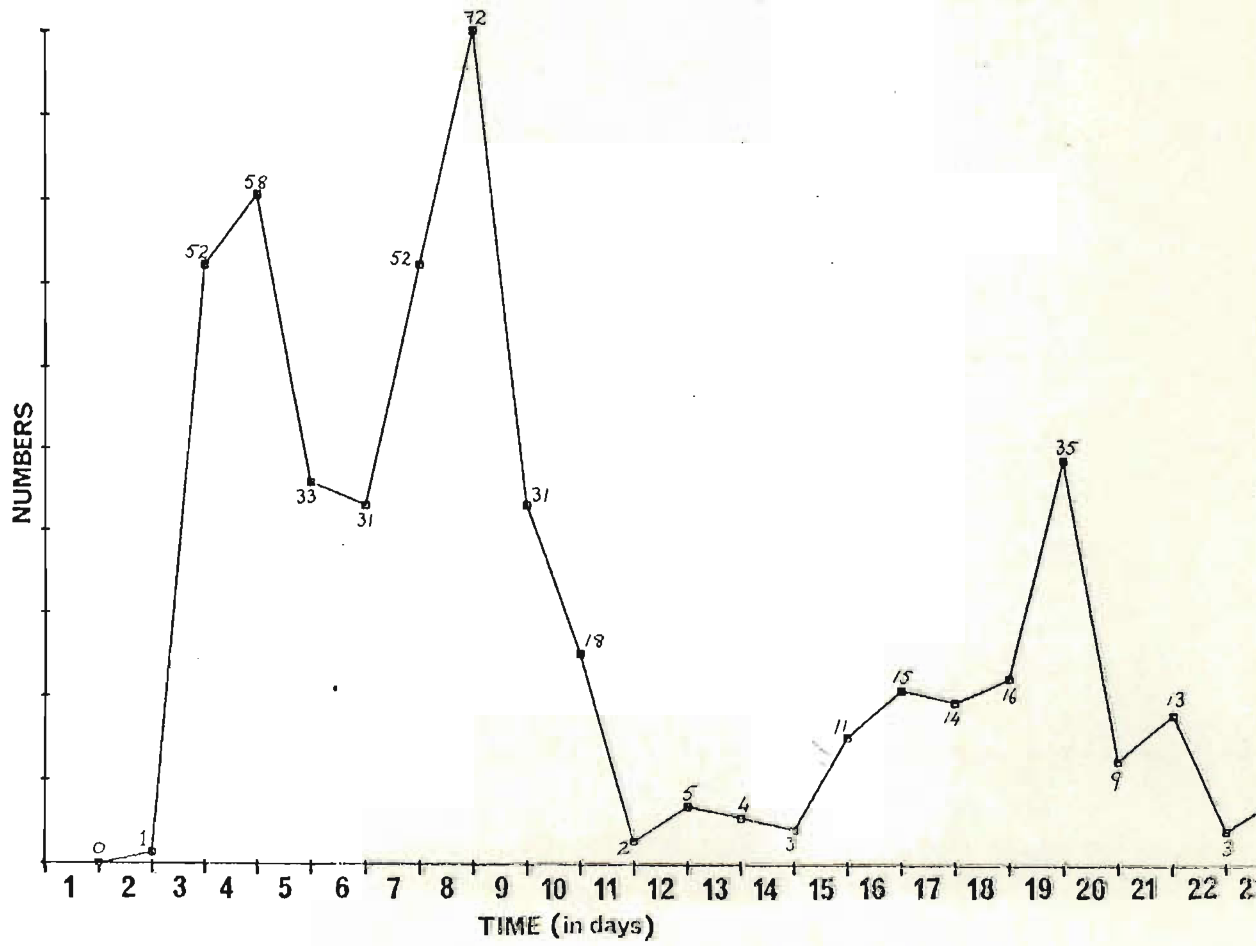


FIGURE 55: Daily totals of adult Necrobia rufipes (Cleridae) present at Carcass B, Pafuri, 14th September to 6th October 1979

Chrysomyia marginalis larvae had left the carcass, at which stage any remaining soft tissues were still moist and pliable. As the carcass dried the number of adults decreased but low numbers remained as long as sinews, fleshy remnants, or fatty deposits on the bones and skin were present. Within each 24-hour cycle their arrival at the carcass habitat was fairly erratic, showing no clearly defined peak activity periods (Fig. 50, 52 & 54). The slight drop in numbers on Days 5 and 6 during Sept. 1979 is presumed to be related to weather factors such as the overcast and breezy conditions present on those particular days. The Cleridae recorded from an impala carcass during a January 1978 survey (Braack 1981) were all N. rufipes and their visitation patterns resembled that presented in January 1979.

ORDER: DIPTERA
FAMILY: PIOPHILIDAE

The Piophilidae form a rather small but widely distributed family of mostly scavenging flies. The adults are small in size and scavenge at carcasses, garbage, excrement, and other proteinaceous plant and animal matter. Larvae typically develop in exposed carcasses, although a few exceptions do exist (McAlpine 1977, Richards & Davies 1977). MacAlpine (1977) divided the family into 23 genera and 67 species, with an additional new species from Pafuri being described later (McAlpine 1978).

Species recorded

Piophila casei (Linnaeus) and P. megastigmata McAlpine were the only members of this family found at carrion. P. megastigmata was first collected from an impala carcass at Pafuri during January 1978, and described as a new species the same year by McAlpine.

Biological notes on Piophila casei and Piophila megastigmata

Piophila casei is well-known as a serious pest in the food-industries on most continents, where the larvae, known as "cheese skippers", infest and spoil meat, leather, and cheese (McAlpine 1977). In the same paper in which he described the new species from Pafuri; McAlpine (1978) remarked "... Judging from the fact that megastigmata was found on the corpse of an impala in a natural habitat in eastern Transvaal and has never been taken elsewhere, it is probably an endemic, rather sedentary, exophilous, asynanthropic fly. Conversely, casei is a highly vagile, endophilous, eusynanthropic species ...". The two species are the same in size, but can easily be separated by colouration and chaetation.

Both P. casei and P. megastigmata are common at carcasses in the K.N.P. thoughout the year. They mix freely at carcasses although both species have the aggressive habit of chasing off other flies in the immediate vicinity, be they members of the same species or flies much larger than themselves. Even blow-flies are chased off by the short darting runs of these flies. Adults are most common soon after Chrysomyia marginalis larvae have swarmed over the carcass resulting in a moist layer being present on the skin. The piophilid flies tend to congregate on the higher-lying areas of the carcass, provided moisture is present, and at such sites males are commonly observed rapidly pursuing females and unceremoniously mounting them for copulation.

Larvae of P. casei and P. megastigmata occur at the same carcass, but seem to be in distinct clumps. The larvae are mostly found between the carcass and soil in damp situations, but they avoid wet areas. They also occur inside the abdominal cavity if the humidity is high, within folds of skin, and any damp area rich in organic content.

No Piophila larvae were encountered at the study carcasses during Jan/Febr. and Sept/Oct. 1979, blow-fly larvae having removed all soft tissues at a very early stage. During May/June 1979, however, soft tissues on Carcass B remained available for a long time (see Fig. 9) and a large organic ooze-poole also formed beside the carcass, providing a rich food-source for Piophila larvae. Despite this abundance of food, the larvae appeared to be very susceptible to competition and were rarely found in association with other maggots such as those of Chrysomyia, Musca, and Ophyra. Small pockets of larvae were present below the legs, under the head and rump and occasional individuals were found around the ooze-pool. The first larvae were observed on 1st June, 15 days after placement of the carcass, and the first puparia were found on 6th June, 20 days after placement. The larvae of both P. casei and P. megastigmata have the unusual habit of looping themselves into a circle by holding on to their posterior end with the mouth-parts, stiffening themselves which creates considerable tension, then suddenly releasing the hold which causes them to be flicked several centimetres into the air and away from the original site - hence the name "cheese skippers".

At the remains of an elephant which had died on the 20th April 1980 at Klopperfontein in the study area, Piophila puparia were collected from a tusk cavity (tusks removed soon after death) on the 16th May, i.e. 27 days after death of the animal. A thorough examination on the 13th June, 55 days after death, revealed many hundreds of Piophila larvae and puparia inside the abdominal cavity in a mixture of dermestid larval frass/dead dermestid larvae/dermestid exuviae, forming a layer several centimetres thick, with an average density of 1 puparium per square centimetre. Collections of puparia were made at intervals from this carcass and kept in jars covered with fine-meshed gauze to determine the percentage successful emergence and parasitism (Table 11).

TABLE 11: Parasitism and adult emergence from Piophila puparia collected from elephant carcass at Klopperfontein, May/June 1980

Date Puparia collected	Number of Puparia	Adults successfully emerged	Parasitised Puparia	Unparasitised Puparia not giving rise to adults	Species
16-05-80	28	14	7	7	P. casei
23-5-80	26	11	11	4	P. casei
30-05-80	13	2	8	3	P. casei
06-6-80	7	4	-	3	P. megastigmata
18-06-80	37	25	-	12	P. megastigmata
TOTAL :	111	56	26	29	

Considering the results for both species together, we find
56 ÷ 111 = 50,49% successful adult emergence
26 ÷ 111 = 23,42% parasitised, and
29 ÷ 111 = 26,12% of the unparasitised shrivelled, which failed to give rise to adults.

If we consider the results for *Piophila casei* alone, we find
27 ÷ 67 = 49,29% successful adult emergence,
26 ÷ 67 = 38,80% parasitised, and
14 ÷ 67 = 20,89% pupal shrivelled which did not result in adults.

Similarly, for *Piophila megastigmata*, we find
29 ÷ 44 = 65,90% successful adult emergence,
no parasitism, and
15 ÷ 44 = 34,09% pupae shrivelled and not giving rise to adults.

All parasites were *Nasonia vitripennis* (Hymenoptera : Pteromalidae), which occurs widespread over South Africa (pers. obs., and Smit 1931) and has a wide range of dipterous hosts (Smit 1931, Cornell & Pimentel 1978), although Piophilids have not previously been recorded as hosts. From the results in Table 11 the impression is presented that *P. megastigmata* is not subject to parasitism, but this is unlikely as the puparia overlap both spatially and temporally in their occurrence (personal observations at many other carcasses) and are, at least on cursory examination, morphologically indistinguishable, so that the results are more likely to be due to "fortuitous" sampling and also based on too small a sample. This pattern emerged upon analysis of field notes after suitable opportunity for further collection of *Piophila* puparia, so that no further work was done to shed light on these anomalous results.

Patterns of carrion-attendance of P. casei and P. megastigmata

Examination of Figures 56 to 62 indicate that piophilids were present in high numbers at Carcass C at Pafuri during each survey period in 1979.

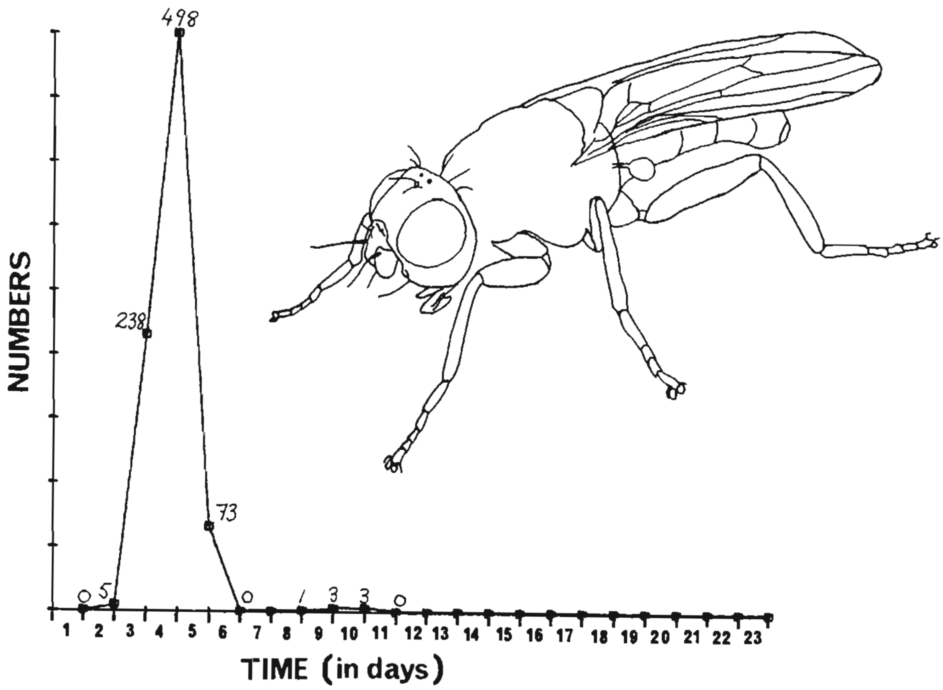


FIGURE 56: Daily totals of adult Piophila (Piophilidae) present at Carcass C, Pafuri, 13th January to 4th February 1979

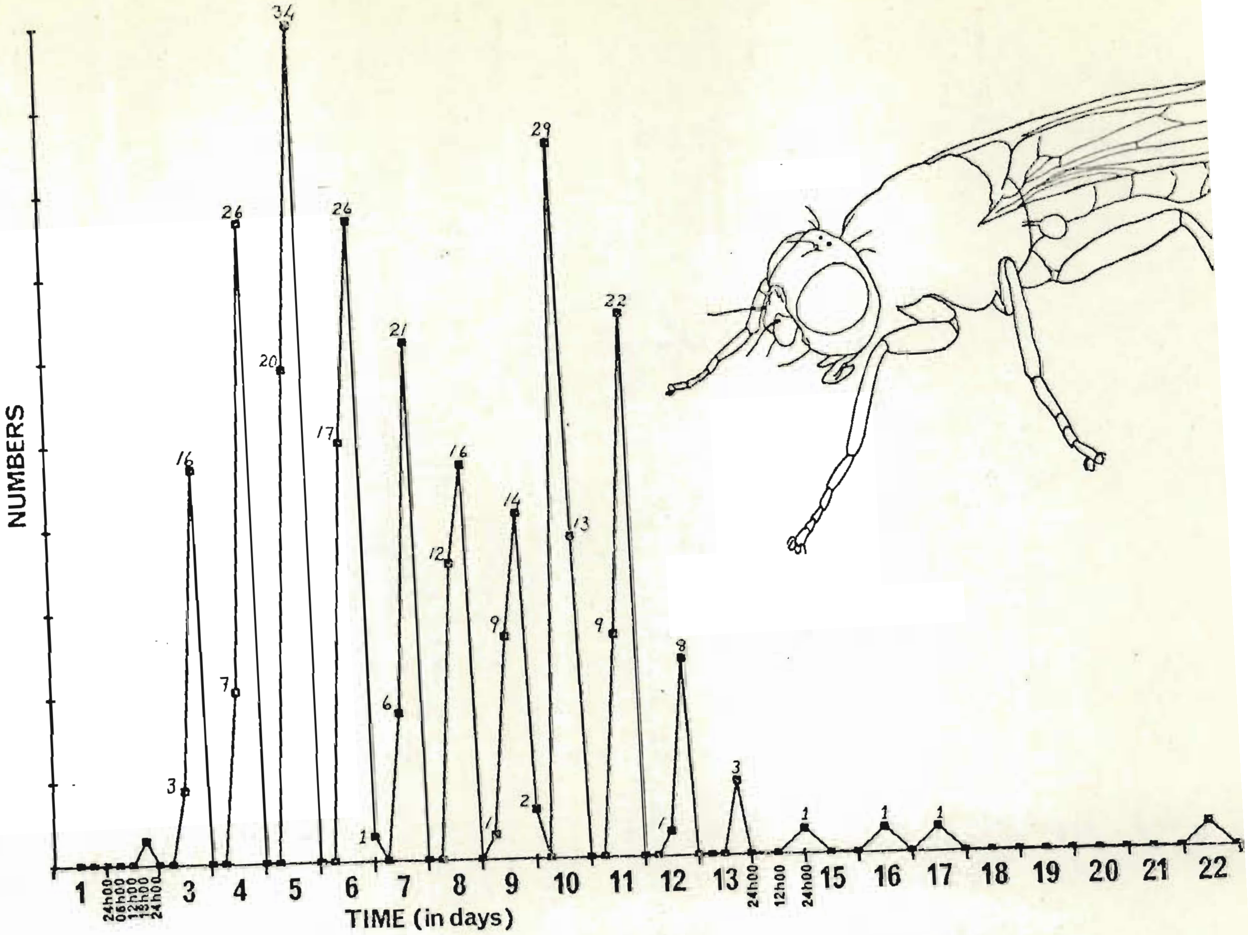


FIGURE 57: Number of adult Piophila casei (Piophilidae) present at each collection period at Carcass C, Pafuri, 18th May to 9th June 1979, to show diel activity cycle

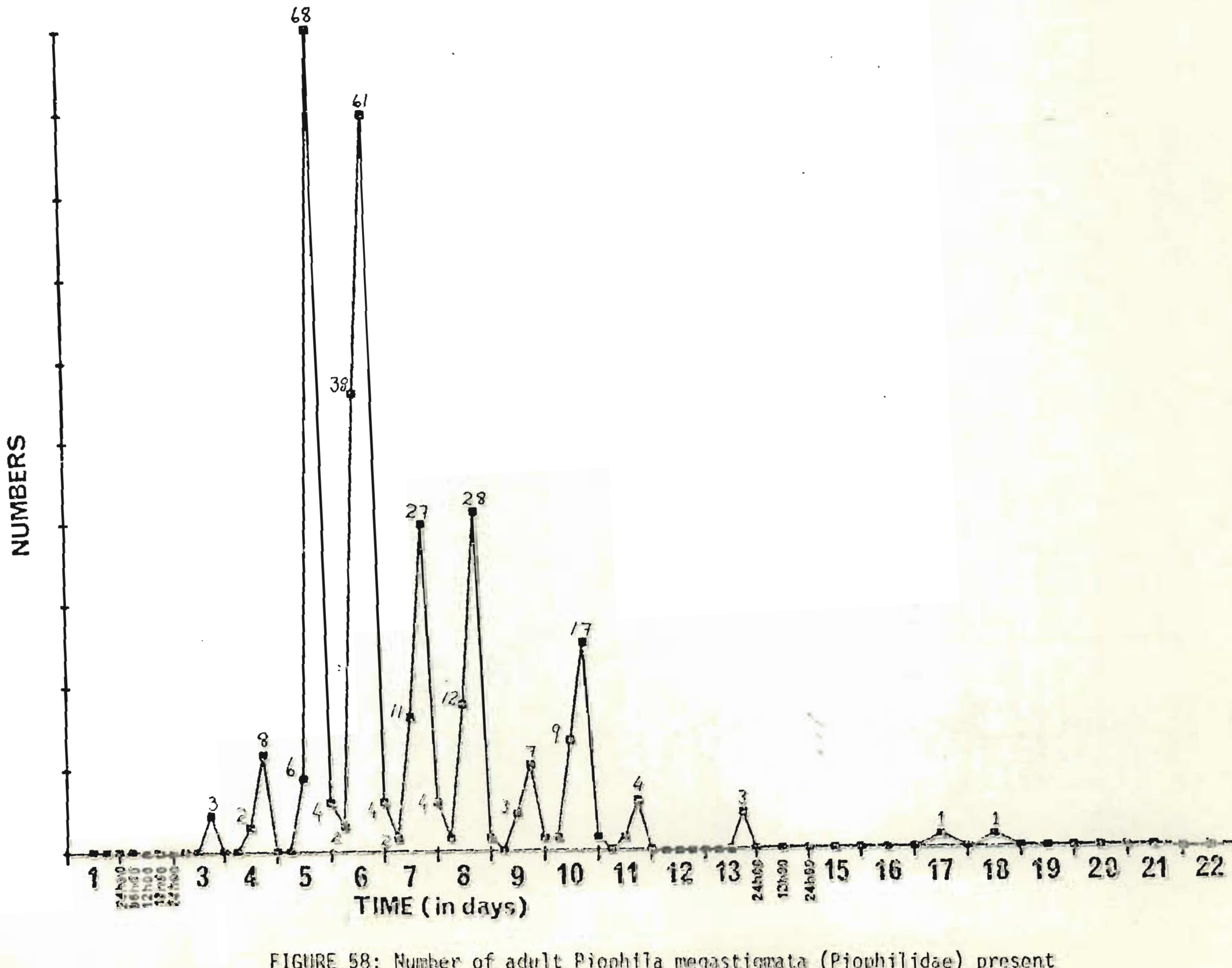


FIGURE 58: Number of adult Piophila megastigmata (Piophilidae) present at each collection period at Carcass C, Pafuri, 18th May to 9th June 1979, to show diel activity cycle.

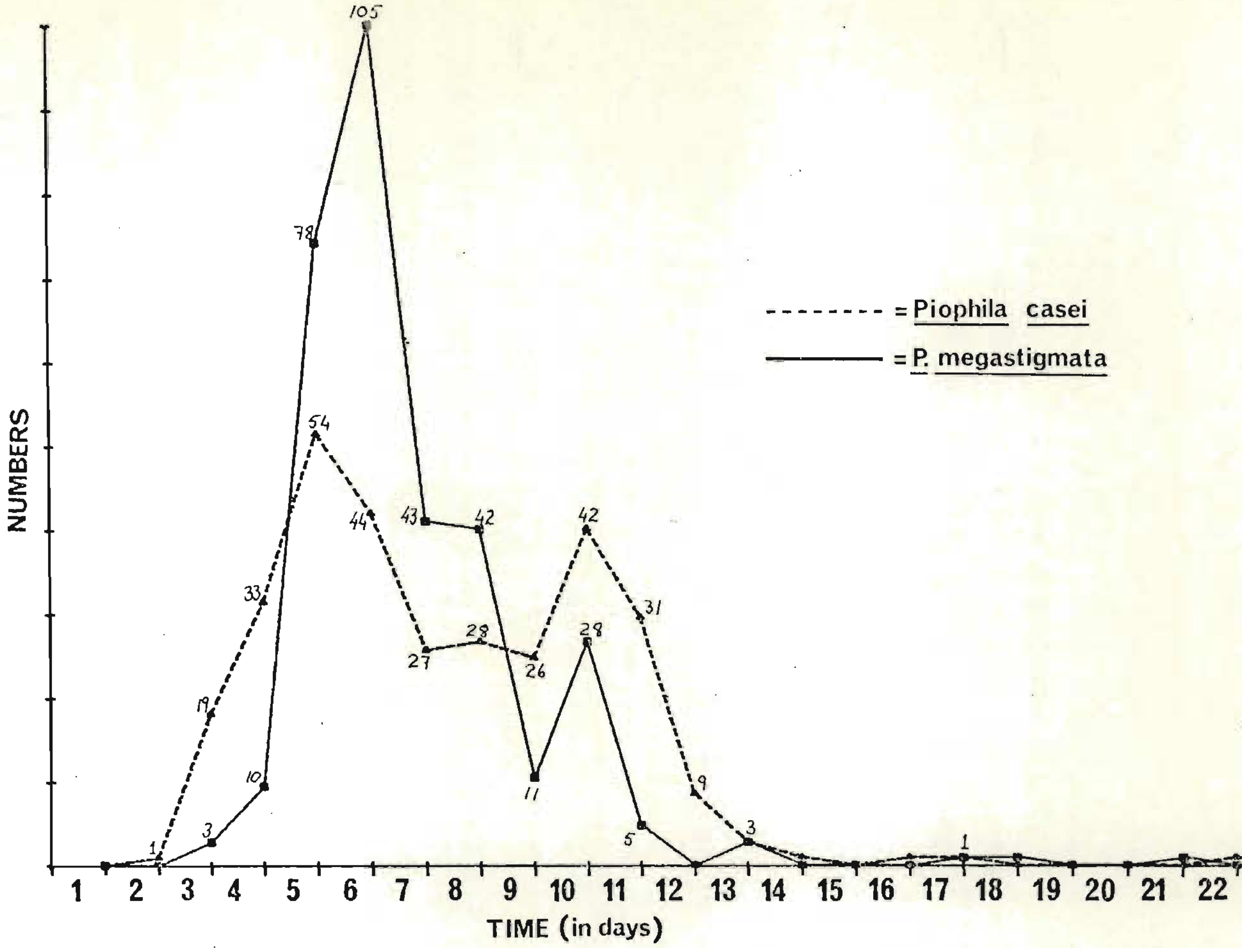


FIGURE 59: Daily totals of adult Piophila casei and Piophila megastigmata (Piophilidae) present at Carcass C, Pafuri, 18th May to 9th June 1979

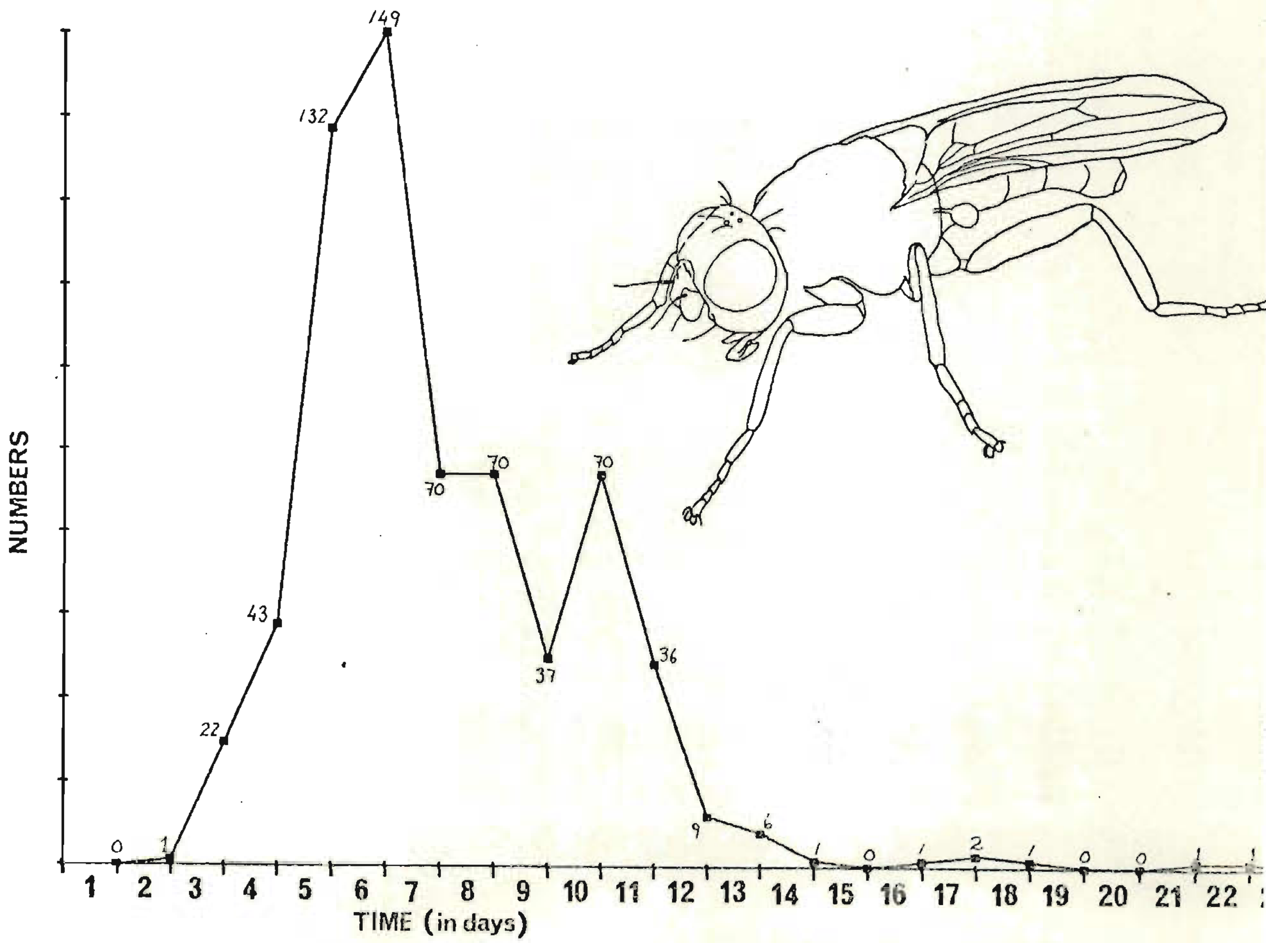


FIGURE 60: Daily totals of all adult Piophila (Piophilidae) present at Carcass C, Pafuri 18th May to 9th June 1979

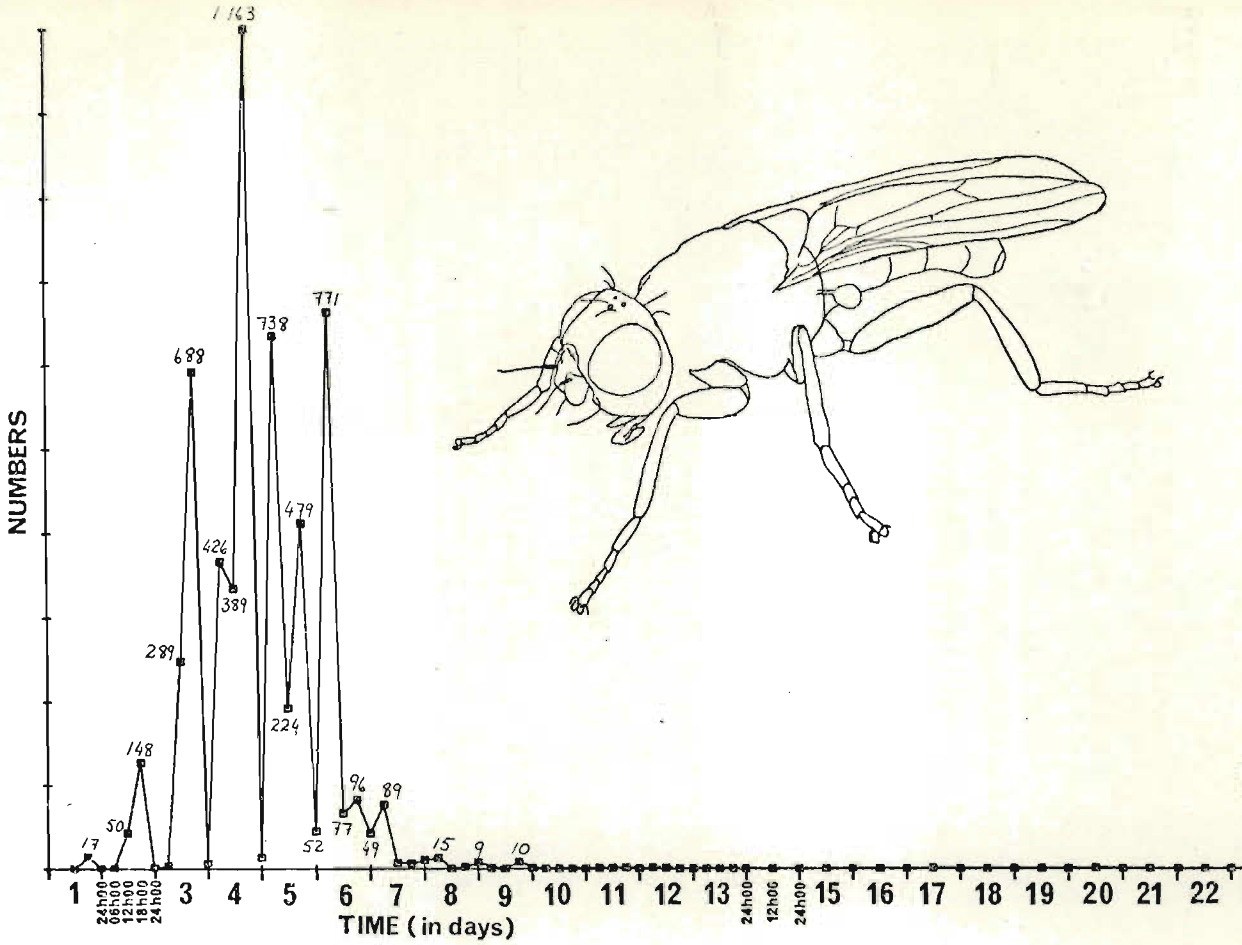


FIGURE 61: Number of adult Piophila (Piophilidae) present at each collection period at Carcass C, Pafuri, 14th September to 6th October 1979, to show diel activity cycle

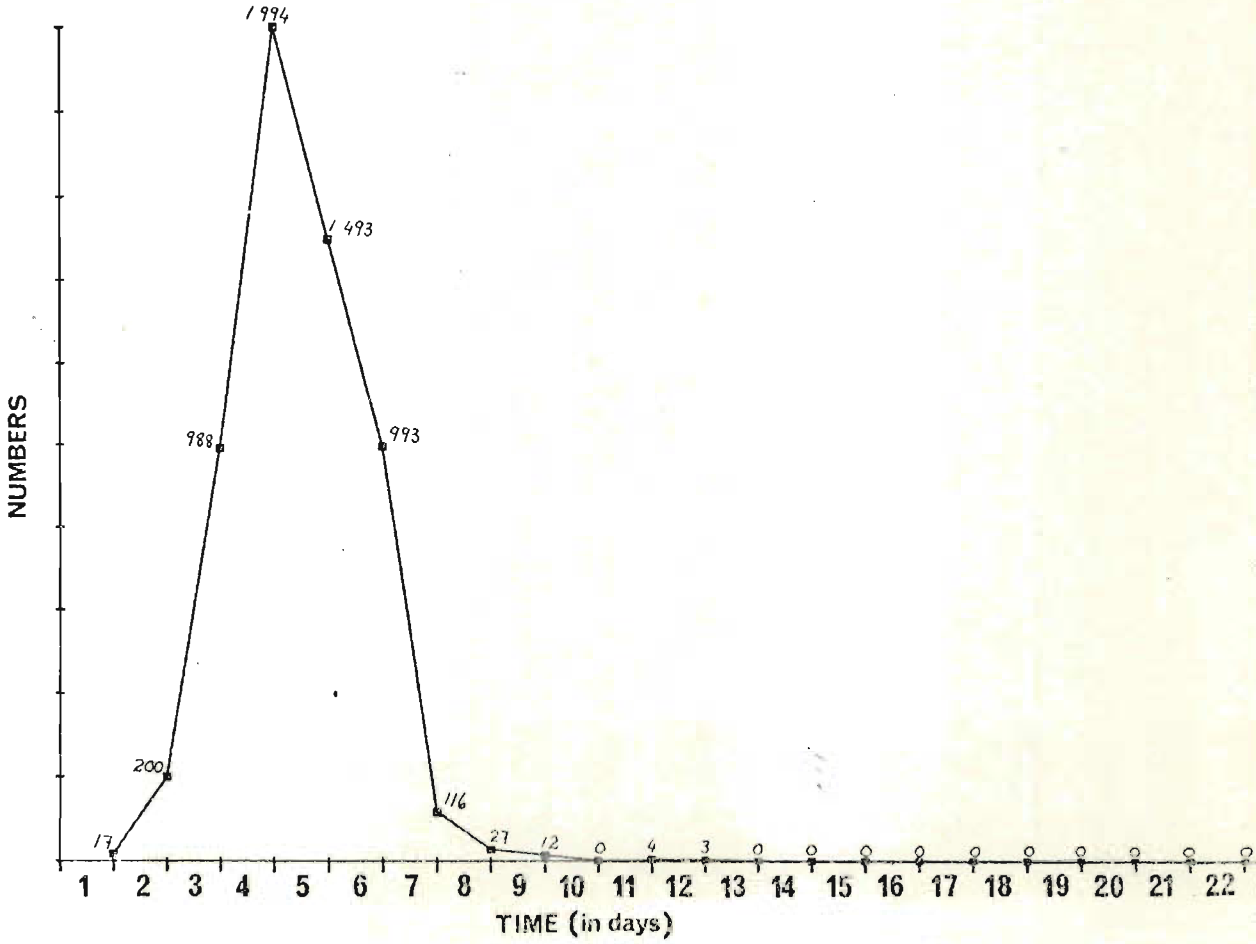


FIGURE 62: Daily totals of adult Piophila (Piophilidae) present at Carcass C, Pafuri, 14th September to 6th October 1979

For the 23-day period in Jan/Febr., 821 individuals (17,69% of all adult Diptera) were recorded; the numbers decreased somewhat to 652 (32,61% of all adult Diptera) in May/June, with a rapid marked rise to 5 849 individuals (36,27% of all adult Diptera) recorded in Sept/Oct.

Figures 56, 60 and 62, representing the daily totals of piophilids visiting the carcass during each survey period, reveal that the carcass initially had a low attraction for these flies due to a lack of suitable moisture. First and second instar C. marginalis larvae generally migrate over a carcass seeking entry into the body and leave a layer of organic moisture behind which renders the carcass highly attractive to piophilid adults. As the carcass dries the attraction decreases with a corresponding drop in the number of piophilid visitors. During Jan/Febr. temperatures were high, blow-fly larval development and carcass decomposition was rapid, so that the period of visitation or carcass utilisation by Piophila was also condensed (Fig. 56). With a slower rate of decomposition and dessication in the cooler months, and a longer stay by blow-fly larvae which add to available moisture at the carcass, piophilids were attracted to this habitat for a longer period (Fig. 60). During Sept/Oct., with average daily temperatures rapidly increasing again, their period of carcass utilisation became less protracted again.

Both Piophila casei and P. megastigmata were present at the carcasses used in the surveys mentioned above, but because of their large numbers, the inability to separate the two species macroscopically, and limited time, the two species were lumped together and treated as a group. To gain some idea of the advisability of this procedure, the Piophila captured during May/June 1979 were separated into the two component species and plotted as shown in Figures 57, 58 and 59. These figures clearly indicate that P. casei and P. megastigmata essentially coincided in their periods of carcass visitation, and that in terms of overall abundance were much the same. P. casei had a more stable plateau in that it did not fluctuate drastically in daily numbers during its period of abundance between Days 3 and 11 (Fig. 59), whereas P. megastigmata rose rapidly to a peak on Days 5 and 6 and dropped steeply thereafter.

Both P. casei and P. megastigmata showed clear preference periods for carcass visitation within each 24 hour cycle, and this diel pattern can be discerned by examining the numbers present on Days 4 and 5 during Sept/Oct. 1979 (Fig. 61). The flies had a preference for dawn and dusk, with depressed numbers at noon, and very low numbers during the hours of darkness. The diel visitation pattern changed somewhat during the cooler months of May and June when temperatures were low at dawn, and here a clear pattern is presented when examining Figures 57 and 58. Few or no piophilids individuals were present in the cold early hours before dawn, but numbers increased during the daylight hours with a peak at dusk, decreasing again thereafter.

ORDER: DIPTERA
FAMILY: SPHAEROCERIDAE (BORBORIDAE)

This is a large and widely distributed family of small flies, usually dark in colour, with the first segment of the hind tarsae characteristically broadened and compressed. The vast majority of species breed in excrement or rotting plant-material (Richards & Davies 1977). Dear (1978) recorded 12 species as having been found at carrion during late summer and autumn. Generally arriving at carrion when the first faint odours develop and the abdomen of the corpse distends, some species remained even when the carrion was completely dry. Skidmore (1978) listed 60 species found in dung, most of these being consistent breeders within excrement.

Species recorded

Twelve species were collected at Pafuri from impala carcasses, these being listed in Table 13. Four were new and of these three were subsequently described by Laszlo Papp (Papp, pers. comm.).

Biology

Hackman (1965) stated that "In the family Sphaeroceridae there are numerous, more or less cosmopolitan, mainly coprophagous species, most of them clearly synanthropous, ..." and included amongst a list of seven examples Limosina bifrons and Coproica ferruginata. He also wrote that Poecilosomella angulata is a very common species in equatorial and southern Africa, Malagasy, but also occurs in the Neotropical region and the Canary Islands. The large number of species of Poecilosomella in Africa suggests that this is its origin from where it was spread probably via cargo ships. Laurence (1955) indicated that many species of Limosina and Copromyza are found at dung, both as adults feeding on moisture on the parts and as larvae living within, but that some species are only attracted to dung during the adult stage with unknown larval habitats.

Relatively few sphaerocerids were collected from carcasses in the present study, but this was possibly due to a lack of exposed rumen-content. Although the abdomen and stomach of each study carcass used for monitoring insect-diversity was punctured, the contents were only minimally exposed until removed by scarabaeids or maggot activity, at which stage the rumen was drenched with carcass juice and may have altered or disguised its attractiveness to these flies.

Patterns of carrion-attendance

A total of 40 spaerocerids were caught during the 23-day study period in Jan/Febr. 1979; during the May/June survey only two were found, whereas over the 23-day period in Sep/Oct. 223 were captured. This latter figure represents 1,38% of the total number of adult Diptera at Carcass C during Sep/Oct. 1979. The sphaerocerids caught during this period were most numerous between Days 2 and 9, with a peak of 50 flies caught on Day 3, but there was no distinguishable pattern. Visitation was erratic with no particular time of day being preferred, and the various species showed no succession sequence to partition the resource between themselves in time. The sphaerocerids observed were all on rumen-content, many with abdomens heavily distended with fluid, and there was no obvious interaction with other species.

ORDER: DIPTERA
FAMILY: CHLOROPIDAE

This is a widespread and common family of small flies which tend to be light-coloured. The larval stages of most species are saprophagous, some phytophagous and a few predaceous.

Species recorded

Nine species were collected from carcasses and are listed in Table 13.

Biology

Dear (1978) stated that two species of Chloropidae have been recorded at carrion during spring, but gave no indication of the species or localities involved.

During the 1979 survey of carrion-insects, individuals of *Siphunculina ornatifrons* were observed walking over the carcass, apparently feeding on the moisture present at many sites. The available evidence suggests that all the chloropids encountered were present at the carcass merely for the fluids, and no obvious interaction with other insects was observed.

Patterns of carrion-attendance

Chloropids were never present in large numbers at any of the study carcasses, except *Siphunculina ornatifrons* (Lw) which briefly attained abundance during September (Figs. 63 & 64). They reached maximum numbers on Days 2, 3, and 4 (Fig. 64) - corresponding to the period when moisture was most easily accessible at the carcass. Numbers increased steadily during each day with maximum numbers recorded at 18h00, whereas few or no individuals were collected at midnight or 06h00 (Fig. 63). A total of 250 specimens of *S. ornatifrons* were collected from Carcass C in Sep/Oct., representing 1,55% of all adult Diptera recorded at this carcass.

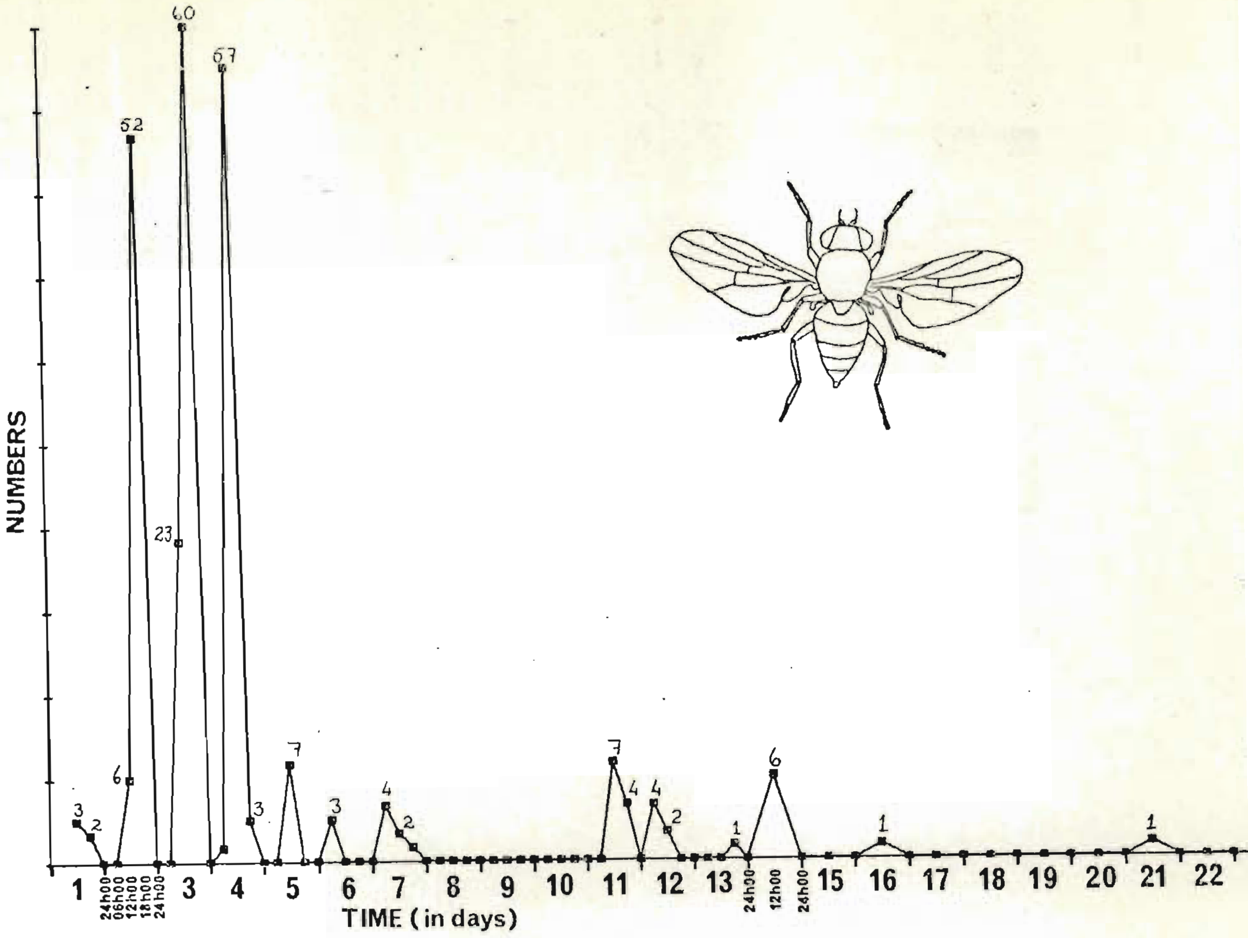


FIGURE 63: Number of adult Siphunculina ornatifrons (Chloropidae) present at each collection period at Carcass C, Pafuri, 14th September to 6th October 1979, to show diel activity cycle

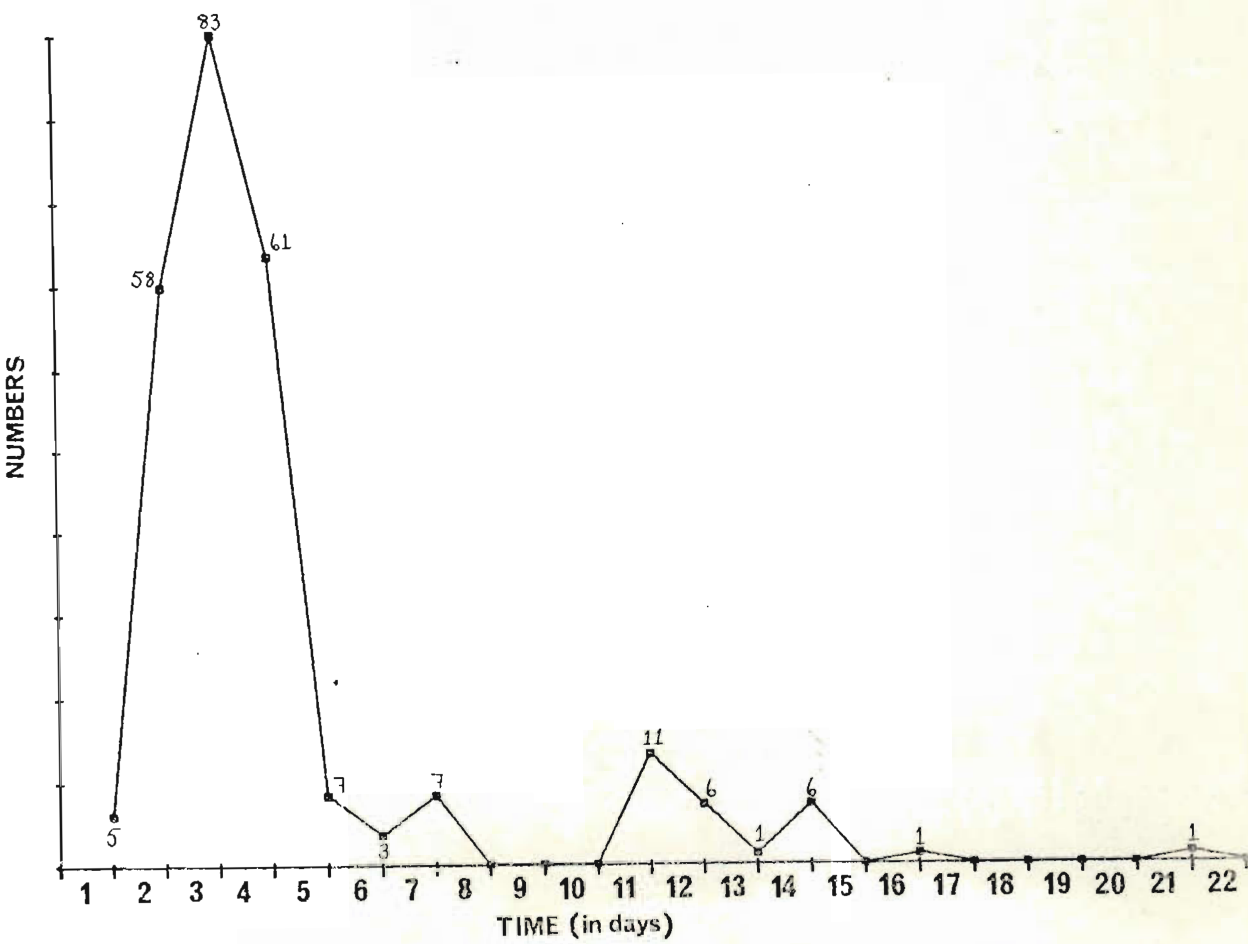


FIGURE 64: Daily totals of adult Siphunculina ornatifrons (Chloropidae) present at Carcass C, Pafuri, 14th September 1979

ORDER: DIPTERA
FAMILY: MILICHIIDAE

The Milichiidae is a common and widely distributed family of small, dark-coloured flies which vary considerably in habits. Although larvae appear to be saprophagous and generally breed in dung or scavenge in burrows or hides, the adults tend to feed at flowers or on organic liquids, such as Desmometopa sucking at haemolymph oozing from injured insects (Oldroyd 1964, Richards & Davies 1977). Skidmore (1978) recorded Leptometopa latipes as breeding in human excrement, and Dear (1978) mentioned that species of Meonura are "important" visitors to carrion during late spring and summer in Europe. He neglected to say why they are important. Specimens of Meonura have been collected from birds nests and off carrion, and the genus is sometimes placed in the family Carnidae (Richards & Davies 1977).

The milichiids recorded during this study were generally dispersed over the entire carcass and appeared to be attracted by fluids. I have also reared four specimens of Milichiella lacteipennis (Lw) from a sample of 20 larvae collected on 13th June 1980 from the moist bottom-most layer of rumen-content spilled from a buffalo which had been killed on the 30th April 1980 near Mahembane, north-east of Punda Maria. No interaction between milichiids and other carrion-attendant insects was observed at any stage.

Patterns of carrion-attendance

Milichiids were present at carcasses as occasional individuals or small groups in summer and winter, but increased in spring. The only species of significant abundance was Meonura n. sp. (Fig. 65 & 66) during September and October. It maintained low numbers until Day 7 when numbers increased considerably, reached a maximum on Day 10 with 502 specimens recorded, declining thereafter to reach a plateau on Day 14. Within each 24-hour cycle Meonura n. sp. was absent at midnight, absent or present only in very low numbers at 06h00, increased steadily to 12h00, followed by a relatively high peak at 18h00. A total of 2 574 specimens of Meonura n. sp. were recorded during the 23-day study period in Sept./Oct. 1977, representing 15,96% of all adult Diptera

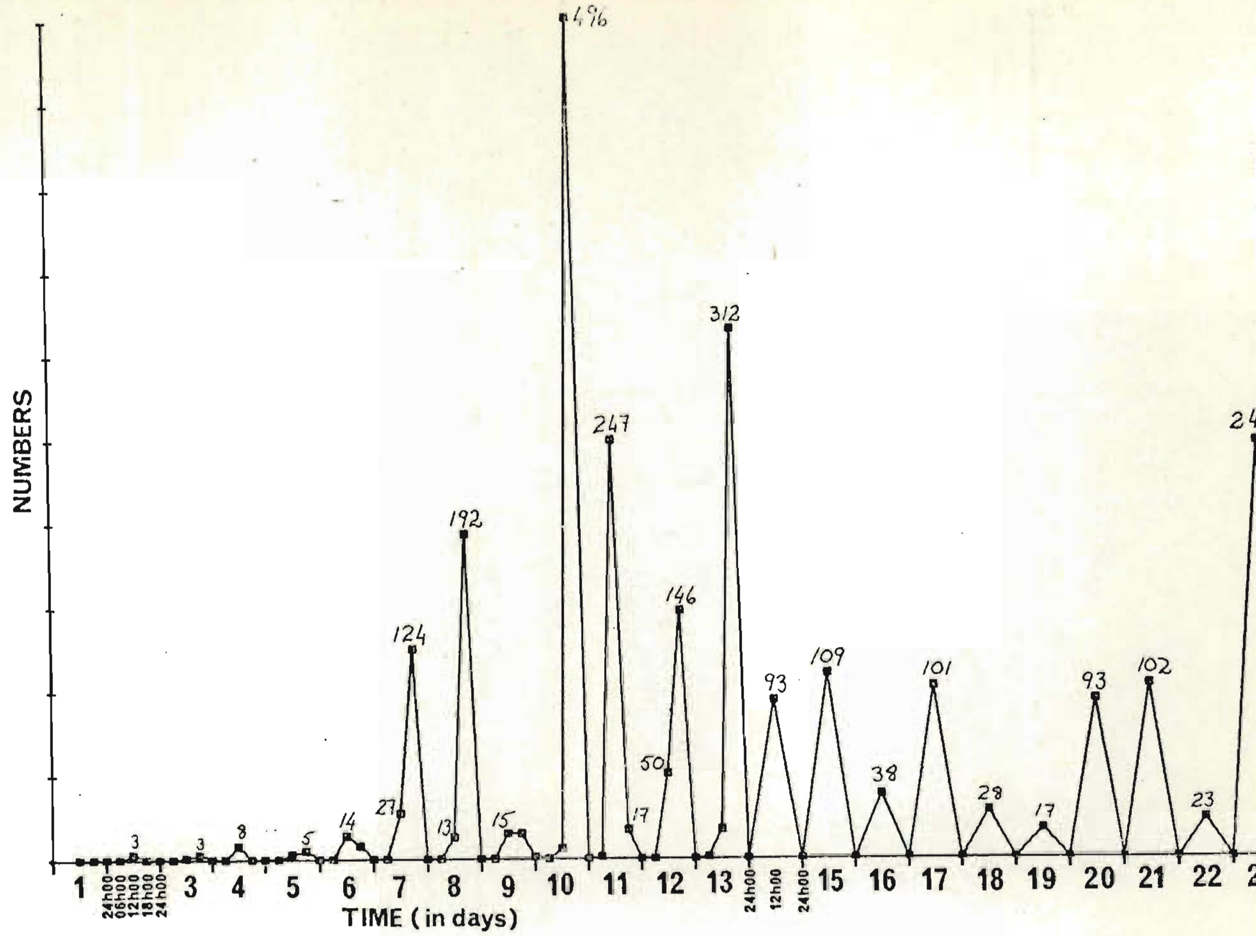


FIGURE 65: Number of adult Meonura n. sp. (Milichiidae) present at each collection period at Carcass C, Pafuri, 14th September to 6th October 1979, to show diel activity cycles

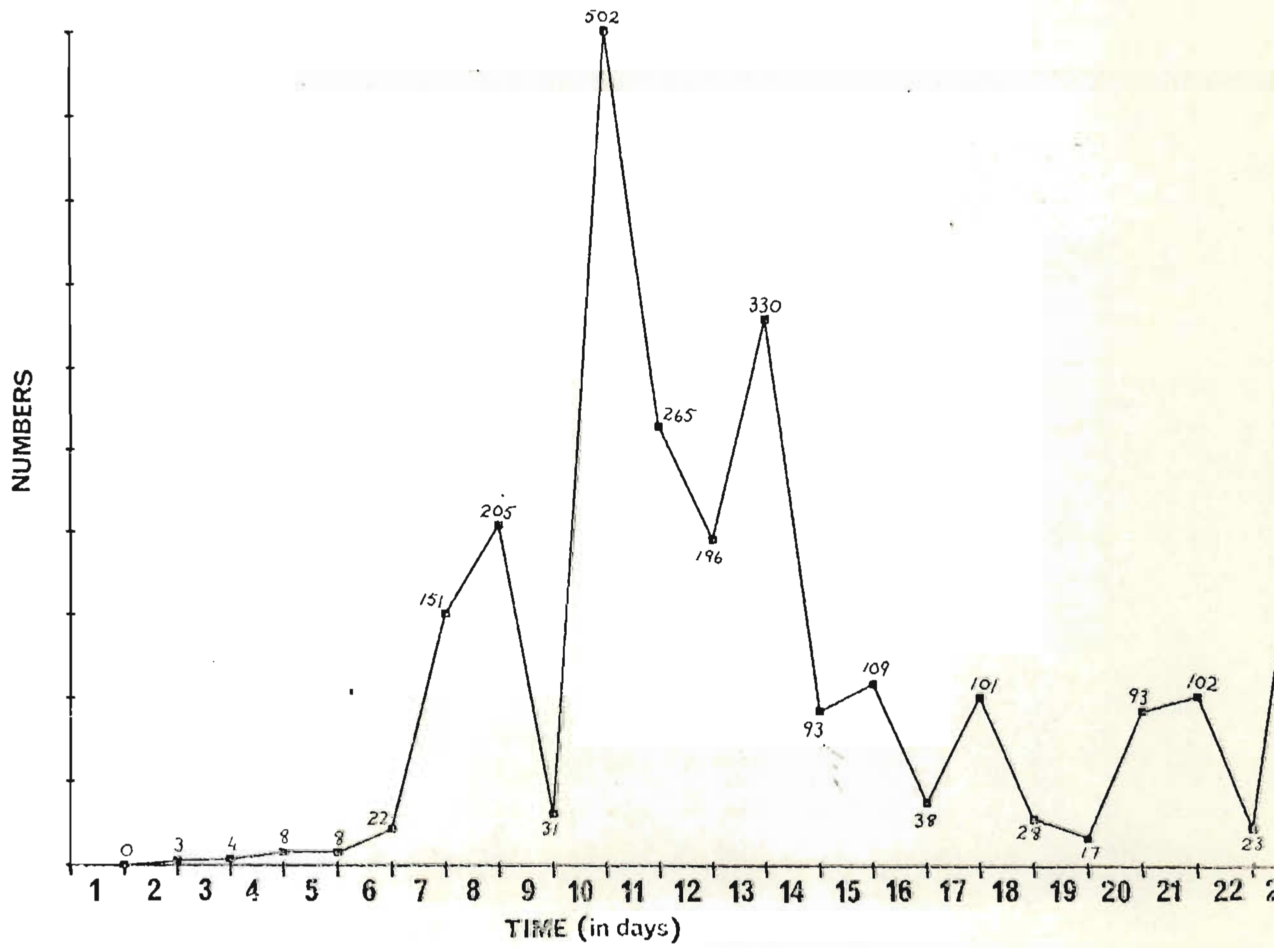


FIGURE 66: Daily totals of adult Meonura n. sp. (Milichiidae) present at Carcass C, Pafuri, 14th September to 6th October 1979

found at Carcass C in that period.

ORDER: DIPTERA
FAMILY: MUSCIDAE

The Muscidae form a very large, widely distributed family of small to fairly large flies with widely divergent habits (Richards & Davies 1977). Several genera have blood-sucking adults with a piercing proboscis but the majority of flies have lapping/sponging mouthparts (Greenberg 1971, Skaife et al 1979). Musca domestica is the best-known member of this family; it has a cosmopolitan distribution with many populations living eusynanthropically and functioning as disease vectors for many diseases, amongst others anthrax, cholera and poliomyelites (Greenberg 1971). Breeding media of muscids are highly diverse and include larvae parasitising nestling birds by imbibing their blood (Skaife et al 1979), predacious larvae which prey on invertebrates in dung or other matter, while the immature stages of most species appear to be saprohagous in decaying organic material, especially those of plant origin (Richards & Davies 1977).

Species recorded

Twenty-one species in eleven genera were recorded at carcasses during 1979, and are listed in Table 13.

Of these, only three genera - Atherigona, Musca, and Ophyra - consistently utilised the carcass habitat and reached abundance. The remaining genera were never recorded in numbers exceeding 20 individuals per carcass and were present only as sporadic isolated specimens. Haematobia, Haematobosca, Stomoxys, and Stygeromyia are all blood-sucking ectoparasites on mammals and do not use the carcass habitat for breeding (Zumpt 1973), so that their presence at the study carcasses can be regarded as incidental. Referring to the muscid flies listed above, A.C. Pont (pers. comm.) mentioned that "... I think that most of these were probably visiting the carcasses for feeding rather than for reproduction."

Biological notes on Atherigona spp

Containing some 180 valid species, the genus Atherigona has a wide distribution throughout the tropical and sub-tropical regions of the Old World (Pont 1981). All the species are divided amongst two subgenera, Acritochaeta and Atherigona, and Pont (pers. comm.) stated that ".. Adult female Atherigona have frequently been observed feeding on dead insects and larger carrion. Presumably this is a source of the proteins and minerals essential for reproduction. Larvae of the typical subgenus are phytophagous, attacking various Graminaceae, whilst species of the subgenus Acritochaeta are predators or scavengers in decaying organic matter, usually of vegetable origin."

At least five species of Atherigona were collected at study carcasses used during the survey on carrion-frequenting insects at Pafuri during 1979. These were A. aberrans Malloch, A. naqvii Steyskal, A. steeleae Emden, and Atherigona spp. indet. The vast majority of captured specimens were females, and as species identification in many cases requires examination of the males, it was not possible to identify all the species present. Furthermore, because of the small size and close morphological similarity of the species mentioned above, no attempt was made to separate them and a collective count was made of all Atherigona for the compilation of visitation patterns.

During four years of work on carrion I have not once seen larvae of Atherigona at carrion, or reared them in any of the many samples of rumen content or organic offal taken at carcasses. All the available evidence points to the adults using the carcasses only as a source of nutrient-rich moisture but that breeding occurs elsewhere. During the stage when adult Atherigona were abundant at carrion, I have on many occasions observed these flies on the carcass itself and on the rumen-content, busily engaged in lapping up available moisture. Other than this, they have no impact on carcass decomposition, and do not appear to have any interaction with other members of the carrion-insect complex.

Patterns of carrion-attendance of Atherigona spp.

Atherigona were by far most abundant during summer, with 1289 individuals (27,78% of all adult Diptera recorded at Carcass C) visiting the study carcass during Jan/Febr. 1979. Figures 67 and 68 reveal that the flies were present at the carcass for a relatively short period, with a distinct peak between Days 2 and 5 when an abundance of moisture and carcass fluids were present. Another small peak is evident on Days 8, 9 and 10, and was caused by rain on those days which soaked the carcass so that nutrient-rich ooze was again available and was also accompanied by a brief increase in smell, acting as an attractant for the flies.

With the exception of three adults captured as individuals on Days 5, 6 and 8, Atherigona flies were conspicuously absent during the survey in May/June 1979, an indication that they were probably sensitive to the low temperatures reigning at this time.

The probable absence of any breeding in winter must lead to a rapid decline in population size, so that with the return of warmer weather in spring the number of adults is still depressed, as is reflected in the relatively low total of 438 individuals visiting Carcass C during Sept/Oct 1979 (2,71% of adult Diptera). Figures 69 and 70 show a definite period of preferential visitation lasting from Day 2 to 7, with a peak on Day 5. As is the case during summer, this coincides with the period of maximum breakdown of carcass material when an abundance of fluids is available. Appraisal of Figure 69 shows that a definite diel visitation preference exists, with a bimodal peak within each 24-hour cycle. Large numbers of flies attended the carcass habitat at dawn and dusk, but were absent or present only in low numbers at midnight and noon. This same diel pattern was evident in summer, and is clearly present in Figure 67.

Biological notes on Musca spp

Saccã (1964) regarded the genus Musca as containing some 6C species, with most occurring in the Old World. Many species are haematophagous but with varying degrees of adaptations and modificatioı

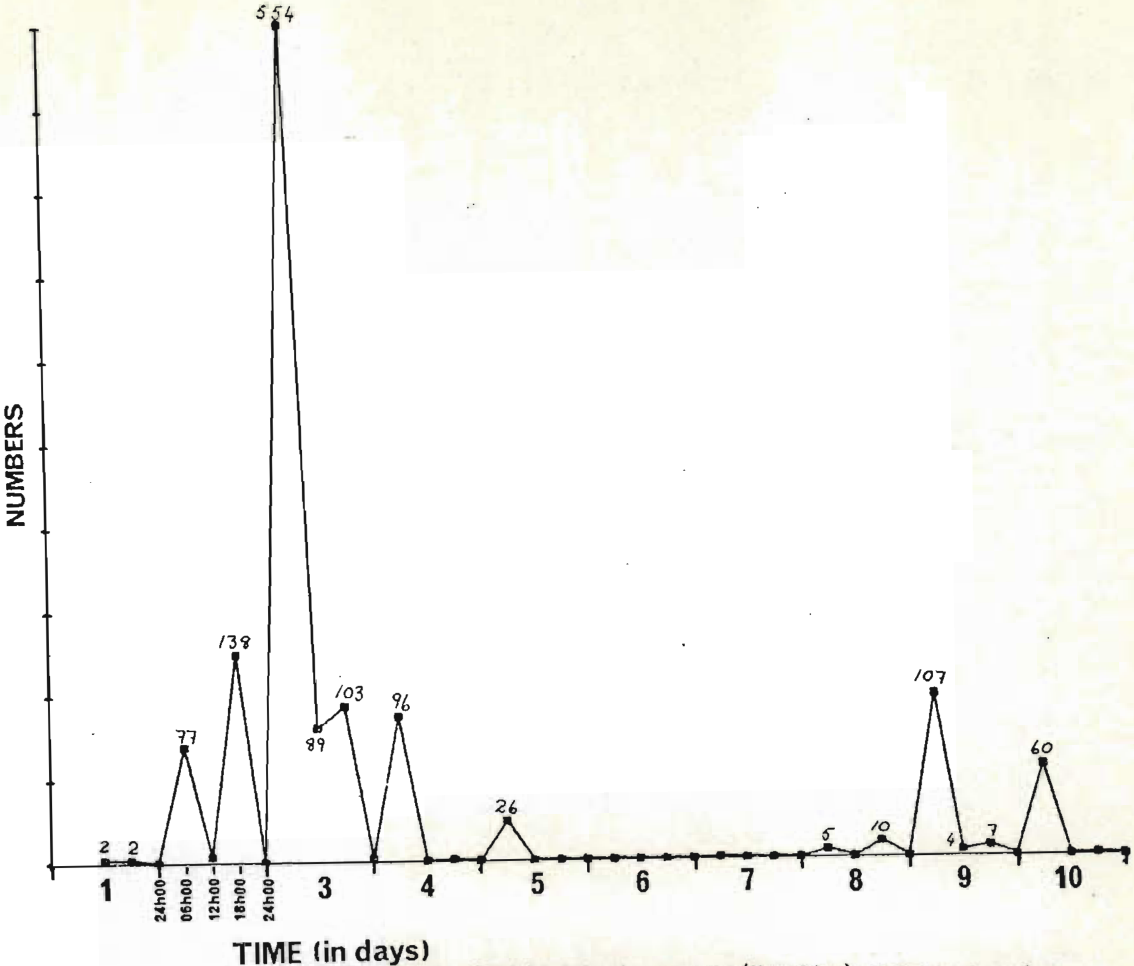


FIGURE 67: Number of adult *Atherigona* spp. (Muscidae) present at each collection period at Carcass C, Pafuri, 13th to 22nd January, 1979, to show diel activity cycles

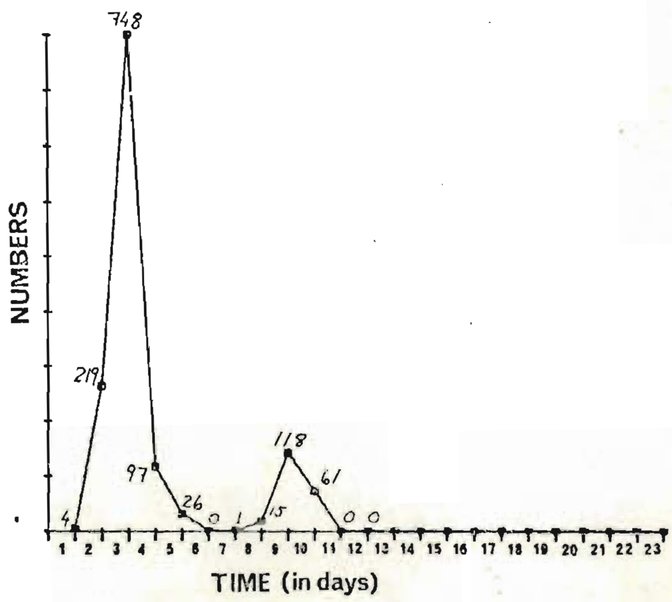


FIGURE 68: Daily totals of adult *Atherigona* spp. (Muscidae) present at Carcass C, Pafuri 13th January to 4th February 1979

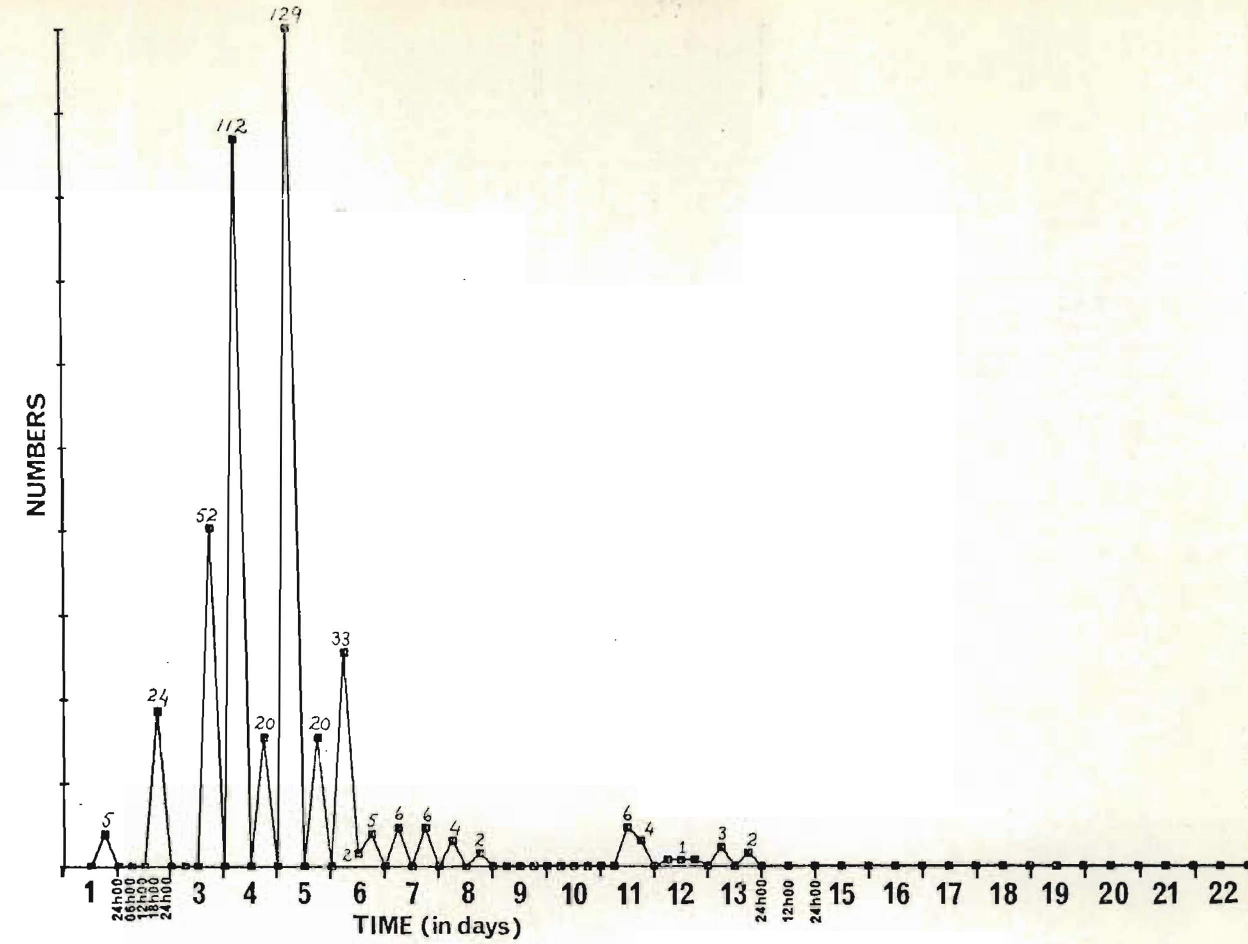


FIGURE 69: Number of adult Atherigona spp. (Muscidae) present at each collection period at Carcass C, Pafuri, 14th September to 6th October 1979, to show diel activity cycles

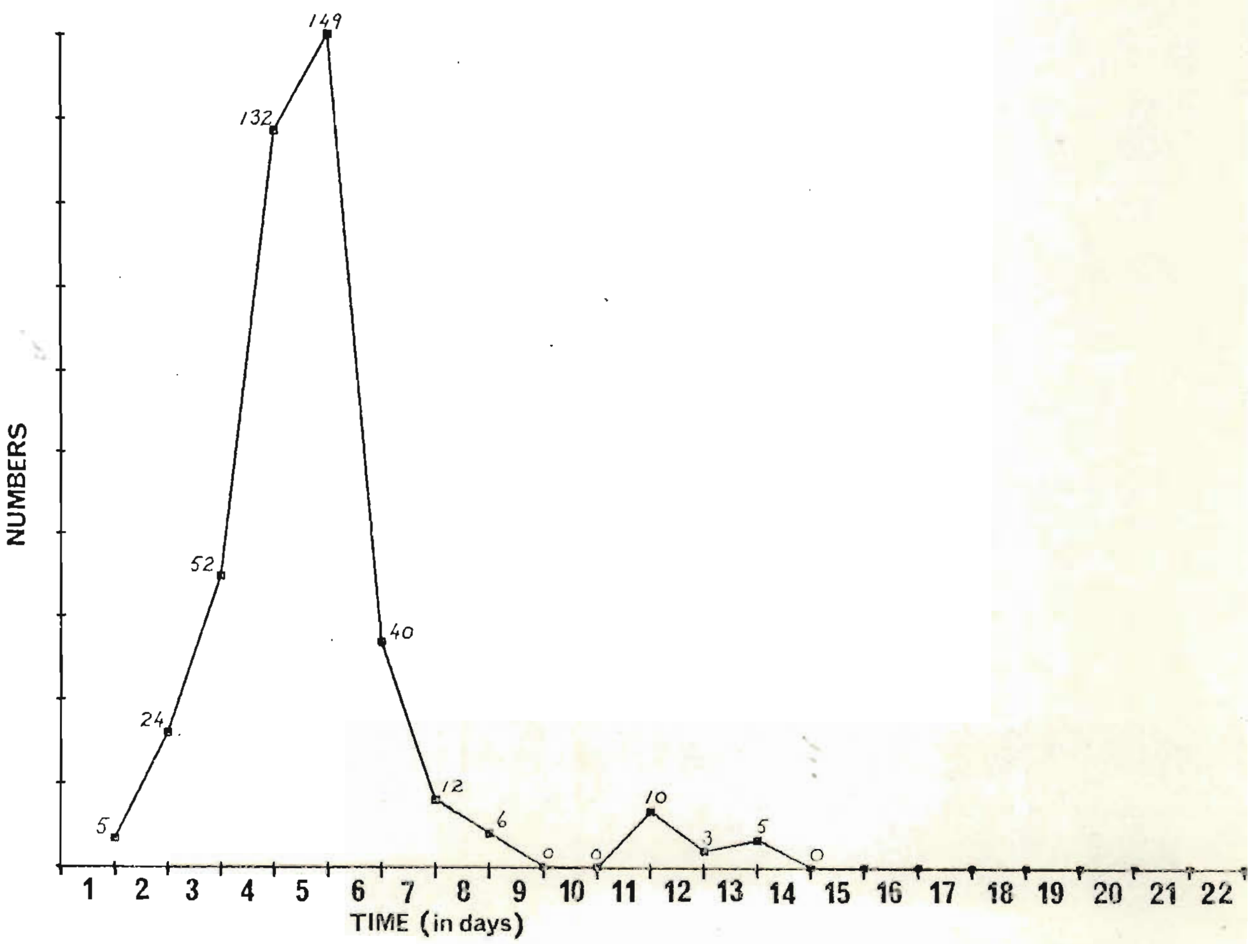


FIGURE 70: Daily totals of adult Atherigona spp. (Muscidae) present at Carcass C, Pafuri, 14th September to 6th October 1979

of the mouthparts to obtain blood: some have piercing mouthparts capable of puncturing the skin of the host animal, others rasp at scabs or partially-healed wounds, while most settle near fresh wounds to ingest exuding blood (Saccã 1964, Greenberg 1971). Members of this genus, including the haematophagous species, are also known to feed on a wide range of other protein-containing substances, such as ocular, nasal and buccal secretions of animals (Saccã 1964), and also moisture in dung, carcasses, food and garbage (Greenberg 1971).

Of the five species of Musca recorded from carrion in 1979, M. conducens was present in very low numbers and is only an incidental visitor to carrion. It is a haematophagous species which rasps away at the skin of the host until bleeding results, and has been positively implicated in the transmission of filarial worms in domestic animals (Greenberg 1971, Howell et al 1978). Cuthbertson (1933) reported this species as also being rare in Rhodesia (Zimbabwe). Musca lusoria, M. sorbens, and M. xanthomelas all are haematophagous species which obtain blood at open wounds or at puncture sites of biting flies, with the larvae developing in the dung of various mammals (Cuthbertson 1933, Greenberg 1971, Howell et al 1978). I have reared M. lusoria from larvae found in fresh buffalo-dung at Pafuri during June 1979, the larvae feeding for 10 days prior to pupariation, and the pupal stage also lasting 10 days. Musca sorbens is known to scrape at sores until perforation results in exudation of lymph or pus, and all three species feed on lachrymal secretions at the eyes of Man and other animals, with M. sorbens considered a prime vector of acute epidemic conjunctivitus in parts of Asia (Greenberg 1971, 1973). M. sorbens is also known to transmit tuberculosis and several other diseases (Saccã 1964).

The only other species of Musca recorded at carrion during 1979 was M. domestica, and within this species two subspecific forms were found, namely M. domestica calleva Walker and M. domestica curviforceps Saccã and Rivosecchi. The literature on M. domestica is vast due to its cosmopolitan distribution, its abundance, and its role in the dissemination of a multitude of organisms causing disease in humans (Greenberg 1971), including amongst others bacillary dysentery, typhoid fever, cholera, salmonellosis, anthrax, leprosy, and parasitic helminths (Skaife et al, 1979). The main method of infection occurs by these flies walking over infected food, faeces, or other sources and then settling on uncontaminated food, and also by ingesting infective material and depositing droplets either by regurgitation or defecation on food intended for human consumption (Howard 1912, Graham-Smith 1913, James & Harwood 1970).

Musca domestica is a well-studied species and its life-history is adequately summarised by Howell et al (1978) and Skaife et al (1979). Females deposit their eggs in batches of 100-150 within dung or other decaying organic matter, and the eggs hatch 8-24 hours later. The larvae pass through three developmental stages, and depending on climatic conditions may be ready to pupate after three days during hot weather, but in winter may take as long as three weeks. The fully-grown larvae depart from the breeding medium and usually burrow into soil for pupation. The pupal stage generally lasts 4-5 days in summer, after which the adults emerge. Under optimal conditions the life-cycle may therefore be completed within 12 days.

Due to the close resemblance of the species of Musca collected, the generally small impact these flies have on carcass decomposition, and relatively low impact or influence on other members of the carrion-complex, it was decided that expenditure of the time required for species-separation was not warranted, and they were accordingly recorded collectively as "Musca".

Because of competition mainly from the larger, more active and rapid-growing larvae of Chrysomyia albiceps and C. marginalis and the disruptive effect of these blow-fly larvae by continually wriggling in and over the dung-component within the carcass and drenching it with digestive enzymes, Musca flies have very little success in breeding at most carcasses. Utilisation of that portion of rumen-content extruded by bloating or scarabaeid-activity is generally not very successful due in part to the usually small component of dung thus extruded, it mostly being flattened and fully exposed to the sun, the very large number of predatory histerid beetles which are attracted to the carcass and the presence of predatory mites such as Macrocheles muscaedomesticae Scopoli.

At medium-sized carcasses such as impala, only small isolated pockets of Musca larvae were found below the carcass, and then usually only in the colder months of the year when blow-fly larval numbers were reduced and development took longer. However, Musca larvae often occurred in enormous numbers in the stomach and other abdominal contents of larger mammals such as buffalo and elephant, especially where the abdominal cavities of such animals had been partially opened by vertebrate scavengers, the soft tissues removed, but the rumen-content left inside the abdomen and the hide of the animal shaded it from the sun so that a high humidity regime was maintained. During June and July 1980 I reared several hundred Musca domestica ssp. calleva taken as samples from amongst many thousands of pupae lying in the rumen-content in buffalo carcasses rejected due to foot-and-mouth disease in the annual culling operations at Pafuri. The buffalo had been culled on 6th June, and the pupae were collected on 30th June.

At other reject buffalo, shot on 30th April 1980 at Mahembane windmill near Punda Maria, I collected a sample of moist rumen-content (dry mass later determined as 34,96 g) containing many near full-grown Musca larvae. On 24th May I counted 202 pupae in this sample. Adult emergence took place between 27-29 May, a total of 184 adults resulting, all being M. domestica ssp. calleva (Pont pers. comm.). At several carcasses of buffalo culled at Manxeba in the Pafuri area on the 2nd June 1980, numerous freshly emerged Musca domestica adults were seen emerging from the abdominal cavity on the 26th June. Many similar observations substantiating the above results have subsequently been made at other large carcasses such as those of hippopotami and elephant throughout the K.N.P.

Patterns of carrion-attendance of Musca spp.

The number of Musca utilising the study carcasses during Jan/Febr. 1979 was relatively low, with only a total of 68 adults being captured at Carcass C, representing 1,47% of all adult Diptera trapped. This was a distinct drop compared to the number present during a short study at the same site during January the previous year (Braack 1978, 1981), and almost certainly resulted from the lower rainfall in the month preceding the January 1979 study as compared with the months preceding the 1978 study. Within limits, a higher rainfall will favourably influence the survival of Musca larvae as it moistens the dung within which these flies breed (pers. obs.) which otherwise rapidly dessicate in the high temperatures experienced in this region during summer.

Examination of Figure 71 reveals that Musca had two periods of abundance at the carcass, the pattern being slightly obscured by a misleading drop in numbers at Carcass C on Day 4. Field-notes taken at the time indicated that the general trend at Carcass B was a gradual decrease from Day 3 to Day 7, but because of the low numbers any "chance" absence of flies at the time of collection will show up as a skewed pattern as revealed in Figure 71. Generalising from the results at Carcasses B and C, the pattern was for Musca to have a peak on Day 3, decreasing slowly thereafter, and another sudden peak on Day 8. The first peak can be ascribed to the smell of decomposition which reached a maximum on Day 3, whilst the rain which fell on Day 8 (see Table 8) released an easily detectable smell of dung by soaking the rumen content lying alongside the carcass, which these flies find very attractive (pers. obs.) and resulted in the second wave of abundance. This second peak was higher than the first, presumably due to the lack of other odours normally present during the early stages of decomposition which would disguise the smell of dung.

The number of Musca decreased as winter approached, with a total of 45 individuals (2,25% of adult Diptera) utilising Carcass C in May/June 1979. Figure 72 indicates a peak of 19 flies visiting the carcass on Day 2, the number of daily visitors decreasing steadily thereafter to a near absence after Day 5.

With the return of warmer weather in spring, combined with a virtual dearth of dung-utilising Scarabeidae which overwinter in the soil and do not emerge until increased temperatures of spring coincide with good rains (Tribe 1976), the Musca population rapidly increased and this is reflected in the high numbers of flies trapped at Carcass C in Sept/Oct. 1979. A total of 3 129 were recorded, being 19,40% of all adult Diptera. Peak utilisation of the carcass occurred on Day 3 (Fig. 74) when the smell of decomposition was at its greatest and the carcass and immediate surrounds was covered in a layer of moisture which the flies feed on. As the smell of the carcass and available moisture decreased, so too did the number of Musca, until by Day 9 few

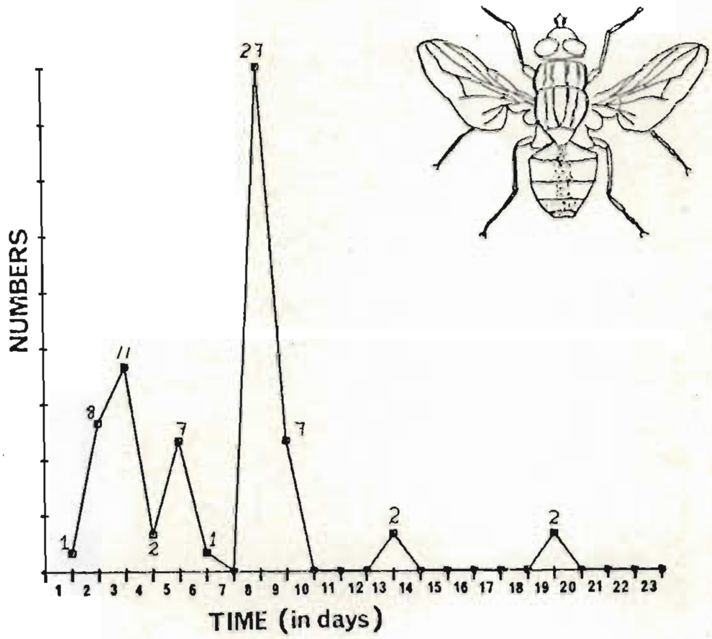


FIGURE 71: Daily totals of adult Musca spp. (Muscidae) present at Carcass C, Pafuri, 13th January to 4th February 1979

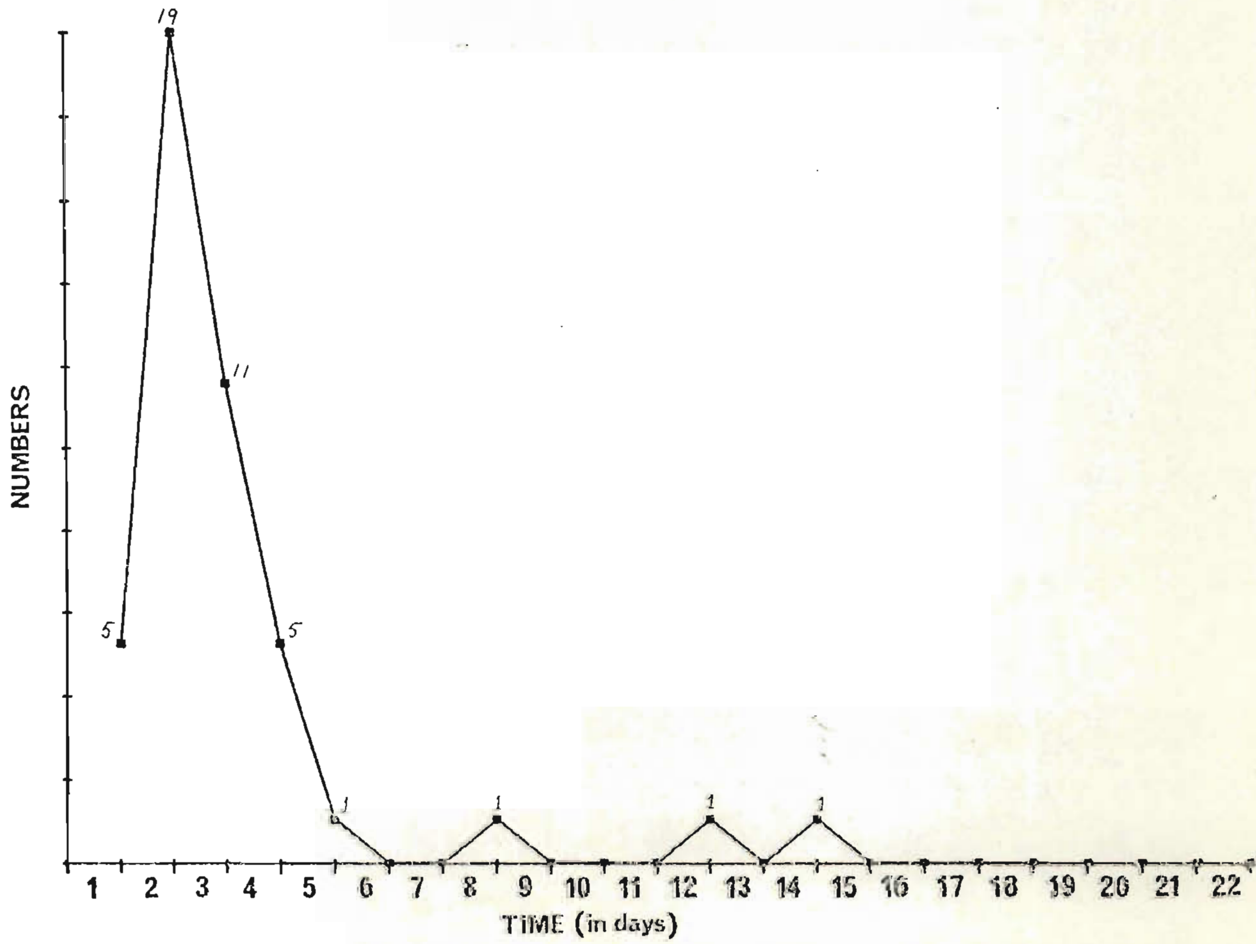


FIGURE 72: Daily totals of adult Musca spp. (Muscidae) present at Carcass C, Pafuri, 18th May to 9th June 1979

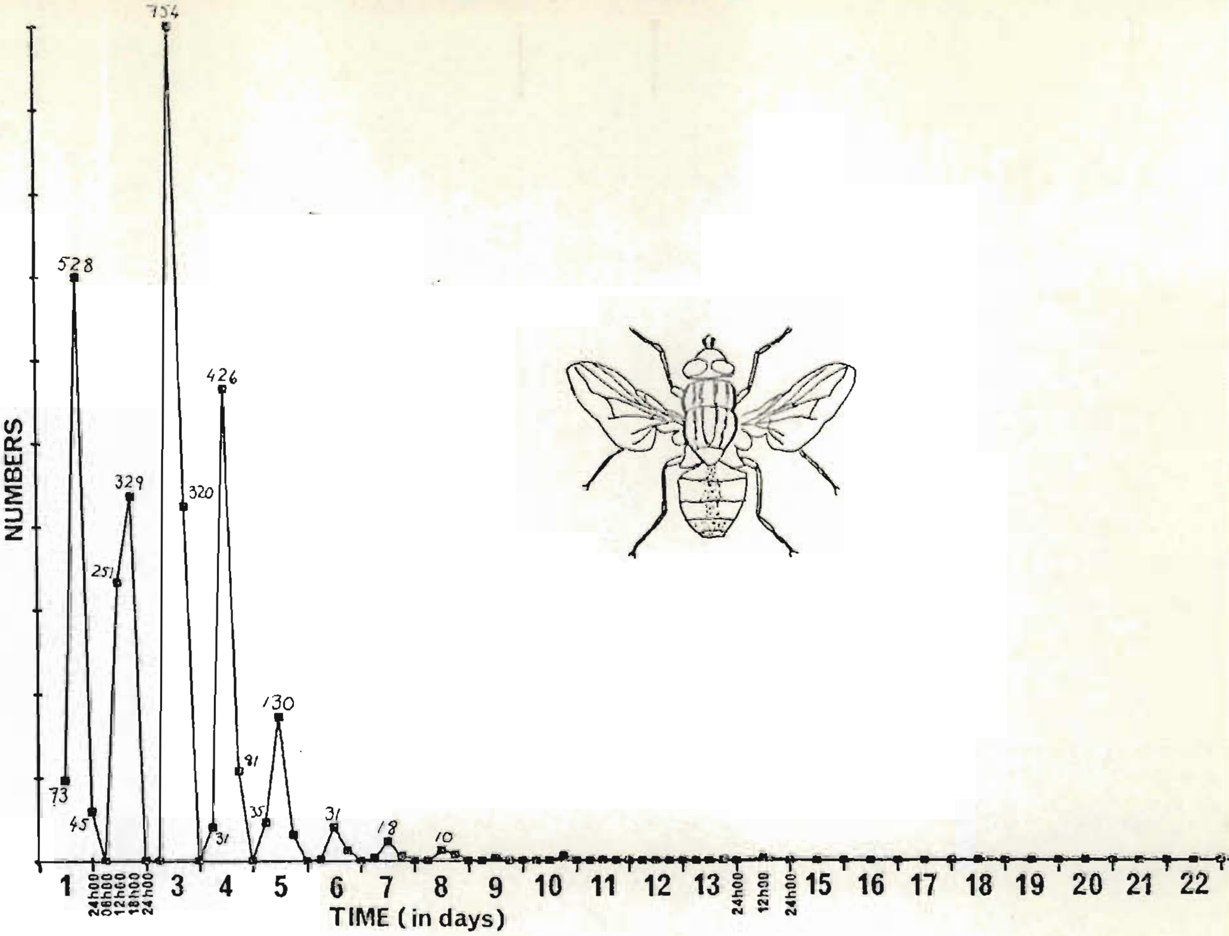


FIGURE 73: Number of adult Musca spp. (Muscidae) present at each collection period at Carcass C, Pafuri, 14th September to 6th October 1979, to show diel activity cycles

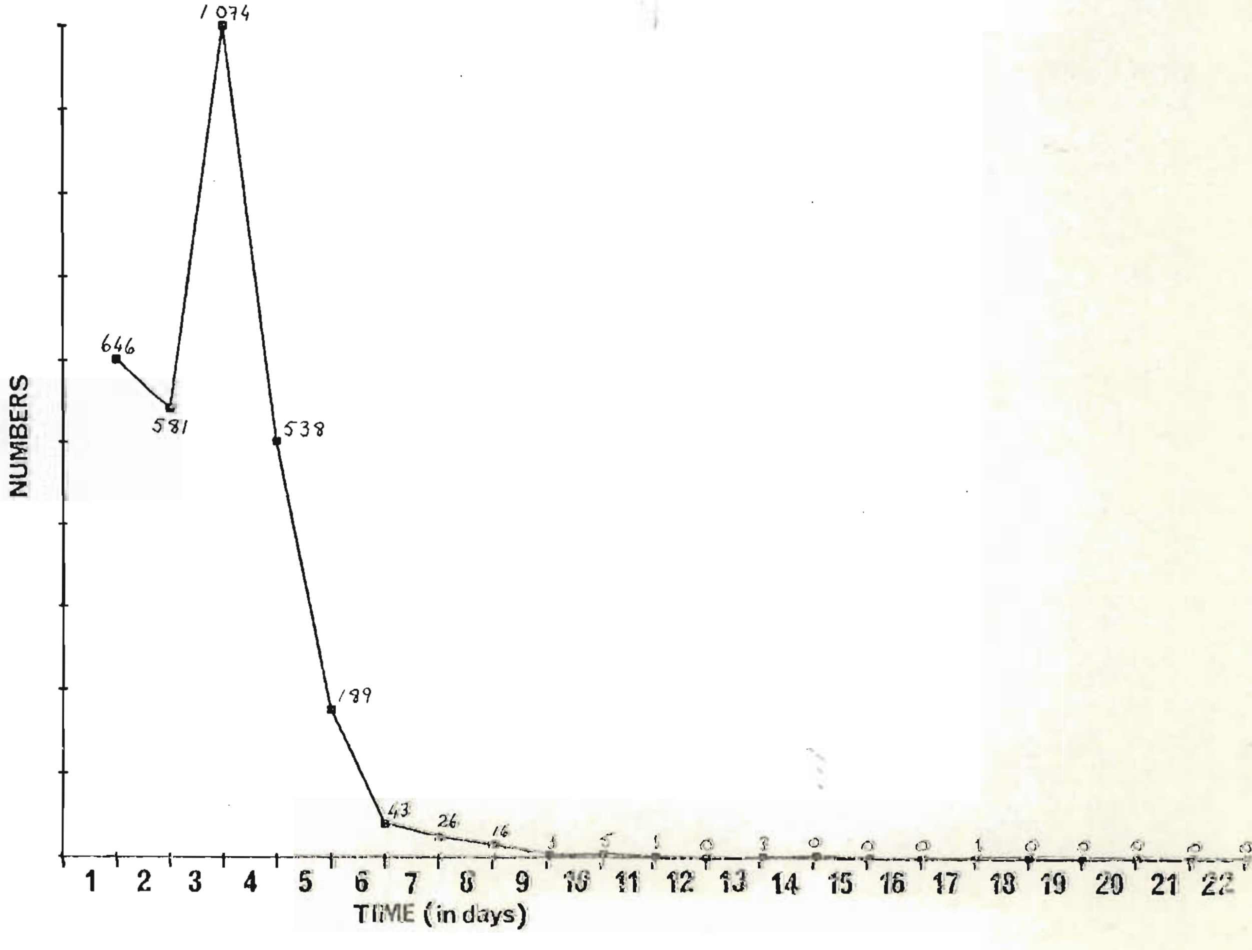


FIGURE 74: Daily totals of adult Musca spp (Muscidae) present at Carcass C, Pafuri, 14th September to 6th October 1979

flies were attracted to the carcass.

Figure 73 reveals that adult Musca did have preference periods for carcass visitation. A general period of inactivity reigned during the hours of darkness, but numbers increased rapidly after dawn so that a high peak was reached at mid-day, with a strong but dwindling presence maintained until dusk.

Because the population of Musca was high during the immediate post-winter period, coinciding with the peak likelihood period of anthrax outbreaks, the importance of these flies, which readily consume carcass liquids, as potential transmitters of disease should not be underestimated. They are unlikely to have the potential importance of blow-flies in anthrax transmission, however, as they are generally present in much lower numbers than blow-flies, consume smaller quantities of food and consequently discard smaller quantities of infective droplets onto vegetation, but most significantly because they only reach maximum abundance well after blow-flies have become abundant.

Biological notes on Ophyra capensis

Members of the genus Ophyra occur fairly widespread on many continents, with some species being common around dwellings where they often enter in search of food in much the same manner as Musca domestica, but they are more commonly recorded at dung, garbage deposits, and decomposing carcasses (Greenberg 1971). The larvae develop in dung and carrion, where the 2nd and 3rd instar larvae of some species are predacious and attack the larvae of Musca and other co-inhabitants (Cuthberton 1933, Thomsen & Hammer 1936, Greenberg 1971).

Ophyra capensis was the only member of the genus recorded at carrion in the K.N.P. during the present study. It has a distribution covering the more southern areas of the Palearctic region, is known to frequent sources of dung and carrion (Greenberg 1971), and the larvae initially feed on these substrates but during the later developmental stages feed on other dipterous larvae (Conway 1970, Greenberg 1971).

Adult O. capensis were regular and common visitors to the carcass habitat, and I observed them at virtually every carcass in the early stages of decay at widely scattered localities in South Africa. Adult flies are attracted to moist situations at the carcass, such as fresh rumen contents or the thin liquid film left when blow-fly larvae move *en masse* over the carcass in search of an entry site into the body, where *Ophyra* can then be observed feeding on the moisture. On many occasions I also observed adults feeding at the remains of partially consumed *Chrysomyia marginalis* larvae which had been killed by histerids.

Larvae were usually present as isolated small batches representing single egg-batches of individual flies, generally below the carcass or in the abdominal cavity. They preferred wet situations, such as soil which was well-drenched with organic ooze from the carcass, and at such sites they occasionally numberred several hundred individuals (representing the offspring of several female flies) and occurred well below the surface, up to a depth of about 4 cm. I never observed predatory behaviour in the larvae of this species, and in breeding experiments successfully reared them to the adult stage in jars filled with buffalo rumen-content lacking other dipterous larvae. The predatory habit as reported by other authors (e.g. Greenberg 1971) is therefore not obligatory, the larvae being quite capable of surviving on the organic-rich moisture generally present in dung. Probably because the soft tissues and fluids at the carcass habitat are so rapidly consumed by blow-fly larvae in summer, *Ophyra* larvae are competitively displaced and indeed very few were present during the warmer months at small and medium-sized carcasses. At larger carcasses, such as those of buffalo and elephant, they were frequently observed in summer, but rarely in numbers exceeding a few hundred. During the cooler winter months however, when carcass decay was prolonged and soft-tissue removal by blow-fly larvae slowed down, *Ophyra* larvae were commonly encountered in low numbers below small and medium-sized carcasses, but occasionally became numerous (in excess of a thousand individuals) below elephant and buffalo carcasses.

An erroneous impression may be gained upon initial examination of the data provided on the following pages where it is stated that the number of adults visiting the carcass was least in winter. This is correct, that relatively few adults utilised the carcass, but the breeding effectiveness and survival rate of larvae was high during these months (for reasons provided above) and this success is reflected in the large numbers of adults produced which visited the carcass in Sept/Oct. (Fig. 81).

Patterns of carrion-attendance of Ophyra capensis

Of the three survey periods in 1979, Figures 75 to 81 indicate that Ophyra were most abundant during Sept/Oct. when a total of 1 303 individuals were recorded, representing 8,08% of all adult Diptera at Carcass C. This seasonal peak in spring agrees with observations noted in the preceding pages regarding the general biology of these flies, where it was indicated that competitively the larvae have better opportunity for survival during the cooler winter months when the number of blow-fly larvae utilising each carcass are less (so that soft tissues are not consumed so rapidly and remain available for a longer period), the rate of carcass decomposition is slowed down (again contributing to soft tissues being available for a longer period), and the formation of an organic ooze-pool below the carcass (due to the slow usage of carcass material by especially blow-fly larvae) in which the immature stages of Ophyra thrive. This breeding success of larvae during winter results in a build-up of adults which reaches a peak in spring.

Figures 75 and 76 indicate that during Jan/Febr. 1979 adult Ophyra were most abundant at the carcass habitat on Days 3 and 4. This corresponds with the stage when the smell of carcass decomposition is at its peak, and an abundance of protein-rich organic fluid is available at the carcass. As the carcass dries, the number of Ophyra rapidly decreases, but a brief resurgance occurred on Days 8, 9 and 10 when rain drenched the carcass and rumen-content lying in the vicinity, releasing fresh odours which served as attractant for these flies. Figure 75 does reveal a diel preference period for visitation, but this is more clearly illustrated in Figure 80 and will be discussed later in this section. A total of 116 individuals were recorded at Carcass C during Jan/Febr, contributing 2,5% towards all adult Diptera at the site.

The number of adult Ophyra utilising Carcass C during May/June

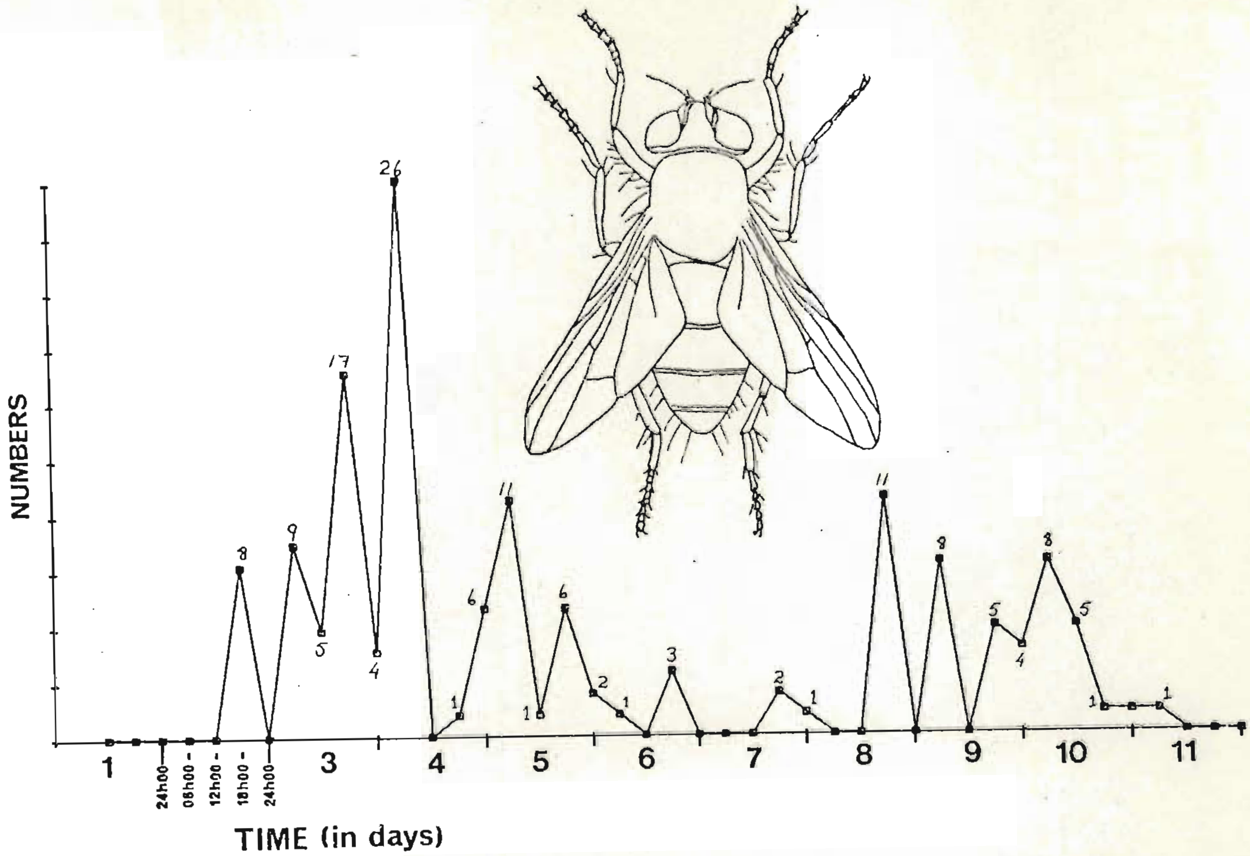


FIGURE 75: Number of adult Ophyra capensis (Muscidae) present at each collection period at Carcass C, Pafuri, 13th to 23rd January 1979, to show diel activity cycles

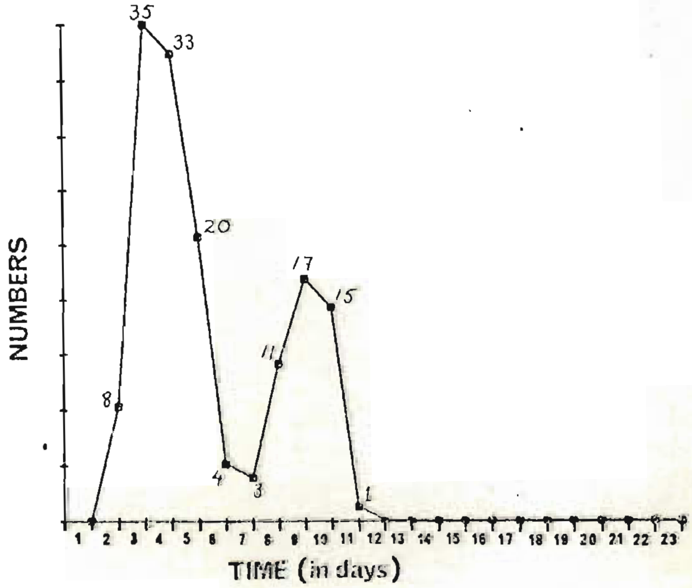


FIGURE 76: Daily totals of adult Ophyra capensis (Muscidae) present at Carcass C, Pafuri, 13th January to 4th February 1979

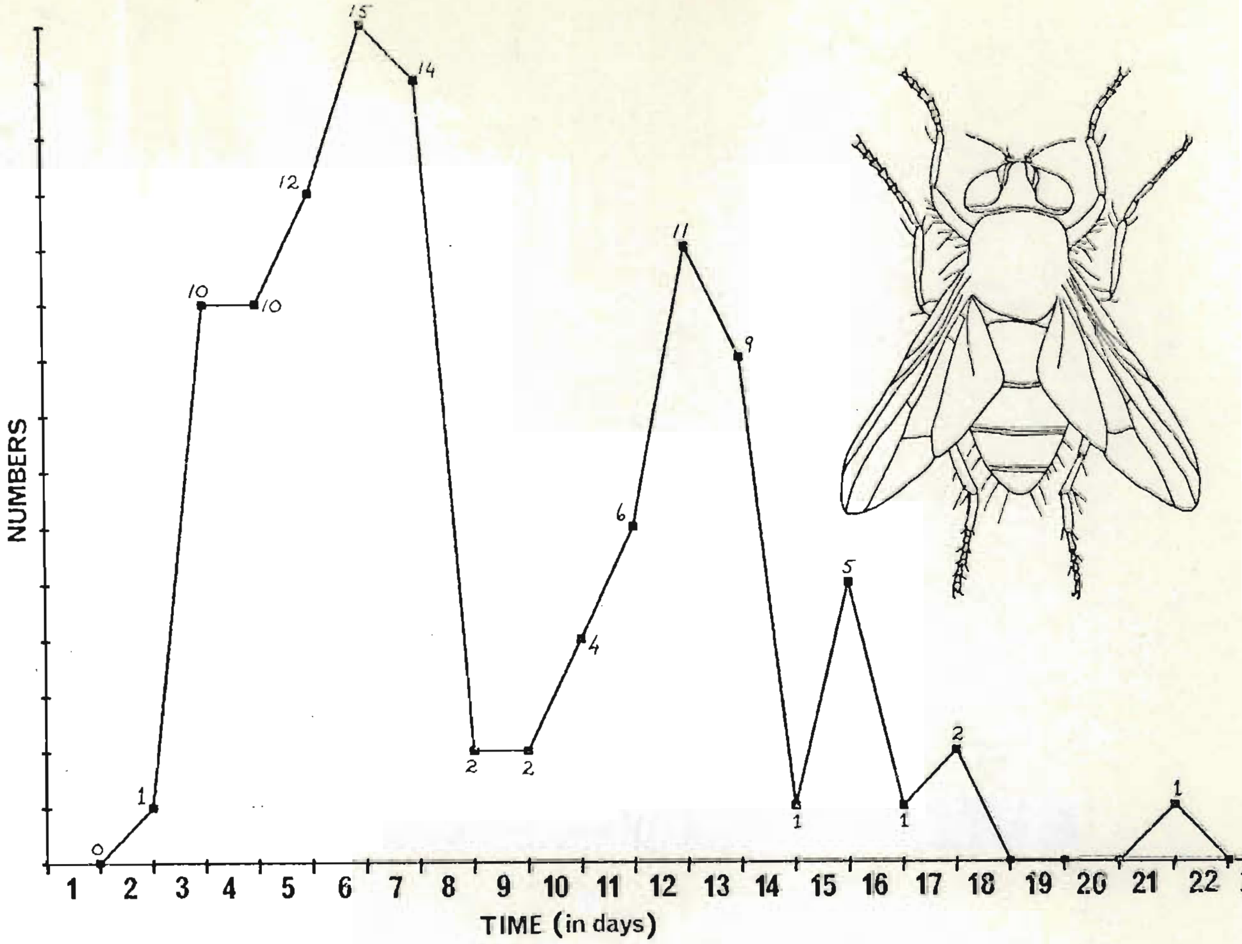


FIGURE 77: Daily totals of adult female Ophyra capensis (Muscidae) present at Carcass C, Pafuri, 18th May to 9th June 1979

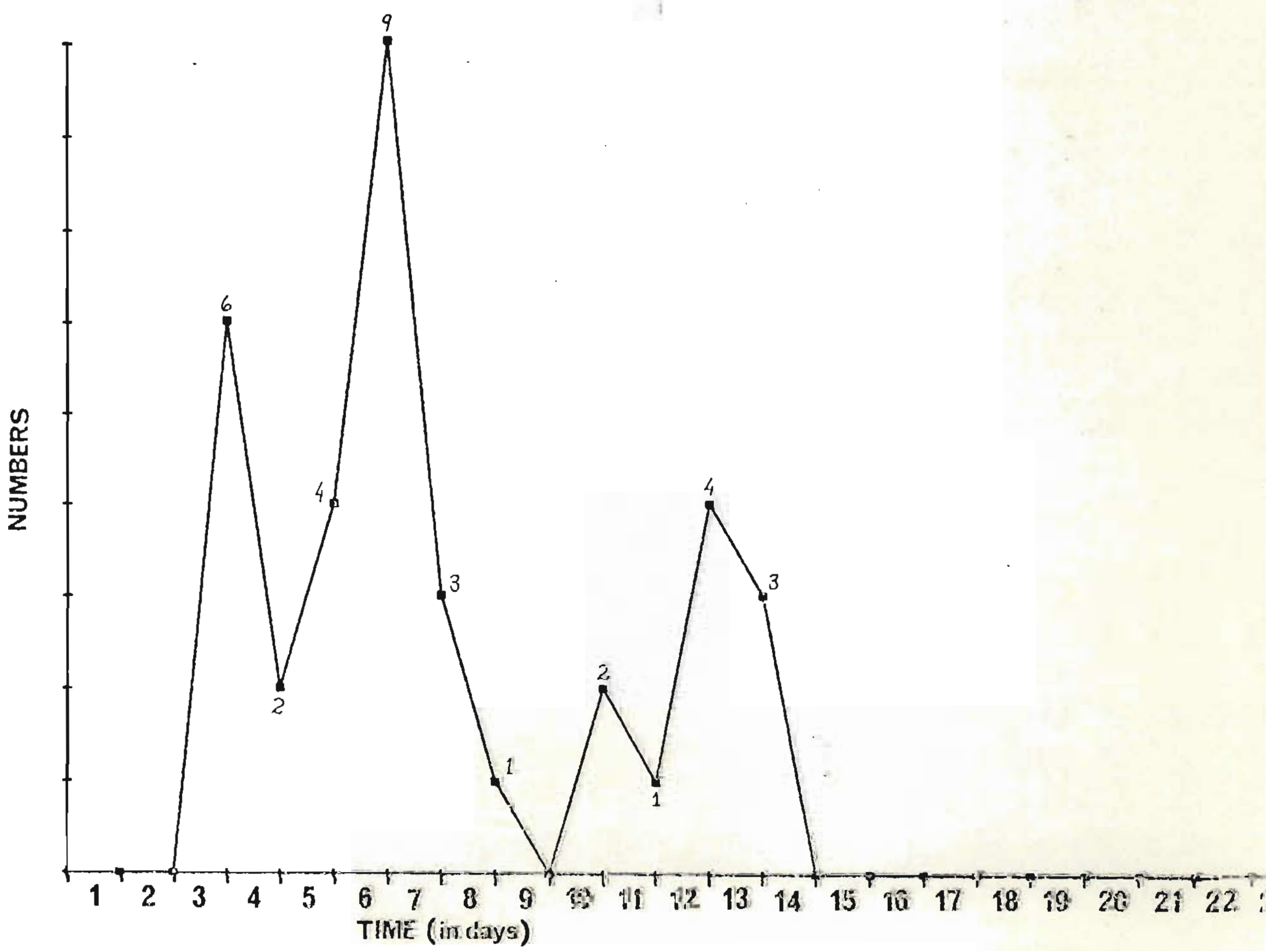


FIGURE 78: Daily totals of adult male Ophyra capensis (Muscidae) present at Carcass C, Pafuri, 18th May to 9th June 1979

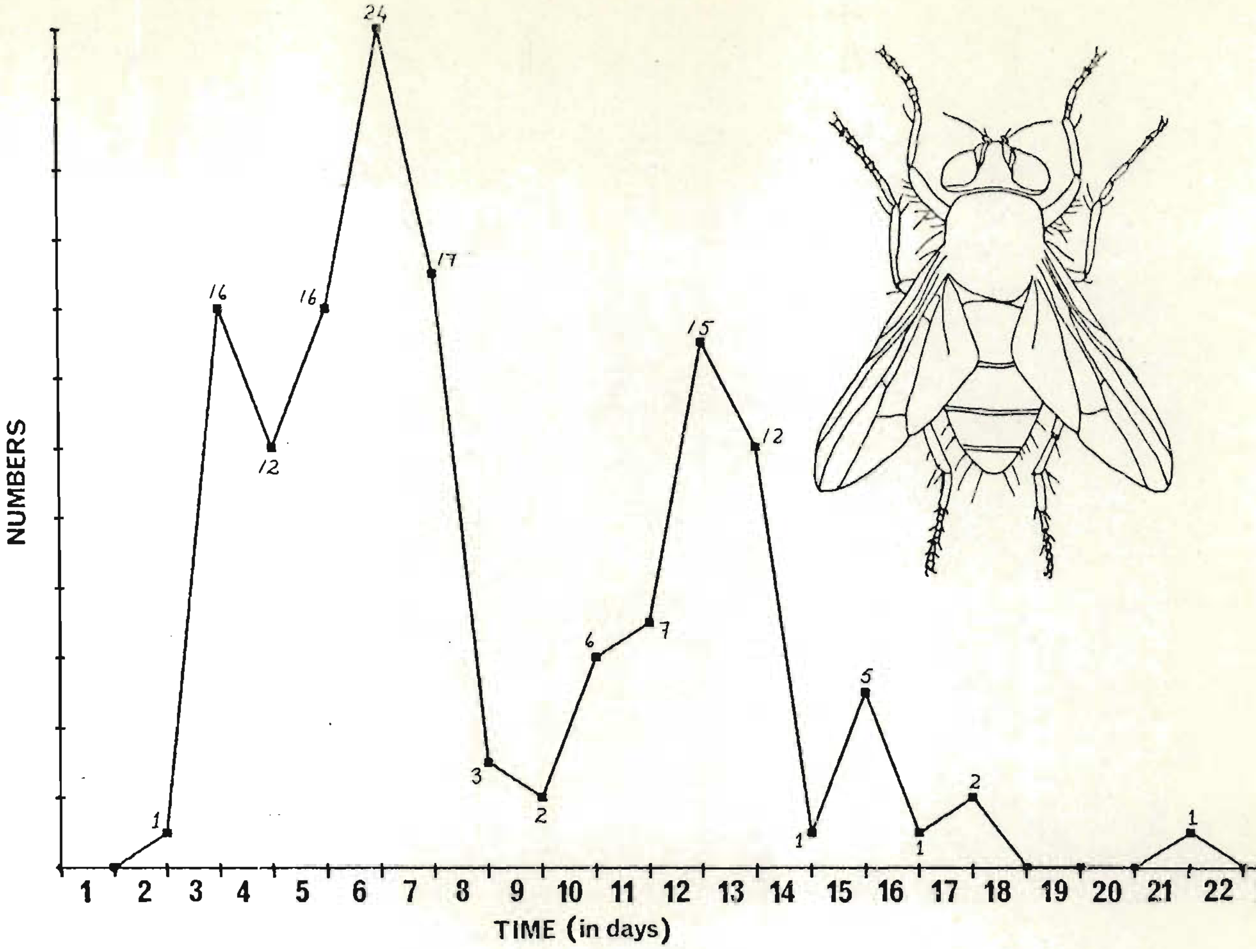


FIGURE 79: Daily totals of all adult Ophyra capensis (Muscidae) present at Carcass C, Pafuri, 18th May to 9th June 1979

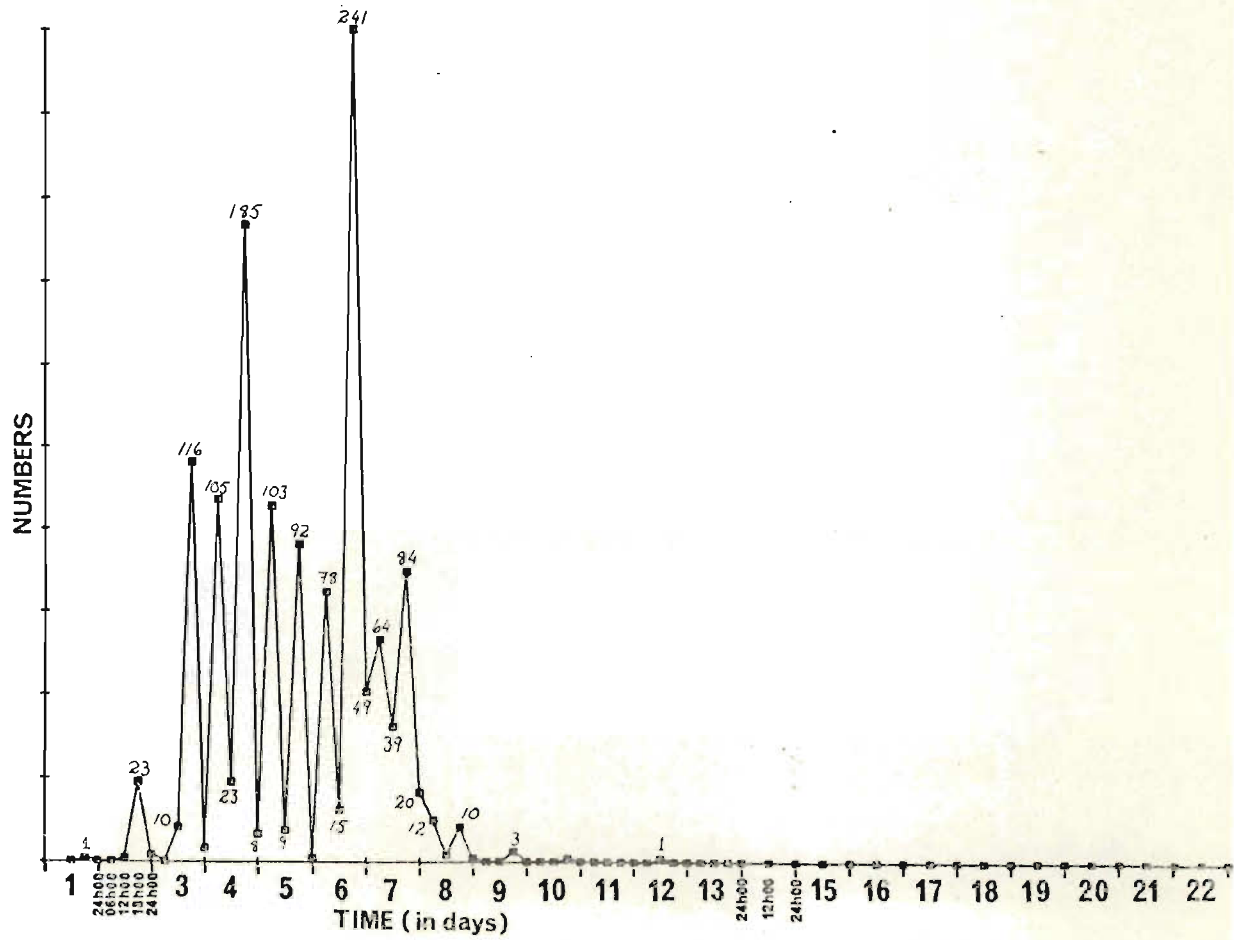


FIGURE 80: Number of adult Ophyra capensis (Muscidae) present at each collection period at Carcass C, Pafuri, 14th September to 6th October 1979, to show diel activity cycles

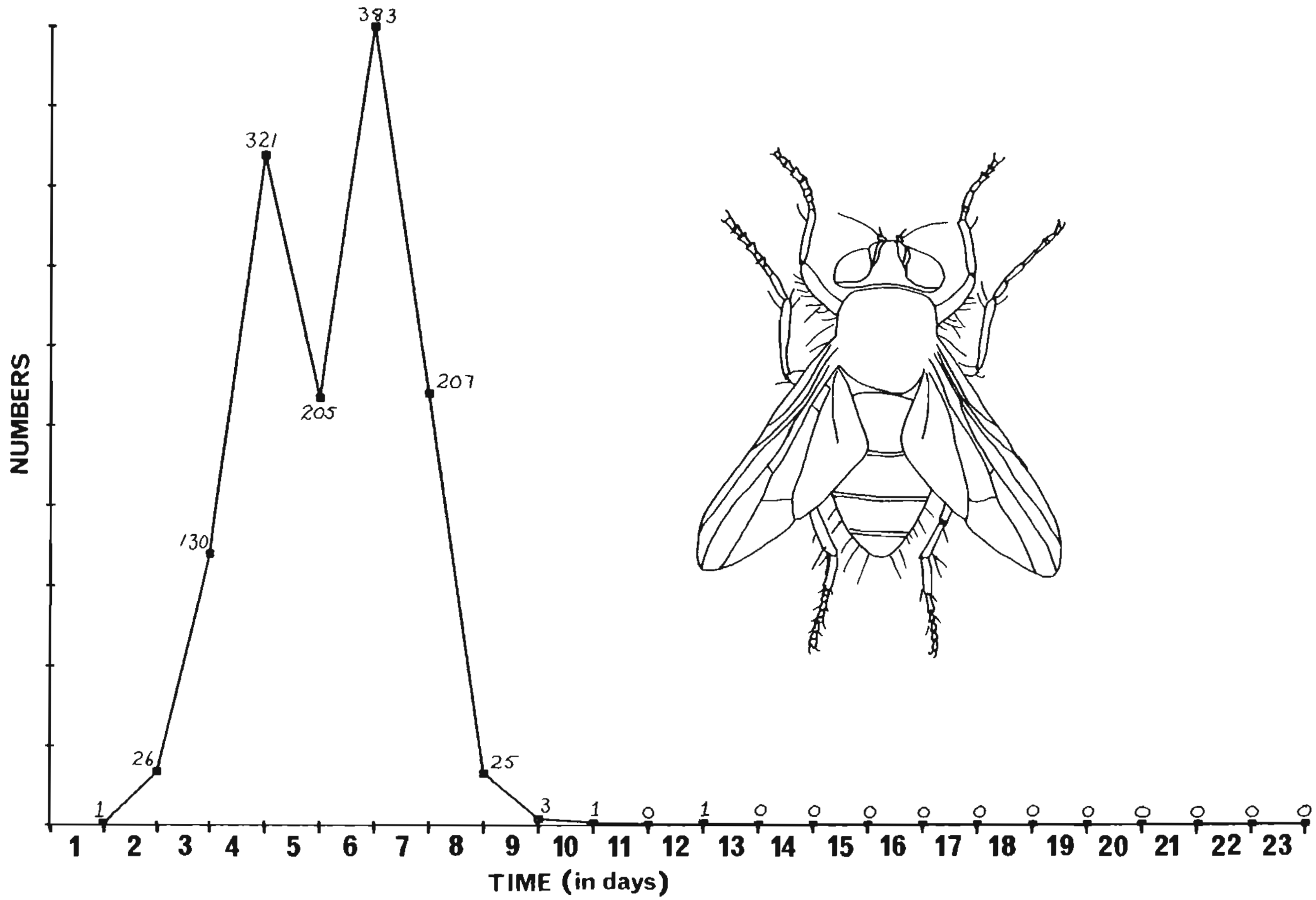


FIGURE 81: Daily totals of *Ophyra capensis* (Muscidae) present at Carcass C, Pafuri, 14th September to 6th October 1979.

was remarkably similar to that recorded in Jan/Febr., but the 141 individuals represented a greater proportionate contribution to the adult Diptera at the carcass, forming 7,05% of the total. Peak visitation occurred between Days 3 and 7 for the same reasons provided above, with a smaller peak on Days 12 and 13. No convincing explanation can be forwarded for this second peak, but it does seem related to a short spell of rain which fell on Day 9 - only measuring 2 mm in total but sufficient to soak the carcass and release distinct odours of decomposition.

By way of comparison with adult Chrysomyia blow-flies which show a clear segregation of peak visitation periods by the two sexes (Fig. 88, 90 & 92), separate counts were made of male and female Ophyra adults trapped at Carcass C during May/June to see whether a similar trend exists. Figure 77 indicates that many more females (106) attended the carcass-habitat than did males (35) (giving a 1:3,03 male : female ratio), but there is no evidence that the sexes had different preferential periods for carcass utilisation in the manner that blow-flies do.

Figures 80 and 81 reveal a fairly extended period of peak visitation by Ophyra adults during Sept/Oct. 1979, lasting from Day 2 through to Day 8 and coinciding with the stage when moisture is readily available at the carcass. Figure 80 clearly shows that Ophyra have distinct periods of preference within each 24-hour cycle for carcass utilisation. Daily bimodal peaks can be detected from Day 2 to Day 7, with most flies being present at dawn and especially dusk, but with a very reduced attendance at midnight and noon.

ORDER: DIPTERA
FAMILY: CALLIPHORIDAE

Other than that all adults are winged (Zumpt 1956) and most are robust and medium to large in size (Skaife et al 1979), it is difficult to make generalised statements concerning this very large family because of the widely divergent range of habits and habitats utilised by the member species. Many species are drab brown in the adult stage, some are an attractive orange, while a few have a resplendant metallic blue or green colour. Adults may be larviparous or oviparous and, depending on the species, the larvae may be saprophagous, coprophagous, necrophagous, haematophagous, or live as parasites on or in the bodies of vertebrates (e.g. *Lucilia* and *Cordylobia*) or invertebrates (e.g. *Calodexia* and some *Sarcophaga*) (Richards & Davies 1977).

Species recorded

The survey of carrion-frequenting insects visiting study-carcasses at Pafuri during 1979 yielded a total of 21 species and these are listed in Table 13. Of these only five species were ever present at any one carcass in numbers exceeding ten individuals in total over each 23-day monitoring period, these being *Chrysomyia albiceps*, *C. marginalis*, *C. putoria*, *Lucilia cuprina*, and *L. sericata*.

Lucilia sp. do become relatively abundant in late winter in especially the stunted Mopane-veld south of Pafuri, but they were never common at the Pafuri survey carcasses and never exceeded a total of 50 at any one carcass. Although they were not an important component of the carrion-complex at Pafuri, a summarised account providing some background and perspective of the two species of *Lucilia* recorded in the K.N.P. will be given later due to their considerable importance in other areas of the country, and the possibility that they may breed in carcasses for a limited period in winter in some areas of the K.N.P.

Chrysomyia putoria was also temporarily abundant on the fresh remains of a puff-adder (*Bitis arietans arietans*) snake near Pafuri Picnic Site, but these derived from an open-pit latrine nearby and never used the carcass for breeding, and were never again observed in abundance at other carcasses. Only a brief discussion will be presented on the calliphorids other than *Chrysomyia albiceps* and *C. marginalis*, the bulk of the continued discussion in this section then concentrating on the latter two species.

Biological notes on calliphorids at Pafuri, excluding Chrysomyia albiceps and C. marginalis

Sarcophaginae:

Although the Sarcophaginae is recognised by some authors as a family in its own right (e.g. Skaife et al 1979), it is retained here for the sake of convenience as a subfamily in accordance with the classification as used by Richards & Davies (1977) and Zumpt (1956, 1965, 1966). Also known as "flesh flies", most species are easily recognised by the abdomen and thorax being characteristically patterned in shades of grey, the shape of the body, and the buzzing noise in flight. The larvae of most species of Sarcophaga occur in decaying animal or vegetable matter, but some are parasites within insects and other animals (Richards & Davies 1977, Zumpt 1965). Despite being larviparous and generally depositing between 40 to 80 1st instar larvae on the breeding medium (Richards & Davies 1977), which should impart a competitive advantage to these flies compared to those laying eggs, I have never found larvae or even observed adults larvipositing on medium-sized to large carcasses. I have, however, on several occasions found sarcophagid larvae - in the absence of other calliphorid larvae - at small carcasses such as those of birds.

During 1979 I placed several such small carcasses for observation of the attendant insects, and found Sarcophaga nodosa to be a frequent breeder within the fresh remains of Helmeted Guinea-Fowl (Numida meleagris), Yellow-billed Hornbill (Tockus flavirostris), and once also in a 497g Puff-adder (Bitis arietans).

Calliphorinae, other than Lucilia:

Eight genera of the Calliphorinae were recorded. Auchmeromyia bequaerti is a larval parasite of warthogs (Phacochoerus aethiopicus) and antbears (Orycteropus afer). Adults are common at the burrow-entrances of these host animals (Zumpt 1965), but are rare visitors at carcasses. The genus Bengalia is well-known due to the unusual habit of the adults to rob food from ants, and are rarely present at carcasses. The larvae are predacious on termite reproductives (Zumpt 1956). Hemigymnochaeta is known only from the Ethiopian region, but aside from H. unicolor and H. varia which were reared from mushrooms and the fungus beds of termites (Zumpt 1956) nothing appears to be known of the biology of this genus.

Rhinia, Rhyncomya and Stegosoma do not utilise carcasses for breeding (Zumpt 1958) and were only recorded as incidental individuals infrequently observed at carrion. Rhinia apicalis is widely distributed and common in the Ethopian region, and the larvae are known to develop in the nests of Dorylus driver-ants, although they are apparently also associated with sand-wasps (Zumpt 1958). Rhyncomya spp. prey on termites and the larvae of Stegosoma have also been found associated with termites and ants (Zumpt 1958).

Two species of Tricyclea were recorded at carrion but never more than ten in total at any one carcass. As in the case of Hemigymnochaeta, very little data exists concerning the biology of this group, other than that one species (T. perpendicularis) deposits its eggs in the temporary nests of driver ants (Zumpt 1956). Specimens of Tricyclea are commonly seen in the Pafuri area and they are frequent visitors to blow-fly traps, but only in low numbers (pers. obs.).

Calliphorinae, Lucilia:
Identification and Systematic notes

The genus Lucilia occurs widespread over the world but is represented in the Ethiopian Region by only three species; Lucilia cuprina and L. sericata are distributed throughout this region but L. infernalis is not present south of the mountainous areas in Zimbabwe (Zumpt 1956). Superficially similar to Chrysomyia albiceps in size and appearance, L. cuprina and L. sericata can nevertheless easily be distinguished from that species by the lack of dark transverse bands across the abdominal segments, the black colour of the face, presence of many strongly-developed bristles dorsally on the thorax, and the narrower form of the body. The two species are widely spread over most continents (Zumpt 1965).

L. cuprina and L. sericata occur sympatrically in many areas and much controversy has arisen over the taxonomic status of these two morphologically near-identical flies (Ullyett 1945, Zumpt 1965, Meskin 1980). Taxonomic characters generally employed to separate the two species include colour of the fore femur, which is black or dark bluish in L. sericata and bright metallic green in L. cuprina (Zumpt 1956, Howell et al 1978). Ullyett (1945) however, correctly pointed out that in a batch of field material there is always a gradation in colouration so that many specimens cannot be relegated to one species or the other using this feature. He showed that the species interbreed readily, that the offspring are viable, and that colour in the F_2 progeny behaves as a Mendelian character with a 1:4:1 ratio. He also contended that hybrid forms appear on an appreciable scale in nature so that colour should not be regarded as a legitimate character for species separation.

Waterhouse and Paramonov (1950) examined additional characters and based on these stated that the two populations were distinct and valid species. This view has been generally accepted (e.g. Zumpt 1956, 1965, Howell et al 1978) but still raises unacceptable doubts as will be seen below.

In entomological texts providing keys to separate the two species (e.g. Zumpt 1956) L. sericata is stated to have 6 to 8 occipital bristles on each side of the head and the same number of setae on the humeral callus, while L. cuprina is held to have only one occipital and 2 to 4 humeral bristles in the corresponding positions. Specimens caught at Pafuri and identified for me by a leading taxonomic specialist in the group (Prof. F. Zumpt) revealed a variation in the number of bristles and setae so that this feature, like colour, also appears unreliable as a means of separating the two species. Meskin (1980, p.179) apparently shared this reluctance to accept the established view of the two species and asks: "Are they really each one species?".

With the above as background it should be clear that the validity of regarding L. cuprina and L. sericata as distinct species is still in doubt and deserves further investigation. For the purposes of this discussion however, L. cuprina and L. sericata will be treated as separate species.

Veterinary impact and areas of occurrence

Both populations of Lucilia are regarded as important veterinary pests which cause myiasis in sheep and result in serious economic losses in many wool-producing regions of the world (Howell 1975, Zumpt 1965). The adult flies are attracted to soiled or wet wool, especially around the buttocks and at the base of the horns, deposit the eggs at such sites, and the resultant larvae cause inflammation of the host skin due to the irritant action of their mouthhooks and the digestive enzyme secreted by the larvae (Smit 1931). The wool fibres become discoloured and at sites where maggot infestation is high the fibres drop out. Chrysomyia chloropyga has similar habits and causes the same cutaneous myiasis as described above, and C. albiceps has also been incriminated of this behaviour but on a lesser scale (Smit 1931).

The two species differ in their impact and importance as agents of so-called sheep-strike in their areas of occurrence. In Europe, L. sericata is very common and is most important as a myiasis-producing agent in living sheep (Salt 1932, Zumpt 1965). In the southern hemisphere such as in South Africa and Australia, L. sericata is abundant in urban and suburban districts, is rare or absent in rural areas, and is of minor importance in the sheep industry (Zumpt 1965). By far the most important myiasis-producing fly responsible for so-called sheep-strike in South Africa and Australia is L. cuprina (Hepburn 1943a, Zumpt 1965), and concern over the economic losses incurred has given rise to a considerable volume of work on this fly (e.g. Mönnig 1942, Hepburn 1943a, b, Mönnig & Cilliers 1944, Potgieter 1945, Norris 1964, Smith et al 1981).

Lucilia spp. in the K.N.P.

Relatively few Lucilia were recorded at the Pafuri study carcasses, with a maximum of 47 being recorded during the 23-day survey period in Sept/Oct. 1979. Analyses of blow-fly trap-catches during 1983, however, have revealed (Chapt. 6) that Lucilia do become relatively abundant from about August to October in the K.N.P.

Although both L. sericata and L. cuprina occur at Pafuri the latter species predominates by far, which supports to some extent the statement by Meskin (1980) that L. cuprina is "restricted" to rural habitats whereas L. sericata is "restricted" to disturbed, man-made habitats.

I have not found these flies breeding in any of the carcasses of more than 150 medium- and large-sized mammals examined throughout the K.N.P. This is in agreement with the findings of most carrion-workers (e.g. Hepburn 1943b, Mönnig & Cilliers 1944, Meskin 1980) in South Africa. It may be that Lucilia breeds opportunistically but in low numbers in some carcasses, but that they can only do so with a reasonable degree of success in the cooler months when competition with Chrysomyia is at a minimum. Even at peak abundance, however, they do not approach the population levels achieved by C. albiceps and C. marginalis, and during most months of the year they exist at a very low level. This aspect is more fully discussed later.

Chrysomyinae, other than Chrysomyia albiceps and C. marginalis

Five species of Chrysomyia were recorded from carcasses in the study area, of which only C. albiceps and C. marginalis are of importance. These two species will be discussed later in detail.

C. inclinata was encountered in very low numbers, the maximum at a particular carcass being six collected over a 23-day period in Jan/Febr. 1979. The fly is superficially very similar in appearance to C. marginalis, is widely distributed over the Ethiopian region but nowhere common, and although on very rare occasions it causes myiasis in wounds it normally breeds in carcasses (Zumpt 1965).

C. chloropyga and C. putoria were formerly regarded as conspecific although polymorphic (Zumpt 1956, 1965), but Paterson (1977) reviewed the relevant data and conclusively showed that two ecologically and morphologically separable species could be distinguished, C. chloropyga breeding in carcasses whereas C. putoria utilises pit latrines.

C. chloropyga has repeatedly been implicated as a myiasis-producing agent in sheep in South Africa (Hepburn 1943a, Smit 1929). The importance of this species varies considerably however, some authors stating that it is equal to Lucilia cuprina in its incidence of attack on sheep (Smit 1931, Smit & Du Plessis 1927), others that it ranks less in importance, such as Hepburn (1943a) who found that in 6% of cases studied C. chloropyga was the only invader but in 20% they were present in association with Lucilia larvae. The surveys of Mönnig and Cilliers (1944) produced no C. chloropyga at all amongst adults reared from maggots obtained from sheep. The probable situation is that C. chloropyga is a myiasis-producing fly but its incidence depends on opportunity, locality, time of year and various factors, and that it is less important than L. cuprina which consistently produces myiasis by the accounts of all the above authors.

C. chloropyga was a very rare visitor to carrion in the study area with no more than ten individuals in total being trapped at any carcass. I have found this species to become relatively abundant in spring further south in the K.N.P. (Skukuza), and at Onderstepoort and parts of the Cape Province they are well-known to breed prolifically in carcasses during winter when competition with C. albiceps and C. marginalis is reduced (Hepburn 1943b, Mönnig & Cilliers 1944). I have never found them breeding in carcasses in the northern K.N.P., and have only on a very few occasions trapped individuals in blow-fly traps placed throughout the study area.

Paterson (1977) stated that C. putoria is a major domestic pest in large areas of tropical Africa and northern Zululand, mainly due to its habit of breeding in pit latrines. My own experience confirms this finding, and I have occasionally observed many thousands of adult C. putoria emerging from larval infested open-pit latrines at the Pafuri Picnic Site and Pafuri Anthrax Camp. I have never found the species to breed in carcasses, although the adults do at times visit carrion for feeding. The only instance where they achieved abundance at carrion, however, was at the fresh remains of a 497g Puff-adder (Bitis arietans arietans) I had accidentally placed within 20 metres of an open-pit latrine at Pafuri.

Chrysomyia albiceps (Wiedemann)

A common species in the Ethiopian region (Zumpt 1956), C. albiceps acquired a reputation in South Africa as a myiasis-producing agent important in the sheep industry in especially the earlier part of this century (Smit 1931). In the 1920's the wool industry was exceeded in importance only by gold-mining, South Africa ranking fifth in the world in terms of the number of sheep possessed (Smit 1929), and the second largest producer of fine (Merino) wool (Smit 1931). Smit (1929) estimated that if sheep did not receive regular attention, 50% of the animals were likely to become infested with maggots, resulting in enormous losses of wool. Rising concern over the impact of so-called "sheep blow-flies" stimulated a considerable volume of research which was to continue for several decades. It soon emerged that three species were concerned, namely Lucilia cuprina, Chrysomyia chloropyga, and C. albiceps (Smit 1929, although he inadvertently referred to L. cuprina as L. sericata), with L. sericata occasionally also being involved but on a negligible scale (Hepburn 1943a). Of these L. cuprina and C. chloropyga were the most important causes of sheep-strike, with C. albiceps the least harmful (Smit 1931). The reduced importance of C. albiceps as a cause of larval infestation on sheep stems from the species not being a primary fly which initiates myiasis - such as L. cuprina and C. chloropyga - but will only deposit its eggs on an established wound infested generally with larvae of one or both of the other myiasis-producing species (Zumpt 1965, Howell et al 1978). With an increase in awareness among farmers of the problem and better prophylactic measures based mainly on the use of insecticides, the incidence of C. albiceps larvae decreased considerably (Hepburn 1943a, Mönnig & Cilliers 1944) to an extent where it is no longer a problem. Much useful work on the bionomics of this species resulted during the early investigations on sheep blow-flies, a noteworthy example being that of Smit (1931).

Distribution and Nomenclature

C. albiceps is widely distributed over Africa and Madagascar, spreading through the Mediterranean, southern Europe, and probably north-western India (Zumpt 1956, 1965). Confusion existed in the earlier part of this century with regard to a morphological and ecologically near-identical counterpart found in Australia and the Oriental region. Regarded at first as being conspecific with C. albiceps, this eastern population was later believed to be distinguishable by its chaetotaxy and genitalia (Holdaway 1933), and is still generally regarded as a separate species known as C. rufifacies (Marquart) (Zumpt 1965). Meskin (1980), however, reiterated Zumpt's earlier (1956) doubts as to their specific distinctness, and after investigating the degree of positive assortative mating by male choice experiments in the two species, the morphologies of the external genitalia of the males, morphologies of the immature stages, and a comparison of the life-histories and biologies, he concluded that the two should be regarded as subspecies of a single species.

C. putoria is also very similar to C. albiceps in appearance, but Holdaway in his 1933 publication showed the distinctness of this species.

Visitation patterns

Examination of Figures 82 to 87 indicate that of the three survey periods undertaken at Pafuri in 1979, C. albiceps were most abundant during September/October and least numerous in May/June.

C. albiceps is well-known to be a so-called secondary fly which normally arrives after other flies such as C. marginalis are already abundant (Hepburn 1943b, Howell et al 1978).

At Pafuri C. albiceps is generally preceded by C. marginalis, the only other blow-fly which attains abundance at carcasses in the area. Adults of C. marginalis arrive within a few minutes or hours - depending on season - after death of the animal, and C. albiceps follow some hours later. A previous study in the same area confirmed the above findings (Braack 1981).

During the Jan/Febr. survey in 1979, comparatively few C. albiceps were present on the first day (Fig. 82 & 83), but fly numbers increased to reach a peak on Day 3, dropping very rapidly so that no flies of this species were present as visitors from Day 5 onwards. They were present on Days 10-13 due to emergence from puparia of larvae having fed on the carcass, but these are not visitors to the carcass. Both C. albiceps and C. marginalis adults were only active during the hours of daylight, and Figure 82 reveals that soon after dawn at 06h00 C. albiceps flies were already arriving, increased steadily with a peak at 18h00, just before dusk. No adults were present on the carcass at

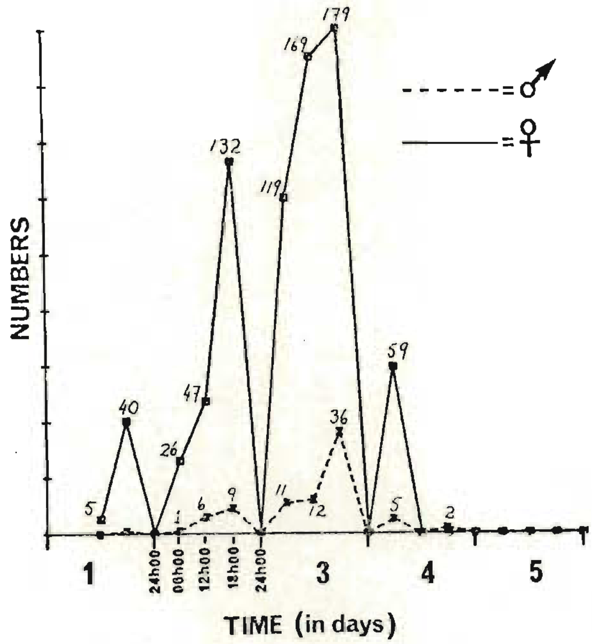


FIGURE 82: Number of adult male and female Chrysomyia albiceps (Calliphoridae) present at each collection period at Carcass C, Pafuri, 13th to 17th January 1979, to show diel activity cycles

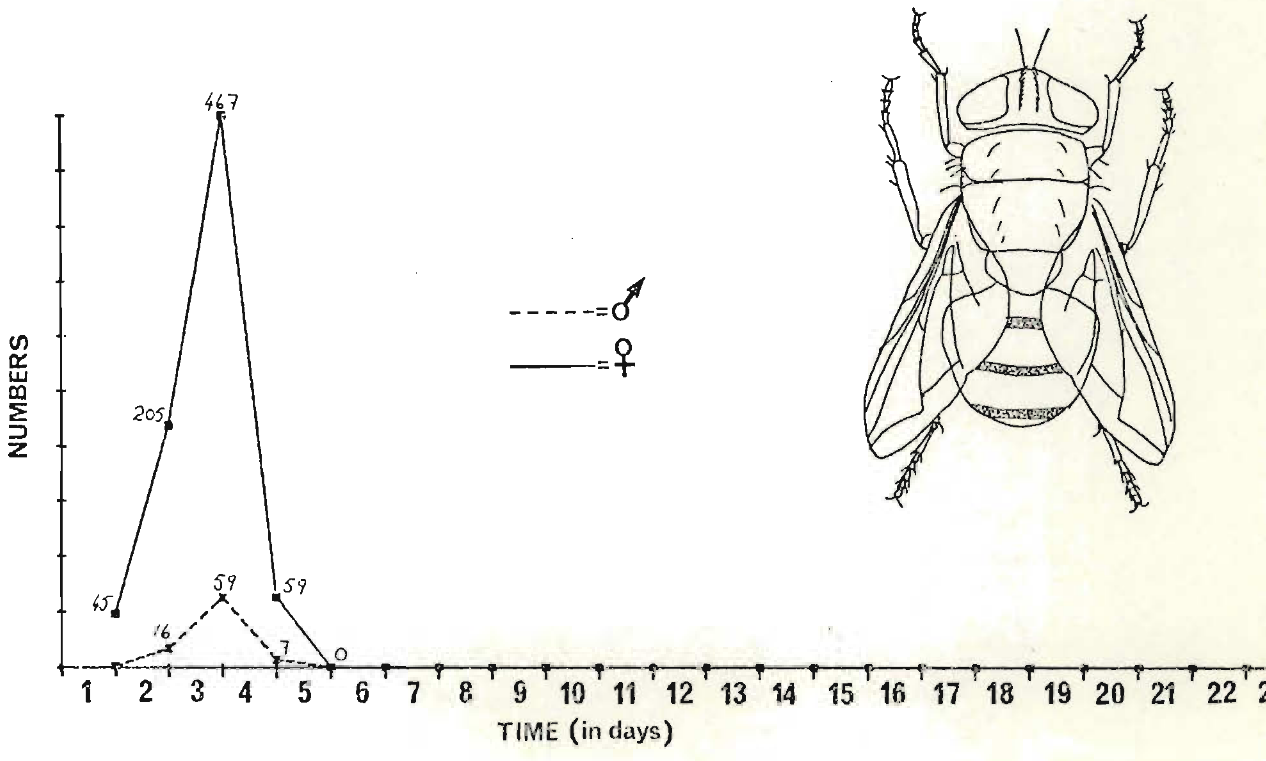


FIGURE 83: Daily totals of adult male and female Chrysomyia albiceps (Calliphoridae) present at Carcass C, Pafuri, 13th January to 4th February 1979

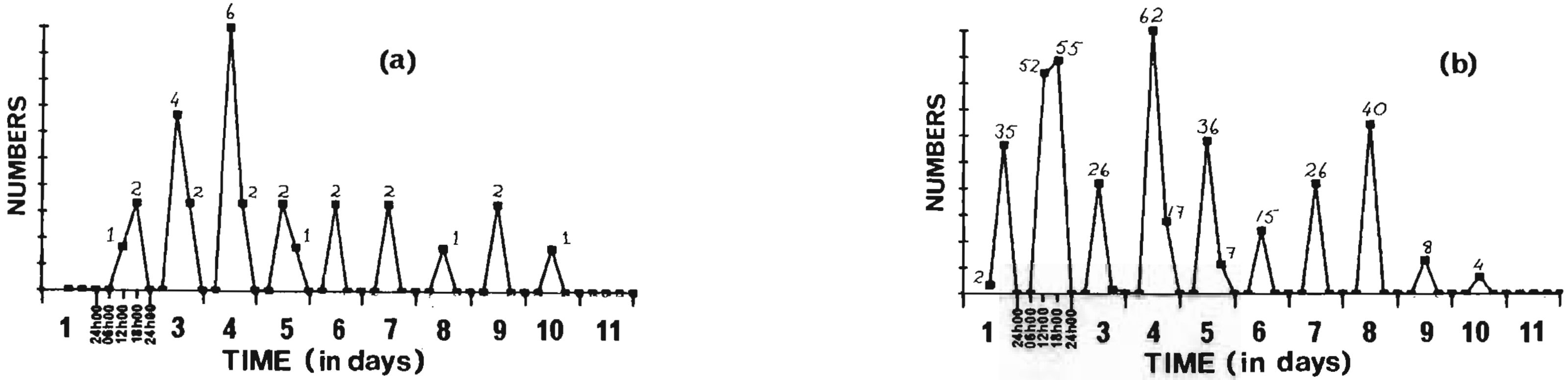


FIGURE 84: Number of adult male (a) and female (b) Chrysomyia albiceps (Calliphoridae) present at each collection period at Carcass C, Pafuri, 18th to 28th May 1979, to show diel activity cycles

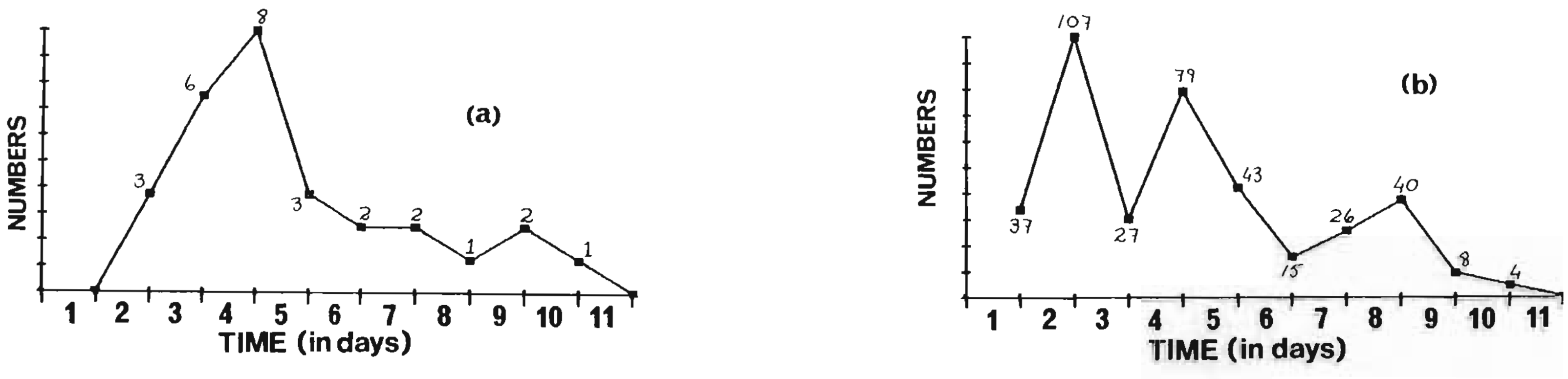


FIGURE 85: Daily totals of adult male (a) and female (b) Chrysomyia albiceps (Calliphoridae) present at Carcass C, Pafuri, 18th to 28th May 1979

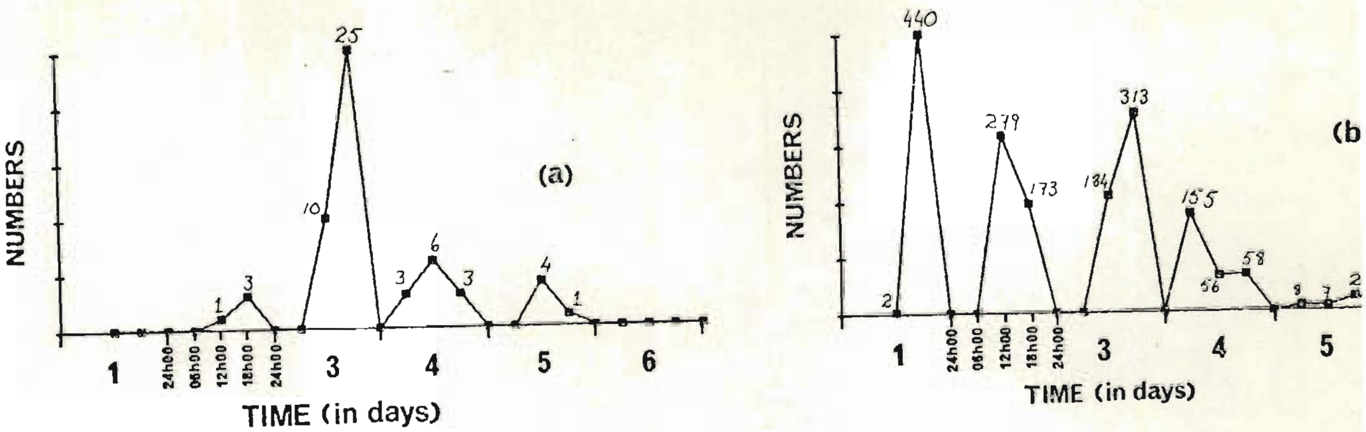


FIGURE 86: Number of adult male (a) and female (b) Chrysomyia albiceps (Calliphoridae) present at each collection period at Carcass C, Pafuri, 14th to 19th September 1979, to show diel activity cycles

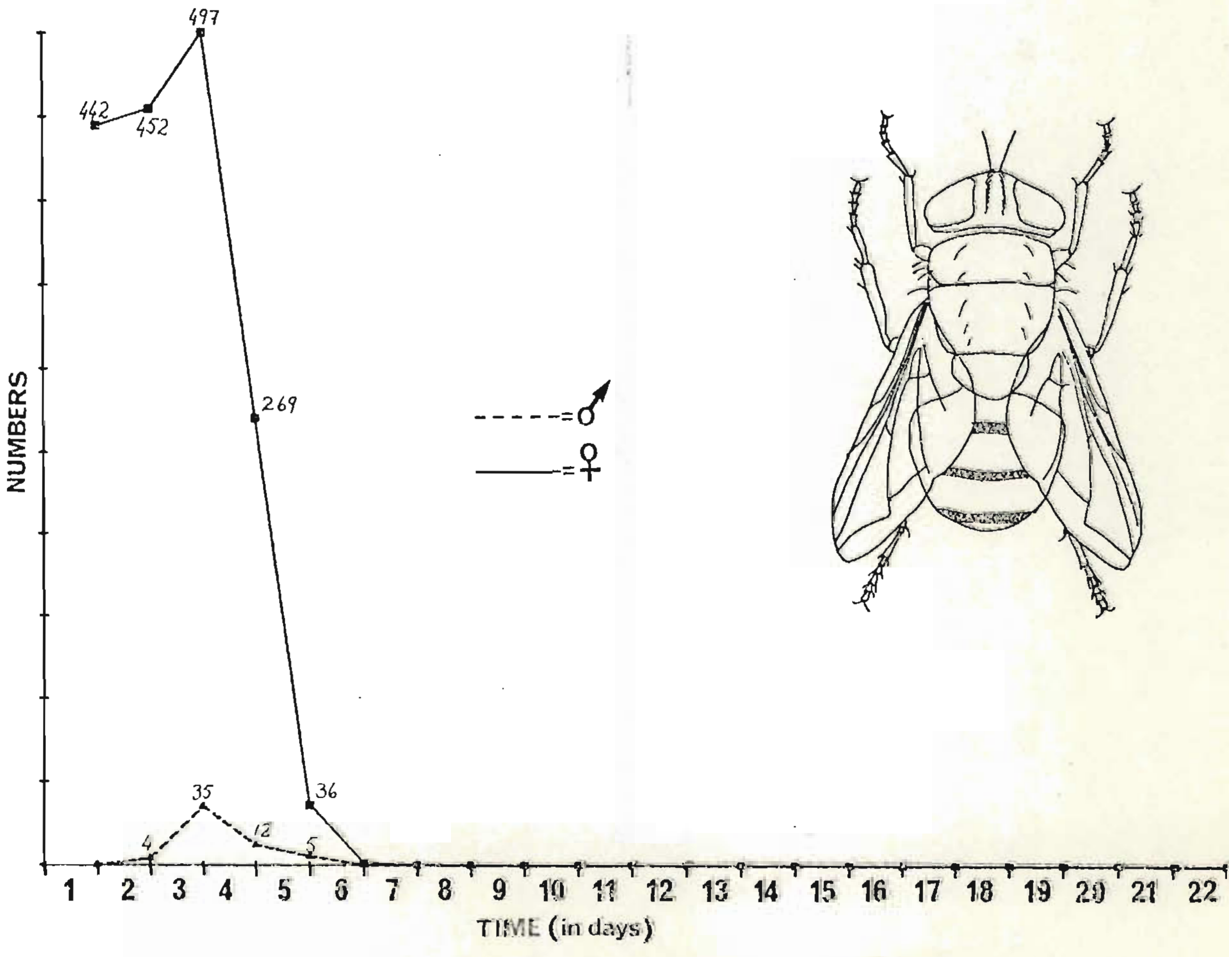


FIGURE 87: Daily totals of adult male and female Chrysomyia albiceps (Calliphoridae) present at Carcass C, Pafuri, 14th September to 6th October 1979

night, the flies settling on twigs and branches of shrubs and trees in the area, generally resting at a height between one and three metres above ground. A total of 859 C. albiceps adults were captured, but many more utilised the carcass between these sampling times or were present outside the radius of the net used to collect flies on the carcass.

The total of 850 flies represents 18,51% of all dipterous adults collected at Carcass C. Another interesting finding was that female flies predominated at a carcass, with 776 of the 859 being female, with only 83 males being recorded. This gives a ♂: ♀ ratio of 1:9,35. The female preponderance does have adaptive significance in that they require protein for maturation of the eggs, whereas the normal requirement for sustaining everyday life-activities is supplied by carbohydrates (Mackerras 1933, Rasso & Fraenkel 1954, Harlow 1956, Dethier 1976, Bowdan 1982). Males therefore do not have the urgent need - and from available evidence the strong drive - to consume blood or other protein-rich fluids present at carcasses. This preponderance of female blow-flies was a consistent feature throughout all the survey-periods.

With the cooler weather in May/June, carcass decomposition was slowed down, the rate of carcass dissolution was slower, carcass fluids were available for a longer period, and this was reflected in the longer period of visitation by C. albiceps adults (Fig. 84 & 85). Flies were present up to Day 10, with females having peak visi-tation on Day 2 and declining steadily thereafter, while males reached a peak on Day 4 (Fig. 85). Figure 84 reveals that a distinct diel visitation pattern is discernable, but differs from the previous survey in Jan/Febr. due to sunrise being much later and sunset much earlier than in summer. The timing of sample collection remaining the same, no flies were present at 06h00 (still relatively dark), peak numbers occurred at noon, with much reduced numbers present at 18h00 (almost dark). Only 414 C. albiceps adults were captured during the May/June survey. This was made up of 386 females and 28 males, giving a ♂: ♀ ratio of 1:13,79. The total of 414 flies represent 20,71% of all dipterous adults recorded at Carcass C.

A very rapid post-winter increase in the number of C. albiceps resulted in 1 753 adults being recorded in the Sept/Oct survey, being

10,87% of the flies at Carcass C. With the return of warmer weather and its effect on carcass decay, the period of visitation is again condensed so that C. albiceps adults were only present up to Day 6. Figure 87 reveals that peak visitation by both species occurred on Day 3 with a steep drop thereafter. A period of daylight activity is again easily discernable in Figure 86, but periods of abundance fluctuate between 12h00 and 18h00. The total of 1 753 adults recorded was made up of 1 697 females and only 56 males, giving a remarkable o : ^{o} ratio of 1:30,30.

Chrysomyia marginalis (Wiedemann)

As in the case of C. albiceps, the investigations in the first half of this century on the bionomics of sheep myiasis-producing flies provided a considerable amount of information on the biology of C. marginalis, despite it being known that this species did not produce larval infestation on living sheep (Hepburn 1943a; Mönnig and Cilliers 1944, Howell 1969, Howell et al 1978). Some confusion appears to have existed (and continues to exist) regarding the competitive role of C. marginalis larvae at carrion, some authors stating that C. marginalis larvae prevent the successful utilisation of carcasses by larval Lucilia and Chrysomyia chloropyga amongst other species (Hepburn 1943b, Mönnig & Cilliers 1944, Howell 1969), whereas Ullyett (1950) did not regard it as an efficient competitor of myiasis-producing flies. C. marginalis has occasionally been stated to cause myiasis (Zumpt 1956, 1965), but Zumpt (1966) contended that most such records were due to misidentification.

Distribution and Nomenclature

C. marginalis is a very common species in sub-Saharan Africa, and is also present in "Southern Arabia", India west of the Indies, and on Madagascar (Zumpt 1956, 1965). It was described in 1830 as Musca marginalis by Wiedemann, and in the same year as Chrysomyia regalis by Robineau-Desvoidy (Zumpt 1956, 1965). The species is widely known as Chrysomyia marginalis, although Prins (1982) referred to it as C. regalis without providing any reason. I have retained use of the more generally-accepted C. marginalis as this work may be referred to on occasion by persons more familiar with that name.

Visitation patterns

Hepburn (1943b) stated that C. marginalis is a very early arrival at carcasses in the Transvaal in summer, but is generally preceeded by Lucilia cuprina and L. sericata. My own findings during the present survey and in a previous study at the same site (Braack 1981) revealed negligible numbers of Lucilia spp. at carcasses in the Pafuri area and that C. marginalis is the first species of insect to arrive, generally within minutes after death of animals in summer and within an hour or slightly longer in the cooler months.

Of the three survey periods undertaken during 1979, C. marginalis adults were most numerous during Jan/Febr, with reduced numbers present in May/June, and only a low number being present in Sept/Oct. A total of 991 adults were recorded in Jan/Febr, representing 21,36% of dipterous adults encountered at Carcass C. As explained in the discussion on visitation patterns of C. albiceps, this only accounts for flies recorded at the four sampling periods within each day, and then only those flies which were on or immediately next to the carcass so they fell within the radius of capture of the net. The figures presented here are therefore only relative indexes reflecting absolute abundance to some extent.

As was found in the case of C. albiceps, a pronounced preponderance of females over males existed at the study carcasses, with 858 of the total 991 C. marginalis adults in the Jan/Febr. survey being females, giving a o : ^{o} ratio of 1:7,45. This preponderance of females is more fully discussed in Chapter 4.

All the flies recorded in Jan/Febr. were present between Days 1 and 4, none being recorded thereafter. Figure 89 also reveals that female attendance at the carcass peaked on Day 2 whilst males had a much lesser but nevertheless distinct peak on Day 3. Examination of Figure 88 shows clear diel visitation preference periods, with most adults being present in the early morning and late afternoon, with reduced numbers present at noon. No activity was recorded at night, the flies

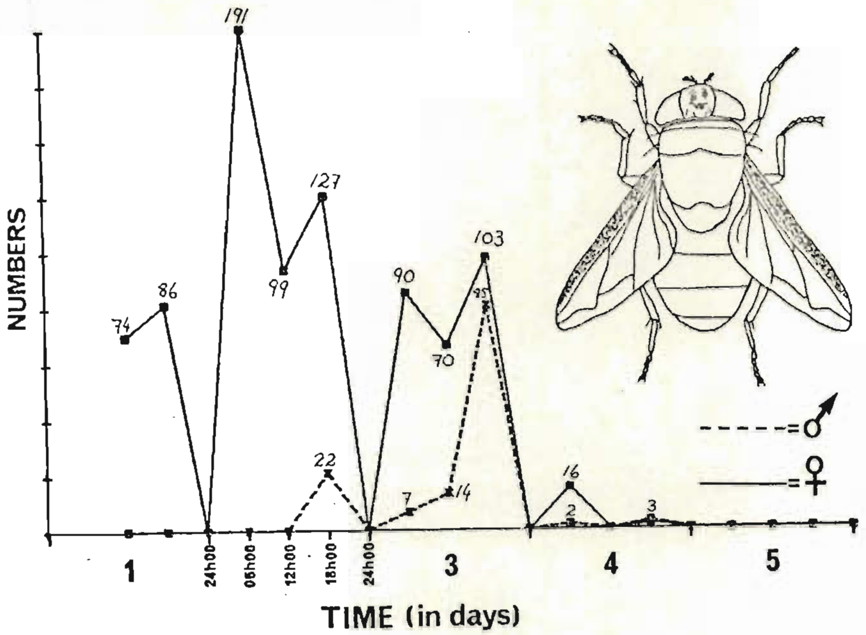


FIGURE 88: Number of adult male and female Chrysomyia marginalis (Calliphoridae) present at each collection period at Carcass C, Pafuri, 13th to 17th January 1979, to show diel activity cycles

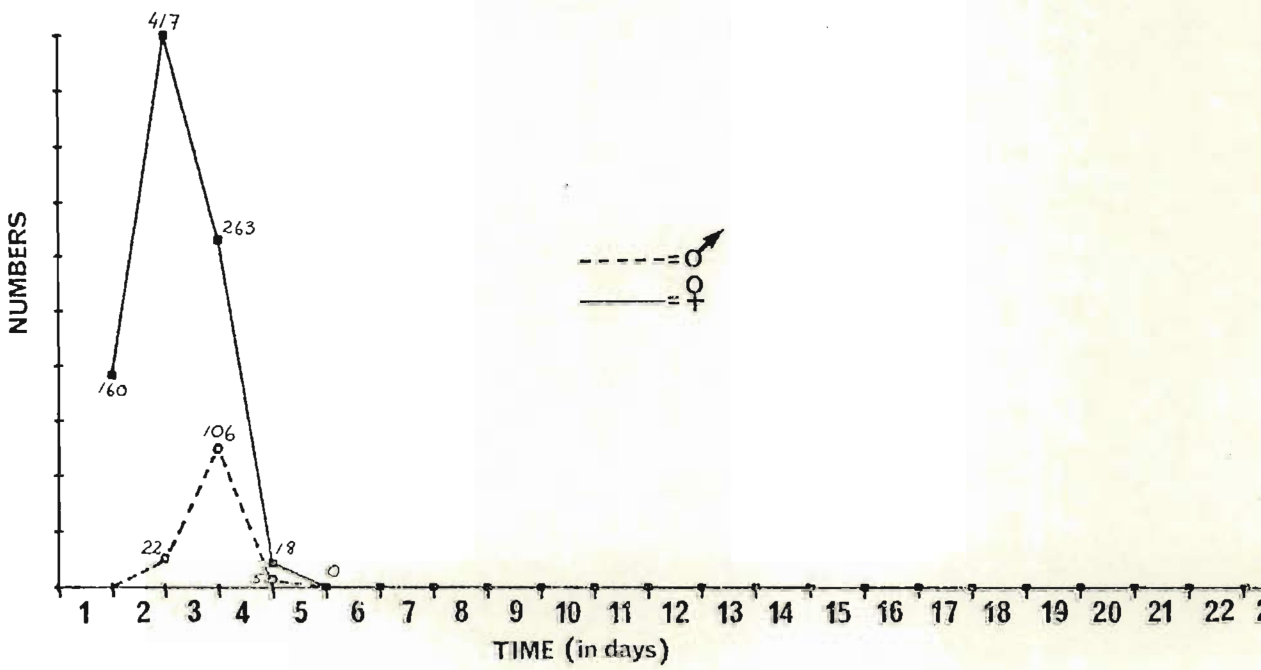


FIGURE 89: Daily totals of adult male and female Chrysomyia marginalis (Calliphoridae) present at Carcass C, Pafuri, 13th January to 4th February 1979

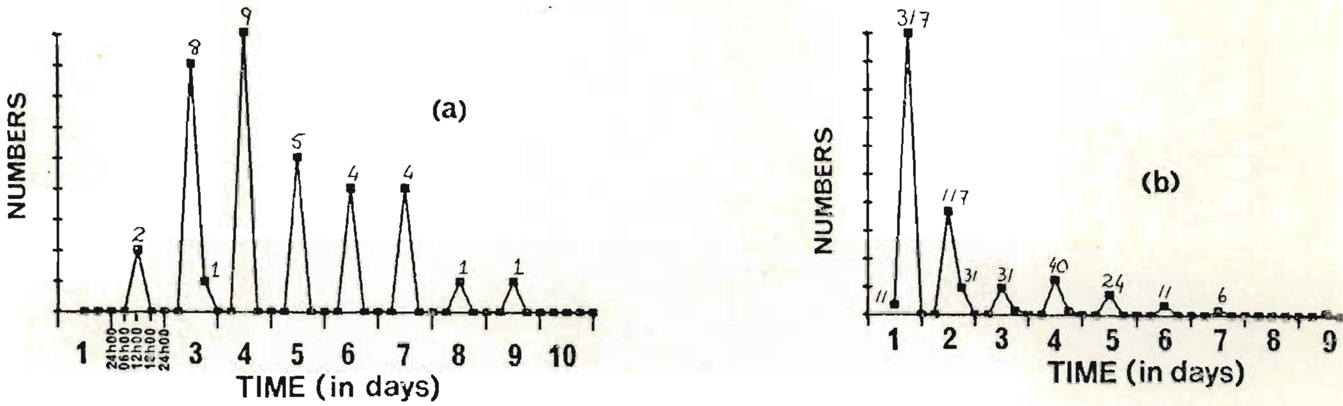


FIGURE 90: Number of adult male (a) and female (b) Chrysomyia marginalis (Calliphoridae) present at each collection period at Carcass C, Pafuri, 18th to 27th May 1979, to show diel activity cycles

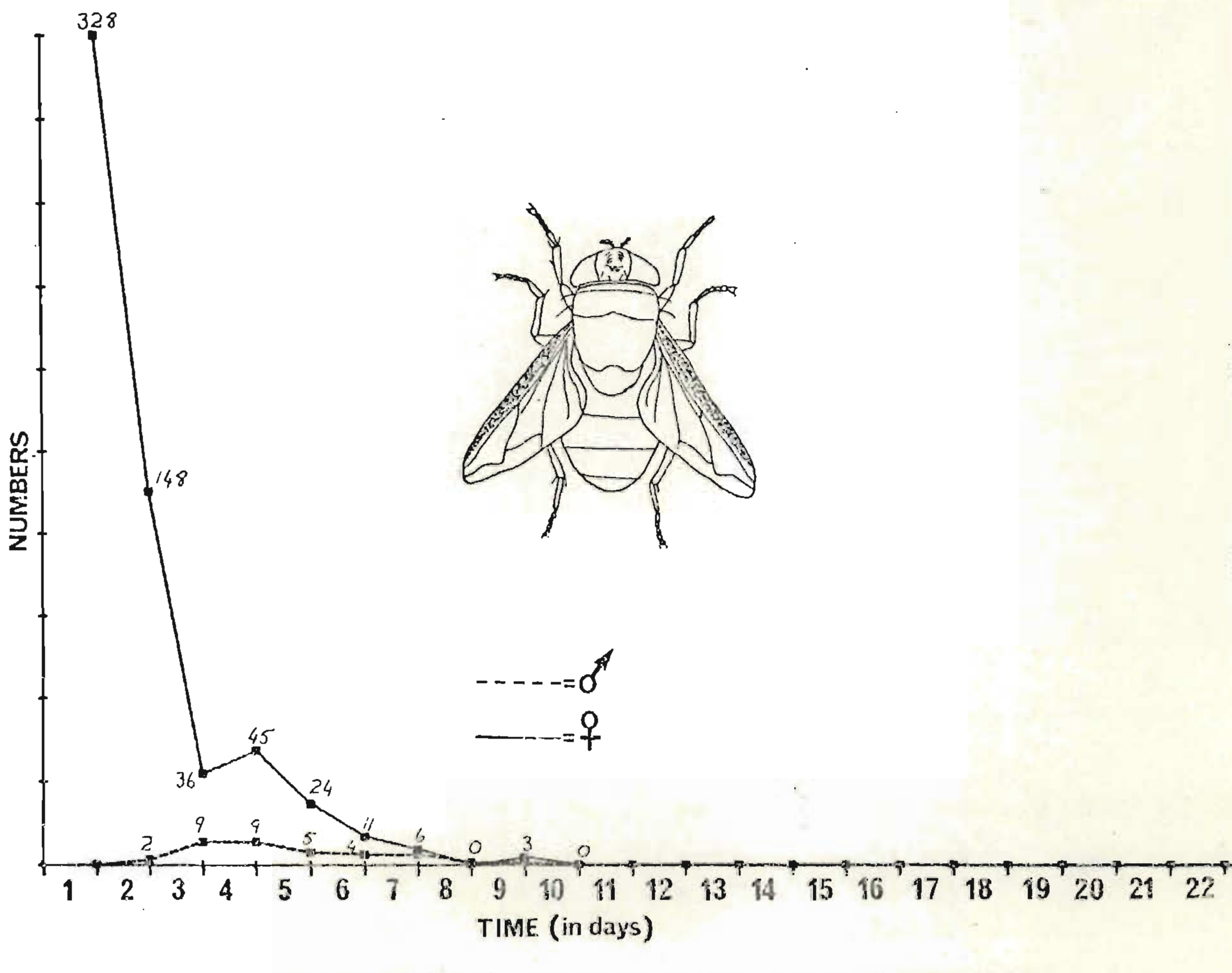


FIGURE 91: Daily totals of adult male and female Chrysomyia marginalis (Calliphoridae) present at Carcass C, Pafuri, 18th May to 9th June 1979

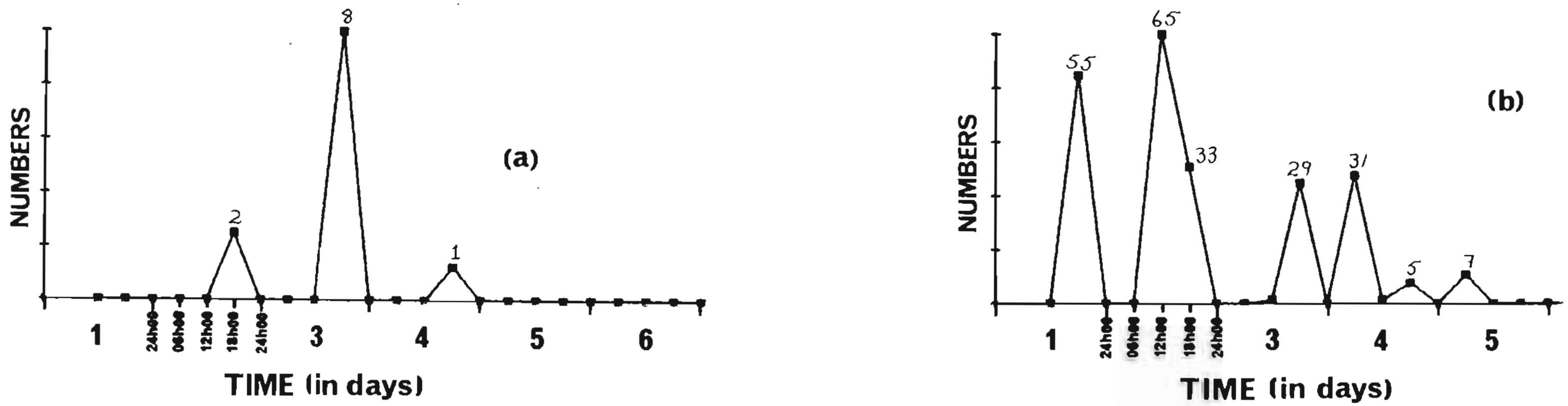


FIGURE 92: Number of adult male (a) and female (b) Chrysomyia marginalis (Calliphoridae) present at each collection period at Carcass C, Pafuri, 14th to 19th September 1979, to show diel activity cycles

FIGURE 93: Daily totals of adult male (a) and female (b) Chrysomyia marginalis (Calliphoridae) at Carcass C, Pafuri, 14th to 19th September 1979

resting on twigs and branches of shrubs and trees in the vicinity of the carcass in the same manner as C. albiceps.

Influenced in the same manner as C. albiceps by the decreased temperatures of approaching winter in May/June, C. marginalis had a more extended visitation period compared with Jan/Febr, with adults being present up to Day 9. Females had a distinct peak on Day 1 and tapered off rapidly thereafter, whilst males only reached maximum abundance on Day 4 (Fig. 90 & 91). Examination of Figure 90 shows that, as in the case of C. albiceps, few flies were present at the 06h00 and 18h00 collection periods due to the relative darkness at these times resulting from decreased daylength. Low temperatures especially in the early morning also inhibited their activity so that peak attendance was achieved at noon.

A total of 636 adults were recorded in May/June (31,82% of dipterous adults at Carcass C, this being made up of 601 females and 35 males, giving a ♂: ♀ ratio of 1:17,17.

Carcass attendance by C. marginalis adults in Sept./Oct. was very low, with only 238 adults in total being recorded (1,48% of dipterous adults at Carcass C). A female preponderance was again obvious, with 227 females as opposed to 11 males, giving a 1:20,64 ♂: ♀ ratio.

With warmer temperatures again reigning so that carcass decomposition is speeded up, adults were only present until Day 5, with a female visitation peak on Day 2 and males on Day 3 (Fig. 93). No clear visitation preference within the hours of daylight is discernable from Figure 92, although most flies did tend to be present at 18h00.

ORDER: LEPIDOPTERA
FAMILY: TINEIDAE

Most members of this widely distributed family are fairly small moths, and are generally some shade of yellow or white, speckled with dots, or mottled orange, sometimes brown or other shades (Pinhey 1975). The family is best known for the relatively few species of the genera Tinea and Tineola, popularly termed "clothes-moths", whose caterpillars devour holes in carpets and clothes (Pinhey 1975).

Species recorded

The 23-day monitoring periods at impala carcasses in 1979 were too short for moths of this family to make their appearance, but larvae were collected from the horns of a wide range of bovid species which had been lying in the field for many months. Dr. L Vari of the Transvaal Museum identified samples of the reared adults, and found them all to be Ceratophaga vastella (Zeller). He stated "However, I expect that there are certainly more of these horn-feeders in the Park, specially the closely-looking tragoptila (Meyrick)."

Biological notes on Ceratophaga vastella

Ceratophaga vastella (Zeller) occurs widespread in the Ethiopian Region and the larvae infest old horns lying in the veld, the pupae and cocoon debris eventually being extruded but remain attached to the horn as the moths emerge (Pinhey 1975). The ability of these and related moth larvae to consume and derive nutritive sustenance from the keratinous sheath is highly unusual in the animal world. Waterhouse (1957) provided some background on the resistance of the keratin protein to proteolytic enzyme attack and its relative insolubility in the usual protein solvents. He mentioned that keratin protein occurs in hair, feathers and other epidermal structures of vertebrates, and is "... characterised by a high, but varying content of cystine, the sulphur of which forms disulphide bonds between adjacent polypeptide chains. These disulphide bridges contribute greatly to the stability of the keratin molecule and, when they are destroyed, the protein becomes more soluble and more readily digested". He continued by saying that the only known animals able to digest keratin are the bird-infesting Mallophaga or chewing-lice, the larvae of some dermestid beetles, and the larvae of a few moths belonging, or related, to the family Tineidae.

Coe (1978) found that Ceratophaga vastella larvae also utilised the soles of the feet of elephant-carcasses in Tsavo (Kenya), and that these were in fact the main agents of removal of these long-persistent items. He made some interesting observations on the construction of the characteristic silken tubes of these larvae. Due to the great heat experienced at certain times of the day, larvae constructed tubes which penetrated the soil where it was cooler. The silken tubes which project upwards from the feeding substrate are only erected when pupation is about to occur, and they also use these aerial tubes as a thermo-regulatory device by moving up and down it according to temperature. The tubes also serve as protection against predators, and when the adult moths eventually emerge they do so relatively quickly.

Richardson (1980) found that when hyaenas consume parts or chips of bovid horns or hooves, these are passed out undigested in the faeces or regurgitated, so that tineid moths are likely to be the only agents responsible for the relatively rapid recycling of nutrients tied up in these body constituents.

Ceratophaga vastella at carcasses

The only consistent fact which emerged from observation of these moths at Pafuri is that they arrive fairly late to very late in the decay sequence of a carcass, but that they have no predictable time of arrival. Some horns lay untouched for many months before being attacked, whilst others in similar circumstances were infested within about two months.

The white, grub-like larvae have brown, well-sclerotised head capsules with well-developed, strong mandibles used for gnawing tunnels through the keratinous sheath of the horn. The tunnel inside the horn-sheath is lined with silk, and if the horn-sheath has separated from the underlying bone the larvae often extend the tunnel inwards by making a silk-lined, tough case. The tunnels are also extended outwards from the horn as characteristic tube-like projections. If these tough tubes are broken off the larvae inside immediately close off the resultant opening with silk strands.

Main sites of initial infestation of bovid horns are at the horn-bases and at contact-points with the soil. At a pair of fresh impala horns tied against a tree one metre above ground at Pafuri on the 7th March 1980, there were 170 larval tubes projecting from each horn on 16th November 1980 with only two adults having emerged. By December 1981 the entire keratinous sheath of each horn had been consumed so that only the inner bony core remained. Another pair of impala horns tied at the same time as the one described above and to the same tree at the same height - but on the opposite side of the stem fully exposed to the sun all day - did not have a single larval tube projecting from it by December 1981.

ORDER: HYMENOPTERA
FAMILY: PTEROMALIDAE

Comprising very small wasps with much-reduced wing-venation characteristic of the Chalcidoidea, this is the largest family in the superfamily and its members are parasites or hyperparasites of most other orders of insects (Richards & Davies 1977).

Species recorded

Only two species, Nasonia vitripennis (Walker) and Spalangia nigroaenea Curtis, were recorded.

Biological notes

Spalangia nigroaenea is well-known as a pupal parasite of several muscoid Diptera such as Musca, Stomoxys and Fannia, and is considered an important limiting agent of these flies in many countries (Legner et al 1967a, 1968). Despite the intensive survey of insects at carrion in 1979, and dissection or rearing of several hundred blow-fly and other puparia at various seasons throughout this study, only two specimens of S. nigroaenea were recorded, both being captured as free-flying adults. Legner et al (1967a, c) implied that this is mainly a parasite of dung-breeding flies, which may explain their near-absence at carcasses.

Discovered in Australia in 1913 and known at first as Nasonia brevicornis Ashmead and Mormoniella vitripennis Walker, this parasitoid was soon found to have a very wide distribution on most continents (Smit 1931). It is a gregarious species with a body length up to 2,8 mm (Legner 1967b) and its presence in South Africa - where it also occurs widespread and commonly - was first discovered in 1924 (Smit 1931).

A summarised account of its life-history is provided below, and, unless otherwise indicated, all details are derived from Cornell and Pimental (1978).

Up to 68 species of Diptera have been found parasited by these wasps, and only the pupal stage of the hosts is susceptible. The female wasp finds the host puparia by olfactory cues, and carefully examines the surface of such puparia by antennal palpation. If found suitable the female inserts her ovipositor into the pupa, feeds on exuding pupal fluids, and finally deposits her eggs within the puparium (Smit 1931). At 26,7°C, the entire life-cycle is generally completed within about lo to 12 days. The eggs hatch 12 to 24 hours after deposition, larvae geed and pass through 3 instars taking 4 to 5 days, pupate within the host puparium and remain in that state for a further 4-5 days before adult emergence. Adults exit through a single hole chewed through the puparial wall but multiple emergence holes are not unusual (pers. obs.). Females are sexually mature after 2 days and oviposition commences within 96 hours of adult emergence. Evans (1933) found that at 17,5°C the first instar lasts one day, the second instar two days and the third instar larva three days.

Of interest is that Nasonia vitripennis attack blow-fly puparia in preference to those of Musca (Cornell & Pimental 1978) or other flies utilising dung (Legner 1967, Legner & Gerling 1967). Also worthy of note is that there appears to be no host sex discrimination so that the sex ratio of emerged flies is not influenced by parasitism (Legner & Olton 1968). Legner (1967) stated that N. vitripennis is a comparatively weak searcher (i.e. not very good at finding host puparia) and that the wasps are incapable of detecting host puparia without physical contact. Successful parasitism is not the only contribution towards mortality of host pupae however, as general probing, feeding by the adult wasp and unsuccessful parasitism also account for additional deaths (Legner & Gerling 1967b).

Legner and Olton (1968) suggested that no justification exists for the use of N. vitripennis as a biological control agent on synanthropic flies such as Musca domestica, Stomoxys calcitrans and others, mainly due to their rare occurrence in these hosts. Smit (1931) also indicated the ineffectivity of this wasp to control blow-flies, due in main part to parasite attacks only being directed at puparia lying exposed above ground.

In a series of simple but very effective experiments, Ullyett (1950) showed that three species of carrion blow-flies, Lucilia sericata, Chrysomya chloropyga, and C. albiceps, differed in their suitability as hosts for Nasonia vitripennis, had corresponding levels of attraction for the parasitoid, and that these fly species had compensated for this difference in suitability by having different pupariation habits for added protection against parasitism. L. sericata is most favoured by Nasonia, C. chloropyga occupies an intermediate position, and C. albiceps is least attractive. Defending themselves against this prefenential attack, 98,87% of Lucilia larvae bury themselves soil and so effectively place themselves out of reach of these wasps, while in contrast only 43% of C. chloropyga and 1,27% of C. albiceps buried themselves.

Nasonia vitripennis

During the 1979 survey of carrion-frequenting insects no Nasonia were recorded in January or February, which concurs with previous findings at the same site (Braack 1981). Four specimens were found walking between C. albiceps puparia under impala Carcass B in May/June, these being present on Days 15, 16 and 20. During the 23-day survey period in Sept./Oct., however, 41 individuals were captured, with 38 of these recorded on Days 6, 7 and 8, and one individual on each of Days 10,13, and 18. The period of peak abundance between Days 6 and 8 coincided with the period of maximum availability of C. albiceps. C. marginalis also pupated on these days, but with the exception of a negligibly small fraction all the larvae buried themselves below soil in the area around the carcass and so escaped being parasitised.

Although only relatively few fly puparia were examined in 1979, a total of 561 C. albiceps and 579 C. marginalis puparia were kept in individual vials during 1980 and 1981. Trichopria lewisi (Hymenoptera: Diapriidae) were frequently reared as parasites from C. albiceps puparia, but no Nasonia were recorded from carcasses in the Pafuri area. From 12 Piophila (Diptera: Piophilidae) puparia collected on 30th May 1980 from the carcass of an adult elephant which had been dead for 40 days at Klopperfontein near Punda Maria, 8 were found to be parasitised by Nasonia vitripennis, each puparium yielding a single wasp. I have also found Nasonia to be a fairly common parasite in C. albiceps puparia in the Southern District of the K.N.P., whilst at Springbuck (Antidorcas marsupialis) carcasses in the Bontebok National Park (Swellendam) during March 1980, 47,56% of C. albiceps puparia were found to be parasitised (n=82). I suspect that the low numbers of Nasonia encountered at Pafuri during the present investigation was not a true reflection of their general abundance in the area over a long period of time. It might be that population numbers were temporarily depressed, or the wasps were attracted to other habitats and hosts more suitable at the time. It may be however, that climatic or other factors are not favourable for the existence of these wasps and made the Pafuri area a marginal habitat. Some support for this possibility is lent by the findings of Legner and Gerling (1967) that N. vitripennis requires a high surface moisture, and that lack of such moisture decreases longevity and productivity of this species. Pafuri falls within the region with the lowest average annual rainfall in the K.N.P., and may be below the threshold for conditions conducive to a sustained, viable population. Nasonia is nevertheless a potentially very important controlling agent of many fly species, and its status in the northern K.N.P. deserves further monitoring.

ORDER: HYMENOPTERA
FAMILY: DIAPRIIDAE

All members of this family are slender, small parasites, the majority of species laying their eggs in the larvae or pupae of Diptera (Bachmaier 1975).

Species recorded

Trichopria lewisi Nixon was the only species recorded at the study carcasses during 1979, and periodic searches for parasites in dipterous puparia at carrion since that time have not resulted in any additional species being found.

Biological notes on Trichopria lewisi

T. lewisi is a widespread species and I have collected specimens throughout the K.N.P., near Pietermaritzburg (Natal), and in the Swellendam area (Cape Province). Lars Huggert (pers. comm.) stated that *T. lewisi* has been reared in Kenya from *Glossina brevipalpis* and *G. fuscipleuris*, and in Tanzania from *Chrysomyia albiceps* and *C. megacephala*.

From a total of 561 *Chrysomyia albiceps* and 579 *C. marginalis* puparia examined mainly during 1980 to determine factors affecting pupal mortality, a total of 29 *C. albiceps* pupuria were found to be parasitised by *T. lewisi* (5,17%), with *C. marginalis* puparia not being utilised at all (Table 12). Because of their different pupariation habits, whereby *C. albiceps* pupal cases lie relatively unprotected above ground and *C. marginalis* burrows into the soil, it would be appropriate that *C. albiceps* should be more susceptible to parasitism.

By dissection of puparia or rearing to adulthood it was found that the number of *Trichopria* within each host-puparium varied between 17 and 44, with an average of 26 (n=14).

TABLE 12: Blow-fly puparia examined in the Pafuri area for parasitism by *Trichopria lewisi*

Date of carcass placement	Date fly puparia collected	Site of collection	Species of puparia	Number of puparia collected	Number pupar parasit
09-02-80	16-02-80	Above ground, randomly below and around carcass	*C. albiceps*	89	-
09-02-80	16-02-80	Below soil, 0,5 m radius from carcass	*C. marginalis*	103	-
17-02-80	26-02-80	Above ground among dried rumen content and bones	*C. albiceps*	103	-
17-02-80	26-02-80	3 to 10 cm below soil, up to 2 m radius around carcass	*C. marginalis*	122	-
12-05-80	27-05-80	Above soil immediately next to carcass	*C. albiceps*	100	-
12-05-80	27-05-80	Above soil immediately below	*C. albiceps*	100	12
12-05-80	27-05-80	Below carcass and partially buried in soil	*C. albiceps*	66	5
12-05-80	27-05-80	Above soil, within 0,75 m of carcass	*C. marginalis*	100	-
12-05-80	27-05-80	Below soil, within 2 m of carcass	*C. marginalis*	100	-
12-05-80	27-05-80	Above soil but immediately below carcass	*C. marginalis*	100	-
12-05-80	20-06-80	Below carcass (whilst examining undamaged, unemerged puparia)	*C. albiceps*	7	7
01-06-80	21-06-80	Above soil below carcass	*C. albiceps*	62	5
01-06-80	21-06-80	Below soil, within 1 m of carcass	*C. marginalis*	54	-
15-01-81	23-01-81	Below carcass	*C. albiceps*	34	-
		TOTALS	*C. albiceps* *C. marginalis*	561 579	29 -

Patterns of carrion attendance of *Trichopria lewisi*

Results obtained in the 1979 survey indicate that *T. lewisi* is rare in summer, increases during winter, and is relatively abundant in spring. During the 23-day survey period in Jan/Febr. 1979 only two individuals were captured (Day 9), a total of ten specimens were present between Days 11 and 23 during May/June, while 37 specimens were observed at Carcass B between Days 6 and 13 during the Sept./Oct. survey, with a definite period of maximum abundance on Days 6, 7 and 8 (16, 5 and 13 individuals respectively). These periods of visitation by *Trichopria* coincide very well with the stage when maximum numbers of freshly pupariated *Chrysomyia* were available.

ORDER: HYMENOPTERA
FAMILY: FORMICIDAE

All ants are embraced within this single very large and widely distributed family. They are distinguished from other Hymenoptera by the presence of a one or two-jointed petiole or pedicel between an anterior propodeum and posterior gaster (Skaife *et al* 1979). All the species are social and, with very few exceptions, have a well-differentiated worker-caste (Richards & Davies 1977).

Species recorded

Ten species were recorded during the 1979 investigations and are listed in Table 13.

Biology

Between 8 and 10 subfamilies are generally recognised in this very large family, and of these the Ponerinae is regarded as the most primitive (Richards & Davies 1977). The ponerine ants include some of the largest ants in Africa and all the workers are armed with a powerful sting. They tend to live in small colonies and are carnivorous (Skaife *et al* 1979). Of the two species of this group recorded at carrion in the study area, only *Megaponera foetens* numbered more than a few individuals at a carcass at any time. The species is also known as Matabele ants, are very common in the Pafuri area, and have foraging parties consisting of a few hundred individuals marching in highly organised columns in search of termites which form their prey (pers. obs.). Their presence at the carcass habitat was in each recorded case incidental in nature as a raiding party disturbed by wandering maggots, and after regrouping the ants would march off without preying on any insects at the carcass.

The Dorylinae are carnivorous and highly polymorphic with blind workers (Richards & Davies 1977). Also known as driver ants, the species are nomadic, do not construct permanent nests, and the workers search for food in leaf litter or just below ground as extensive foraging parties (Skaife _et al_ 1979). Two species of this group were recorded, with _D. fulvus_ being more common. In 1980 I witnessed many thousands of _D. fulvus_ workers present at a Day 3 impala carcass at Pafuri as a thick swath of ants around the perimeter of the carcass, picking off maggots which dropped from the carcass or strayed from the main body of maggots, but not venturing onto the carcass itself due to the intense wriggling activity of the blow-fly larvae. The ants made regular raids for two full days before departing.

The subfamily Myrmicinae is the most diverse and includes the most numerous of the ants in Africa (Skaife _et al_ 1979). The habits of the constituent members vary considerably, and although most are catholic in their diet, some are carnivorous whilst others are granivorous (Skaife _et al_ 1979). The most common members of this group at carrion at Pafuri were of the genus _Pheidole_, with _P. liengmei_ especially abundant. These ants were present in all stages of decay, opportunistically feeding on blow-fly eggs, scraps of muscle tissue and other carcass material, capturing small larvae or feeding at remnants of larger maggots left by predatory beetles, and even in groups attacking blow-fly adults during eclosion.

The genus _Camponotus_ belongs in the subfamily Formicinae, which is considered to be the most advanced of the subfamilies in morphology and behaviour (Skaife _et al_ 1979). _C. rufoglaucus_ was the only species recorded at carrion, but only as isolated and infrequent individuals.

In general it can be said that, unless present as the spectacularly concentrated mass of Dorylus fulvus mentioned above, the ants normally attendant at a carcass cannot have any considerable impact on the carcass itself or on the member-species of the carrion-complex of insects. The number of blow-fly eggs and young larvae carried off by the ants is small compared to that fraction which remains, and may even serve to lessen to some extent the intense competition for food which exists among the surviving larvae during the latter stages of growth.

Patterns of carrion-attendance

The ants utilising the carrion-habitat must be regarded as purely opportunistic attendents which do not present a consistant and clear pattern of visitation. Ants were present at nearly every collection period throughout the 23-day study in each season, varying from solitary stragglers to actively cooperating groups. The abundance of ants varied accordingly to the availability of food material, with peak numbers being noted during the early stages of carcass-decay when large numbers of blow-fly eggs and larvae were available. Ants were commonly seen carrying off eggs, and maggot remnants left by predatory beetles were soon removed by ants. Pheidole liengmei was the most common of the ant species recorded, but even at peak abundance they never numbered more than a few hundred individuals at most. Workers were commonly seen carrying blow-fly eggs and small larvae. Members of this species, together with others, were noted to occasionally co-operate in capturing on blow-fly adults emerging from their puparia, the teneral flies being overpowered by the ants.

CLASS: ARACHNIDA
ORDER: ACARINA
FAMILIES: ACARIDAE, MACROCHELIDAE AND PYGMEPHORIDAE

The Acaridae is essentially a family of free-living mites, many of which are pests of stored products, and some are known to cause allergic reactions in humans (Zumpt 1961).

Members of the Macrochelidae can generally be found in large numbers in the litter layer of soil, within dung, in compost, while some are associated with insects (Meyer et al 1973).

The Pygmephoridae contains mites parasitic on insects, and some species have been collected as adventitious and temporary parasites on moles and mice in Europe (Zumpt 1961).

Species recorded

Four species of mites were recorded at the study-carcasses, these being:

Acaridae: Lardoglyphus sp.
Macrochelidae: Macrocheles muscae-domesticae
Macrocheles n. sp.
Pygmephoridae: Pygmephorus sp.

Biology

The only occasion on which mites at Pafuri were commonly found and functioned as actual participating members of the carrion-complex was in rumen-content in early winter 1979. Specimens of these mites sent in for specialist identification showed that the only species involved were Macrocheles n. sp. and M. muscae-domestica. Axtell (1963) found the latter species and other Macrocheles to be very common in manure of dairy cattle, horses, sheep, chickens and ducks in New York (U.S.A.). M. muscae-domestica is known as an effective predator on house-fly eggs and first-instar larvae in manure and has been studied as a potential biological control agent of house-flies (Axtell 1963).

Lardoglyphus and Pygmephorus were recorded as incidental mites phoretic or parasitic on insects which visited the carcasses. Many mites were collected from flies and beetles where they were clinging to the bodies of these temporary hosts. Ophyra capensis (Muscidae) frequently carried mites, but other flies from which mites were frequently recovered included Siphunculina ornatifrons (Chloropidae), Piophila megastigmata and P. casei (Piophilidae), and Milichiidae and Sphaeroceridae. Macrocheles muscae-domesticae was a frequent phoretic mite especially on dung-beetles. This habit of some mites using transient habitats to rely on insects or other arthropods as a means of transport is well-known and ensures that the mites will be conveyed to a new resource (Mitchell 1970).

Patterns of carrion-attendance

The rumen-content drenched with carcass-fluid in May/June had a considerable number of small *Ophyra capensis* (Muscidae) larvae at a depth of about 2 cm, and it was in this layer that *Macrocheles* were most numerous. Mites were first noticed on Day 6 at Carcass B, and were a common sight by Day 12, retaining this status throughout the remainder of the study-period.

Although mites were retrieved from the bodies of flies and beetles in Jan./Feb. and Sept./Oct., none were observed below the carcasses in the extruded rumen-content. The activity-pattern of blow-fly larvae may be the deciding factor for the suitability of the rumen-content for oviposition by muscid-flies, which in turn will influence the attraction of this habitat to these mites. Unlike the cooler winter months, the activity of blow-fly maggots in summer and spring is more intense and their developmental period greatly shortened. The larger numbers and activity of maggots inhibits oviposition by muscids, and when the maggots depart - generally as a mass emigration within a relatively short space of time - the rumen-content rapidly dries which also leaves this habitat unattractive to muscids. The lack of fly-eggs would therefore render the carcass-habitat unattractive to *Macrocheles*.

INSECTS RECORDED IN LOW NUMBERS AND OTHER INCIDENTAL SPECIES AT CARRION

In addition to the main groups of insects already discussed, a number of others were collected at the carcass-habitat but in very low numbers so that they were not regular attendants at carcasses or true components of the carrion-complex. Their presence should therefore be regarded as accidental, incidental, or temporarily opportunistic. In many instances only ten individuals were recorded from carcasses over the entire period of the 1979 investigations, so that in some groups where difficulty was experienced in finding a specialist to identify the specimens only generic names were obtained and considered sufficient. Ten specimens was considered the minimum; any species recorded in lower numbers as a cumulative total at all carcasses used in 1979 were ignored. These included such arthropods as occasional grasshoppers, butterflies sipping moisture, wasps, solifugids, a scorpion, and several isolated spiders of different species.

Some of the main groups of such incidental species are briefly discussed below, the remainder being listed in Table 13. Unless otherwise indicated, the information on the general biology of these groups is derived from Richards and Davies (1977).

Order: Hemiptera
Family: Reduviidae

Also known as assassin bugs, most members of this rather large and widely distributed family are predacious on other insects. Four species were recorded, of which *Rhinocoris albopunctatus* and *R. violentus* were captured whilst feeding on *Chrysomyia albiceps* flies. *Fusius rubricosus* was present on several occasions, and I have noticed them commonly at elephant dung in the northern K.N.P., presumably preying on some of the dung-utilising fauna.

Order: Hemiptera
Family: Anthocoridae

This is a small family of small, predacious heteropterans which generally feed on other small arthropods. Only one species, *Xylocoris* (*Proxylocoris*) *afer*, was recorded, but I was unable to determine its feeding habits. Referring to a congeneric species, Dolling (1979 pers. comm.) wrote that "*Xylocoris*" (*P.*) *galactinus* (Fieber) in Europe feeds on a wide variety of small arthropods but especially (and particularly the younger instars) on mites. *X. afer* was common at times in the extruded moist rumen-content below the impala carcasses used at Pafuri, and mites were also present at this site so that these anthocorids may well have utilised the mites as prey.

Order: Diptera
Family: Asilidae

Frequently referred to as "Robber flies", these moderate to large elongate flies make up a large family of aggressive insect predators which attack their prey in flight. Eight species were recorded at the Pafuri study-carcasses, of which *Ommatius* spp. and *Hoplistomerus nobilis* was observed most frequently. All species were irregular and infrequent daytime visitors. *Neolophonotus* sp. was seen feeding on *Chrysomyia marginalis* flies.

Order: Diptera
Family: Phoridae

This is a large family of small to minute flies with an unusual hump-backed appearance. They vary considerably in habits, with some occurring in decaying vegetation, some parasitic in honeybee larvae (Rietschel 1975), others living within ant and termite colonies, and some living on dead animals. Four specimens were recorded at the Pafuri carcasses, although none were found to breed in the carrion. I found *Megaselia* commonly breeding in moist batches of dead *Chrysomyia marginalis* flies kept exposed at camp for drying and counting.

Order: Diptera
Family: Sepsidae

These are small to medium-sized flies which have an ant-like appearance and an unusual habit of waving their wings whilst walking. The larvae are saprophagous and are frequently found in dung. Four species of sepsids were noted at the Pafuri carcasses, always associated with moist rumen-content. Adults were frequently seen imbibing the brown rumen-fluids until their abdomens were distended. No breeding was recorded but this is to be expected due to the great activity of blow-fly larvae over the rumen-content and the secretion of proteolytic enzymes by these maggots which drench the rumen-content together with other carcass-fluids. The masses of predatory histerid beetles attracted by blow-fly larvae would also curtail breeding by these flies which normally breed in dung.

Order: Hymenoptera
Family: Sphecidae

This is a large family with several subfamilies of wasps, of which only the Nyssoninae will be considered here. This latter group is also large and its component members vary considerably in habits. Only one species, *Bembix olivata* Dahlbom, was recorded at Pafuri.

B. olivata are fairly large brightly-coloured wasps well-known in many parts of South Africa. They catch dipterous prey in flight and at times of peak blow-fly abundance such flies may account for 80 percent of prey captured, but drops to 5 percent or less as blow-fly numbers decrease (Ullyet & De Vries 1940). The wasps are polyphagous, capturing whatever flies happen to be abundant. Ullyett and De Vries (1940) found that although they probably have an important role in the natural control of blowflies at certain times of the year, the wasps are restricted to the relative proximity of sandy riverbanks due to their mode of nest construction, so that their impact is limited.

A total of eleven specimens were captured at the 1979 study carcasses, these arriving at irregular and infrequent intervals.

ABLE 13: Systematic listing of the Arthropoda attendant at carcasses at Pafuri and their status within the habitat

RDER / FAMILY / SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
ERMAPTERA												
Anisolabis sp.	< 10											*
Bormansia meridionalis Burr	< 10											*
Euborellia annulipes (Lucas)	< 10											*
EMIPTERA												
Reduviidae												
Fusius rubricosus (Stål)	< 10							*			*	
Lisarda rhodesiensis Miller	< 10							*			*	
Rhinocoris albopunctatus (Stål)	< 10							*			*	
R. violentus (Germar)	< 10							*			*	
Anthocoridae												
Xylocoris (Proxylocoris) afer Reuter	± 60							*?			*	
Scutelleridae												
Solenostethium liligerum Thunberg var. sehestedii (Fabricius)	< 10											*

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
COLEOPTERA												
Carabidae												
Metagonum sp.	< 10							*			*	
Platymetopus curtulus Peringuey	< 10							*			*	
Xenodochus melanarius Boheman	< 10							*			*	
Histeridae	)											
Acritus apicestrigosis Bickh.	)											
A. infimus Desb.	)											
A. rugosus Bickh.	)											
A. serratus Burg.	)											
Atholus geminus (Er.)	)											
A. ruptistrius Lew.	)											
Chaetabraeus echinaceus (Schm.)	)											
Chalcionellus amoenulus (Fahrs.)	)											
C. splendidulus (Schm.)	)											
Hister gehini Mars.	)											
H. ignavus Fahrs.	)											
H. tropicus Payk.	)20 662	Late						*		*		
Hypocacculus harmonicus (Mars.)	)	autumn										

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
H. metallescens (Er.)	)											
Pachylister caffer (Er.)	)											
P. nigrinus (Er.)	)											
Paratropus aptistrius Lew.	)											
Saprinus bicolor Fabr.	)											
S. cruciatus flavipennis Pering	)											
S. cupreus Er.	)											
S. intricatus Er.	)											
S. rhytipterus Mars.	)											
S. splendens (Payk.)	)											
S. strigil Mars.	)											
Silphidae												
Thanatophilus (Chalcosilpha) micans Fabricius	265	Summer		*				*		*		

ORDER FAMILY SPECIES		GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
				Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
Staphylinidae													
Aleochara bohemani B. and S.	)									*		*	
A. punctipennis Bernh.	)									*		*	
A. quadripunctata Cam.	)									*		*	
A. trivialis Kraats	)									*		*	
Aleochara sp. 1, 2 and 3	)									*		*	
Atheta sp. 1 and 2	)								*			*	
Erichsonius sp.	)								*			*	
Gabronthus sp. 1, 2 and 3	)	625	Summer						*			*	
Philonthus? aemulus Tott.	)								*			*	
P. bisignatus Boh.	)								*			*	
P. cinctus Fauvel	)								*			*	
P. labdanus Tott.	)								*			*	
P. reinecki Schub.	)								*			*	
P. sp. cf. minutus Boh.	)								*			*	
Philonthus sp. 1, 2 and 3	)								*			*	
Trogidae													
Trox melancholicus Fahr.	)					*	*	*	*	*		*	
T. mutabilis Haaf.	)					*	*	*	*	*		*	
T. radula Erichs.	)	1 422	Summer		*	*	*	*	*		*		

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermma-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
T. rusticus Fahr.)				*	*	*	*	*		*		
T. squalidus Ol.)				*	*	*	*	*		*		
T. tuberosus Klug.)				*	*	*	*	*		*		
Scarabaeidae												
Allogymnopleurus thallassinus Klug												
Anachalcos convexus Boheman	1 164	Summer	*	*	*						*	
Aphodius sp. 1 and 2												
Caccobius convexifrons Roth												
C. nigritulus Klug												
Catharsius philus Kolbe												
Copris amyntor Klug												
C. elphenor Klug												
C. evanidus Klug												
C. mesacanthus Harold												
Garreta nitens (Olivier)												
Gymnopleurus virens Erichson												
Metacatharsius opacus Waterhouse												

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	ASSOCIATION WITH CARRION HABITAT Consis-tant	Opportu-nistic	Inci-dental
Milichus sp. probably *apicalis* (Fahraeus)												
Onitis fulgidus Klug												
O. granulisetosus Ferreira												
O. inversidens Lansberge												
O. obenbergeri Balthasar												
O. picticollis Fabricius												
Onthophagus (*Proagoderus*) *dives* Klug)												
O. (P.) *rectefurcatus* Fairmaire)												
O. aeruginosus Roth.)												
O. anomalus Klug)												
O. carbonarius Klug)												
O. ebenus Péringuey)												
O. gazella (Fabricius))												
O. herus Péringuey)	5 670	Summer	*	*						*		
O. jeaneli D'Orbigny)												
O. lamelliger Gerstaecker)												

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
O. plebejus Klug)												
O. sp. near teitanicus D'Orbigny)												
O. vinctus Erichson)												
O. sp. fimetarius/leroyi complex)												
Pedaria sp.												
Phaeochrous madagascariensis Westwood	4 486	Summer		*			*			*		
Phalops ardea Klug												
Sarophorus costatus (Fahraeus)												
Scarabaeus ebenus Klug												
Sisyphus calcaratus Klug												
S. goryi Harold												
S. impressipennis Lansberge												
S. infuscatus Klug												
S. seminulum Gerstaecker												
Sybax distortus Schaum												
Tiniocellus spinipes Peringuey												

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
Dermestidae												
<u>Dermestes</u> <u>maculatus</u> De Geer	3 191	Late autumn		*	*		*	*		*		
Cleridae												
<u>Necrobia</u> <u>rufipes</u> (De Geer)	2 572	Summer		*			*	*		*		
<u>Phloeocopus</u> sp.	1	Summer						*				*
Nitidulidae												
<u>Carpophilus</u> nr. <u>quadrisignatus</u> Er.	<10											*
<u>Carpophilus</u> sp.	<10											*
PTERA												
Asilidae												
<u>Bactria</u> sp.	< 10							*			*	
<u>Euscelidia</u> <u>rapax</u> Westwood	< 10							*			*	
<u>Hoplistomerus</u> <u>nobilis</u> Loew.	< 10							*			*	
<u>Neolophonotus</u> (<u>Lophopeltis</u>) sp.	<10							*			*	

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
Ommatius sp.	< 10							*			*	
Stichopogon caffer Hermann	< 10							*			*	
S. punctum Loew.	< 10							*			*	
Empididae												
Crossopalpus n. sp. near *aenescens*	< 10											
Phoridae												
Hypocerides spinulicosta Beyer	< 10										*	
Megaselia curtineura (Brues)	< 10										*	
Megaselia sp. near *pauculitincta*	< 10										*	
Plethysmochaeta sp.	< 10										*	
Sepsidae												
Australosepsis niveipennis Becker			*								*	
Paratoxopoda depilis Walker			*								*	
Xenosepsis sp.			*								*	

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
Piophilidae												
Piophila casei (Linnaeus))	5 849	Spring		*						*		
P. megastigmata McAlpine)				*						*		
Lauxaniidae												
Cestrotus n. sp.	<10											*
Homoneura (*Keisomyia*) n. sp.	<10											*
Curtonotidae												
Curtonotum cuthbertsoni Duda	<10											*
Sphaeroceridae												
Coproica demeteri Papp)			*								*	
C. ferruginata Stenh.)			*								*	
Coproica sp.)			*								*	
Copromyza (*Borborillus*))			*								*	
marginatus Adams)												
C. (*B*) *sarcophaga* Papp.)			*								*	

RDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	ASSOCIATION WITH CARRION HABITAT Consis-tant	Opportu-nistic	Inci-dental
C. (*Gymnometopina*) sp.)			*								*	
Elachisoma braacki Papp)			*								*	
Limosina (*Bifronsina*) *bifrons* Stenh.)	223	Spring	*								*	
Limosina sp. 1 and 2)			*								*	
Lotobia sp.)			*								*	
Poecilosomella angulata Thom.)			*								*	
Ephydridae												
Chlorichaeta albipennis (Loew.)	< 10										*	
Discomyza eritrea Cresson	< 10										*	
Mosillus beckeri (Cresson)	< 10										*	
Chloropidae												
Apotropina n. sp.												
Chloropsina sp.												
Conioscinella sp. 1, 2 and 3												
Oscinella sp.												
Siphunculina ornatifrons (Lw)	250	Spring					*					
S. punctifrons (Sabr.)												
Siphunculina sp.												

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	ASSOCIATION WITH CARRION HABITAT Consis-tant	Opportu-nistic	Inci-dental
Milichiidae												
Desmometopa m-nigrum (Zett.)												
Leptometopa latipes (Mg.)			*									
Leptometopa n. sp.												
Meonura n. sp.	2 574	Spring					*					
Milichiella lacteipennis (Lw)			*				*				*	
Muscidae												
Atherigona aberrans Malloch)												
A. naqvii Steyskal)	1 289	Summer	*	*			*				*	
A. steeleae Emden)												
Atherigona spp. indet.)												
Fannia leucosticta Meigen	1											
Graphomya leucomelas Wiedemann	1											
Gymnodia mervinia												
Gymnodia tonitrui Wiedemann												
Haematobosca latifrons Malloch	1											
H. spinigera Malloch	6											

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
H. thirouxi ssp. potans Bezzi	7											
Morellia nilotica Loew	3											
Musca conducens Walker)												
M. domestica ssp. calleva Walker)												
M. domestica ssp. curviforceps)												
Sâcca and Rivosecchi)	3 129	Spring	*	*			*				*	
M. lusoria Wiedemann)												
M. sorbens Wiedemann)												
M. xanthomelas Wiedemann)												
Ophyra capensis Wiedemann	1 303	Spring	*	*			*	*			*	
Stomoxys sp. indet	1											
Stygeromyia maculosa Austen												
Calliphoridae												
Auchmeromyia bequaerti Roubaud	< 10								*			*
Bengalia sp.	< 10							*			*	

RDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
Chrysomyia albiceps (Wd.)	1 753	Spring		*				*		*		
C. chloropyga (Wd.)	< 10			*					*	*		
C. inclinata Walker	6			*								
C. marginalis (Wd.)	991	Summer		*						*		
C. putoria (Wd.)	< 10		*				*				*	
Hemigymnochaeta incerta Zumpt	< 10											*
H. unicolor (Bigot)	< 10											*
Hemigymnochaeta spp.	< 10											*
Lucilia cuprina (Wd.))	47	Winter		*					*		*	
L. sericata (Mg.))				*					*		*	
Rhinia apicalis (Wd.)	< 10											*
Rhyncomya forcipata	< 10											*
Sarcophaga haemorrhoidalis (Fallén)	< 10			*							*	
S. hirtipes (Wd.)	< 10			*							*	
S. nodosa Engel	< 10			*							*	
Stegosoma vinculatum Loew.	< 10											*
Tricyclea semicinerea Bezzi	< 10											*
Tricyclea sp.	< 10											*

RDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
EPIDOPTERA												
Tineidae												
Ceratophaga vastella (Zeller)	>300	All year				*				*		
YMENOPTERA												
Chalcididae												
Brachymeria podagrica (Fabr.)	< 10								*			
Pteromalidae												
Nasonia vitripennis (Walker)	>40	Spring/ Summer							*		*	
Spalangia nigroaenea Curtis	2								*		*	
Diapriidae												
Trichopria lewisi Nixon	>35	Spring/ Summer							*		*	
Formicidae												
Brachyponera sennaarensis (Mayr)												*

RDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
Camponotus rufoglaucus (Jerd.) ssp. *zulu* Em.												*
Crematogaster castanea Sm.												*
Dorylus fulvus Westw. ssp. *badius* Gerst	>15 000							*			*	
D. helvolus (L.)								*			*	
Megaponera foetens (Fab.)												*
Ocymyrmex weitzeckeri Em *foreli* Arn.												*
Pheidole crassinoda Em.				*			*	*			*	
P. liengmei For.				*			*	*			*	
Tetramorium pusillum Em.												*
Sphecidae												
Bembix olivata Dahlbom	< 10							*			*	
Apidae												
Axestotrigona togoensis Cockerell	30-50						*				*	
Trigona (*Hypotrigona*) *gribodei* Magretti	30-50						*				*	
ARINA												
Acaridae												
Lardoglyphus sp.	< 100										*	

ORDER FAMILY SPECIES	GREATEST NUMBER PER CARCASS	SEASON OF GREATEST ABUNDANCE	FOOD RELATIONS							ASSOCIATION WITH CARRION HABITAT		
			Copro-phagous	Sarco-phagous	Dermato-phagous	Kerato-phagous	Sapro-phagous	Preda-cious	Para-sitic	Consis-tant	Opportu-nistic	Inci-dental
Macrochelidae												
<u>Macrocheles</u> <u>muscae-domesticae</u> (Scopoli)	< 100										*	
Pygmephoridae												
<u>Pygmephorus</u> sp.	< 100										*	

CHAPTER 4

TROPHIC RELATIONS AND COMMUNITY STRUCTURE OF THE CARRION-ATTENDANT ARTHROPOD-COMPLEX

In Chapter 3 a detailed account was given of the species attracted to the carcass-habitat, their abundance, feeding preferences, periods of attendance and aspects of their general biology. In this section it is proposed to summarise and synthesise these findings by examining the major trophic pathways available at the carcass-habitat, the competitive interactions between members utilising this habitat, and the successional pattern they exhibit.

TROPHIC RELATIONS

Throughout Chapter 3 a clear but unstated attribute of the carcass was used as base for the discrete and narrow range of food substances consumed by most of the groups of carrion-attendant insects. This attribute is the fact that the carcass is not a single homogeneous entity as is conveyed especially by the term "carrion", but is composed of a number of clearly separable units which serve as feeding substrates. These include flesh, fatty deposits, fluids, rumen-content, skin, horns and hooves, and each of these component units may serve as an independent source of attractant and resource for a group of user-arthropods. The carrion-community is not described and defined by only the sum of the insects attracted to these components, but includes also the arthropods which are attracted to feed on those insects feeding on the carcass. In the same manner, the carrion community also includes those species which arrive not necessarily to feed, but use the carcass as a cue to parasitise other species they associate by evolutionary adaptation with the carcass-habitat.

To be precise, however, it is necessary to include in the carrion-community only those species which are <u>regularly</u> attracted to carcasses in numbers considered <u>abundant</u> for the particular species so it can be regarded as a <u>concentration</u> of members. Some of these may be consistently and exclusively associated with carcasses, such as larvae of <u>Chrysomyia marginalis</u>, <u>Ceratophaga vastella</u>, <u>Dermestes maculatus</u>, Necrobia rufipes and others, whilst some may be opportunistic, such as scarabaeids and ants. At certain carcasses, in this case herbivore carcasses, such opportunistic groups as scarabaeids are nevertheless regularly and abundantly attracted and must therefore be considered as part of the carrion community, despite the high likelihood that most scarabaeid species would be absent at a carnivore carcass.

Figure 94 represents in diagrammatic form the food-web which exists at carcasses at Pafuri, whilst Figure 95 shows the major trophic categories at this habitat.

Definition of terms

When describing events and interactions at the carcass it is necessary to be precise in the usage of descriptive terms. This is especially important at the carcass habitat where a wide range of trophic interactions occur. Fichter (1949) indicated the confusion which stemmed from early observers describing necrophilous species as necrophagous. There is a vast difference between these terms.

In the following discussion coprophagous will be used to describe the habit of feeding on dung or components thereof, keratophagous to describe those feeding on horns and hooves, dermatophagous those feeding on skin, and those subsisting on fragmentary or particulate organic remains discarded by other organisms will be referred to as detritivores. Some uncertainty exists as to an appropriate term to describe those arthropods which feed on muscle and other soft fleshy tissues and the organic-rich moisture on or in it. The term necrophagous is defined in a dictionary of biological terms (Kenneth 1975) as meaning "Feeding on dead bodies" - which is not sufficiently specific as to components - while sarcophagous is stated as meaning "Subsisting on flesh". For the purpose of this discussion "sarcophagous" will be regarded as the more appropriate term, and will be used in the sense of decomposing flesh which includes blood and the film of moisture which often accompanies it and attracts some species of adult flies.

It must be emphasised that some of the arthropods have feeding habits which cannot adequately be compartmentalised into a single cate-

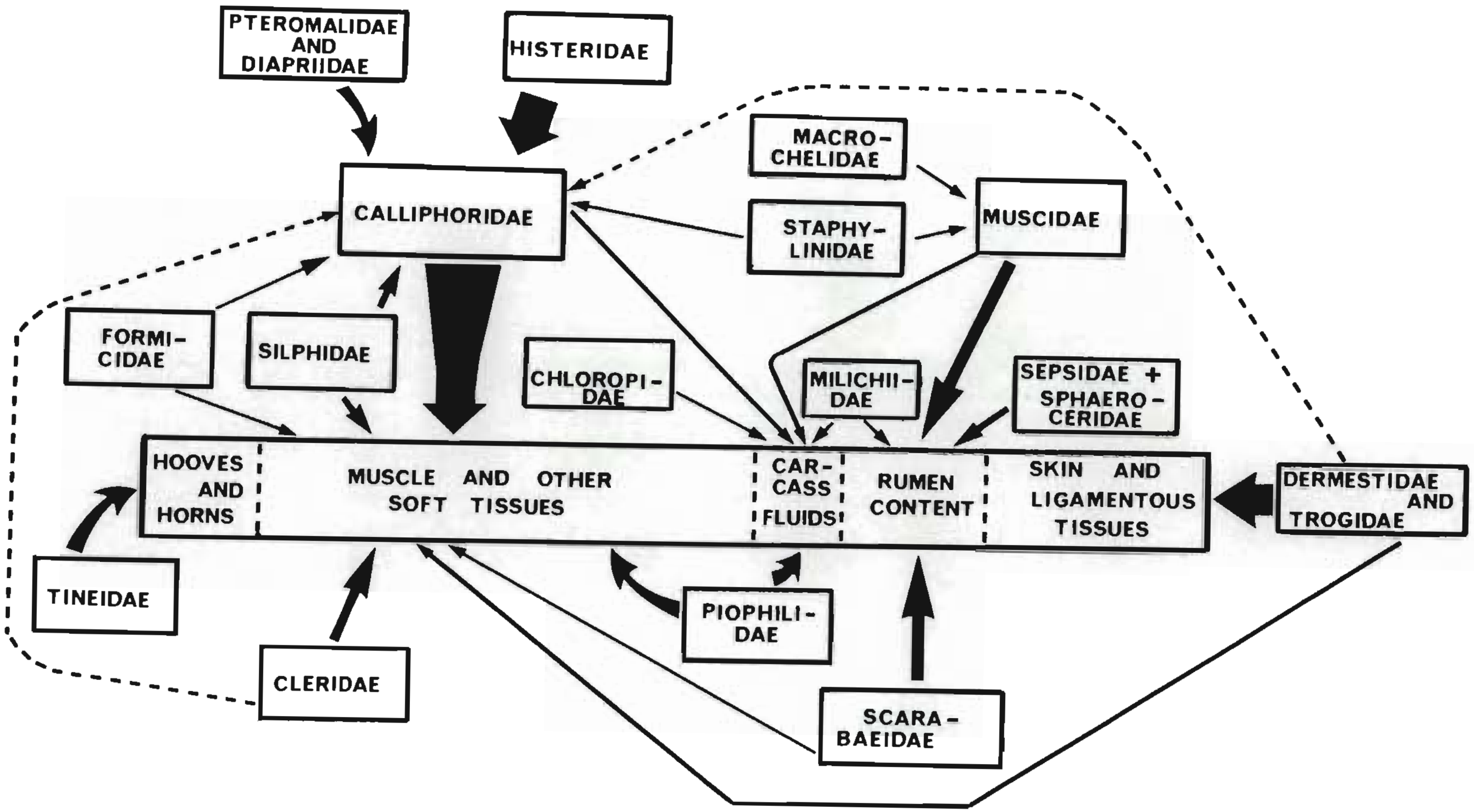


FIGURE 94: Food-web structure of the carrion-attendant arthropod-complex

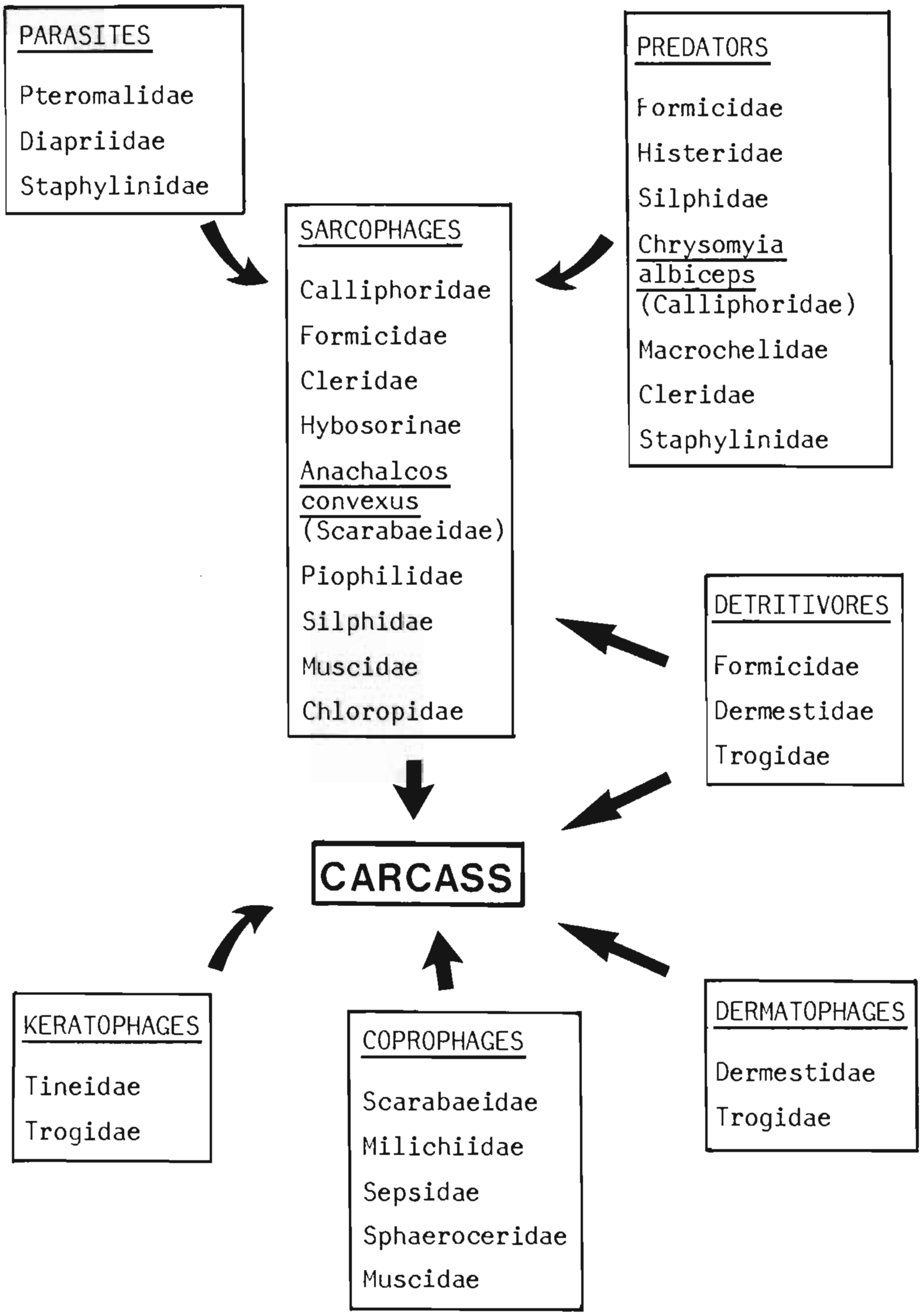


FIGURE 95: Simplified representation of trophic interactions at the carcass-habitat

gory as described above. Whereas blow-flies and piophilids (the species discussed here at least), for example, can be categorised as sarcophagous in the larval and adult stages, this is not possible for certain muscids and the scarabaeid Anachalcos convexus where the larval stages utilise dung but the adults prefer muscle tissues or their associated fluids. Similarly, dermestid adults may spend most of their time feeding on nearly-dry skin and ligamentous tissues, but they occasionally also scavenge on maggots caught by predatory beetles and at times even capture their own maggot prey. In this discussion, therefore, the species have been categorised according to their preferred source of nutrient intake where they spend most of their feeding time.

The sarcophagous component

Carcass soft-tissues represent the most abundant of the resources offered by the carcass-habitat and supports the largest biomass of attendant arthropods. Of these the most numerous are calliphorid larvae which may number in excess of 210 000 at an impala carcass (pers. obs.). The blow-fly larvae, especially those of Chrysomyia marginalis, are also the most important of the insects attendant at carcasses because of the influence they have on the carcass and as an abundant prey item for predatory members of the community. Although C. albiceps larvae are wholly dependent upon soft tissues in the first instar, they do resort to opportunistic predacious behaviour in the second and third larval stages when they prey heavily upon C. marginalis larvae. Other species which rely either wholly or to a large extent upon muscle and other soft tissues are Phaeochrous madagascariensis and Anachalcos convexus of the Scarabaeidae, piophilid larvae, silphid adults and larvae, Ophyra capensis (Muscidae) larvae, and larval and adult Necrobia rufipes (Cleridae). Ants occasionally also have opportunity to feed on the soft tissue component of the carcass, leaving a characteristic pitted appearance due to the removal of minute particulate portions of tissue. This generally occurs in winter when blow-fly activity is reduced; in summer ants rarely have opportunity to gain access to the carcass which is covered in a dense, highly active layer of maggots. Also included in this category are those arthropods which imbibe blood or the organic-rich fluids which bathe the tissues as a thin film, such as piophilid, muscid, chloropid and calliphorid adults.

In addition to forming the largest component in terms of biomass of the carrion-attendant complex of arthropods, the sarcophagous segment (effectively the larvae of C. marginalis) also forms the pivotal basis for a considerable food-web which acts upon it. This food-web includes at least three additional trophic levels, namely predators, parasites, and detritivores. These interactions are illustrated in Figures 94 and 95.

The coprophagous component

This comprises those species which are attracted to the rumen-contents of essentially herbivorous mammals. The bulk of these species belong to the family Scarabaeidae although Musca larvae (Muscidae) also utilise this resource heavily at times, especially where it exists in large quantity such as at buffalo and elephant carcasses. Sphaerocerids, sepsids and milichiids also breed in dung or rumen-content, and the adults of these and Musca species obtain nutrients from the liquid fraction of this commodity. In the absence of blood or other carcass moisture, blow-fly adults also readily imbibe rumen liquids. Generally the most numerous contribution to the coprophagous community is made up by the scarabaeid genus Onthophagus which may exceed 5 600 individuals at a carcass in summer.

The dermatophagous component

Despite its relative abundance at the carcass-habitat, skin is utilised almost exclusively by Dermestes maculatus with a negligible portion also consumed by trogid beetles. Although in excess of 3 000 adult D. maculatus beetles have been recorded at a single carcass, it is mainly the larvae which are responsible for the complete consumption of this resource. Offered a choice, adult D. maculatus prefer moist muscle tissue and ligamentous remains to skin and subsist on fragmentary remains of these tissues to a large extent during their stay at the carcass. Adults may occasionally also function as predators by preying on larvae of C. marginalis, and frequently act as detritivores by scavenging upon the remains of dead insects lying around the carcass, especially blow-fly larvae left by predatory beetles.

The keratophagous component

As in the case of skin mentioned above, the keratinous sheath of bovid horns and animal hooves are a narrowly exploited resource which in the study area is utilised only by the tineid moth *Ceratophaga vastella*, except for a very minor consumption by trogid beetles. The paucity of species feeding on keratinous substances is due to the extraordinarily high stability of the keratin protein and its resistance to proteolytic enzymes, making it difficult to digest. This aspect is discussed by Waterhouse (1957). Although a true member of the carrion-community which is exclusively dependent upon keratinous substances for its survival, *C. vastella* is rarely contemporaneous with any of the other community members because of its very late arrival at the carcass-habitat.

The detritivorous component

This group is represented by a few opportunistic species which are not always consistent or predictable in their pattern of attendance at the carcass. The majority are ants which arrive soon after death of the animal and usually at least a few individuals are present at this habitat at any given time. They tend to be more numerous during the initial stage of decay when an abundance of carrion materials are available and numerous insects are present at the carrion-habitat. They function both as predators by feeding on blow-fly eggs, larva, and emerging adults, and as detritivores by utilising any particles of organic offal present at the carcass. Of the ant species *Pheidole liengmei* was the most common.

Although more often encountered in its role as dermatophage, *Dermestes maculatus* displays great readiness to function additionally as a detritivore by frequently feeding on the moist cuticular remains of *C. marginalis* larvae which have been partially consumed by histerid and other beetles, and will also feed on other dead insects such as blow-flies at the carrion habitat.

The predacious component

The majority of species in the considerable assemblage of predators present at the carcass-habitat devote their attention to a single prey species, that being the immature stages of Chrysomyia marginalis. The most numerous coleopterous group is the Histeridae which includes many species and collectively reach great abundance.

Aside from the histerids - which may number in excess of 20 600 individuals at an impala carcass - the second and third instar larvae of C. albiceps also prey heavily upon their congeneric partners. More than 114 900 C. albiceps larvae may be present at a single impala carcass (Chapt. 5). Together with the histerids they account for the vast majority of mortalities amongst C. marginalis larvae.

Other groups which function permanently or temporarily as predators and feed not only on blow-fly eggs, larvae and emerging adults, but also on the immature and adults of other insects such as Musca, Ophyra and Piophila, are ants, silphids, and to a much lesser extent clerids, dermestids, trogids, staphylinids and macrochelid mites.

The parasitic component

Aside from a few incidental individuals, the two main species encountered were Nasonia vitripennis (Pteromalidae) and Trichopria lewisi (Diapriidae). Both were found mainly in Chrysomyia albiceps puparia, although N. vitripennis was also collected from puparia of Piophila (Piophilidae). Based on a sample of 561 C. albiceps puparia and 579 C. marginalis collected in different seasons, T. lewisi was found to parasitise 5,17% of C. albiceps while C. marginalis was not subjected to parasitism at all. This lack of parasitism in the latter species is related to the difference in pupariation behaviour displayed by C. albiceps and C. marginalis, whereby C. albiceps lies exposed in a concentrated mass above-ground and C. marginalis disperses and burrows into the soil prior to pupariation.

Although reputed to be parasitic on pupae of cyclorrhaphous flies, no parasitism by species of Aleochara (Staphylinidae) was recorded, despite the presence of these beetles at the habitat.

COMPETITION AT THE CARCASS-HABITAT

Carrion is a temporary resource which is unpredictable and inconsistent both in its availability and locality. Because of the competition by vertebrate scavengers and other species which have opted to utilise this resource, most invertebrate members of the carrion-community need therefore to rapidly discover, colonise and maximally utilise the habitat. These are features characteristic of "r-selected" organisms (Pianka 1970), which in many species, such as blow-flies, are also characterised by high rates of reproduction and growth (Odum 1971). A rapid rate of growth in individual and population size would represent in this instance a desirable adaptation for optimal use of a newly opened habitat as represented by a fresh carcass. Resources such as space and nutrients are limited, however, and as the habitat rapidly fills with individuals and species competition results between members utilising or searching for the same resource. The well-known "competitive exclusion-" or "competitive displacement principle" (Hardin 1960, De Bach 1966) states that "different species having identical ecological niches (that is, ecological homologues) cannot coexist for long in the same habitat" (De Bach 1966). In the long term this should lead to the complete exclusion of one species from a particular habitat, or to the specialisation of species with acquisition of adaptations which render them competitively superior to other species in a particular portion of the habitat (niche specialisation), or to partitioning of the resource so that the competitive interface is decreased.

Partitioning of resources

For two or more species to utilise the same specific resource the competitive interaction can be minimised by division of this resource so that the greater number of individuals in each species occupy a different position on the resource. This is referred to as spatial partitioning and allows the species to reach abundance at the resource at the same time. Alternatively the species can each occupy the whole of the space occupied by the resource by having different periods of peak attendance, this being called temporal partitioning.

When applied as above with reference to competitive selection the term "resource" must be used very specifically and narrowly. "Carrion" or "carcass" are broad terms more descriptive of a habitat than a resource, and embrace amongst others a range of feeding substrates such as muscle and other soft tissues, fluids, skin, hooves, horns, and rumen- or stomach-contents.

(a) Between-carcass partitioning

Seasonal partitioning

Although some species like Dermestes maculatus are present and utilise the carcass-habitat throughout the year, there are some species which show a distinct seasonal peak and are replaced by another species utilising the same resource in another season. When referring to food requirements this can be applied to the family Histeridae with members preying heavily upon Chrysomyia marginalis larvae. The genus Hister tends to be abundant in summer but far less common in winter when the numbers of Saprinus, especially Saprinus cupreus, are considerably elevated. Perhaps a more clear example (though not applicable in the K.N.P.) is the marked changeover in the use of carcasses by Chrysomyia larvae in the Cape Province. Here C. marginalis utilises carcasses in summer to the near total exclusion of C. chloropyga, but the situation in reversed in the cooler winter months (pers. obs.).

An example of combined food and also space seasonal partitioning is afforded by the dominance of scarabaeids at rumen-content in summer when their activity - combined with that of blow-fly maggots - prevents the effective use of this resource for breeding by Musca flies. Scarabaeid activity is negligible in winter, and especially in late winter/early spring Musca flies capitalise on the opportunity thus afforded for breeding.

Carcass-size partitioning

There is evidence that some carrion-attendant species are adapted to more optimally utilise carcasses of a certain size-range, thus exemplifying another class of resource partitioning. Sarcophagids were never found breeding in any of the more than 200 medium- to large-mammal carcasses examined during the course of this study. On several occasions, however, I did find these flies successfully breeding in small carcasses such as mice and yellow-billed hornbill, without competition from Chrysomyia larvae. Denno and Cothran (1975) provided evidence which suggests this is a widespread adaptation to minimise competition between sarcophagids and calliphorids. Working in California they found that of the flies breeding in rat carrion, 64% were sarcophagids, whereas in rabbit carcasses these flies formed only 2,8%. In a later publication Denno and Cothran (1976) found that, although calliphorids were competitively far superior to sarcophagids, species of these two families could coexist at rabbit carcasses in California, but with sarcophagids present only in very low numbers. Observations in the K.N.P. suggest that rabbits represent about the upper range of the size-class wherein a changeover occurs from sarcophagid utilization to calliphorid utilisation.

Observations at 304 small carcasses near Bredasdorp in the Cape Province convinced Mönnig and Cilliers (1944) that carcasses up to about 500 g attracted different flies compared with larger carcasses. Meskin (1980) found that C. marginalis did not breed in small carcasses in the highveld region of the Transvaal, and he suggested that this species utilises larger carcasses for larval food resources. This is in agreement with the findings of Mönnig and Cilliers (1944) and also my own findings in the K.N.P., so that collectively the evidence strongly supports the view that some species have preferences for specific carcass sizes, which will serve to lessen competition between species having the same nutritional requirements.

Within-carcass partitioning

Interspecific competition amongst member-species of the carrion-attendant arthropod community for the same food resource appears to be minimal upon initial examination as most species utilise discrete non-overlapping resources and have differing strategies of carcass-utilisation. Blow-flies, piophilid and muscid adults, for example, all feed on moisture at the carcass but avoid direct competition by having a preference for specific fluids and reaching abundance at different times in the decay sequence. Blow-fly adults are first to arrive and prefer the fluid-blood component. Piophilid and muscid adults arrive some days later but Piophila prefer the thin layer of moisture present on the carcass soon after C. marginalis larvae have swarmed over the carcass. Musca also feed on this moisture, blood, and especially fluid-drenched rumen-content and soil around the carcass, but Piophila has a tendency to be crepuscular and nocturnal whereas Musca has distinctly diurnal activity peaks. In a similar manner Dermestes maculatus has a strong and narrow feeding preference for skin and moist fleshy or ligamentous tissue, and Trox spp avoid excessive competition with this dermestid by having a wider resource selection enabling them to feed with apparent equal facility on skin, suet, hooves, and general organic offal including freshly killed blow-fly larvae. In this manner many other members of the carrion community can be shown to have specific non-overlapping preferences, such as tineids feeding almost exclusively on the horns of bovids.

Some apparent anomalies do exist however. The two species Piophila casei and P. megastigmata have the adults overlapping entirely in their visitation patterns at the carcass and appear to have the same nutrient preferences. Although abundant, P. casei is nevertheless significantly less numerous than P. megastigmata but persists at the carrion-habitat for a slightly longer period (Fig. 59) which renders unlikely the possibility that it is competitively suppressed by P. megastigmata.

With both species feeding in the adult stage on moisture at the carcass, especially the liquid film left by maggots moving over the carcass, it appears the resource is under-utilised and sufficient to support both species simultaneously. Rather than provide an answer, however, this prompts the question why the resource is not more fully utilised by more Piophila adults. It seems likely that the adults are relatively free of limiting factors, but that the larval stages are subjected to severe limiting factors and are unable to produce a large adult population which can fully exploit available resources at the habitat. The available evidence supports this latter possibility as Piophila larvae at medium-sized carcasses such as impala are restricted to very small pockets of resource material left available by calliphorid larvae. With regard to the apparent coexistence of the larvae of the two species at the same carcass, the following statement by Hutchinson

(1964) provides a possible answer "If the two species were almost equally efficient over a wide range of environmental variables, competitive exclusion would be a slow process. Both species then might oscillate in varying numbers, but persist almost indefinitely."

However, as Levin (1970) indicated using mathematical models to support his views, species are not always necessarily resource-limited as is so persistently indicated in the literature. He convincingly showed that two prey species (such as Piophila casei and P. megastigmata) using a common resource (muscle tissue in our example) could coexist if each is limited by an independent combination of predation and resource limitation, as two independent factors would be serving to limit the two species.

Returning to resource competition at the carcass-habitat, such resources are not restricted to food however. An interspecific competitive interface may exist between species utilising different feeding substrates but require overlapping space, such as when larvae of Chrysomyia marginalis swarm over the carcass during the latter stages of growth and prevent adult flies such as piophilids, Musca and Ophyra from settling to feed on moisture and also preventing coprophagous species from reaching the rumen content.

The most clear example of intraspecific competition at carcasses is that which exists amongst blow-fly larvae - particularly those of Chrysomyia marginalis - not only for food but also for space. This aspect is discussed more fully in the next section.

Interspecific conflict also occurs between the species of Chrysomyia at a carcass and almost certainly exemplifies a condition known as character displacement. First defined by Brown and Wilson in 1956, character displacement describes the acquisition of features by two competing species to utilise slightly different aspects of a niche and so reduce competitive conflict. At the carcass-habitat, C. marginalis is generally first to arrive and oviposit at the carcass, and with this advantage together with an inherent larger size and vigorous activity the later C. albiceps larvae are ousted from the carcass-body itself to peripheral areas to feed on draining carrion-fluids and less attractive carcass components such as the limb-extremities. Both C.

albiceps and C. marginalis are sarcophagous in the 1st larval instar stage, but C. albiceps becomes a facultative predator upon C. marginalis larvae in the 2nd and 3rd larval stages. It is not difficult to see how this could have been a secondary adaptation in response to severe competition by larvae such as those of C. marginalis, which would be a perfect example of character displacement.

A different example of interspecific competition exists in Dermestes maculatus (Coleoptera) where the potential for mortality-inducing feeding-conflict between adults and larvae is reduced by the adults having an earlier abundance period and a preference for moist muscle or ligamentous tissue-remains left by blow-fly maggots. The larvae - no doubt left no alternative but nevertheless doing well on this fare - subsist upon skin and are most numerous when most of the adults have departed.

An interesting phenomenon which does have a bearing upon intraspecific competition is the delayed period of peak abundance of Chrysomyia marginalis males feeding at the carcass relative to that of the females (Fig. 88 & 90). This is advantageous to the females who have a more urgent requirement for a protein-rich meal necessary for proper ovarial development and the production of viable eggs (Dethier 1976, Bowden 1982). The segregated periods of abundance do not seem likely to result from direct conflict as in the traditional concept of intraspecific competition, but may have been selected for in the species due to the benefits which accrue in reproductive advantage. Not only do the two sexes have differential periods of peak abundance, however, but the overall male:female ratio is distorted. By examining the totals of all C. marginalis captured whilst visiting Carcass C in 1979 (i.e. excluding adults arising from larvae utilising the carcass) we find a male: female ratio of 1:5,53 (n = 991) in January, 1:17,17 (n = 636) in May, and 1:20,64 (n = 238) in September. More females visit a carcass therefore. No doubt this can also be attributed in large part to the reduced need of males for carcass resources, but the effect nevertheless is to reduce intraspecific competition for a commodity (blood) which females more urgently require.

The same phenomemon of initial female preponderance has been observed in C. albiceps (though to a lesser extent, see Fig. 86) but was not detected in Ophyra capensis (Muscidae) (Fig. 77 & 78). The distorted male:female ratio was also present in C. albiceps, with a maximum skewed proportionality of 1:30,30 (n = 1 753) reached in September.

Although not so much a feature of the Pafuri carcasses as further south in the K.N.P., intraspecific competition amongst parasites such as Nasonia vitripennis can also be considerable. It has been shown (Chapter 3) that female Nasonia wasps will not oviposit in fly-puparia already parasitised, and especially in areas such as Swellendam where I have recorded 47,56% parasitism amongst Chrysomyia albiceps puparia (n = 82) such competition for suitable hosts is high. This competition, although on a lesser scale, can also be expected to be operative in the other wasp, Trichopria lewisi, which parasitises C. albiceps in the northern K.N.P.

To summarise certain of these competitive interactions; if a species is competitively superior to another, then it may cause it to occupy the same "niche" at a different time (temporal competitive exclusion), or cause it to utilise the fringes of the niche or not to utilise it at all (spatial competitive exclusion). The interaction is competition, the effect is competitive exclusion, and if it resulted in adaptations to reduce competition it is character displacement. However, character displacement is a relatively long-term effect. In the short-term, when species A competitively excludes species B spatially or temporally the niche occupied by each species is its competitive refugium.

Competition in the blow-fly guild

Competition between blow-fly larvae for available resources is a complex phenomenon influenced by many factors such as the species involved, the number of larvae of each species, the difference in time between oviposition of the species involved, the quantity of food available, environmental temperature, and most likely several other as yet undetermined factors. Two apparently similar carcasses can be placed alongside each other and be exposed to the same external environmental factors, and yet the eventual total numbers of larvae and their proportionate make-up will differ - often drastically (Chapt. 5) - almost leading one to conclude that a considerable element of chance is involved.

It is unlikely that any worker having dealt with blow-fly larvae at carrion in South Africa will have failed to note the vigorous attacks of Chrysomyia albiceps larvae upon other maggots attendant at a carcass. These larvae are predatory in their 2nd and 3rd instars, attacking C. marginalis and larvae of other fly species. C. albiceps individuals join in until the prey-larva is subdued so that eventually a tight clump of up to eleven C. albiceps larvae may be holding onto a single prey maggot. The larvae rasp and tear at the prey cuticle until the soft body contents are exposed, and this is consumed until eventually only a shrivelled cuticle remains.

Chrysomyia marginalis adults arrive before C. albiceps in the successionary sequence of flies at the carcass and are first to oviposit. The larvae, especially in the third instar, are extremely vigorous, tenacious, and they swarm over the carcass always maintaining their frantic rate of movement and are very adept at gaining and maintaining a position on the carcass. So adept are they at retaining a hold at the feeding site that it is very common to see thousands of these larvae packed tightly alongside each other such that only a wide expanse of circular posterior ends is visible, the whole mass rhythmically pulsating as each individual thrusts itself forward to retain its proximity to the feeding surface, but having to counteract the jostling movements and lateral pressure of the mass of maggots surrounding it. Occasionally the pressure is too great and large "blobs" of these larvae fall away to the ground, giving rise to a mass of larvae surging over the exposed site, and the fallen larvae crawling around at a considerable rate in an attempt to locate the carcass.

The vigorous movement of C. marginalis larvae, combined with their size advantage due to earlier oviposition and an inherent larger maximum size, results in the more sluggishly-moving C. albiceps larvae not being able to gain a hold on the carcass itself except at a few isolated positions, generally on the limbs. C. marginalis larvae almost invariably occupy the carcass body itself, while C. albiceps is arranged along the periphery and, generally during the latter stages of growth, as a wide swath around the carcass. Often all the larval stages of C. albiceps will feed on carrion juices soaking the soil and can frequently be found in organic ooze-pools of carrion-fluid. The 2nd and 3rd instar stages also prey to a considerable extent upon C. marginalis larvae falling to the ground or crawling through the layer of C. albiceps along the periphery.

Although Lucilia is not a major component of the blow-fly population in the study-area under discussion, it is periodically abundant in other parts of the country and is of considerable importance to the sheep industry as a cause of "sheep-strike" (Smit 1931, Howell et al 1978). It differs from C. albiceps and C. marginalis in that it gains abundance during the cooler months of the year, this generally being attributed to its competitive exclusion from carcasses by Chrysomyia during the warmer months (Mönnig 1942, Howell 1969, Howell et al 1978). In the only quantitative study thus far on competition in blow-fly larvae in this country, Ullyett (1950) found that, although heavily preyed on by C. albiceps larvae, Lucilia is an effective competitor. Some doubt therefore still exists as to the exact relationship between Lucilia and other carcass-frequenting flies, and it is possible that Lucilia has an inherent self-governing population peak in the cooler months quite independent of competitive effects.

As clearly revealed during my own studies and also indicated by Ullyett (1950) and others (e.g. Levot et al 1979, Bennettova & Fraenkel 1981), a manifestation of both inter- but more specifically intra-specific competition was a reduction in the average size of larvae at pupariation. The mortality rate was decreased by allowing successful pupariation in smaller, less well-fed maggots which will give rise to sub-sized adults. In controlled experiments Ullyett (1950) found that the fecundity of such undersized flies was reduced. Caged flies at Pafuri showed that, at least with the degree of size-reduction generally produced by competition in naturally-occurring large carcasses, the production of eggs and their viability falls within the range normally occurring from full-sized individuals.

Furthermore, the findings of Ullyett are in agreement with mine that, although such eggs in his experiments were somewhat less in number, they were nevertheless equal in size and viability to those produced by normal full-grown flies. They ".. give rise to larvae which are healthy, are of normal size and which will, given the opportunity, produce pupae and adults which tend to conform to the mean maximum size for the species" (Ullyett 1950).

With increased competition, or with the premature removal of carrion-material by vertebrate scavengers, the nutrient intake may be insufficient for the formation of pupae, resulting not only in a reduction of average size but also reduction in numbers.

In general, blow-flies should be regarded as exceptionally adept competitors. They have occupied a niche which probably represents one of the ultimate examples of opportunism, and exemplifies the phrase "struggle for survival" in a particularly intense form. They utilise as larval breeding medium a commodity which is sought after with equal intensity by an array of vertebrate scavengers so that its availability becomes infrequent and unpredictable. The carrion material must also be in an attractive form with regard to its stage of decomposition, which in summer means the carcass is acceptable for only one, or at most two days, else it may be rejected as unsuitable for oviposition. These conditions having been fulfilled, so many flies generally deposit their eggs that the available carrion material cannot support to maturity all the resultant larvae. Such larvae must therefore not only compete amongst members of their own and other blow-fly species for what is a compact, finite resource, but they must do so in the minimum possible time due to the constant risk of the carcass being discovered by hyaenas, jackals, vultures, and several smaller vertebrate scavengers. In the face of this competition, they are exposed to attack from predatory beetles and ants, from drowning in the soup of decomposition fluids, from desiccation by the sun, and the intense heat generated in the depths of the carcass which frequently reaches 55°C. Having survived this meleē, they are further preyed on and parasitised during their pupal stages. Despite this pressure on survival, they remain successful and abundant.

SUCCESSION

Although recognised by several persons before him, the concept of succession was first studied and expounded in depth by Clements in the early part of this century (Drury and Nisbet 1973). This concept has found wide application in general ecology but has yet to be satisfactorily defined.

Succession is generally understood to mean sequences of vegetational associations or animal groups in time. These sequential changes can exist simultaneously in closely adjoining spaces (such as the gradient of species dependent upon wave-action in the intertidal zone across a beach) or in the same space at different times (such as the "waves" of species arriving and departing from a carcass). Succession is manifested as recognisable communities which follow each other in a sequence. Each community in the successional sequence is referred to as a "seral stage" (Colinvaux 1973).

Such a pattern of sequential utilisation of resources has long been known to exist at carcasses. The consistent and predictable nature of this phenomenon is such that it has been applied in criminal law situations to determine the amount of time elapsed since death by examining the organisms present at the carcass (e.g. Mégnin 1894, Nuorteva 1977, Prins 1980). Many other workers have commented on succession at carrion (e.g. Fuller 1934, Bornemissza 1957, Reed 1958, Payne 1967, Johnson 1975, Smith 1975, Braack 1981, Jiron & Cartin 1981) but other than an account of the sequence of species attendance few (e.g. McKinnerney 1978) made any significant analyses or theoretical contribution to the understanding of carrion succession.

Succession at the Pafuri study-carcasses

All the species of arthropods encountered had preference periods for attendance at the carcass habitat when they reached maximum abundance, and being absent or present only in low numbers at other times. These periods of abundance or maximal attendance for nearly all species may be short-lived or of long duration depending on the availability and condition of the food resource. In this way adult blow-flies, which feed on blood and other moisture and also oviposit at the carcass, were present for a very short period generally lasting only a few days. On the other hand trogid beetles, which have a wide resource selection including moist muscle tissue, suet, skin, hooves and even preying on blow-fly larvae, are present at the habitat for a very long time. Most species, however, have a peak preference-period for carcass-attendance which is of short duration.

Despite the seeming array of resources available at the carcass-habitat, there can be no doubt that the presence of blow-flies - especially Chrysomyia marginalis - is of central importance to almost the entire carrion-insect complex, and a crucial determinant of community structure. A large number of species depend either directly on the blow-fly larvae as a food-source or indirectly on the influence of maggots on the carcass. The activity of the maggots not only has a tremendous accellerating effect on carcass decomposition, but their effects - such as providing organic-rich liquids by secreting digestive enzymes which dissolve muscle and other soft tissue, by opening up the carcass, by leaving strands of ligamentous and other tissue which rapidly dry, etc. - also provide a whole range of different species with their particular food and space requirements. The presence of maggots therefore, and their duration of stay, is a prime factor in determining succession at carcasses.

Chrysomyia marginalis flies are almost invariably the first to appear at the carcass and oviposition by females soon follows, with adult C. albiceps following a very similar but slightly delayed pattern. Ants are also early arrivals which utilise blood or moisture oozing from body cavities, prey on blow-fly eggs, and later prey on larvae or feed on organic detritus at the carcass. With the hatching of blow-fly larvae, a large number of mainly histerid beetles arrive as predators and are soon joined by staphylinid and silphid beetles. With the moult to the second instar, numerous predatory larvae of C. albiceps also join the attack on C. marginalis larvae. As C. marginalis larvae travel over the carcass abandoning exhausted feeding sites and seeking other sites, they leave an abundant supply of nutrient-rich moisture which is utilised by large numbers of piophilid, milichiid, chloropid and muscid flies. When maggots disperse to find pupariation sites they are again attacked by ants previously unable to reach the seething mass on the carcass. Pupariation in C. marginalis generally occurs on Days 5 and 6 in summer and Days 9 to 14 in winter.

This event marks the end of the most intense period of activity at the carcass and also a steep decline in the number of species present at the carcass. Pupariation of C. albiceps commences a day or two later and signals the arrival of diapriid and pteromalid wasps which parasitise C. albiceps puparia above-ground. With the emergence of blow-flies from their puparia a few days later, ants become abundant again to use the opportunity for capturing any flies not rapid enough in their escape from the protective puparia.

Whilst the above sequence is in progress, and to a large degree independent of calliphorid activity (except in competition for space where blow-fly larvae at least for a while prevent them from reaching their resource) the rumen-content component of the carcass has also attracted a series of scarabaeid beetles, milichiid, sepsid, sphaerocerid and muscid flies.

As more and more of the carcass surface becomes exposed due to maggots moving to the inner recesses of the carcass to obtain fast-diminishing resources, moist tissue-remains become available and the number of dermestid and clerid beetles increase rapidly. The dermestid adults deposit eggs and as the carcass dries after departure of the blow-fly maggots, so these beetles also steadily depart. The dermestid eggs soon hatch and larvae feed on the now near-dry skin. Trogid beetles remain common at this stage to scavenge on any organic remains. Although quiescent and not visible, parasitic diapriid and pteromalid wasp-larvae are present in many of the C. albiceps puparia which lie around long after the remainder have yielded adult blow-flies.

The last member of the successional sequence is the tineid Ceratophaga vastella which oviposits in the horns of bovids, arriving several weeks or even months after death of the animal. The larvae reveal their presence by the characteristic frass-studded silken tubes which protrude from the keratinous horn-sheath.

The above is a generalised account of the sequence of events which characterises most carcasses in the northern K.N.P. Because of the rapid rate of development of C. marginalis maggots in summer the sequence is condensed into a very short period. With cool temperatures slowing their metabolic rate in winter, the process is more extended and the successional pattern more easily observed. These successionary sequences are depicted in Figures 96 to 98.

Discussion

The initial view of succession as developed by Clements in the early 20th century (Drury & Nisbet 1973) held that species replace others in a progressive, directional, and predictable manner to an eventual climax community which was regarded as a kind of "superorganism". Contemporary views do not differ much although the "superorganic" nature of the climax community is denied (Colinvaux 1973). Ricklefs (1973) also showed that succession does not always lead to a climax community and cited carcasses as an example where no buildup to a stable commmunity exists. No concensus appears to exist, however, on the mechanism driving succession and how the climax community or "society" is brought about. A considerable amount of detail characterising earlier communities as opposed to later communities in the successional sequence has been compiled during the course of a multitude of mainly botanical studies on succession, and much of this is summarised as a tabular model by Odum (1971: p. 252). Difficulty exists in propounding a single generalised theory embracing and explaining succession, and stems from a number of different phenomena usually falling under the umbrella of the term "succession". These include (a) sequential development through time on a single site with stable climate and physiography, (b) sequential development through time on a single site which changes due to extrinsic influence such as climatic change, and (c) sequential changes along sites adjoining each other (such as between tide-levels on a beach slope) (Drury & Nisbet 1973).

The long-enduring obsession with succession - especially in its application to the diversity and stability of climax communites - suggests a difficulty in grasping the essential nature of this phenomenon and a desire for an explanation of its functional mechanism which is intuitively and logically satisfying. Succession should be viewed in proper perspective however. A series of species - be they sarcophagous, coprophagous, predatory, parasitic, etc., - utilising a carcass in a staggered pattern, each having its own period of distinctive

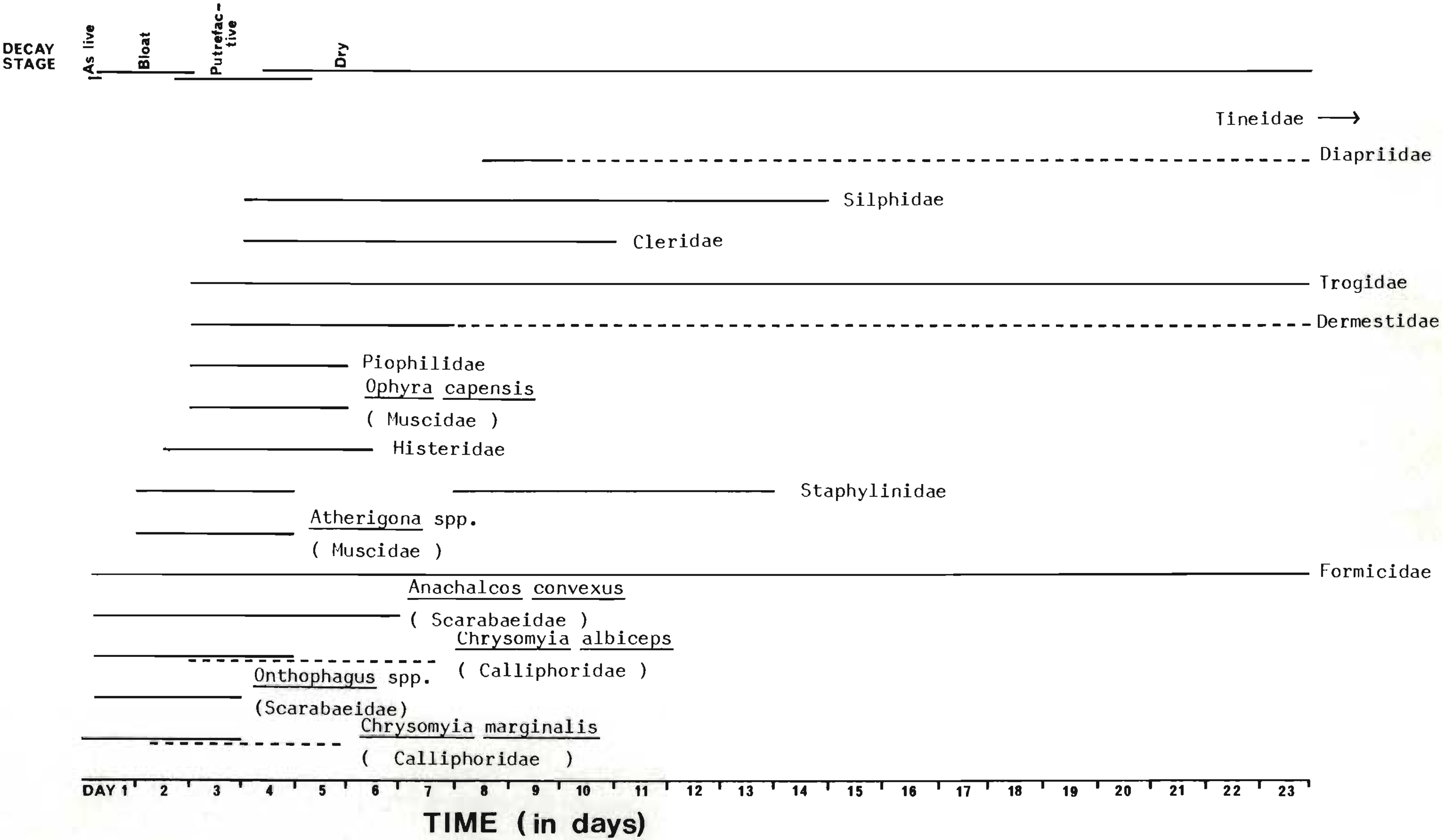


FIGURE 96: Periods of peak attendance of the main carcass-frequenting

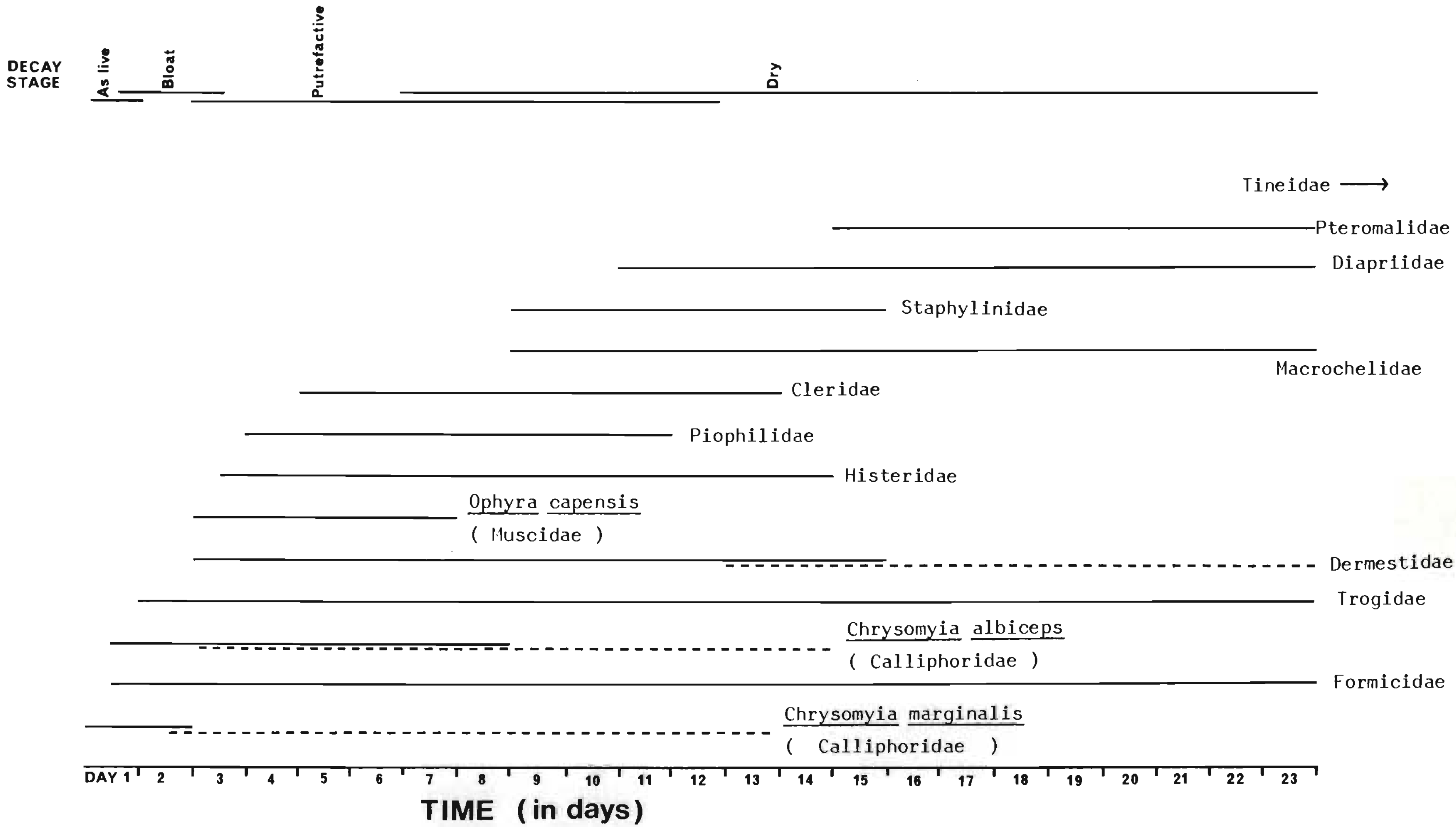
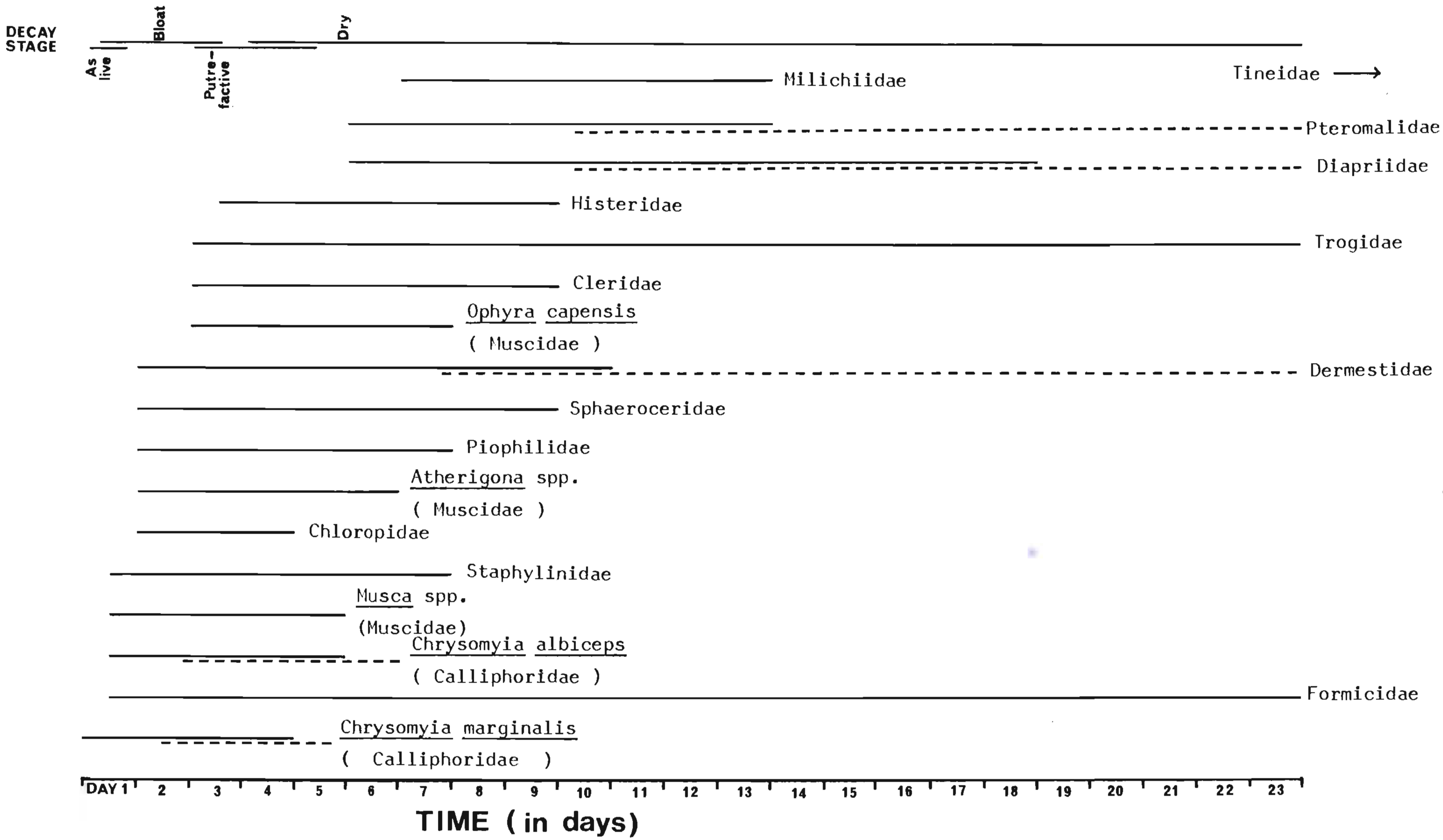


FIGURE 97: Periods of peak attendance of the main carcass-frequenting



DECAY STAGE
As live
Bloat
Putre-factive
Dry
Milichiidae
Tineidae
Pteromalidae
Diapriidae
Histeridae
Trogidae
Cleridae
Ophyra capensis
(Muscidae)
Dermestidae
Sphaeroceridae
Piophilidae
Atherigona spp.
(Muscidae)
Chloropidae
Staphylinidae
Musca spp.
(Muscidae)
Chrysomyia albiceps
(Calliphoridae)
Formicidae
Chrysomyia marginalis
(Calliphoridae)
DAY 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
TIME (in days)

abundance, appears to be a prime example of the traditional concept of succession. Species having the same resources and utilising these in a staggered manner, however, exhibit the result of competitive exclusion, and yet its manifestation can also be described as succession. Succession in this simple example is a mixture of visitation periods determined by competitive and non-competitive situations. It shows that the staggered pattern termed succession is driven by sometimes unrelated mechanisms which of necessity complicates description and understanding of the term considerably. Given the generalised concept of succession existent today, it is perhaps a moot point to discuss the necessity of distinguishing between the outward manifestation of competitive exclusion on the one hand, and competitively unrelated serial utilisation of carcass components on the other.

Succession at carrion to a very large extent results from the addition, not replacement, of species to the community present at the carcass. The addition of species arises from new resources becoming available and these resources most often in turn arise as a result of the action of one or more of the community members in the community. For example, the emergence of blow-fly larvae at the carcass stimulates the arrival of large numbers of predatory histerid beetles; the activity of the maggots leaves a liquid deposit on the carcass which attracts moisture-seeking piophilid and other flies; the continued feeding efforts of the maggots rapidly exposes the rumen-content in initially undamaged carcasses which is utilised by scarabaeids; the departure of maggots creates space for more individuals of certain species such as clerids (the sudden change in proportionate make-up of a community must also be regarded as a seral stage in succession as the community structure may be radically changed). Note also that when discussing succession the carcass is regarded as a single substrate and, unlike when discussing competition, no strict adherence is given to limiting ourselves to a single component such as skin. Succession arises from the collective attraction afforded by all the constituent components of the carcass habitat, and this includes both the carcass itself (e.g. flesh attracting flies to oviposit) and the organisms acting upon it (e.g maggots attracting histerids). Succession is by the very meaning of the term a dynamic process, based upon interactions which change and/or create resources.

In succession at carcasses, one community (seral stage) does not cause another to succeed, it merely often enables it by providing essential conditions favourable to succession by another community. Usage of the term "succession" often implies a change in the component species making up a community (seral stage). This need not necessarily be the case, as a different community with different properties may result simply from a change in the relative abundances of the species in the community. Thus it may be more correct to state that succession is a change in community* structure (whether by a species or group of species being replaced by another or others, or simply a significant change in the relative abundances of the species) at a particular habitat through time. This succession may be due to abiotic or biotic influence, i.e. as a result of a change in the physical environment either due to external factor(s) or due to exerted influence of the species present, or due to arrival of new species attracted to species already present, e.g. predatory histerids attracted to blow-fly larvae.

In conclusion, carrion represents an ephemeral resource with no steady progression to a stable climax community having a reasonable prospect of long-term existence. The climax community in the traditional sense is generally dependent upon the existence of a closely-adapted interacting group of biotic components which act upon a supporting substrate to varying degrees (e.g. carcass, rocky beach transect). In a climax forest community for example, a climax population of trees has dying individuals broken down by decomposers into inorganic components which are re-assimilable by young trees. This represents an idealised situation of minimal requirements, but will in reality probably include a number of other producers, and also herbivores and predators, parasites and decomposers each having differing nutritional requirements in different amounts and proportions so that a series of populations of organisms balanced in their proportionate contribution to the community is essential to a stable climax situation. An imbalanced condition where, for example insufficient nutrients exist

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* A single species may also be considered as a community, e.g. end-stage Tineidae, just as much as members of a single species may belong to different seral stages (e.g. adult and larval blow-flies - their needs are widely divergent).

will not result in a stable climax community. At the carcass-habitat the only resource items remaining available for a relatively long period of time are skin, hooves and horn-sheaths utilised by dermestids, trogids and tineids. The substrate is non-replenishing and is depleted in direct proportion to the population of insects it supports. The insects destroy their own habitat therefore and render it temporary.

CHAPTER 5

BIOLOGY AND ECOLOGY OF THE IMMATURE STAGES OF *CHRYSOMYIA ALBICEPS* AND *C. MARGINALIS*.

From the evidence presented in Chapter 4 it should be abundantly clear that the two blow-fly species *Chrysomyia albiceps* and *C. marginalis* are of crucial importance at the carcass-habitat because of their ability to rapidly consume all the soft tissues on a carcass within a relatively short period of time, and also by their presence and action on the carcass drastically influencing other members of the carrion-community. The presence of the larvae stimulates the arrival of large numbers of predators such as beetles, and their action on the carcass and duration of stay influences the timing of peak arrivals and numbers of insects such as piophilids, clerids and dermestids. It is not incorrect to state therefore that these two species are the most important determinants of community structure at the carrion-habitat, directly and indirectly.

Given their status in the carrion-community, their remarkable efficiency as removal-agents of soft carcass-material, and the potential importance of the adults in the epidemiology of anthrax, it is appropriate that more attention be devoted to the biology and ecology of these two species of blow-flies.

DEVELOPMENTAL STAGES

Although some calliphorids do larviposit, *C. albiceps* and *C. marginalis* deposit eggs which require a period of development before larval eclosion. The larvae pass through three instars during which they imbibe liquid substances partially or wholly digested externally by proteolytic enzymes (lipolytic and other enzymes internal) (Hobson 1931, 1932a, 1932b), finely fragmented particles of tissue (Mackerras and Freney 1933), while 2nd and 3rd instar *C. albiceps* also frequently prey mainly upon *C. marginalis* larvae (Ullyett 1950, Coe 1978, Meskin 1980).

Upon cessation of feeding the larvae of C. marginalis move away from the carcass and bury themselves in the soil for pupariation, whereas larvae of C. albiceps remain at the carcass site and pupariate above ground either alongside or below the carcass. The terminology as suggested by Fraenkel and Bhaskaran (1973) is used throughout, so that that stage of the third instar larva between cessation of feeding and pupariation is referred to as the post-feeding larva; pupariation is applied to the process whereby the post-feeding larva contracts and the cuticle forms a hard, protective, barrel-like structure called the puparium. The prepupa refers to the stage between formation of the puparium and the next moult (larval-pupal apolysis). The prepupa is a necessary distinction as it is neither a larva nor a pupa, the latter lying free within the puparium. During pupariation the puparium initially has a white colour, then passes through orange/red to brown as tanning of the cuticle progresses. The larvae pass through three instars before assuming the non-feeding behaviour of the brief prepupal stage. The prepupae become inactive and shrivel up, the cuticle becoming a hard reddish-brown protective puparium within which the pupa develops. Adult emergence occurs by haemolymph pressure distending the ptilinal sac which forces open the opercular cap at the anterior end of the puparium. Teneral adults climb onto vegetation where they remain for the short period necessary for hardening of the cuticle and wings before flying off.

OVIPOSITION

Although it has been shown that certain species of Diptera, including blow-flies, have adult females capable of maturing their first batch of eggs by utilising the larval fat body as a protein reservoir (Spradbery & Sands 1981), the necessity in general for adult female blow-flies to ingest a protein-rich meal to ensure maximal production of eggs, proper yolk formation and maturation of the eggs has been well-documented (Dethier 1976, Bowdan 1982). Barton Browne et al (1979, 1981) showed that with only a limited supply or absence of protein-rich material oosorption of many of the oocytes occurred. Females generally obtain their protein in the form of a blood-meal at fresh carcasses, but may also derive such nutrients from other carcass-fluids and dung-liquids. If no suitable opportunity arises for egg-deposition, it is known that the females may resorb such eggs and that the oocytes can also be resorbed in time of need - such as during stress periods due to lack of food or low temperatures (Hinton 1981).

In the study area, C. marginalis was generally the first arthropod species to arrive at the carcass after death of an animal. Arrival frequently occurred within minutes of death and several hundred of these flies were often present within a few hours. As indicated earlier (Chapter 3, Fig. 88 & 90, and Chapter 4) there was a marked preponderance of females among the initial arrivals, and these flies congregated and fed at sites where blood or other fluids exuded from the carcass, such as from the mouth, in the nose, on the eyes, and from any wounds. Observations at carcasses and more specifically at experimental portions of meat clearly showed that C. marginalis females rarely oviposit at anything but fresh meat. Freshly killed rabbits frozen and later thawed did not elicit egg-laying, nor did more than 50 other offerings of either thawed or decomposed 500 g chunks of lean baboon meat. Female C. marginalis flies were also extremely reluctant to oviposit at small quantities of fresh meat (200 g portions), but readily deposited eggs on rabbit-sized carcasses or larger. This behaviour supports the findings of Mönnig and Cilliers (1944) and explains why Meskin (1980) found C. marginalis to be absent from his small-mammal (laboratory rats) carcasses in the Highveld region of the Transvaal, and also why persons such as Smit (1931) and Hepburn (1943a) found it very difficult to maintain laboratory populations of this species.

Eggs of C. marginalis were noticed at carcasses within four hours in summer and ten hours in winter, although during the colder months egg-laying was subject to considerable variation, sometimes occurring until Day 3. In summer however, maximal egg-deposition by C. marginalis occurred within the first sixteen hours after placement of the carcass. Oviposition occurred only during the hours of daylight, adults being inactive at night. Individual flies deposited their eggs in clusters, but more often in large contiguous masses together with other females, in protected and shaded positions such as the axil regions, within the abdominal cavity if opened by scavenging, in the mouth, nostrils, and especially at the interface between carcass and soil (Braack 1981). The females crawled as deep as possible into these situations and extended their ovipositors to a considerable length before ovipositing. Smit (1931) and Meskin (1980) also recorded this preferance for oviposition sites with high humidity and low illuminance. Positioning of the eggs was also such that they would not be exposed to the sun despite its shift in position through time. If the eggs became accidentally exposed due to a shift in carcass position, as when moved by scavengers, they soon became desiccated, shrivelled, and died.

Observations and experiments with C. albiceps revealed their behavior to be much the same as described above for C. marginalis. They displayed a delayed pattern of arrival at the carcass habitat however, so that peak deposition of eggs occurred on Day 2 in summer and correspondingly later in winter. Experiments also revealed that C. albiceps readily oviposited at large carcasses or on small 150 g portions of baboon meat, and that they had no reluctance doing so at thawed meat. Meskin (1980) reported that at the rat carcasses he used during his studies, C. albiceps females deposited their eggs singly and never in clusters. I have never observed this behavious at any of the large carcasses I have studied, the flies always ovipositing in clusters with the component eggs adhering to each other. The soil/carcass interface was also a prime site for egg-deposition.

Fecundity

The fecundity of both species of blow-flies was determined by keeping reared pairs in spacious flight cages. The flies were periodically offered 150 g (C. albiceps) and 500 g (C. marginalis) portions of fresh lean baboon meat. When oviposition had occurred each egg-clump was microscopically teased apart with needles and the individual eggs counted. The results of these counts showed that C. albiceps deposited an average of 260 eggs per laying (n=11, range=196-308) and C. marginalis 324 eggs per laying (n=8, range=297-357). Females of both species were found to be capable of producing eggs throughout their adult life. In summer C. albiceps flies kept in flight cages were found to oviposit by the 4th day after emergence from puparia and to oviposit up to nine batches during their adult lives (up to 41 days in summer). Although C. marginalis were found to deposit eggs within 10 days after adult emergence, the oviposition behaviour of this species was negatively influenced to some extent by only offering them 500 g portions of meat due to practical study limitations and this quantity not being of optimal size to stimulate peak response. Both C. albiceps and C. marginalis were observed to oviposit during June and July (the coldest months in the study area) although the number of females laying eggs and the frequency of oviposition was greatly reduced. Thus, for example, from a total of 100 C. albiceps and 100 C. marginalis adults kept in flight cages between 2nd June to 5th July 1980, only 7 egg-clusters were obtained from C. albiceps and 1 from C. marginalis, despite fresh meat being made available to these flies every second day.

Coe (1978) found by dissection of gravid female flies in Kenya that C. albiceps yielded a mean of 214 eggs and C. marginalis 341.

Workers have indicated that there is a relationship between the number of eggs deposited and the size of the adult blow-fly (Ullyett 1950, Webber 1955). They reported that the size of the adult fly is largely determined by the quantity of food available to the larval stages and that inadequately fed larvae would result in sub-sized adults. My own experiments have indicated that this also occurs in C. albiceps and C. marginalis. Using Lucilia cuprina adults in Austria, Webber (1955) showed that there was a predictable relationship between adult size and the number of ovarioles. Meskin (1980) repeated these experiments in the Transvaal using Lucilia sericata and Calliphora croceipalpis, constructing regression equations for the correlation between female size and total ovariole number. Bennettova and Fraenkel (1981) also showed this to be true for Phormia regina and Sarcophaga bullata. Adult size influencing fecundity therefore appears to be a general phenomenon among blow-flies, smaller females depositing less eggs.

An additional interesting finding from keeping paired flies in flight cages in the study area for obtaining specific data on eggs, was the frequent observation that female C. albiceps and C. marginalis were repeatedly capable of depositing clusters of viable eggs several days after all males had died. This indicated that sperm storage occurred (for at least 5 days in both species) and oocytes could be fertilised long after copulation, Egg-incubation

The time elapsed from egg-deposition to hatching of the larva is referred to here as the incubation period. This was determined by using eggs laid by wild females kept in flight cages. Portions of lean baboon meat (150 g for C. albiceps; 500 g for C. marginalis) were offered to these females as substrate, and close observation was maintained on the resultant eggs. These incubation periods, together with related data, are presented below in Table 14.

TABLE 14 : Egg-incubation for Chrysomyia albiceps and C. marginalis

SPECIES	Time elapsed from oviposition to larval eclosion	Ambient Temperature (°C)		% Relative Humidit	
		Min.	Max.	Min.	Max.
C. albiceps	12 hr. 18 min.	28,0	39,5	18	54
C. albiceps	12 hr. 35 min.	23,5	31,0	60	80
C. albiceps	13 hr. 54 min.	28,0	39,5	18	54
C. albiceps	14 hr. 30 min.	21,5	30,5	48	90
C. albiceps	17 hr. 39 min.	20,0	29,5	38	73
C. albiceps	18 hr. 05 min.	20,0	29,5	38	73
C. marginalis	10 hr. 03 min.	32,0	35,5	33	46
C. marginalis	10 hr. 21 min.	27,5	35,5	33	73
C. marginalis	10 hr. 40 min.	27,0	34,0	41	81
C. marginalis	11 hr 29 min.	25,0	33,0	52	88
C. marginalis	13 hr. 00 min.	23,5	30,0	65	80
C. marginalis	13 hr. 25 min.	23,5	28,0	60	85
C. marginalis	14 hr. 55 min.	22,5	26,0	94	96

The above results were all obtained during the warmer months (November to March), and observations at carrion suggested that these periods are roughly doubled in winter. Concerning C. albiceps, Zumpt (1965) reported incubation periods of 24-36 hours "depending on temperature", whereas Prins (1982) found that at 25-28°C C. albiceps hatched 21 hours after oviposition. The above results are confusing when compared with the Pafuri findings, but Prins (1984, pers. comm.) stated that his results were based on observations of only two egg-batches, and Zumpt (pers. comm.) had informed him that emergence could take place between 12-15 hours at high temperatures (although these findings do not appear to have been published).

The trend presented by the data in Table 12 suggests a more rapid rate of development with increasing temperatures. This pattern is confirmed by the findings of Vogt and Woodburn (1980) for Lucilia cuprina, who also showed that the rate of egg-development is not only linked with temperature, but that with increasing saturation deficits (lower relative humidity) the rate of egg development is decreased in a non-linear manner. They also found that survival of eggs declined with increased saturation deficits, which would explain why the Pafuri blow-flies always selected crevices and similar positions where humidity may remain higher than general environmental humidity.

"EPIDERMAL STREAMING" AND OTHER EXPLORATORY BEHAVIOUR DISPLAYED BY LARVAE OF CHRYSOMYIA MARGINALIS

The developmental period of maggots resulting from eggs deposited at the carcass by blow-flies is such that several days are required before sufficient nutrients are ingested to allow successful pupariation by the larvae. Vertebrate scavengers such as hyaenas and vultures therefore represent a serious threat to successful completion of larval development in blow-fly species which depend solely on carrion as a breeding medium, and considerable evolutionary pressure must therefore have been exerted on such blow-flies to minimise or compensate for this threat. One of the adaptive features exhibited by larvae of such blow-flies as Chrysomyia marginalis appears to be epidermal streaming, a phenomenon commonly observed at carcasses.

Epidermal streaming describes the process whereby recently emerged blow-fly larvae, mostly from eggs laid at the soil/carcass interface, enter beneath the thin outer layer of skin and migrate upwards to the top of the carcass and often over to the opposite side, leaving a blackened, almost entirely dehaired hide covered with a thin film of moisture which soon dries. This behaviour was first briefly referred to in an earlier publication (Braack 1981).

Considering the necessity for rapid access by the maggots to carcass soft-tissues below the skin, two alternatives appear to be available to maggots when hatching: either secrete sufficient digestive enzymes to dissolve the skin and then enter the abdomen from below, or move up the carcass to where vertrebrate predators or scavengers are likely to have punctured the carcass thus providing a more easy and quick route to the tissues inside. Observations at study carcasses showed that the maggots display both behavioural patterns. The most feasible explanation for the migratory movement over the carcass would seem that natural selection had favoured this as an exploratory phase to find the most rapid means of entering a carcass, as there exists a very real need for the carcass to be utilised as quickly as possible due to the high likelihood of further scavenging by vertebrates. Should no point of entry be encountered, the skin is dissolved from below the carcass by enzyme action.

In mutilated carcasses, epidermal streaming generally proceeded only as far as the wounds where the whole mass of maggots would move into the cavity. At scratches or superficial wounds not penetrating the body wall the maggots ignored such sites and continued their exploratory movement upwards and forwards. Provided a site was not directly exposed to the full desiccating rays of the sun, blow-fly larvae occasionally congregated around superficial wounds and used these as entry sites into the abdomen. If fully exposed to the sun, even open wounds were passed over.

The exploratory movement of C. marginalis was also observed at large carcasses such as buffalo, although not as frequently or as dramatically. At such carcasses they occasionally engaged in limited upward epidermal streaming and if the maggots encountered tick puncture sites of a suitable nature, they at times enlarged these to enter the body.

In cases where liquid exuded from a wound due to bloating or scavenging, larvae often moved directly along the liquid path in a compact mass over the skin from the carcass/soil interface to the wound site without further exploratory behaviour.

Although the mass exploratory migration was more often exhibited by young larvae, it was occasionally observed in near full-grown maggots generally when competition for limited resources was particularly intense and alternate locations were sought. In such cases where large larvae undertook exploratory movement they did so externally by moving above the skin between the hairs.

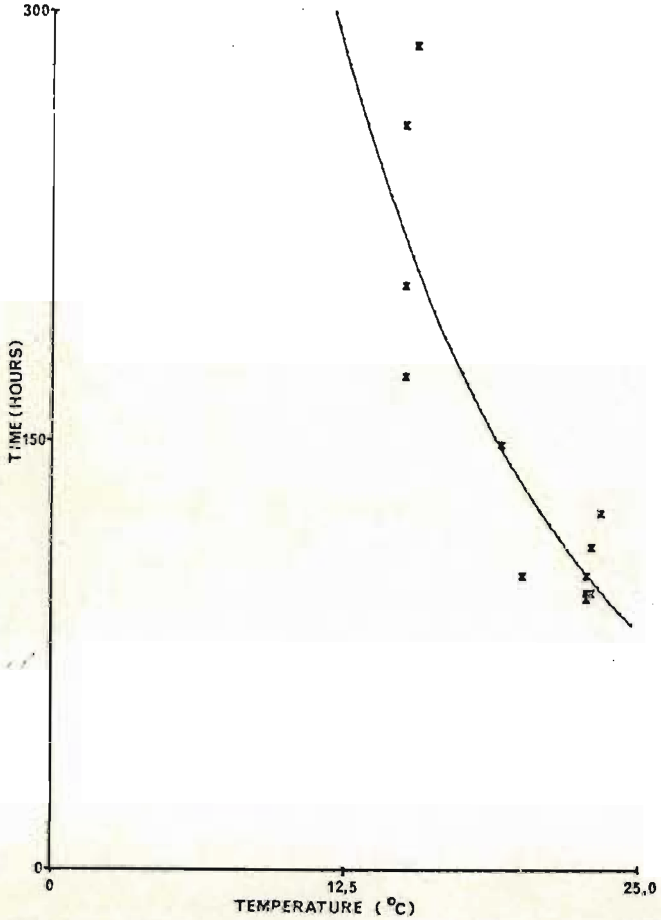
Several advantages appear to be accrued by epidermal streaming as a means of performing the exploratory phase. By moving below the outer layer of skin the larvae avoid tumbling off the side of the carcass, and friction is provided for the upward climb. Some protection against the drying sun is provided, and the high humidity within this protective sheath also reduces the potential for desiccation in the highly susceptible first instar stage. Additionally, some protection is afforded against predatory beetles and ants which are present soon after hatching of the maggots.

LARVAL DEVELOPMENT

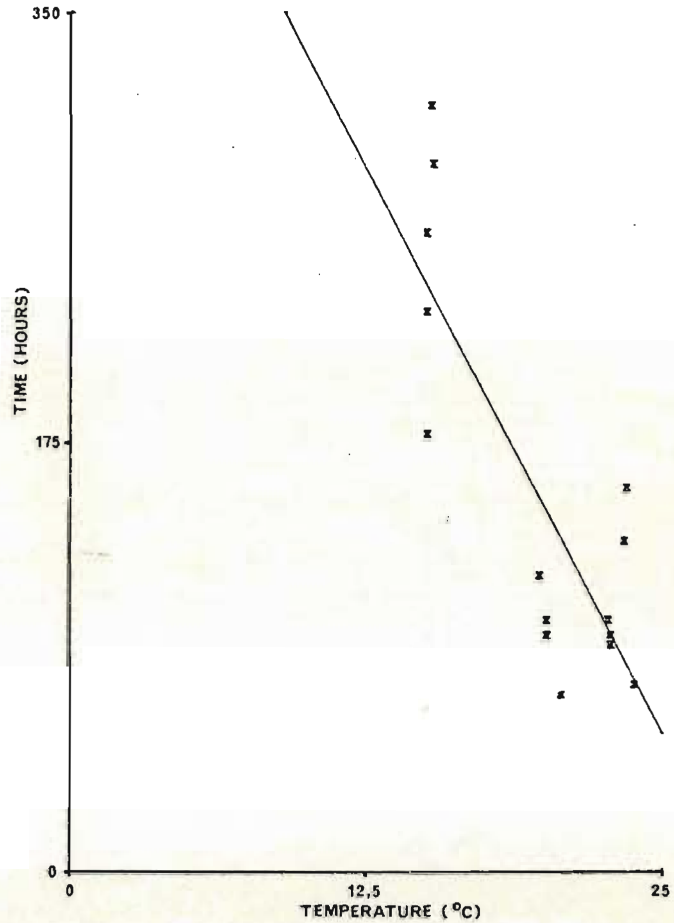
The rate of development of sarcophagous blow-fly larvae is little short of astounding, but the necessity and adaptive significance of this rapid growth becomes clear when examining the selective pressures exerted on the larvae. As other authors have indicated (Ullyett 1950, Levot et al 1979, Meskin 1980) and personal observations as related in Chapter 4 have shown, intra- and inter-specific competition between blow-fly larvae for the confined and finite resources at the carrion-habitat is severe. An array of predatory insect species, especially histerid beetles, prey on the larvae in large numbers, and the constant high likelihood of complete removal of resources by vertebrate scavengers all contribute to selective advantage being placed on a rapid rate of development. This necessitates optimal utilisation of available nutrients, but the energetics of food assimilation has been studied by relatively few workers. Hanski (1976a) found that efficiency was highest at temperatures between 25 to 30°C, and at such temperatures Lucilia illustris larvae had instantaneous net production efficiencies (i.e. increase in biomass divided by assimilation) up to 82% (carbon units) or 84% (energy units). These values are very high when compared to the estimates of below 50% for most insect larvae, while a value of only 39% is suggested as a mean for all saprohagous invertebrates (Hanski 1976a). Using Calliphora erythrocephala, Putman (1977) found that mean total assimilation per larva up to the prepupal stage was 186,18 cal (S.D.70,81 cal), while daily non-cumulative mean assimilation per larva was in the order of 9,73 ± 2,66 cal in the first day after hatching, and 32,18 ± 28,15; 121,95 ± 67,10 and 40,91 ± 32,17 for Day 2, 3 and 4, the larvae leaving the carcass on Day 5.

The work of these authors, Hanski (1977) and especially Levot et al (1979) indicated that there is a distinct period of most rapid growth which generally coincides with the early third larval instar, and that the highest assimilatory rate (highest value for instantaneous net production efficiency) occurs during this period of maximal biomass production.

The rates of development of Chrysomyia albiceps and C. marginalis larvae in the study area are provided in Figures 99 and 100 as regressions by plotting time (from egg-deposition to post-feeding 3rd stage larvae seeking pupariation sites) against the mean minimum air temperature during this period. As Richardson (1980) correctly pointed out, ambient temperature is not a desirable parameter as the temperatures to which the larvae are exposed in the carcass differ considerably from general atmospheric temperature. Measurement of internal carcass temperature is even less suitable however, as the microclimate varies so considerably over short distances and the constant movement of larvae is such that they are exposed to a widely fluctuating temperature regime within short spaces of time. Thus it is that the collective heat generated by the maggots inside the carcass may result in temperatures over 50°C, (Fig. 10) while only a few centimetres away at the carcass/atmosphere interface temperatures may be less than 30°C. Maggots constantly traverse these temperature boundaries so that for practical purposes it is more desirable to use ambient temperature, even though this should only serve as a relative index.



<u>FIGURE 99</u>: Relationship between mean minimum ambient temperature and time in the development of <u>Chrysomyia albiceps</u> from oviposition to post-feeding third instar larva. (Fitted curve is the exponential curve y = 998,456; r = 0,895; p <0,01; df = 10)



<u>FIGURE 100</u>: Relationship between mean minimum ambient temperature and time in the development of <u>Chrysomyia marginalis</u> from oviposition to post-feeding third instar larva. (Fitted line is the straight line y = 18,505; r = 0,815; p <0,01; df = 13)

The data used for the compilation of Figures 99 and 100 were obtained from observations at carcasses under natural conditions (other than vertebrate scavengers being excluded by fencing wire). To generalise from these results, and supposing for the purposes of this generalisation that oviposition occurred on Day 1 by C. marginalis and Day 2 by C. albiceps at a carcass placed early on Day 1, C. marginalis larvae were found to have completed feeding and moved off to seek pupariation sites by between Days 4 and 6 in summer, and C. albiceps between Days 5 and 7. In winter the developmental rate was considerably slowed down so that C. marginalis and C. albiceps larvae generally ceased feeding between Days 9 to 14.

The general pattern of blow-fly larvae behaviour during development was for recently emerged C. marginalis larvae to enter the carcass and then to spend the bulk of their larval lives either in or on the carcass. After eclosion from the egg-stage C. albiceps larvae were also found to often move onto the carcass, but with few exceptions were soon ousted and limited to peripheral areas of the carcass by competition with C. marginalis larvae. Most C. albiceps larvae occurred as a wide swath around the carcass and also below it, thus spending the bulk of their time off the carcass. During the final stages of growth large masses of C. marginalis larvae were also present alongside the carcass due to insufficient food and space resources, but they tended to occupy positions separate from C. albiceps larvae. C. marginalis were completely dependent upon carcass material during their entire larval life, whereas the 2nd and 3rd larval stages of C. albiceps were facultative predators which preyed heavily upon C. marginalis larvae falling onto or crawling through the swath of C. albiceps surrounding the carcass. This predatory nature of C. albiceps is a well-known phenomenon (Smit 1931, Mönnig & Cilliers 1944, Ullyett 1950, Zumpt 1965, Meskin 1980, Prins 1980, 1982). Experiments conducted in February 1981 in the study area using multiple replicates of mixed and separate C. albiceps and C. marginalis larval populations on baboon meat revealed that on a diet of meat only, C. albiceps larval development was successful and produced viable flies (5 replicates of 10 larvae each, one of 50 pupae failed to produce an adult). When offered both meat and live C. marginalis larvae as food resources, C. albiceps 2nd and 3rd stage larvae utilised both but developed at the same rate and as successfully as those with meat only (40% of C. marginalis larvae killed, but this was under confined conditions). The most interesting results were that when 30 2nd instar (6 mm average) were placed with 90 2nd instar C. marginalis larvae in dishes with no meat, all the larvae died. This suggests therefore that meat - or the broth draining from a carcass to the peripherally situated C. albiceps larvae - is essential to the development of these flies, and that predation is opportunistic but not sufficient in itself.

Although young 3rd stage C. albiceps larvae offered only C. marginalis larvae as resource did produce some sub-sized puparia, the results were ambiguous as those successful could equally have been attributed to sufficient reserves in the larvae from earlier feeding on meat. More extensive trials are needed to clarify this aspect.

Having completed their feeding and stored sufficient reserves for the pupal stage, C. marginalis larvae frequently departed en masse from the carcass to dig into the soil for pupariation several metres away from the carcass. This departure en masse has definite survival value as they have to move through or over the swath of C. albiceps which thus have less opportunity to prey on the collective mass than on scattered individuals. The mass emigration, or if not quite so concentrated then departure of maggots is nevertheless generally within a relatively short period of each other, is also a reflection on the limited period over which C. marginalis females oviposit, thus enabling the larvae to reach maturity at much the same time. By way of contrast, larvae of C. albiceps did not display such a near-synchronised period for entering the prepupal stage, this occurring over several days (also mentioned in Braack 1981). Only on very rare exceptional occasions did C. albiceps larvae depart from the carcass-site or dig into the soil (in each case prompted by being severely disturbed or sudden complete removal of the carcass), the usual pattern being for the larvae to pupariate above soil below or immediately alongside the carcass. Another interesting phenomenon associated with the mass departure of C. marginalis larvae from the carcass, was the frequency at which this departure occurred at night, this being especially noticeable in summer. This would of course have high adaptive significance as night-emigration would not expose the larvae to the desiccating effects of the hot summer days (and would probably have added benefits to some extent by concealment from reptilian and avian predators). Supporting this conclusion to some extent was the frequent observation that, again most prominent under hot summer conditions, less larvae of C. marginalis would be visible by day as they tended to move into the carcass whereas at night they swarmed all over the carcass.

Smit (1931) briefly remarked that sheep blow-flies (known then as Lucilia sericata, but probably were L. cuprina) departed at night, and Smith et al (1981) also observed the same tendency in larvae of Lucilia cuprina for night-time departure from parasitised sheep and rearing-medium in trays. Smith et al speculated on the significance of this behaviour but failed to relate it to the natural environment at carcasses where the value of this phenomenon may be more easily determined.

Prins (1982) found that under a laboratory temperature regime between 25-28°C the 1st instar larvae of C. albiceps lasted 15-20 hours with a length of about 3 mm 12 hours after hatching, the second stage larvae occupied 26-30 hours reaching 6-7 mm after that period, whilst final stage larvae varied from 153 to 158 hours, the entire larval lifespan thus taking 199 to 204 hours. His observations showed the larval lifespan of C. marginalis (which he called C. regalis) to be about 11 days during late summer in the south-western Cape Province (cool climate).

Miscellaneous observations concerning physical stresses on blow-fly larvae

Observations at carcasses where blow-fly larvae were occasionally temporarily submerged by rain-water or carcass-fluids prompted a short test to determine the ability of these larvae to successfully withstand submersion. Twenty full-grown 3rd stage larvae of each of C. albiceps and C. marginalis were placed in net-bags and totally submersed in water at room temperature for 60 minutes. The larvae became sluggish and near quiescent towards the end of this period, but when removed and placed on sand, all pupariated and successfully produced adults. On another occasion in summer four sand-filled jars each containing between 50-100 near full-grown 3rd stage C. marginalis larvae were accidentally thoroughly wetted (but not drenched) by rain. The larvae crawled around until the upper layers of sand had sufficiently dried more than one week later before pupariating. This observation indicated that these larvae can, when suitable sites are unavailable, delay pupariation for a considerable length of time.

Temperatures were often found to reach very high levels within carcasses (Fig. 10) and especially *C. marginalis* larvae were regularly exposed to such heat. At a decomposing hippopotamus, general atmospheric temperature was measured as 33,5°C whereas the temperature inside the hollowed out cavity was 40,0°C, and inside a mass of *C. marginalis* larvae within the abdominal cavity temperature measured 43,5°C. Surprisingly the temperature within a mass of *C. albiceps* larvae *outside* the carcass was also found to be very high at 42,5°C. As corroborating evidence, Coe (1978) recorded temperatures of 47,5°C in the external meatus of an ear of a decomposing elephant and 51°C "on the surface of the soil surrounding the corpse".

Vertebrate predators of larval stages

In addition to the array of invertebrate predators of *C. albiceps* and especially *C. marginalis* larvae discussed in Chapters 3 and 4, a number of vertebrates were observed feeding on mainly *C. marginalis* larvae during their dispersive phase away from the carcass in search of pupariation sites. These included Common Variable Skinks (*Mabuya varia*), a Rock Leguaan (*Varanus exanthematicus*), Blue-eared Glossy Starlings (*Lamprotornis chalybaeus*), Crested Francolins (*Francolinus sephaena*), Yellow-billed Hornbills (*Tockus flavirostris*) and Red-billed Hornbills (*Tockus erythrorhynchus*). These were all sporadic, exceptional cases and direct vertebrate predation probably has a negligible impact on the blow-fly population. Vultures, hyaenas and jackals presumably consume considerable quantities of larvae at some carcasses during the scavenging process. As has already been indicated elsewhere however, the adult blow-fly population is almost certainly sustained by larvae developing at large (elephant/buffalo/giraffe etc.) carcasses or medium and smaller-sized carcasses undiscvoered by vertebrates, so that this scavenging has been adapted for in the species.

PLATE 2: Immature stages of *Chrysomyia albiceps*

a) Dorsal view of egg showing median strip. X 75.

b) Median strip at anterior pole of egg. X 2 000.

c) First instar larva, lateral view. X 35.

d) Second instar larva, anterior spiracles. X 750.

e) Second instar larva, posterior spiracle. X 1 000.

f) Second instar larva, lateral view. X 35.

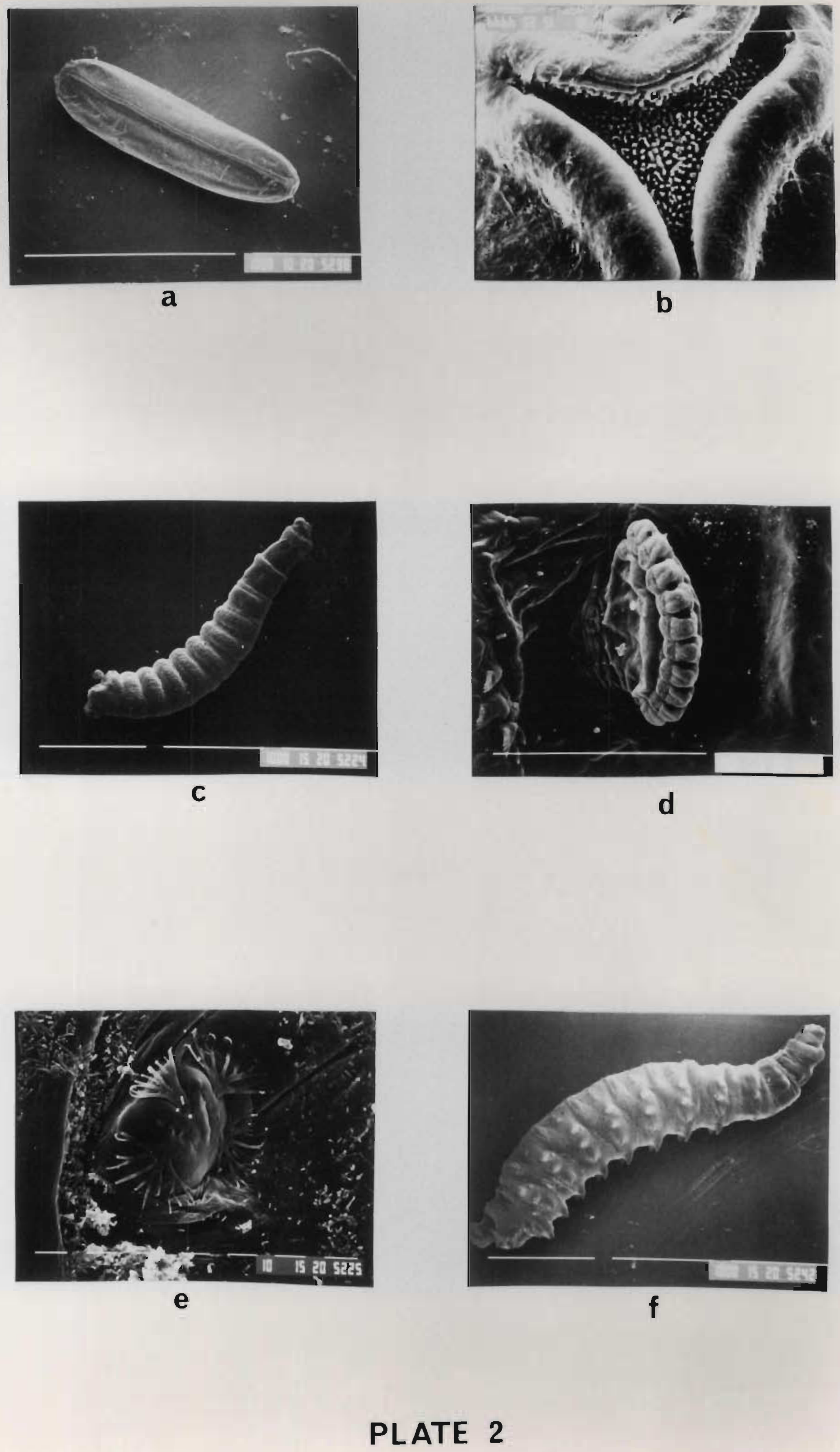


PLATE 2

PLATE 3: Immature stages of *Chrysomyia marginalis*

a) Dorsal view of egg showing median strip. X 75.

b) Median strip at anterior pole of egg. X 5 000.

c) Outer meshwork layer of chorionic plastron comprising median strip on egg. X 10 000.

d) First instar larva, lateral view. X 50.

e) First instar larva, anterior view. X 200.

f) Second instar larva, posterior spiracle. X 500.

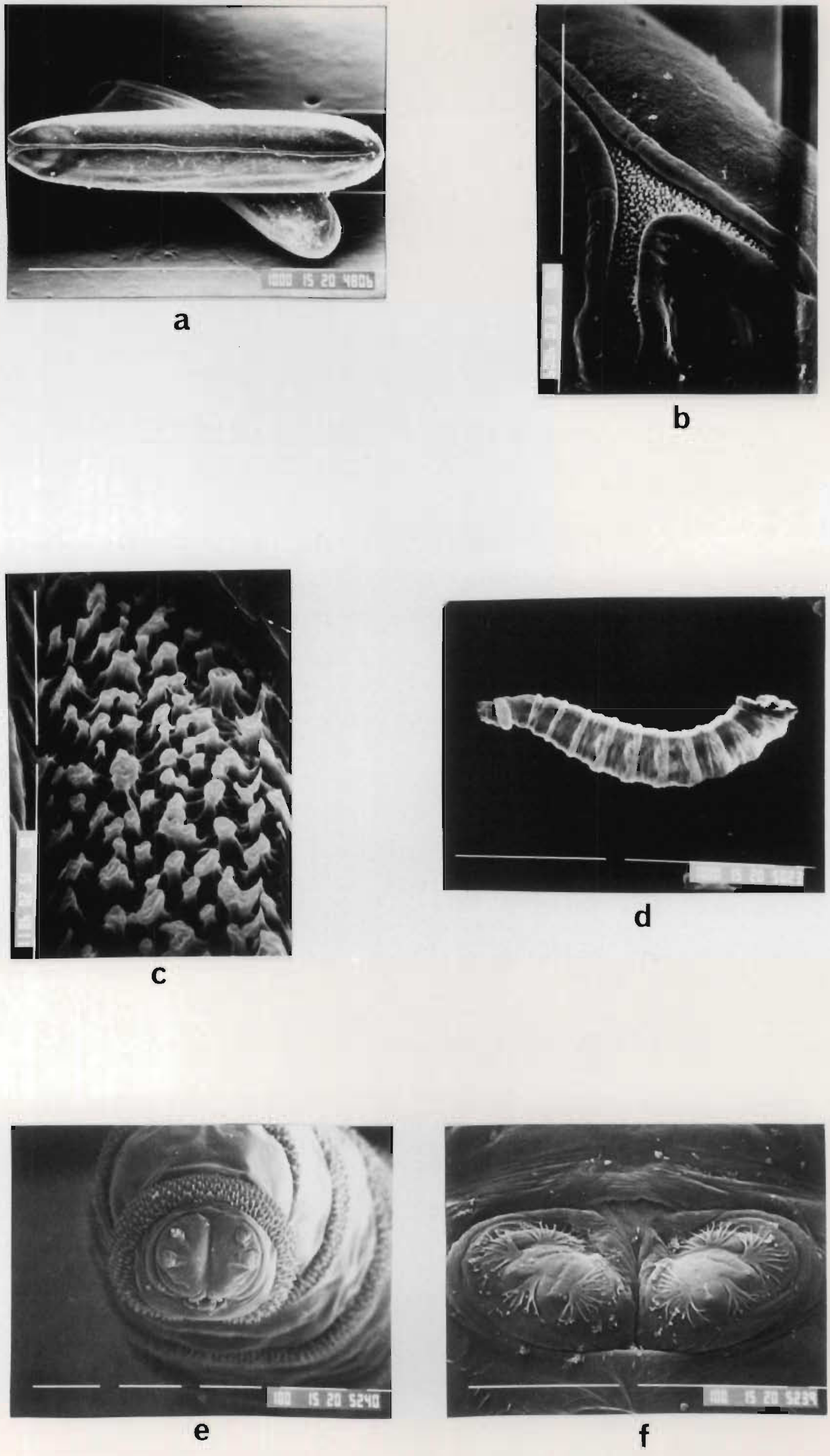


PLATE 3

Larval mortality in vulture intestines

In the foregoing section it was indicated that relatively few carcasses were available for utilisation by blow-flies as breeding-medium. Scavenging vertebrates, however, were occasionally observed feeding at large carcasses (giraffe, buffalo, elephant) where maggots had established feeding sites and reached near full-grown proportions. The idea arose that if blow-fly larvae swallowed by especially vultures during feeding could survive passage through the digestive tract of a vulture, the high population level of C. albiceps and C. marginalis in the study area could at least in theory be more easily sustained than a population exclusively dependent upon that fraction of carcasses remaining undiscovered or incompletely consumed. Larvae of Calliphoridae, Sarcophagidae, and a variety of other dipteran species have been reported by Zumpt (1965) and James and Harwood (1970) as having survived extended periods in mammalian digestive tracts, so that the possibility of larval blow-fly survival in vulture intestines increases.

Three vultures (one adult Cape vulture, Gyps coprotheres; one immature Whiteheaded vulture, Trigonoceps occipitalis; and one immature Whitebacked vulture, Gyps africanus) were caught between 6-9 June 1980 using nylon leg-traps set at a buffalo carcass in the Pafuri area and transported to the Anthrax Research Camp at Pafuri and each placed in a metal-barred cage measuring 1,2m x 1,8m x 1,2m.

The vultures were each provided daily at 08h00 with a basin of fresh water and a basin containing fresh baboon meat cut into small lumps (about golf-ball size) with between 150-200 C. albiceps and 200-300 C. marginalis 2nd and 3rd instar larvae added to the meat. At 12h30 the basin with any leftover meat and larvae was removed and large trays placed below each cage to receive faeces and regurgitation. Inspections were made at hourly intervals until 22h00 for the presence of larvae in the trays.

The above procedure was followed for seven days, after which it was decided to withhold all meat for six days and then to give each vulture 200g baboon meat again cut into small lumps, blow-fly larvae of all sizes being added to the meat. Trays were again placed under each cage during the six-day pre-feeding period, and for four days afterwards.

During February 1981 three adult Whitebacked vultures were kept in the same cages and fed 450g portions of baboon meat with blow-fly larvae of all sizes. They were fed at five-day intervals for fifteen days. Trays were placed below each cage as before.

During the initial July 1980 experiments the vultures were not yet accustomed to the proximity of humans, so that occasionally when approaching the cages they would regurgitate some of the contents of the crop. Blow-fly larvae were often expelled with meat in this way, and in each case all the larvae of both species were dead.

No viable larvae were found in the faeces during any of the trials, but clean, flattened larval skins of both species were frequently found lying individually or in small batches in the trays.

On two occasions in February 1981 "hairballs" or pellets (vultures had been fed whole baboons in January and early February), approximately 3cm x 2cm, were found in which larval skins of both species of blow-fly were matted.

The above results indicated that larvae of _C. albiceps_ and _C. marginalis_ appear unable to survive the conditions in the alimentary canal of the three species of vultures mentioned.

The other species of vertebrate scavenger responsible for bulk removal of carrion in the northern Kruger Park is the spotted hyaena, and it seems inconceivable that blow-fly larvae would be able to survive the unusually potent digestive enzymes present in the stomach of that animal.

It seems likely therefore that blow-fly larvae establishing themselves at carcasses and consumed by vultures and hyaenas are precluded from forming any contribution to the adult blow-fly population.

Number of larvae attendent at carrion

Chrysomyia albiceps and _C. marginalis_ flies occur widespread and abundantly in southern Africa (Smit & Du Plessis 1927, Smit 1931, Mönnig & Cilliers 1944, Zumpt 1965), and breed most commonly in large carcasses (Smit 1929, 1931, Mönnig & Cilliers 1944, Zumpt 1965). In the northern K.N.P. they are especially common and their average annual abundance by far exceeds that of any other carrion-utilising flies (Chapt. 6). To gain some idea of the potential recruitment to this population offered by breeding sources it was decided to determine the number of full-grown or near full-grown larvae present at carcasses such as those of impala. As the major portion of the mortality affecting blow-flies occurs in the earlier larval stages due to competition and predation (Ullyett 1950) and a correction factor can be incorporated for pupal mortality (see next section) the number of full-grown larvae would allow a fair estimate to be made of the number of adult flies which would result from such a carcass. A number of carcasses were therefore placed at intervals in the Pafuri area to determine the larval load, but success was only achieved at three carcasses due to mishaps and scavenging.

All the carcasses used were adult male impala and after weighing were placed at site A (area enclosed with fencing wire, Fig. 11) on a large mesh fencing-wire platform. Close observation was maintained until the first post-feeding larvae were noticed, at which stage the carcass was raised by means of lifting the platform, all the larvae on the ground were scooped into a large basin containing formalin and this was then positioned below the carcass. Formalin was poured over the carcass to encourage departure of the remaining larvae which eventually dropped into the basin. The edges of the basin were curved sharply inwards so maggots were unable to escape. The basin was left in position for two additional days so that all larvae were collected. The contents of the basin was then poured through a sieve (2 m square of mosquito netting), the retrieved maggots rinsed, and finallly thoroughly mixed by alternatively moving corners of the sieve to their opposite sides for several minutes. Five random samples of maggots 100 g in weight were taken and the contents later counted and these figures averaged to a mean number of larvae for each species per 100 g of maggots. The entire remainder of maggots on the sieve were then weighed and by extrapolation from the number of larvae in the averaged 100 g sample, the total number of larvae per carcass and their proportionate contribution could be determined. The same procedure was used to determine the larval load at a sheep carcass placed in the

Bontebok National Park (Swellendam, Cape Province) for comparison (Table 15).

TABLE 15: Number of 3rd instar larvae attendant at carcasses at Pafuri and Swellendam

Date	Carcass	Mass in Kg.	Locality	Number of larvae		Total number of larvae
				C. albiceps	*C. marginalis*	
February 1980	Impala	55,0	Pafuri	114 943 ± 9 920	95 097 ± 5 760	210 040 ± 15 680
January 1981	Impala	58,5	Pafuri	25 977 ± 2 400	139 086 ± 6 230	165 063 ± 8 630
January 1983	Impala	62,7	Pafuri	56 603 ± 7,011	116 966 ± 5 236	173 569 ± 12 247
March 1979	Sheep	33,25	Swellen-dam	28 948 ± 5 580	95 328 ± 7 803	124 276 ± 13 383

From the above it can be seen that there is no definite correlation between carcass-size and number of attendant larvae. The figures do confirm, however, observations that large numbers of larvae do utilise available carcasses in summer in the study area. These determinations (Table 15) only reflect summer conditions which are optimal for larval development (increased adult population so more eggs laid per carcass, shortened growth period due to higher metabolic rate so less time for predation by histerids etc., also less likelihood of carcass discovery by vertebrate scavengers due to period of exposure less and vegetational cover better). Far fewer larvae utilise carcasses at Pafuri during the cooler months (personal observations) and during June/July larval numbers per impala-carcass are reduced to a few thousand.

A number of persons in South Africa have made determinations of the number of larvae or adult flies emerging from carrion and these provide good measures for general comparison. Hepburn (1943b) placed sheep carcasses during most months of the year at Onderstepoort (Transvaal) and Middelburg (Cape) and recorded the number of flies reared from them (Tables 16 & 17).

The pattern presented by Hepburn's (1943b) Onderstepoort carcasses indicate that (1) Chrysomyia albiceps and C. marginalis were the most consistent of the blow-fly species utilising carrion, (2) they were generally the most abundant of the various species, (3) they utilised carcasses throughout the year, (4) they emerged more prolifically from carcasses in the warmer months, (5) their numbers were low during the cooler winter months and (6) Lucilia spp. and especially Chrysomyia chloropyga were often more plentiful in winter and early spring. His results from Middelburg (Cape) showed that in this cooler region Chrysomyia chloropyga was the most successful species utilising carrion. Of the remaining species C. marginalis was by far the most numerous, but in comparison with the Onderstepoort results this species and C. albiceps were less successful in utilising carcasses during cooler months when Lucilia spp. and C. chloropyga became abundant. C. albiceps and C. marginalis were nevertheless the most numerous of blow-flies in the warmer months when they utilised carcasses to the virtual exclusion of other species.

TABLE 16: Number of blow-flies reared from sheep carcasses at Onderstepoort (Transvaal) (Adapted from Hepburn 1943b)

Date experiment commenced	Days of carcass exposure for oviposition	Number of flies reared from carcass						
		Lucilia cuprina	*Lucilia sericata*	*Chrysomyia chloropyga*	*Chrysomyia albiceps*	*Chrysomyia marginalis*	Other species	Total flies
5/6/40	10	13	43	17 253	14 054	2 044	-	33 407
15/11/40	7	-	-	-	16 477	6 435	226	23 138
3/2/41	2	-	-	-	7 960	14 249	699	22 908
2/6/41	7	-	-	4 635	4 350	36	69	9 090
20/8/41	13	411	838	15 465	982	402	194	18 292
30/9/41	7	-	-	-	9 396	31 232	12	40 640
31/10/41	7	-	-	-	8 991	4 920	-	13 911
31/12/41	3	-	-	-	1 427	1 488	-	2 915
17/3/42	5	-	1	4	14 636	13 769	101	28 511
23/4/42	6	6	1	-	15 650	3 952	1	19 610
23/6/42	14	249	12 528	22 978	62	2	218	36 037
5/8/42	12	391	3 965	40 244	2 938	2 394	40	48 972
25/9/42	7	-	-	2	8 263	16 690	1	24 956

TABLE 17: Number of blow-flies reared from sheep carcasses at Middelburg (Cape Province)(Adapted from Hepburn 1943b)

Date experiment commenced	Days of carcass exposure for oviposition	Number of flies reared from carcass						
		Lucilia cuprina	*Lucilia sericata*	*Chrysomyia chloropyga*	*Chrysomyia albiceps*	*Chrysomyia marginalis*	Other species	Total flies
4/7/41	10	15 371	25 948	23 925	28	-	186	65 458
6/8/41	10	25 767	20 589	47 228	-	-	30	93 614
11/9/41	10	896	633	38 226	97	-	-	39 852
10/10/41	10	977	899	21 234	438	-	-	23 548
10/11/41	10	14	-	17 343	7 213	-	4	24 574
13/12/41	10	-	-	-	12 080	27 397	-	39 477
14/1/42	10	-	-	-	11 811	37 829	-	49 640
12/2/42	10	-	-	50	7 923	25 650	1 698	35 321
14/3/42	10	-	-	9	2 419	4 544	63	7 035
9/4/42	10	-	-	-	5 656	11 226	16	16 898
	TOTAL	43 025	48 069	148 015	47 665	106 646		

An additional important finding by Hepburn (1943b) was that *C. marginalis* rarely visited small carcasses - such as those of rats - as breeding medium, which was confirmed by Meskin (1980) and my own observations in the study area. Low numbers of *C. albiceps* larvae did occasionally utilise such small larvae in the study by Hepburn, but *Lucilia* spp were by far the most numerous and consistently used such small carcasses. Larger carcasses, such as cats and rabbits, were frequently used by *C. marginalis* for breeding. From the results obtained at carcasses of 304 small animals, such as birds, rats, lizards, frogs etc. in the Cape winter rainfall area, Mönnig and Cilliers (1944) concluded that there was a qualitative difference - a transitional phase between carcasses over and under about 500g, those less than that mass being utilised mostly by larvae of *Lucilia*, *Calliphora croceipalpis* and *Sarcophaga* spp. Those above 500g attracted generally the same species and proportionate make-up of flies as those attracted to sheep carcasses. At such carcasses they found that *C. albiceps* and *C. marginalis* predominated during the warmer months while *Lucilia sericata* and especially *Chrysomyia chloropyga* increased in winter (Table 18).

Coe (1978) calculated that 144 600 *C. albiceps* and roughly 11 500 *C. marginalis* "prepupae" had utilised an elephant carcass he had observed in the Tsavo National Park, Kenya. The number of *C. albiceps* he calculated would be in broad general agreement with an estimated 250 000 similar larvae I observed at the 5 day old remains of a minimally scavenged decomposing elephant in October 1982 near Lower Sabie in the southern K.N.P. His estimate of 11 500 is considerably lower, however, than the more than 500 000 *C. marginalis* larvae observed at this carcass. At the 3 day old carcass of a young elephant near Shingwedzi in October 1982 heavily scavenged by hyaenas and vultures, I estimated between 40 to 50 000 *C. marginalis* larvae to be present, but could find only a few hundred *C. albiceps* larvae. At the 10 day old remains of yet another elephant carcass - a full grown adult partially scavenged by hyaenas and cultures - near Shingwedzi in September 1982 I estimated about 130 000 *C. albiceps* but only about 50 000 *C. marginalis* larvae to be utilising the carcass. At the 6 day old remains of an adult giraffe killed and extensively fed on by five lions near Skukuza in October 1982, I collected and counted all the blow-fly present at the site. All that remained of the carcass at the time were the neck and limbs which had been essentially unused by vertebrate scavengers.

TABLE 18: Number of blow-flies reared from sheep carcasses at Bredasdorp (Cape Province) (Adapted from Mönnig and Cilliers (1944)

Date experiment commenced	Days of carcass exposure for oviposition	Number of flies reared from carcass					
		Lucilia cuprina	*Lucilia sericata*	*Chrysomyia chloropyga*	*Chrysomyia albiceps*	*Chrysomyia marginalis*	*Calliphora croceipalpis*
8/7/42	10	0	396	61 304	129	0	488
25/8/42	7	0	0	59 780	9 671	2 776	0
13/10/42	7	0	0	5 246	6 820	525	0
17/11/42	7	0	0	0	1 567	683	0
22/12/42	7	0	0	16	24 061	185	0
16/2/43	7	0	0	236	11 342	4 091	0
29/3/43	7	0	0	0	8 864	24 128	0
11/5/43	7	0	0	0	972	3 456	0
	TOTAL	0	396	126 582	63 426	35 844	488

The counts (by counting the number of larvae in 5 x 100g samples and extrapolating to the entire mass of larvae collected) indicated that between 197 727 and 220 727 C. marginalis larva and 67 106 (± 4 403) C. albiceps larvae were present at the carcass.

From the results above it should become clear that there is an element of chance in the number of larvae developing at a carcass. There is no direct correlation between carcass size and the number of larvae present; certainly it is true that more larvae are able to develop at larger carcasses, but it does not necessarily mean - and in fact very rarely happens - that progressively larger portions of carrion will support proportionately more larvae. By way of example, two similarly sized impala carcasses in the same condition can be placed directly alongside each other at the same time under the same conditions, but the number of larvae developing in each will rarely be similar in number. Indeed, as is indicated in Table 15, the proportionate contribution of larvae of each blow-fly species towards the total number of larvae present varies from carcass to carcass, with one species being more numerous that another species at one carcass but less so at another, within the same season and not as a result of normal seasonal changes in population fluctuations. Hepburn (1943b) also raised this phenomenon of randomness in larval populations at smaller carcasses.

Despite this element of randomness discussed above, the number of larvae is nevertheless generally such that - at least in the warmer months of the year - all the soft tissues present at medium-sized carcasses, such as impala and considerably larger animals such as kudu, will be rapidly consumed in their entirety by the larvae without any assistance from vertebrate scavengers. During the severe drought of 1982 I had opportunity to witness evidence of several buffalo carcasses which had been stripped of soft tissues by the action of blow-fly larvae only, this serving as an indication of their efficiency.

PUPARIATION AND PUPAL MORTALITY

The pupal stage is potentially highly vulnerable to attack from both invertebrate and vertebrate predators. To counteract this to some extent larvae of C. albiceps and especially C. marginalis seek concealed positions prior to entering the pupal stage.

Larvae of Chrysomyia marginalis tend to 'pupariate' as a collective, concentrated effort which is generally obvious in warm weather but less distinct in winter. Departure from the carcass in such cases was found to take the form of a mass migration which lasted only a few hours from time of departure from carcass to the vast majority being buried below ground. This occurred despite the larvae being the offspring of a number of different females and the eggs almost certainly having been deposited at different times. Some mechanism thus appeared to trigger a behavioural response for collective movement away from the carcass. The mass migration resulted in pupariation over a short period of time with very few C. marginalis remaining at the carcass.

Pupariation in Chrysomyia albiceps, however, represented a contrasting strategy. At no stage was any concentrated, near-simultaneous pupariation behaviour observed in the collective mass of larvae present at the carcass. Instead they tended to pupariate as individuals over a protracted period of several days irrespective of season and situation. Whereas C. marginalis larvae moved away from the carcass for a distance of several metres and buried themselves below one to ten centimetres of soft soil, C. albiceps larvae only in exceptional instances buried themselves and in most cases pupariated above soil below or immediately next to the carcass - the great majority of puparia being directly below the cascass. The puparia were considerably thicker and tougher than those of C. marginalis, and reflect similar properties displayed by the 3rd stage larval cuticles.

Although C. albiceps puparia were sufficiently protective as a shield against possible desiccation by being often directly exposed to the sun, they were vulnerable to parasitic attack by such wasps as Nasonia vitripennis (Pteromalidae) and Trichopria lewisi (Diapriidae). Tables 19 and 20 summarise the results obtained from a sample of 1 033 puparia of both C. albiceps and C. marginalis at different times and conditions.

TABLE 19: Mortality in *Chrysomyia albiceps* pupal stage. Pupae were kept individually in net-topped glass-bottles until ten days after last adult blow-fly had emerged, the unemerged puparia then broken open for examination.

Date of carcass placement	Date puparia collected	Site of collection	Number of puparia collected	Successfully emerged adults	Unemerged Parasitised puparia	Unemerged Brittle concretion inside puparium	Unemerged Flaky yellowish mass inside puparium	Unemerged Dead, fully formed flies inside puparium	Unemerged Puparium partially chewed by insects
9/2/80	16/2/80	Above ground, randomly below and around carcass	89	15	-	22	36	16	-
17/2/80	26/2/80	Above ground among rumen-content and bones	103	80	3	-	1	17	2
12/5/80	27/5/80	Above ground immediately next to carcass	100	26	-	14	17	39	4
12/5/80	27/5/80	Above ground below carcass	100	51	12 (*Trichopria*)	4	5	21	7
12/5/80	27/5/80	Below carcass partially buried in soil	66	52	5 (*Trichopria*)	4	-	5	-
1/6/80	21/6/80	Above ground below carcass	62	55	5 (*Trichopria*)	1	-	1	-
15/1/81	23/1/81	Above ground, randomly below and around carcass	34	30	-	-	-	4	-
		Totals	554	309	25	45	59	103	13
		Percentage of total	100	55.7	4.5	8.1	10.6	18.5	2.3

TABLE 20: Mortality in *Chrysomyia marginalis* pupal stage. Pupae were kept individually in net-topped glass-bottles until ten days after last adult blow-fly had emerged, the unemerged puparia then broken open for examination.

Date of carcass placement	Date puparia collected	Site of collection	Number of puparia collected	Successfully emerged adults	Unemerged Parasitised puparia	Unemerged Brittle concretion inside puparium	Unemerged Flaky yellowish mass inside puparium	Unemerged Dead, fully formed flies inside puparium	Unemerged Puparium partially chewed by insects
9/2/80	16/2/80	Below soil, 0,5 m radius from carcass	103	56	2 (undetermined insects)	15	3	16	11
17/2/80	26/2/80	3-10 cm below soil, up to 2 m radius around carcass	122	96	1 (undetermined sect)	-	2	17	6
12/5/80	27/5/80	Above soil, within 0,75 m of carcass	100	38	-	27	8	21	6
12/5/80	27/5/80	2 to 7 cm below soil, within 2 m of carcass	100	45	-	7	1	45	2
1/6/80	21/6/80	Below soil, 1 m radius from carcass	54	39	-	9	-	3	3
		Totals	479	274	3	58	14	102	28
		Percentage of total ..	100	57,2	0,6	12,1	2,9	21,2	5,8

The tables indicate an average 44,3% mortality in the pupal stage of _C. albiceps_ whilst _C. marginalis_ was subject to an average 42,8% pupal mortality. This natural mortality contrasts strongly with large numbers of 3rd stage post-feeding larvae which I collected on numerous occasions for placement in netting-covered sand-basins to obtain adults where a mortality rate in the pupal stage of only one to two percent was the norm. Given suitable conditions a very high survival rate through the pupal stage was therefore possible. Tables 19 and 20 also indicate a 4,5% parasitism in _C. albiceps_ and a mere 0,6% in _C. marginalis_.

Figures 101 and 102 graphically depict the rate of development of the two species from oviposition to adult emergence. By comparison with Figures 99 and 100 which depict the rate of larval development from oviposition to the post-feeding third stage larvae, it can therefore be deduced that the pupal stage in summer for both species generally lasts approximately four days whilst in winter it may be six days or longer.

The divergent pupal strategies of the two species can thus be briefly contrasted: (1a) By moving away from the carcass and finally dispersing prior to digging into the soil _C. marginalis_ escapes the occasionally heavy toll taken by parasitism; (1b) By remaining at the carcass in a relatively confined area and pupariating predominantly above ground (but below the carcass) _C. albiceps_ exposes itself to, and is subjected to, occasional heavy parasitism; (2a) By moving away from the carcass, even in a concentrated effort, _C. marginalis_ is at times subjected to heavy predation especially by birds, although it escapes parasitism; (2b) By remaining under the carcass _C. albiceps_ exposes itself to parasitism but appears to escape vertebrate predation almost entirely. This last mentioned situation is not intuitively satisfying however, as _C. albiceps_ puparia were at virtually all carcasses fairly easily accessible to birds and lizards, but were never seen to be fed on by these animals. Their tough skin and the spiky projections covering the body to some extent may be a repellent factor. In general, however, the two strategies appear counterbalanced, both conferring advantages but also having disadvantages. The prime reason for departure from the carcass habitat by _C. marginalis_ prior to becoming immobile however, is almost certain a response to escape from _C. albiceps_ larvae which would prey very heavily upon the defenceless prepupae.

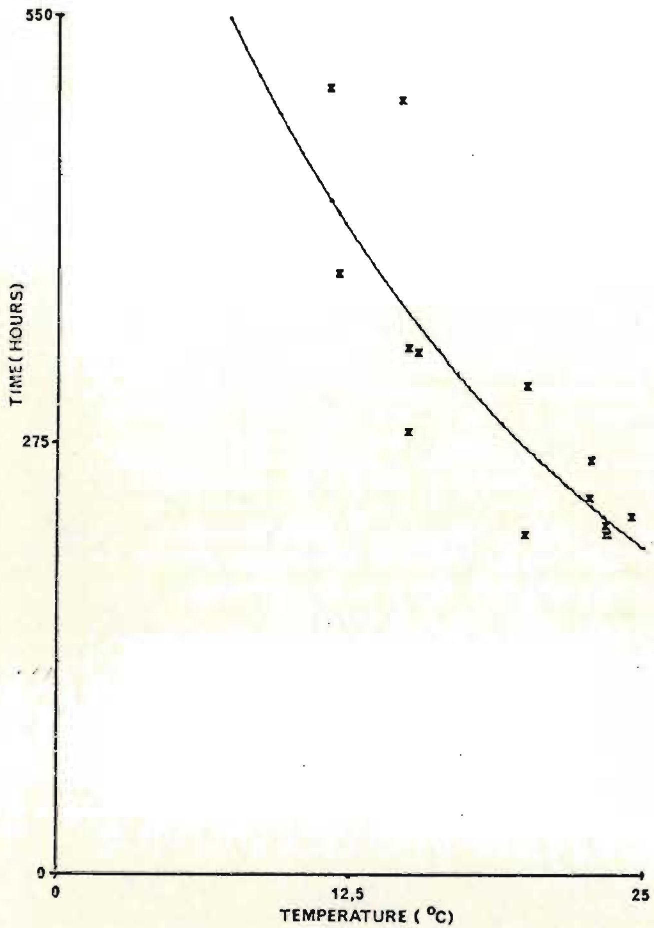


FIGURE 101: Relationship between mean minimum ambient temperature and time in the development of *Chrysomyia albiceps* from oviposition to adult emergence from the puparium. (Fitted curve is the exponential curve y = 818,255; r = 0,865; $p < 0,01$; df = 12)

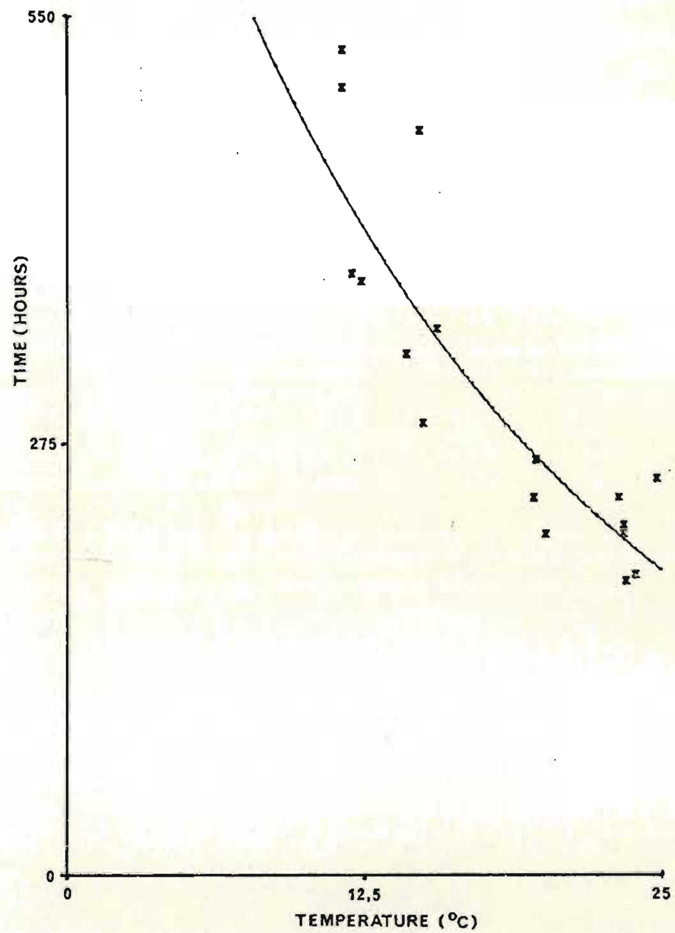


FIGURE 102: Relationship between mean minimum ambient temperature and time in the development of *Chrysomyia marginalis* from oviposition to adult emergence from the puparium. (Fitted curve is the exponential curve y = 889,266; r = 0,895; $p < 0,01$; df = 15)

CHAPTER 6

POPULATION DYNAMICS OF ADULT *CHRYSOMYIA ALBICEPS* AND *C. MARGINALIS*

To learn more of the behaviour and dispersal patterns of the adults it was decided that the most practical and effective method would be to rear large numbers of blow-flies and mark the adults in such a manner that they would be easily recognisable for a number of weeks. Such flies would then be released from a central point and after allowing them to disperse unhindered for a period of about one week, place traps in different localities at varying distances to recapture marked flies. An operation such as this would permit the assessment of dispersal patterns, flight range, rate of movement, habitat preferences, and by examining the proportion of marked flies to unmarked flies, would also enable population density to be determined.

After examination of the various alternatives available it was decided that feeding adult blow-flies a radioactive substance, phosphorous-32 (P^{32}), would be the most effective method satisfying all the requirements mentioned above if administered correctly. P^{32} was decided upon due to its relative safety to the operator (no alpha or gamma emission), its short half-life (14,2 days), and the success achieved by other workers using this isotope to mark flies (Lindquist *et al* 1951, MacLeod & Donnelly 1957, Quarterman *et al* 1954a, b, Schoof & Mail 1953, Southwood 1978, Yates *et al* 1952).

The method employed was to obtain large numbers of full-grown third-stage *C. albiceps* and *C. marginalis* larvae from deliberately-placed impala carcasses and to allow such larvae to pupariate in sand-filled basins which were covered with netting against parasite attack. The impala carcasses and surrounding area were drenched with paraffin and thoroughly burnt so as to destroy all remaining larvae which would have represented an unnatural increase in blow-fly populations. The sand-filled basins were sieved at the Anthrax Research Camp to retrieve

PLATE 4: Colour illustrations of adult *Chrysomyia albiceps*, *C. chloropyga*, *C. marginalis* , and *Lucilia cuprina* (From Howell *et al* 1978).

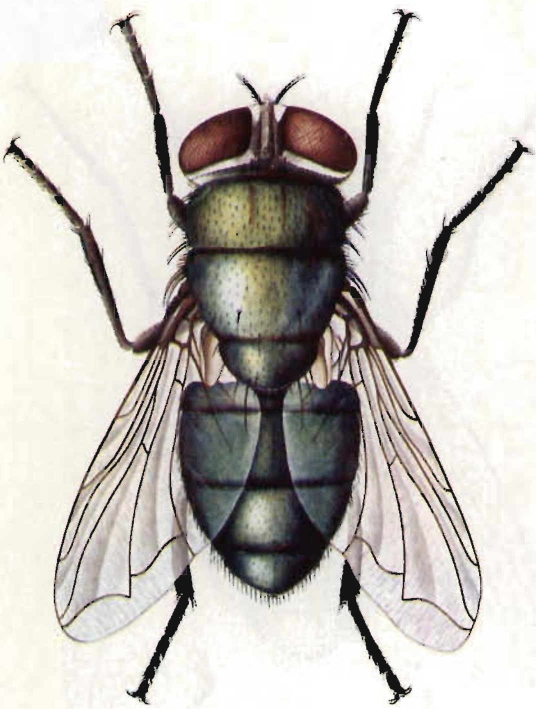
a) *Chrysomyia albiceps*.

b) *Chrysomyia marginalis*.

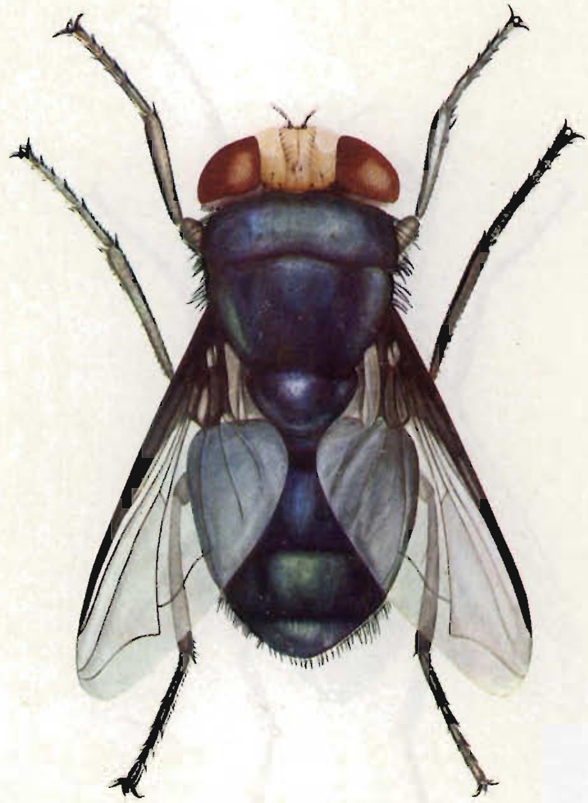
c) *Lucilia cuprina*)

) overleaf

d) *Chrysomyia chloropyga*)



a



b

Chrysomyia albiceps, the banded blowfly

This fly is green-coloured with a dark band around each of the abdominal segments. The legs are reddish-brown to black

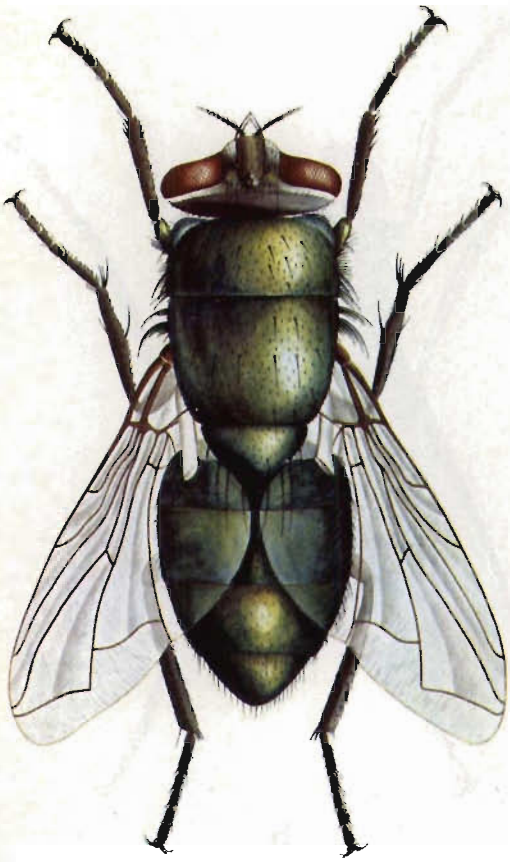
The banded blowflies will not initiate a strike on live animals but they lay their eggs on sheep that have previously been struck and their hairy larvae extend the wounds already present

Chrysomyia marginalis, the blue-bottle

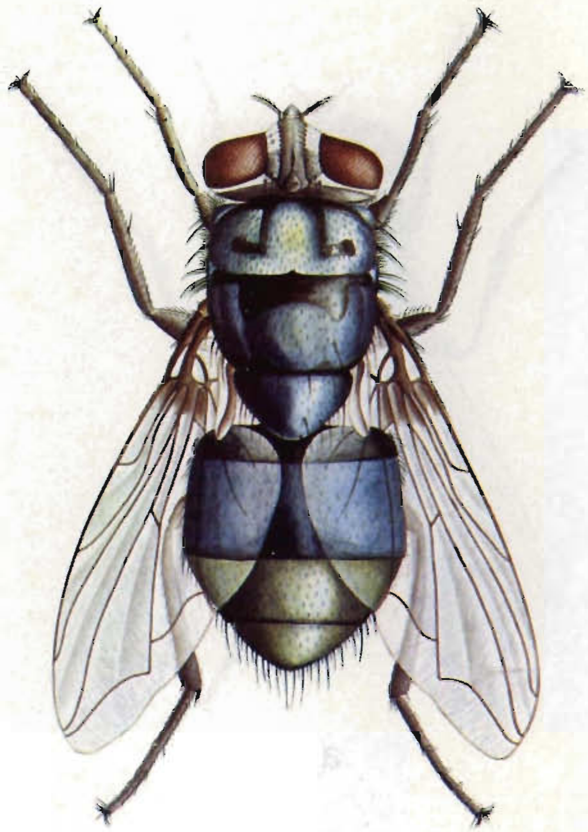
This is a big, clumsy, noisy blowfly, bluish-green to dark blue in colour, with black fore-margins to its wings. It is much larger than the other blowflies and has a yellow face and reddish-brown eyes

Blue-bottles do not attack live animals but play a very important role as competitors for any available carrion

PLATE 4



c



d

Lucilia cuprina, the green blowfly

The adult fly is medium-sized, averaging 8-10 mm in length, and brilliant green with a coppery tinge in colour. The eyes are brownish-red and the legs black, except the femora of the first pair, which are characteristically bright green
This is the most important sheep blowfly, occurring all over South Africa. Under certain conditions it will attack living sheep
L. sericata, the European green blowfly, looks very like *L. cuprina* but has uniformly black legs. In Southern Africa it is common in urban areas but rare in country districts

Chrysomyia chloropyga, the green-tailed blowfly

This fly is slightly larger than the green blowfly and is easily recognised by the brassy-green colour of the last 2 abdominal segments, contrasting sharply with the blue of the thorax and the rest of the abdomen. In addition it has a characteristic black omega-shaped mark on the 1st thoracic segment just behind the head
It will also attack live sheep

the puparia which were then placed in flight-cages, 2 000 puparia per cage. The flight-cages consisted of mosquito-netting suspended between two plastic basins and had six petri-dishes holding food and sugar-water in each cage, the petri-dishes being stacked one above each other at intervals and supported by string from the top basin. Each cage measured approximately 140 cm in length and 33 cm in width, and had a zipper fitted longitudinally for access to the petri-dishes (Plate 5a). Emergence of adults from the pupal stage generally occurred over a period of two days. On the first day of emergence only sugar-water was given to the adults as a source of moisture and carbohydrates, and a 1:4 mixture of yeast hydrolysate:sugar as a protein and additional carbohydrate source. On the second and third days after emergence the flies were fed a solution of 0,020 milliCuries (mCi)P^{32} per millilitre of sugar-water. The P^{32} was obtained from the Isotope Production Unit of the Nuclear Development Corporation of S.A., Pelindaba, who prepared the P^{32} as a 10 ml aqueous solution. After further dilution with 6,25 litres H_2O the solution contained the desired activity of 0,020 mCi/ml on the first day of feeding to the flies. During the afternoon of the second day of feeding a random sample of flies from various cages was taken to monitor the level of radioactivity and the proportionate number of flies having reached the desired level of radioactivity (between 1 000 and 80 000 cts/min). Having been found satisfactory, the flies were transferred in their cages to the release point in a vehicle with protective tarpaulin shielding the flies from excessive continuous exposure to the sun and a possible dehydrating draught during transfer. The flies were released at dusk by slitting open the cages and allowing them to escape. Dusk was chosen as the release time as blow-fly adults are inactive at night, so that released flies would not travel far before settling down for the night. By morning they were presumed to have recovered from any shock-effect or escape-tendency induced by the process of transfer, so that dispersal and further flight-behaviour would closely approximate a natural pattern. The flies were left undisturbed for a full week, and on the eighth day after release blow-fly traps were placed in varying compass directions up to 40 km radius around the Central Release Point (C.R.P.), approximately 300 metres southeast of Baobab Hill (Fig. 103).

Three trials were made to run such an operation as described above to a successful conclusion, these being in September/October/No-

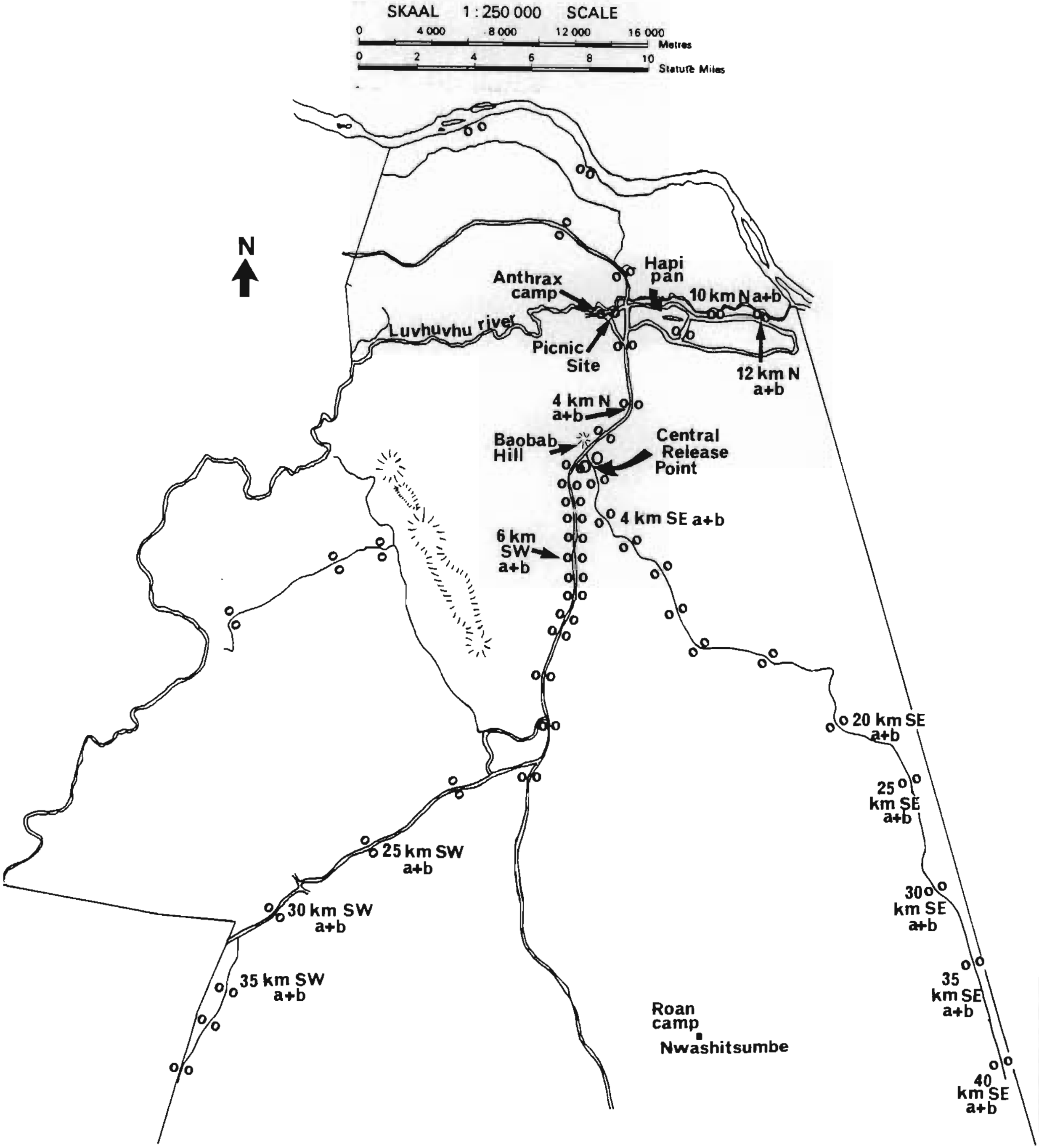


FIGURE 103: Map of the northern Kruger National Park to show Central Release Point of radioactive flies and positions of placement of traps for subsequent recapture of blow-flies (each small circle represents one trap).

vember 1980, March/April/May 1981, and January/February/March 1982. Although the methodology for rearing, marking, and releasing of flies worked well in all three attempts, rain and cloudy weather at critical periods and ineffective bait (insufficient water to keep bait wet) in the fly traps resulted in failure of the first two. The final attempt progressed well in most aspects, the only disappointment being the lack of large numbers of C. albiceps larvae at the carcasses for rearing to adulthood.

For the third attempt a new mixture for blow-fly bait was experimented with and proved highly effective. The bait eventually decided upon for each trap consisted of 1 kg fresh lean buffalo meat cut into golf-ball sized portions, 1 kg fresh fish cut into similar portions, one handfull (approximately 100g) of buffalo rumen-content, this all mixed with 2 litres of water taken from a 200 ℓ drum of water in which a full-grown baboon had been allowed to decompose for one week. All the traps were suspended from tree branches away from the main trunk and at a height such that the lower basin generally reached about two metres above ground, out of reach of most scavengers (Plate 5b).

For the final 1982 study three impala carcasses were placed on the 22nd January and full-grown larvae of C. albiceps and C. marginalis collected between 23h00 and midnight of 25th January. The carcasses were burnt immediately thereafter. A total of 16 000 C. albiceps and 52 000 C. marginalis puparia were placed in flight cages, 2 000 per cage. Adult flies emerged on the 30th and 31st January and were presented with P^{32} on the 1st and 2nd February. Release of the flies occurred at dusk on the 2nd February, and baited traps were placed on the 10th, 11th and 12th February. A total of 90 traps were originally placed at varying distances from the C.R.P.(Fig. 103), but several of these were ripped apart or disturbed by lions, hyaenas, leopards, and smaller mammals despite attempts at placing traps in reasonably inaccessible positions. Eventually only 76 traps remained effective. Trap collection and emptying occurred on the 17th, 18th and 19th February, and was performed in the same sequence as placement so that all traps had an equal trapping period. The traps were all sealed at the site of collection so that no flies could enter elsewhere. Great caution was exercised throughout the operation to ensure that no contamination occurred or that radio-active flies were not transferred with bait from

PLATE 5: Blow-fly cages, traps, and discard droplets

a) Flight cages used for rearing blow-flies for radioactive marking. Newspaper strips were added to increase surface area for resting flies. Ruler suspended between the two upper basins = 30 cm.

b) Traps used for blow-fly captures.

c) *Chrysomyia marginalis* male facing discard droplet from another blow-fly.

d) Discard droplets on *Colophospermum mopane* leaves.

a

b

c

d

PLATE 5

one site to another which could result in spurious findings. The traps were emptied at the Anthrax Research Camp where the catches were transferred to sealed paper-bags, except for the outermost rows of traps (35 to 40 km, and also the 63,5 km traps discussed later) which were tipped out bit by bit and examined to determine the relative position of radioactive flies in the trap. Each bag was in time spread on paper as a single layer of flies which was meticulously checked with a Thiac II Geiger-counter for the presence of radioactive flies which were then removed. Once examined the flies were again sealed in their bags and total counts of trap-catches made at a later date at Skukuza.

A small temporary weather station was established at the Central Release Point to monitor temperatures and rainfall during the study period. Readings for percentage relative humidity were taken at 08h00 at the C.R.P., and at 14h00 and 20h00 at the Anthrax Camp each day (Table 21). The relative humidity reflects the lowest and highest values of the three readings taken each day, the lowest value always being at 14h00.

TABLE 21: Weather data as recorded at Central Release Point (except relative humidity, see text) from date of blow-fly release to last day of trap removal.

Date	Temperature °C		Percentage Relative Humidity	Rainfall
	Minimum	Maximum		
2/2/82	22,0	32,0	26 - 28	-
3/2/82	26,5	37,0	33 - 64	-
4/2/82	23,0	37,0	42 - 77	-
5/2/82	24,0	44,0	30 - 65	-
6/2/82	25,5	39,5	33 - 65	-
7/2/82	24,0	38,5	31 - 64	-
8/2/82	23,5	38,5	42 - 84	4 mm
9/2/82	23,0	38,5	39 - 74	-
10/2/82	22,5	43,5	35 - 64	-
11/2/82	26,0	27,5	50 - 80	3 mm
12/2/82	22,0	34,0	40 - 76	-
13/2/82	22,0	37,0	37 - 78	-
14/2/82	21,0	37,5	32 - 66	-
15/2/82	21,0	38,0	34 - 65	-
16/2/82	23,0	38,0	44 - 74	-
17/2/82	21,5	38,0	27 - 87	-
18/2/82	21,5	26,0	82 - 95	64,0 mm
19/2/82	22,0	28,0	50 - 64	21,0 mm

DISPERSAL AND FLIGHT RANGE

A total of 1 625 radioactive blow-flies were recaptured in the study area up to 40 km from the release point. Although only 132 of these were C. albiceps, this represents a remarkably good recapture rate considering the low number of radioactive adults of this species released, and the large area from which recaptures were made. Table 22 shows the radioactive C. albiceps recaptures in all the distance-classes from the release point. Of the ten recaptures between 30 to 40 km from the C.R.P., 5 had been at a distance of 30 km, 4 at 35 km, 1 at 37,5 km, and none at 40 km. 37,5 km thus appears to have been the apparent maximum distance covered during the 17 days elapsed since release of the flies and removal of the last trap-line. The corresponding data for C. marginalis shows relatively high numbers of radioactive recaptures in all distance-classes from the C.R.P., with a total of 1 493 recaptures. Of these 46 were caught between 30 to 40 km from the C.R.P., consisting of 18 at 30 km, 16 at 35 km, 4 at 37,5 km, and 8 at 40 km.

Of interest is that the furthermost radioactive recaptures of C. albiceps and C. marginalis were in the upper layer of flies in the traps, suggesting that these flies had arrived close to the time of trap removal. It also indicates a minimum rate of movement of 2,35 km per day for C. marginalis if the flies had indeed been captured very near the time of trap removal, and 2,20 km per day for C. albiceps.

On the 15th February a journey had to be made to Shingwedzi (south of the study area) and this opportunity was utilised to place two additional traps in Mopane shrubveld along the Mphongolo River at a point 63,5 km from the C.R.P. These traps were recovered on the 24th February (22 days after release of the radioactive flies) and two marked C. marginalis flies were found in each of the traps. These flies were also in the upper layers and suggest a minimum rate of movement of 2,88 km per day.

The numbers of radioactive C. albiceps and C. marginalis recaptured were the highest in the distance-class 6-10 km from the C.R.P., the next highest being 12-18,5 km (Table 22). It should be noted that a direct comparison of radioactive recaptures in the two classes is

TABLE 22: Captures of radioactive and non-radioactive blow-flies 10 - 19 February 1982.

Distance from Central Release Point	Number of traps	Total number of *Chrysomyia albiceps* captured	Number of radioactive *C. albiceps* recaptured	% of total *C. albiceps* formed by radioactive recaptures	Total number of *Chrysomyia marginalis* captured	Number of radioactive *C. marginalis* recaptured	% of total *C. marginalis* formed by radioactive recaptures
0 - 4 km	12	4 066	8	0,20%	21 226	133	0,62%
6 - 10 km	19	14 270	65	0,45%	93 698	880	0,93%
12 - 18,5 km	16	10 801	40	0,37%	63 738	379	0,59%
20 - 29 km	8	5 992	9	0,15%	30 904	55	0,18%
30 - 40 km	12	10 455	10	0,10%	34 965	46	0,13%
Total	67	45 584	132		244 531	1 493	

not valid because differing numbers of traps were used, and most importantly because the 12-18,5 km swath around the C.R.P. covers a much greater area than the 6-10 km band, so that even with an equal number of traps in each band the outer band would still represent a far greater area into which flies could disperse with proportionately fewer traps per unit area and therefore less chance for recapture. With this in mind, the 141 flies recaptured in the relatively small area of the 4 kilometre radius around the release point, which was relatively "saturated" with 12 traps, should be considered as a very low number of recaptures compared with the, say, 56 recaptures in the 30-40 km band which represent an enormous area with only 12 traps to cover the area. Following this line of reasoning therefore, it should be obvious from Table 22 that the released flies moved away from the area of release and relatively few either remained or returned to the area. That this is a natural response is suggested by the findings in another radioactive study discussed in Chapter 7 where "wild" blow-flies fed at an impala carcass which had been injected with P^{32}, and some of these flies were caught 32,5 km from the carcass some days later.

The data gained from this experiment suggest that these two species of blow-flies dispersed in a random direction away from a point of release and that they covered considerable distances within a relatively short period of time. This would have definite advantage as both species are specialists which utilise only carcasses as breeding medium. Not only do the flies have to contend with severe competition from vertebrate scavengers for such a resource (Chapter 2), but they prefer carcasses of a certain size and in a certain condition (fresh or near fresh). Such carcasses are rare and selective pressure most likely necessitates these flies to search extensively over enormous areas to locate a suitable breeding medium.

The Luvuvhu River, which at that time reached approximately 30 metres in width, did not present an obstacle to blow-fly flight nor did it serve as an inhibitory boundary. This clearly revealed by the radioactive recaptures north of the river as far as the Limpopo bank beyond which no farther traps could be placed. Eight traps had been placed north of the Luvuvhu (Fig. 103), with 31 C. albiceps being recaptured and 357 C. marginalis. These two totals represent a remarkably similar 23,48% and 23,91% of the total number of radioactive recaptures of C. albiceps and C. marginalis, respectively, throughout the study area (excluding the 4 C. marginalis at 63,5 km). This high percentage of recaptures from only 8 traps in a relatively confined area can most likely be ascribed to the lush riverine forest adjoining the Luvuvhu and Limpopo rivers, the stands of fairly tall and dense mopane trees in many areas between the two rivers, and the strong attraction such well-wooded areas have for blow-flies (see next section).

Mountainous terrain similarly offered no obstacle to flight. A series of hills up to about 192 metres in height and stretching from Matekevele to Makahanya (Fig. 2) formed a near continuous line of division between the C.R.P. and five traps placed well to the west of these hills. The five traps recaptured 14 radioactive C. albiceps (10,61% of all radioactive recaptures of C. albiceps) and 74 C. marginalis (4,96% of all radioactive recaptures of C. marginalis), despite the area being predominantly fairly arid mopane shrubveld and Punda Maria sandveld (Gertenbach 1983). Hilly terrain is also a characteristic feature of much of the region between the C.R.P. and the Luvuvhu River (Fig. 2) and also proved to be no barrier to blow-fly movement. Schoof and Mail (1953) in England also found that blow-flies of the species Phormia regina were not deterred by rivers or wooded ridges 400 to 500 feet in height. MacLeod and Donnelly (1960) similarly found that Lucilia ceasar and Calliphora erythrocephala readily crossed a 200 yd wide river in England and that a steep hill 500 feet in height failed to stop their crossing. The most important factor influencing blow-fly movement would appear not to be of a direct geological nature, but rather the nature of the vegetation in the area. This aspect is discussed in the next section.

Norris (1964) and Johnson (1969) provided useful summaries of the results of several workers in diverse localities who had determined flight distances through fixed time periods, although most studies were confined to the northern hemisphere. The findings of some of these workers indicated that while Musca domestica may travel as much as 11,4 km during the first 24 hours after release (Bishop & Laake 1921), they may at other times be found within 640 metres of the release point nine days after release (Johnson 1969). The only data found in the literature for flight range of Chrysomyia spp. is for C. albiceps in Australia where the species covered 16 km in less than 12 days (Gurney & Woodhill

1926), although the flies in that part of their range were subsequently called C. rufifacies and are still known by that name (Zumpt 1965, Meskin 1980). Other data revealed that blow-flies such as Calliphora vicina regularly cross a distance of 35,4 km across open sea to a lighthouse off the Belgian coast, and that Callitroga hominivorax has been recorded covering 289 km within a two-week period (Johnson 1969).

HABITAT PREFERENCE

Periodic observations during 1980 and 1981 at carcasses and at single trap-catches in differing habitat conditions suggested that blow-flies had a preference for well-wooded, lush environments, but insufficient evidence was available to allow definite conclusions. The large number of traps placed in differing habitat types during the January/February 1982 study for radioactive recaptures allowed more conclusive comparisons to be made of the influence of contrasting landscape zones on blow-fly abundance.

In Table 23 (p. 212) the trap-catches for six traps in each of four different habitat types are given. The traps were situated completely in the particular habitat type and not in a transition zone, and were not selected because of particularly high or low catches in the particular traps. The trap-numbers provided for the arid Wambiya sandveld are not paired as are the traps in the other habitat categories because scavengers damaged many of the traps.

Trap catches show that larger concentrations of both C. albiceps and C. marginalis occurred in densely wooded forest environments such as the riverine forest along the Luvuvhu River and the tall mopane forest to the southeast of Punda Maria. Very low numbers of flies were captured in the arid Wambiya sandveld, and intermediate although still somewhat low numbers of blow-flies were captured in the mopane shrubveld in the area around Baobab Hill. Although not indicated in Table 23, the short, stunted mopane scrub on the Hlamalala plains between Klopperfontein and Nwashitsumbe also supported a very low number of blow-flies similar to that in the arid Wambiya sandveld.

PLATE 6: Vegetational types monitored for blow-fly habitat preference.

a) Open mixed mopane-veld at Central Release Point.

b) Riverine forest adjoining Luvuvhu River.

c) Tall *Colophospermum mopane* forest east of Punda Maria.

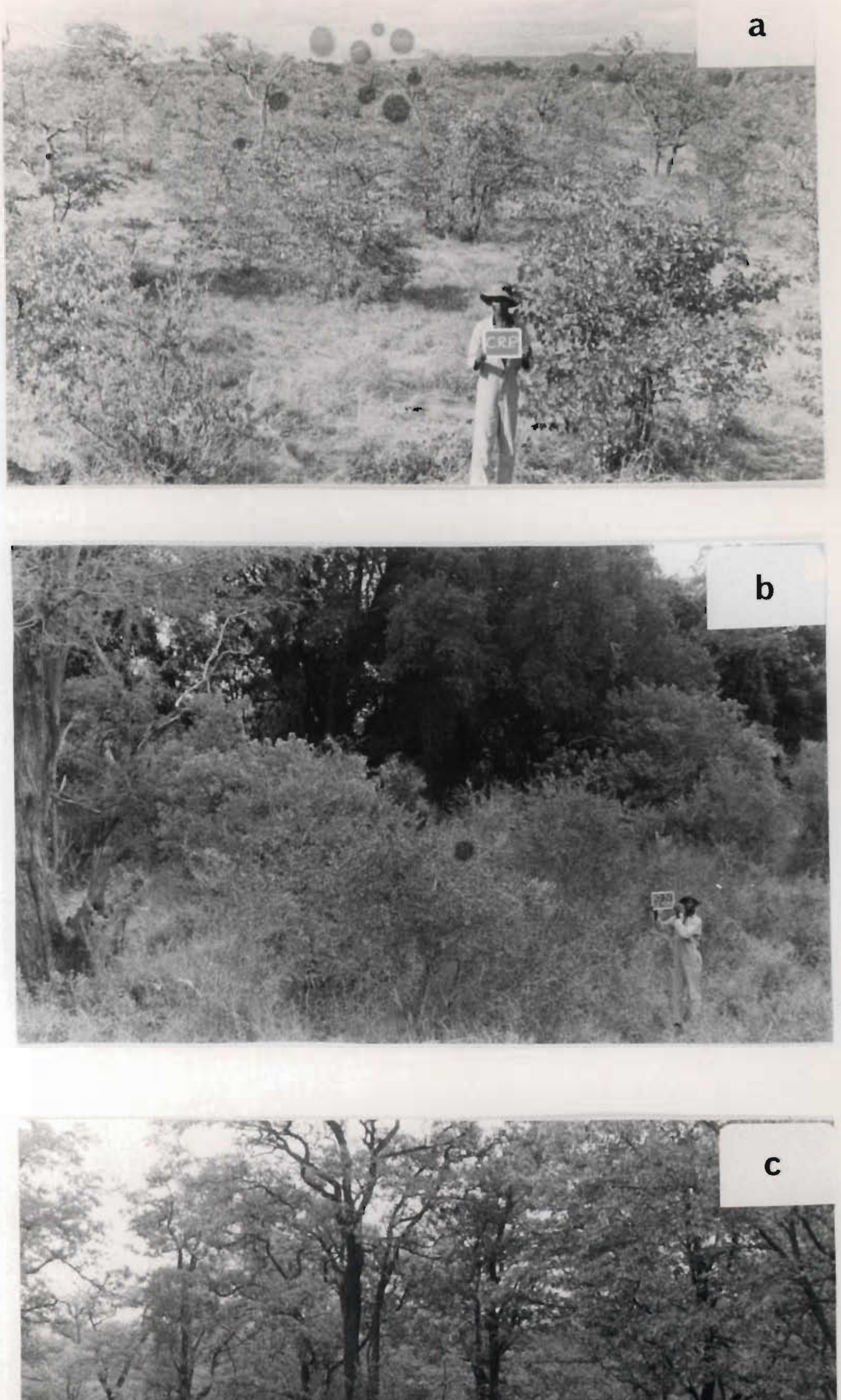


PLATE 6

Part of the distinct preference of *C. albiceps* and *C. marginalis* adults for well-wooded, forested environments can be explained by a need for moisture. During the 1980 and 1981 experiments when adult blow-flies were kept in cages for reproductive and other studies, it soon became clear that the adults were subject to rapid dehydration especially in summer and that the adults had to have daily access to liquid if fatal dehydration was to be avoided. On hot summer days the adults generally had several drinks of water at dishes provided. Also influencing blow-fly preference for well-wooded environments is an avoidance reaction displayed by these flies to excessive radiation intensity from the sun. Observation revealed that, when resting, adults rarely remained for long in positions where they were directly exposed to the sun on hot days, although they would rest for considerable periods in shade. Figures 82 and 88 reveal that *C. albiceps* and *C. marginalis* have a bimodal daily activity peak in summer a depressed activity at noon, whereas this pattern is not evident in late autumn (Fig. 84 & 90). Forested environments allow a greater proportion of adult activities to take place in shade.

Although difficult to prove, probably the single greatest factor drawing blow-fly adults to well-wooded environments is the greater probability of finding carcasses. Arid, sparsely vegetated environments generally support a reduced mammal population compared with better vegetated environments, so that the likelihood of a carcass occurring in an arid environment, such as in the Wambiya sandveld and Hlamalala plains, is decreased. More important perhaps is that any carcasses occurring in such open arid environments are likely to be discovered by vultures very soon which then strip the carcass of soft tissues. The probability of locating a carcass suitable for blow-fly utilisation is increased in riverine or forested enviornments, and this is discussed further in Chapter 2 under "Availability of carcasses for arthropod utilisation". It would therefore appear that a combination of factors are responsible for adult *C. albiceps* and *C. marginalis* showing a clear preference for such forested habitat types.

POPULATION DENSITIES

The simplest method for estimating population density is by

TABLE 23: Trap catches of *Chrysomyia albiceps* and *C. marginalis* in differir landscape zones to indicate habitat preference (Trap numbers indi cate distance, e.g. 20 km, and general direction, e.g. SW = South west in relation to Central Release Point.

Trap number	Landscape	Total number of *C. albiceps* captured	Total numbe of *C. margina* captured
Anthrax Camp 7,5 Km N	Riverine forest	2 716	14 817
Picnic Site 7,5 km N		693	4 012
Luvuvhu 10 km Na		1 418	5 702
Luvuvhu 10 km Nb		1 091	8 527
Luvuvhu 12 km Na		1 047	7 856
Luvuvhu 12 km Nb		616	4 171
	Totals:	7 581	45 085
25 km SWa	Generally tall, dense mopane forest, no river nearby	1 936	9 756
25 km SWb		2 743	15 701
30 km SWa		2 841	5 159
30 km SWb		1 164	2 853
35 km SWa		749	3 914
35 km SWb		1 606	6 932
	Totals:	11 039	44 315
20 km SEa	Arid Wambiya sandveld	30	217
20 km SEb		59	322
25 km SEa		69	440
30 km SEa		47	374
35 km SEb		11	198
40 km SEb		166	1 905
	Totals:	313	3 456
4 km Na	Mopane shrubveld representative of large part of study area	973	4 590
4 km Nb		556	4 341
4 km SEa		228	890
4 km SEb		141	442
6 km SWa		222	1 595
6 km SWb		157	754
	Totals:	2 277	12 612

single recapture of marked flies released for dispersal into the population under study and application of the Lincoln Index to the results achieved (Southwood 1978). Although it is an estimate it is the most practical method as an absolute count of every individual fly in such a large area as the northern K.N.P. is clearly impossible. A good measure of accuracy can be achieved however, by using large numbers of released flies and recapturing with a large number of traps (Vogt et al 1981). The method is also subject to a number of conditions being fulfilled if accuracy is to be achieved: (1) the marking procedure should not influence the subsequent behaviour of marked flies; (2) such marked flies should have an equal "catchability" as unmarked flies, (3) the flies should disperse throughout the area in which population density is to be determined; (4) the population must be closed, or if not, it should be possible to determine immigration and emigration.

A total of 16 000 C. albiceps and 52 000 C. marginalis puparia of sufficiently large size were obtained for rearing adults in January 1982 as described in the preceding sections. After release of the radioactively marked (P^{32}) flies at the Central Release Point (C.R.P.) near Boabab Hill, traps were placed on the 8th day after release in all the main directions around the C.R.P. (Fig. 103) up to 40 km away. Of the traps placed only 76 traps (still a large number) ultimately proved effective.

An additional 200 puparia of each of C. albiceps and C. marginalis were reared separately from those placed in flight cages for rearing adults for marking. From these pupal mortality was determined, indicating a 97% successful adult emergence in C. albiceps and 96,65% for C. marginalis. This theoretically reduced the caged population of C. albiceps to 15 520 (97% x 16 000) and C. marginalis to 50 258 (96,65% x 52 000).

After two feeds of a 0,020 mCi P^{32} per millilitre sugar-water a random sampling of the caged flies was made immediately prior to release to determine the proportion of flies which had imbibed enough of the mixture to retain a level radioactivity to register a suitable response in the Geiger-counter for a period of at least 3-4 weeks. Background radiation in the study area had been determined as varying between 20 to 60 counts per minute (cts/min.), and it was therefore decided that only flies registering a pre-release level of 500 cts/min. would be regarded as marked flies. Such a pre-release random sampling indicated that 96,43% of 56 C. albiceps and 90% of 40 C. marginalis exceeded 500 cts/min. This further reduced the populations of marked flies to 14 965 (96,43% x 15 520) for C. albiceps and 45 232 (90% x 50 258) in C. marginalis.

Many workers attempting estimates of insect population densities fail to consider mortality in the marked population from the time of release to time of recapture (e.g. Norris 1959, Vogt et al 1981). This was accounted for in the present study by keeping control populations of marked and unmarked flies of each species in flight cages to assess mortality during the period of study. The caged flies, 200 marked of each species, indicated that only 38,54% (5 767) of C. albiceps and 82,47% (37 302) of C. marginalis survived by the last day of trap removal (19th February 1982).

Statistically the population surviving midway through the trapping period would be a more appropriate figure for use in the Lincoln Index, but this could not be determined directly. Data obtained from caged flies during 1981 shown that mortality in both C. albiceps and C. marginalis approximated a normal bell-shaped curve and that under summer conditions maximum adult life expectancy for C. albiceps was 30-32 days and for C. marginalis 62-63 days. By extrapolation from this data the expected differential mortality for any period during adult life can be estimated, and shows that an additional 14% (i.e. 52,54%) of C. albiceps and 8% (i.e. 90,47%) of C. marginalis could reasonably be expected to have survived to the middle of the trapping period. Calculation thus indicates 7 862 (14 965 x 52,54%) C. albiceps and 40 921 (45 232 x 90,47%) C. marginalis adults to have survived, and it was accepted that for the purposes of this discussion these figures represent the marked populations available for trapping.

That the amount of P^{32} ingested by the flies had no marked deleterious effects is evidenced by the fact that a radioactive C. marginalis female had deposited a weakly radioactive batch of eggs at fish being cut at the Anthrax Camp, showing that fertility was not afffected by the level of P^{32} imbibed. Non-radioactive control flies of both species kept in flight cages at the Anthrax Camp for the duration of the study, compared with radioactive flies also kept for observation during this period, revealed that the P^{32} did not increase the natural mortality rate. Based on caged populations of 200 unmarked and 200 marked flies for each of C. albiceps and C. marginalis, the mortality from the time of adult emergence (31/1/82 and 1/2/82) to the last day of trap collection (19/2/82) the mortality recorded amongst unmarked and marked C. albiceps was 56,85% and 61,46% respectively, and amongst C. marginalis 26,18% and 17,53% respectively.

Worthy of note was that a small proportion of radioactive flies were undersized due to insufficient nourishment during the larval stages, but observations revealed that the flight viability of such flies was not greatly impaired. A considerably undersized radioactively marked male C. albiceps was recovered from a trap 25 km from the release point, indicating that such apparently handicapped flies are capable of flight over long distances.

One of the requisites for using the Lincoln Index is that the released flies should mix completely with the population for which density is to be determined. Radioactive flies were recaptured in all habitat types and in all zones throughout the study area, thus showing that this requisite was satisfied. It was shown earlier that both C. albiceps and C. marginalis display clear preferences for certain habitat types so that aggregations of these flies occur especially in well-wooded areas. The placement of traps, however, was done in an essentially random manner with regard to habitat type and in all directions around the release point (Fig. 103) so that for all practical purposes trap-catches were not biased towards any habitat type or designed to capture excessively high or low numbers of radioactive flies.

A potential problem arises with application of the values for total marked recaptures to the Lincoln Index. As indicated the available evidence is that marked flies only arrived at the outer periphery of the trapping area during the last few days of the trapping period, so that significantly more time was available for trapping unmarked flies by these peripheral traps than marked flies. To negate this bias it was decided to use only the values of marked and unmarked recaptures in an inner circle around the release point with 19,25 km as radius (midway between the 18,5 and 20,0 km series of traps), and to calculate the number of marked flies within this inner area for use in the Lincoln Index. A far more reliable estimate of population density would be obtained in this manner.

In order to calculate the number of marked flies in the outer area (19,25 km to 40 km) at the end of the trapping period the following equation was used:

$$\text{Number (Outer)} = \frac{FT_O}{FT_I} \times \frac{\text{Area (outer)}}{\text{Area (Inner)}} \times \text{Number (Inner)}$$

where FT_O = the number of marked flies captured per trap in the outer circle,

FT_I = the number of marked flies captured per trap in the inner circle and

Number (Inner) = the total number of marked flies in the inner area

By using the data from Table 22 and as indicated subsequently, the computation for C. albiceps is as follows:

$$\text{Number (Outer)} = \frac{0{,}95}{2{,}40} \times \frac{3\ 862{,}39}{1\ 164{,}16} \times \text{Number (Inner)}$$

$$= 1{,}3133 \text{ Number (Inner)}$$

By mathematical substitution and entering the total number of marked C. albiceps released we find:

$$\text{Number (Outer)} = 1{,}3133\ (7\ 862 - \text{Number (Outer)})$$

$$= (1{,}3133)(7\ 862) - 1{,}3133 \text{ Number (Outer)}$$

$$2{,}3133\ (\text{Number (Outer)} = (1{,}3133)(7\ 862)$$

$$\text{Number (Outer)} = \frac{(1{,}3133)(7\ 862)}{2{,}3133}$$

$$= 4\ 463$$

Subtracting this from 7 862 we derive a figure of 3 399 marked *C. albiceps* in the inner circle.

Using the same method for *C. marginalis* we find:

$$\text{Number (Outer)} = \frac{5,5}{29,61} \times \frac{3\ 862,39}{1164,16} \times \text{Number (Inner)}$$

$$= 0,5658 \text{ Number (Inner)}$$

$$= 0,5658\ (40\ 921) - 0,5658 \text{ Number (Outer)}$$

$$= \frac{0,5658\ (40\ 921)}{1,5658}$$

$$= 14\ 787$$

and by subtracting this from 40 921 we derive a figure of 26 134 marked *C. marginalis* in the inner circle.

The Lincoln Index is generally written as follows:

$$N = \frac{an}{r}$$

where N = the estimate of the number of individuals in the population, n = total number of flies captured, a = number of marked flies and r = total marked recaptures.

For *C. albiceps* therefore, we obtain an estimate of

$$N = \frac{(3\ 399)(29\ 137 + 113)}{113}$$

$$= \frac{(3\ 399)(29\ 250)}{113}$$

= 879 899 flies in the inner circle with 19,25 km as radius (1164,16 km²), which when computed provides a figure of 756 *C. albiceps* per km² or 7,56 adults per hectare.

The corresponding values for *C. marginalis* are

$$N = \frac{(26\ 134)(178\ 662 + 1\ 392)}{1\ 392}$$

= 3 380 410 flies in the area with the C.R.P. as focus and 19,25 km as radius, which gives an estimate of 2 903 *C. marginalis* per km² or 29,03 adults per hectare.

That these estimates are workable approximations of true density is given credence by comparing these results with those obtained by other workers attempting to determine blow-fly densities. Working in Australia, Gilmour et al (1946) released large numbers of Lucilia sericata at the centre of an area (6,4 km radius) throughout which they had distributed 100 traps, and by correcting for death rate and emigration from the study area they calculated a density of 0,3 to 5,7 flies per acre (1 acre = 0,404 hectare). Also in Australia, Norris (1959) used a similar technique but did not take into account fly mortality, thus obtaining tentative densitites for the following species: Calliphora stygia = 100/acre, C. augur = 350/acre, Chrysomyia ruficacies = 50/acre, and Microcalliphora varipes = 10 to 20 flies per acre. Cragg and Hobart (1955) also attempted population estimates of blow-flies in England but failed to correct for such factors as mortality or emigration, thus arriving at tentative densities of 23 Lucilia sericata per acre, and between 6 and 238 females of the "L. ceaser group" per acre. Macleod (1958) used another method with several assumptions regarding rates of mortality, dispersal, and zones of influence of traps, and showed that densities in England varied markedly at different times of the year. He measured densities of Calliphora vicina as 50 - 200 per acre in August, 400 - 1 000/acre in September, and 700 to 1 000/acre in October, whereas in another year he only recorded 11-27/acre in August and 67/acre in October. For Lucilia sericata he computed densities of 2,8 and 0,8/acre in August and 1 per acre in October.

The estimates of density for C. albiceps and C. marginalis in the Punda Maria/Pafuri/Wambiya study area can therefore be regarded as being realistic. The estimates should be viewed as average values for the study area as a whole, so that the value for each species will be higher in well-wooded areas and lower in open mopane-veld.

SEASONAL ABUNDANCE

A number of workers (Smit & Du Plessis 1927, Smit 1931, Hepburn 1943a, Mönnig & Cilliers 1944) have indicated that there is a marked seasonality in the abundance of blow-flies, with different species having periods of distinct population build-ups which do not necessarily coincide with each other. The periods of population increase

TABLE 24: Months of peak abundance of *Lucilia*, *Chrysomyia albiceps* and *C. marginalis* as determined by various workers using trap-catches from baited blow-fly traps.

Author	Locality	*Lucilia*	*Chrysomyia albiceps*	*C. marginalis*
Hepburn (1943a)	Onderstepoort (Tvl.)	August/September December February/March	October to March May	October to February
Mönnig and Cilliers (1944)	Bredasdorp (Cape Prov.)	September/October/November	December to May	January to April
Smit and Du Plessis (1927)	Cape Province	Spring		Autumn
	Eastern Tvl.		October/November/December	Autumn
	North-Eastern Tvl.		October/November7December	Autumn
Smit (1931)	Grootfontein (Cape Prov.)	April/May October/November/December	November/December/January April/May	March/April/May

and the extent of increase vary according to geographic locality, climatic factors and the availability and accessibility of food, but general trends are nevertheless discernable. Table 24 summarises the relevant data of the authors mentioned above, indicating the months of peak abundance of selected blow-fly species as derived from trap-catches.

As the northern K.N.P. study area is situated in a zone which amongst other factors differs clearly in climate and vegetation from the Cape Province where the bulk of blow-fly studies in this country have concentrated, it was decided to test the applicability of the findings of the above authors by monitoring the seasonal population fluctuation of blow-flies in this area. This would provide a better concept of blow-fly numbers during the dry post-winter months when the risk of an anthrax epizootic is at its greatest. The trap-catches discussed in this section provide only a relative index of abundance and as such are only a poor reflection of the absolute abundance of flies in the area.

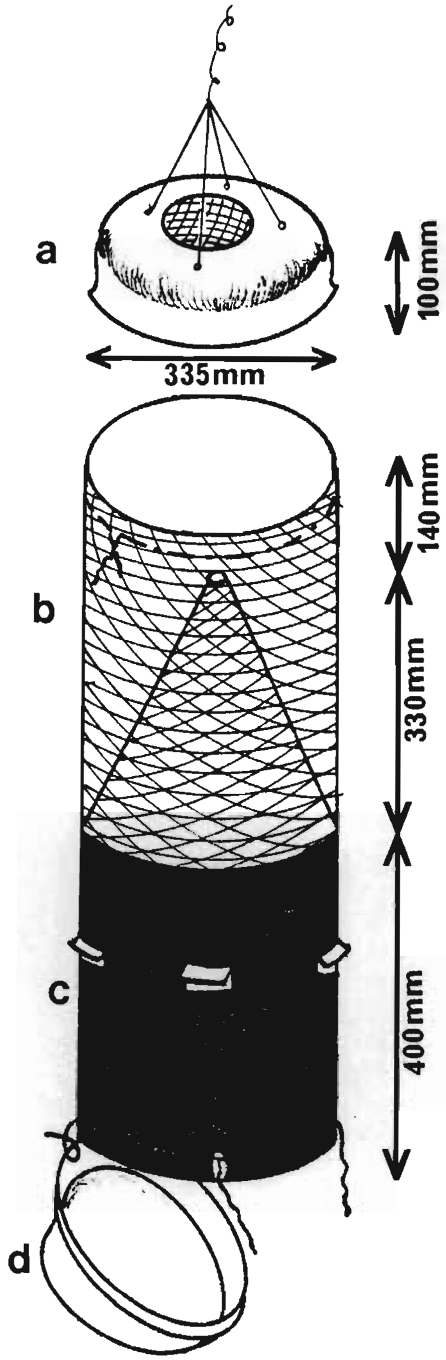
Three blow-fly traps were used for monthly monitoring. The northernmost trap was placed near Hapi Pan approximately one kilometre south of the Luvuvhu river on a flat expanse dominated by near uniformly distributed Colophospermum mopane trees averaging between four and six metres in height. Another trap was located at Baobab Hill in a shallow valley with mixed vegetation consisting mainly of Colophospermum mopane, Terminalia prunioides, Commiphora sp., Adansonia digitata, and Combretum imberbe trees which ranged between about four and fifteen metres in height. The remaining trap was placed further south near the Nwashitsumbe Roan Camp in a grass-filled scrub-mopane plain dominated by stunted Colophospermum mopane averaging between 1,5 and 4 metres, with occasional larger Combretum imberbe and Sclerocarya birrea. The traps were all suspended from branches such that the lower end was approximately 1,75 metres above ground level, out of reach of hyenas and smaller scavengers. The traps were placed for a full seven-day period, generally during the last week of every month, and each trap was baited with a mixture comprising 1 kg fresh lean impala meat cut into small chunks, 1 kg fresh fish similarly cut into golf-ball sized portions, a handful (± 135 g) of impala rumen-content, and two litres of water. The traps were designed according to a well-known principle whereby flies are attracted to bait in a darkened area, and upon completion of feeding fly upwards through a funnel into an enclosed area from which they cannot escape. Such traps have been widely used in blow-fly studies and the basic construction thereof is described by Blair (1945) and Smit (1945). The traps used in this study are depicted in Figure 104 and Plate 5b.

Data are graphically represented in Figures 105 to 108. The traps placed at Hapi Pan in September 1983 and at Nwaswitshumbe in June 1983 were tampered with by scavenging mammals, but this break in data did not obscure the general trend in population fluctuation.

From the data it is evident that a clear seasonality also exists in the blow-fly population of the K.N.P. Chrysomyia albiceps and C. marginalis follow a similar trend and only reach abundance during the warmer months of the year. C. marginalis is more numerous than C. albiceps and has a longer abundance period, with a rapid increase from September through to February. C. albiceps has an abundance period from October/November to February, with a maximum population in January.

Another factor again clearly revealed is the distinct avoidance of both C. albiceps and C. marginalis of the arid open scrub-mopane country which the Nwashitsumbe trap represents. The data also reveal higher numbers of Lucilia at Nwashitsumbe. Although these flies never reached the level of abundance attained by Chrysomyia they had a clear preponderance during winter and early spring, showing a distinct population increase beginning in June, peaking in July/August and rapidly declining in September/October.

Reasons for the depressed C. albiceps and C. marginalis populations during the cooler months are almost certainly related to the sensitivity of these flies to low temperatures. Smit (1931) found that no eggs were laid in the colder winter months, and although minimum winter temperatures in the northern K.N.P. are not as severe as in the Cape observations at Pafuri confirm that during the latter half of June and in July very few eggs are laid even if an abundance of meat is made available. Furthermore, during the immediate pre- and post winter months the relatively cold night-time temperatures retards the rate of development of the larvae. This exposes them to a longer period of predation by ants, histerids, etc., and, more importantly, increases the likelihood of vertebrate scavengers discovering the carcass or carrion



a) Plastic basin for lid. Central portion replaced with gauze to allow additional light.

b) Mosquito gauzing.

c) Black plastic sheeting covering gauze to darken lower area. Small 100 mm windows to allow entry by blow-flies.

d) Plastic bait basin.

FIGURE 104: Design of blow-fly traps used during the present study.

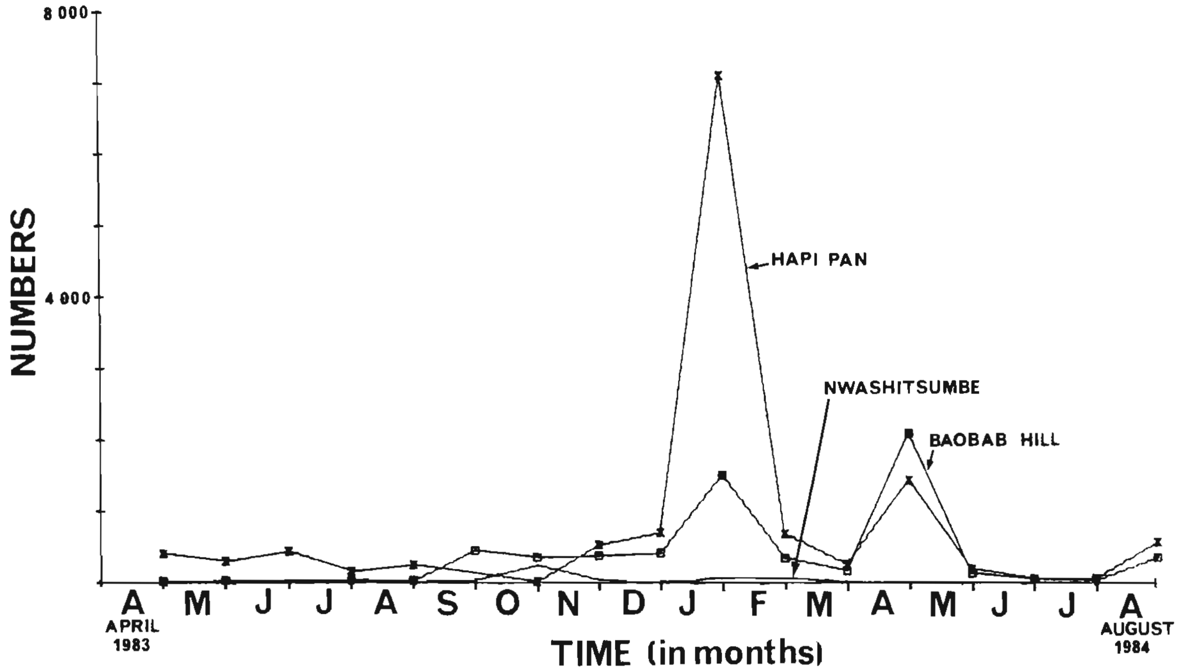


FIGURE 105: Monthly results of Chrysomyia albiceps trapped at three sites in the northern K.N.P. to show seasonal abundance

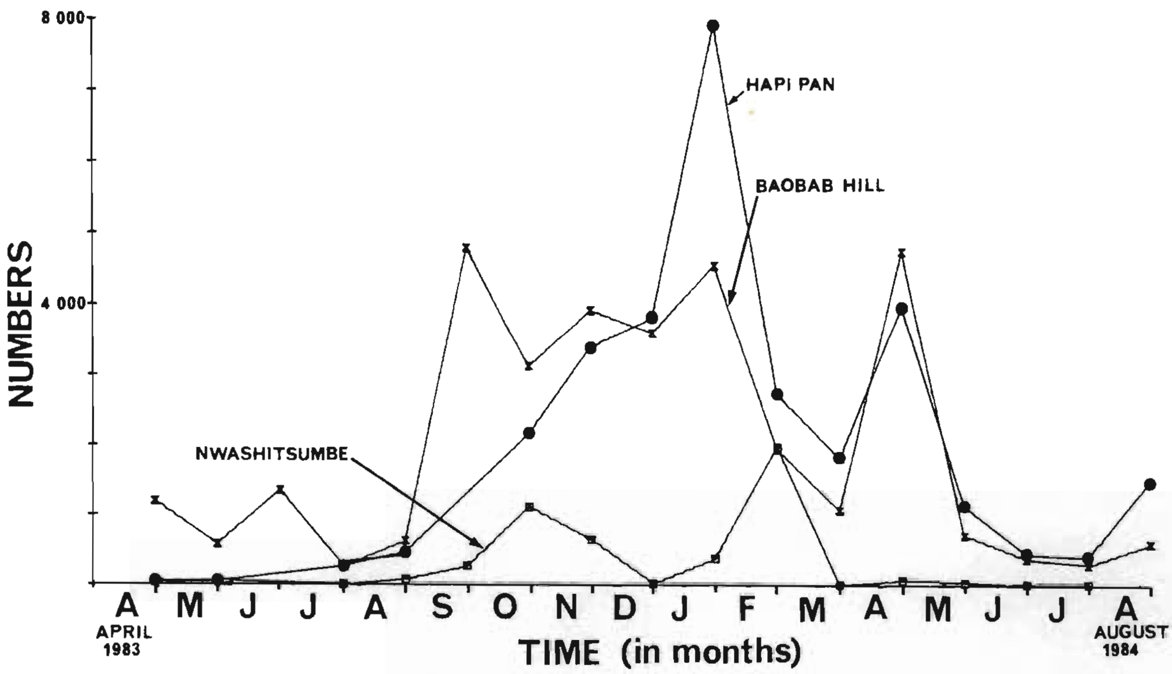


FIGURE 106: Monthly results of Chrysomyia marginalis trapped at three sites in the northern K.N.P. to show seasonal abundance

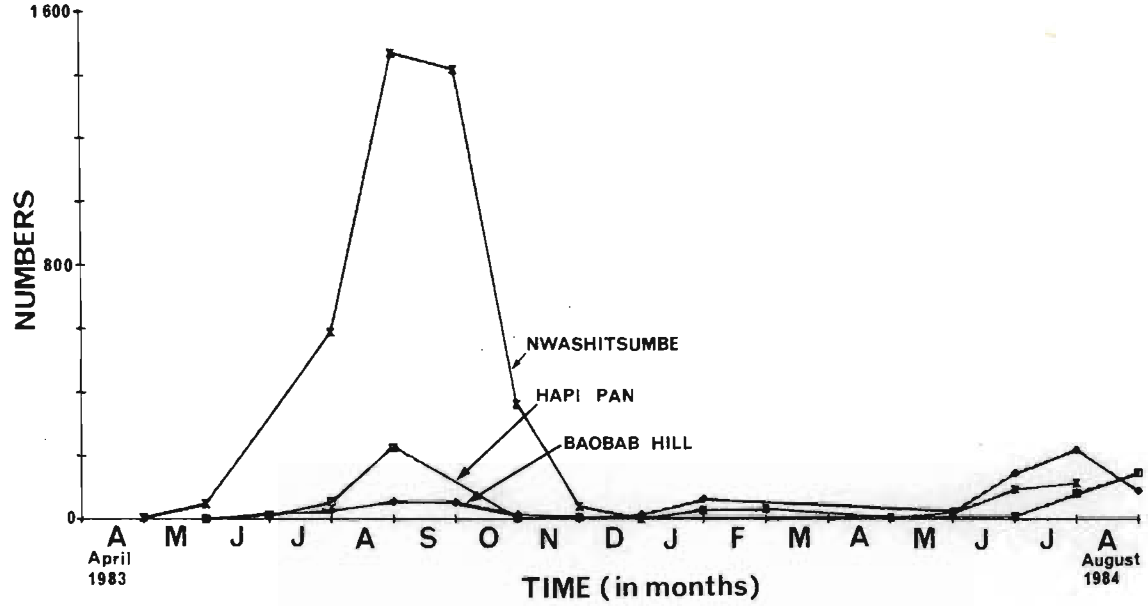


FIGURE 107: Monthly results of *Lucilia* spp. trapped at three sites in the northern K.N.P. to show seasonal abundance

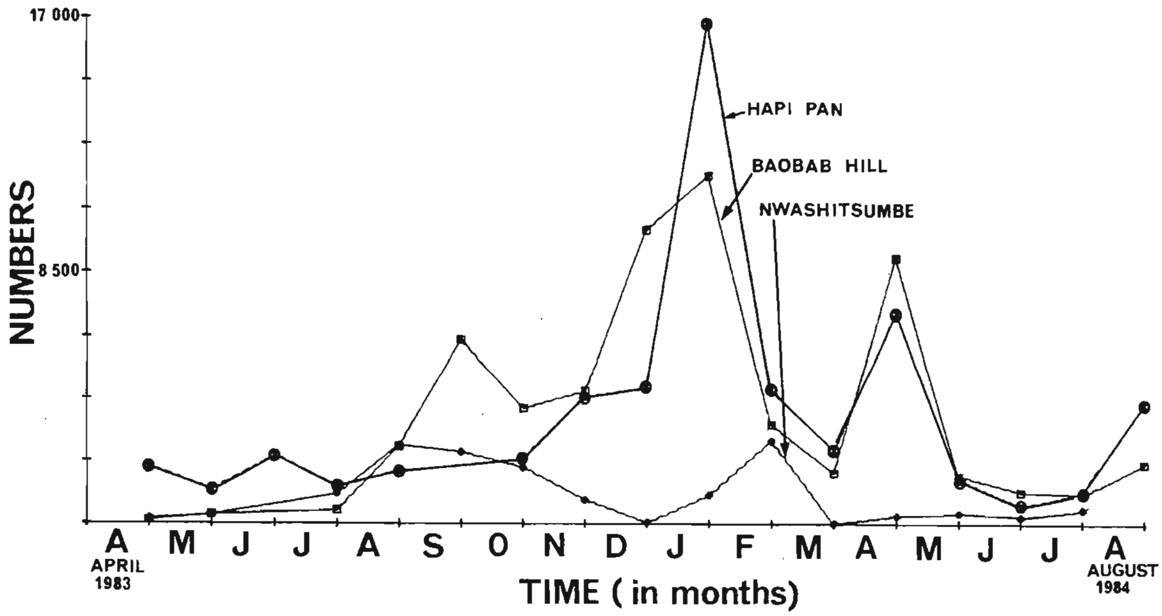


FIGURE 108: Monthly results of all flies trapped at three sites in the northern K.N.P. to show seasonal abundance

so that the soft tissues are removed before the larvae reach a growth stage sufficiently advanced for successful pupariation.

Another factor which favours an increased blow-fly population in the warmer months is that this coincides with the raining season and concommitant vegetational growth period. The increased vegetational cover increases the possibility of vertebrate scavengers overlooking an occasional carcass which will then be utilised by blow-flies.

CHAPTER 7

FEEDING BEHAVIOUR AND DISEASE-TRANSMISSION POTENTIAL OF *CHRYSOMYIA ALBICEPS* AND *C. MARGINALIS*

Flies have long been known to be important in the transmission of disease, not only by serving as essential hosts for the parasites causing malaria, trypanosomiasis, leishmaniasis, filariasis, and others, but also by walking or feeding on infected material and mechanically spreading this to other sites as often occurs with cholera, anthrax, and other bacterial diseases (Graham-Smith 1913, Howard 1913, James and Harwood 1970, Greenberg 1973).

Yet another potential avenue of infection occurs by flies feeding on disease sources, and depositing undigested or semi-digested intestinal contents in the surrounding vicinity. This latter phenomenon is of particular importance in the northern K.N.P. where periodic outbreaks of anthrax (*Bacillus anthracis*) occurs, and blow-flies promote spreading of the disease by depositing large numbers of infected blood-droplets in the area around an animal killed by anthrax (Pienaar 1961, De Vos 1973). These blood droplets have traditionally been referred to as "vomit drops", an unusual and as yet not fully understood phenomenon associated with blow-flies and various cyclorrhaphous Diptera lacking piercing mouthparts (Horsfall 1962). Vomit drops have been reported to be a major cause of the stains or spots so abundantly encountered at and near fly-feeding sites (Graham-Smith 1913, De Vos 1973, Greenberg 1973). Observations at carcasses during the present study suggested that this is not applicable to all flies capable of producing vomit drops, and that at least in *Chrysomyia albiceps* and *C. marginalis* the blood droplets around a carcass are for the most part produced in other ways.

As indicated in earlier chapters, *C. albiceps* and *C. marginalis* are usually the first insects to arrive at the carcass, and because of their feeding habits and abundance they are responsible for the removal of considerable amounts of moisture from the carcass, and deposition of potentially infective reject material in the surrounding area. To gain insight into the distribution and density of this discarded material away from the carcass, an experiment was designed to determine the pattern of droplets in the immediate vicinity of a carcass. The flight range of these flies visiting the cascass under natural conditions was also determined as this would indicate how far such infective material could be dispersed. It is necessary first, however, to provide some information concerning the various kinds of droplets likely to be encountered at a carcass, with observations on feeding behaviour, for a better perspective on the potential of these flies as disease transmitters.

VOMIT DROPLETS, DISCARD DROPLETS, AND FAECAL DROPLETS

Vomit drops are partially regurgitated droplets of liquid food commonly seen suspended from the proboscides of stationary flies after the act of feeding. Various reasons have been forwarded for this phenomenon, but none of them experimentally proven. Graham-Smith (1913) stated that "... the impression is conveyed that the insects have distended their crops to an uncomfortable degree and that some of the food is regurgitated in order to relieve the distension". Horsfall (1962) also implied this by stating that flies often "regurgitate the contents of the gut" when having ingested "food more rapidly than they digest it", and that this drop is held by the cupped labella and expands and contracts by alternate regurgitation and ingestion. Saccā (1964) and Rietschel (1975) suggested that the partial regurgitation is in response to a need for proper mixing of saliva with the ingested food, and that mixing can best be achieved by moving droplets of food back and forth via the mouth.

Discard droplets and faecal droplets are both voided via the anus, but they are considered by me as qualitatively different. Faecal material, in the normally accepted sense, is regarded as matter which has remained in the body of an animal for some time while being subjected to digestive processes, and consists of essentially unusable waste. Discard droplets, in contrast, are voided soon after the act of feeding and consists of undigested material. This can clearly be seen by placing microscope slides alongside a wound on a freshly killed animal; blood droplets are soon voided onto them by the flies. Microscopic examination of these slides will indicate that red-blood corpuscles have passed through the alimentary canal in an undamaged condition. The feeding behaviour suggests that flies are presented with an infrequently available rich source of protein, which under natural conditions is most likely to be removed soon by predatory or scavenging mammals or birds, and that selection pressure has favoured those flies which make most of the opportunity by imbibing blood copiously. The flies then extract those nutrients from the blood which can rapidly and easily be extracted, allowing semidigested or partially utilised blood to be voided. Comparable mechanisms appear to be at work in mosquitos where rapid diuresis results in the discharge of fluid almost immediately after termination of feeding (Nijhout & Carrow 1978), and also in fleas where blood is voided soon after ingestion (Rothschild 1965).

MECHANISM OF FEEDING

From the many sophisticated experiments of Dethier and others (Dethier 1966, 1976, Vernays & Simpson 1982) it appears that the ingestion of food by blow-flies occurs in a series on interacting steps or events which eventually lead to food entering the intestines. This pathway in most feeding sequences can be summarised as follows: when brought into contact with food, chemoreceptors on the tarsi are stimulated and the sensory input results in extension of the proboscis. Odour wafted onto the antennae, in a sufficiently high concentration, initiates the same response. When brought into contact with food due to extension of the proboscis, chemosensory hairs on the aboral surface are stimulated and result in the labellar lobes being opened, which in turn brings the oral papillae into contact with the food. Stimulation of these papillae causes a sucking response so that food enters the oral cavity and passes into the midgut and crop. The midgut does not have a large capacity and is sealed off by the cardiac valve when filled, the remaining intake of food then passing into the crop. The oral receptors in the meantime have been adapting to the constant stimulus of food, until a threshold is reached after which feeding ceases. Disadaptation of the labellar receptors occurs soon again however, so that feeding recommences, and a meal is therefore made up of a series of interrupted drinks or feeds (Dethier 1966). Final cessation of ingestion, i.e. termination of the meal, is determined by nerve impulses from stretch receptors present in the oesophagus and around the crop, so that the amount of food ingested in one meal is essentially determined by volumetric factors (Bernays & Simpson 1982).

The crop duct valve has considerable pressure exerted on it by the contents of the crop, resulting in slight leakage causing regurgitation (Dethier 1976, Green 1964). As food in the midgut is used, the crop valve (crop duct) and cardiac valve (proventriculus) open sequentially so that food can be driven to the midgut by peristalsis. As the crop progressively empties the pressure on the crop valve decreases with a corresponding decrease in vomit drops.

The food supply of a fly is not always of the same viscosity or consistency, and the structure of the proboscis has been adapted to cope with this eventuality. The distal part of the proboscis, the labella, is capable of assuming different degrees of cupping which enables it to either filter liquid food through a series of fine channels termed pseudotracheae, or to expose a series of prestomal teeth which are used to rasp at solid particles prior to wetting it with saliva or crop contents for dissolving, or in the extreme cupping position to expose the lumen of the mouth so that semi-solid material can be ingested (Dethier 1976, Harlow 1956).

FEEDING BEHAVIOUR

Both male and female C. albiceps and C. marginalis readily partake of blood-meals, although other liquids are also taken up, such as lachrymal secretions on the eyes of fresh carcasses, the thin moisture film on the intestines and other organs, and also moisture in rumen or dung. They also feed on nectar of flowers, and in captivity imbibe sugar solutions made up in a wide range of concentrations. It is now well-known that blow-flies need carbohydrates for maintenance of life and can be kept alive for considerable periods on a pure diet of sugar and water alone, but protein is essential for the production of viable eggs (Mackerras 1933, Rasso & Fraenkel 1954, Harlow 1956, Dethier 1976, Bowdan 1982).

If food is present only in solid form, such as congealed blood or sugar crystals, they express through the proboscis a layer of moisture to partially dissolve the food, this then being sucked up in the usual manner. The process of feeding, however, is best portrayed when observed at a pool of blood, and the following description is based on observations at carcasses with easily accessible blood.

The flies approach a pool or source of liquid blood, and then extend the proboscis against the surface of the pool. They rarely remain in one position for more than a few seconds, but rather move on or around the blood-source in a continuous erratic movement, retracting and pressing the labellae against the blood all the while. After a variable period of time, which is usually less than a minute after commencement of feeding but may be several minutes, they move away and "preen" or clean themselves, then remain stationary. During this stationary phase, or occasionally whilst preening,they often excrete in a very rapid movement a droplet of liquid which is clear to dark brown or red in colour. Following this action they may preen or fly off, but more often return for another feed on the blood, again followed by the actions leading up to the excretion of the liquid drop.

The cumulative effect of all these excreted droplets (discard droplets) is to give the carcass a spotted appearance, and this is not the result of vomit-drops which are discussed below.

If the flies have fed sufficiently they may remain sitting on the carcass, but more frequently fly off to nearby vegetation. Here they alternate between preening themselves, standing motionless, and sometimes partially regurgitating droplets of blood which hang suspended from the proboscis. The flies generally remain on the vegetation for several minutes, sometimes in excess of three hours. When pushing out vomit drops they allow the drop to remain suspended for periods of three to fifty seconds, rarely longer, taking them up again but pushing out another droplet after a few seconds. Only on very rare occasions (less than 1%) do they allow the droplet to come into contact with the resting substrate, and this is usually accidental such as when another fly bumps into it. Whilst discharging vomit drops, the flies may briefly interrupt this behaviour to void droplets via the anus.

The above description is based on observation of 43 males and females of C. albiceps and C. marginalis. The behaviour varies widely according to the quantity, quality, availability and location of the food, ambient temperature and other climatic factors, and other parameters such as sex, age and physiological state of the adult fly (Strangways-Dixon 1959, Belzer 1978, Dethier 1961, Johansson 1964).

Two specific examples have been selected as being fairly "typical" and are presented below:

On 11/4/81, 10h30, at an impala carcass (dead 27 hours), a C. marginalis female was observed to approach and commence feeding at a thoracic incision where muscle tissue was exposed but with only a very thin layer of more or less dried blood available. She fed for 1 minute 45 seconds, preened 5 seconds, resumed feeding for 1 minute 8 seconds, preened for 1 minute 25 seconds, voided a dark red discard droplet, resumed preening for 48 seconds, then walked briefly and stood motionless for 28 seconds, preened for 2 minutes 42 seconds, flew away to a leaf about 15cm from the carcass and 33cm above the ground. She preened the forelegs, eyes and proboscis for 77 seconds, remained motionless for 12 seconds, preened hindlegs, wings and mid-legs for 46 seconds, voided a small red discard droplet, briskly walked onto a nearby leaf (2 seconds), remained motionless for 26 seconds, preened for 22 seconds, stood motionless for 23 seconds, then flew back to the carcass for another feed.

It will be noticed that no vomit drops appeared, and in 54% of flies observed no vomit drops did in fact appear, although every fly did give off one or more discard droplets. In the case of flies where vomit drops were observed, a more or less typical sequence was as follows:

In another observation, a female C. marginalis after feeding flew to a leaf approximately 10cm from the carcass and 30cm above the ground. It walked on the leaf for 12 seconds, preened for 37 seconds, stood motionless for 4 seconds, preened 25 seconds, walked 8 seconds, preened 31 seconds, walked to another leaf taking 13 seconds, preened 14 seconds, remained motionless 3 seconds, preened 35 seconds, stood motionless 13 seconds, preened 18 seconds, stood motionless 93 seconds, preened 6 seconds, stood motionless 12 seconds, preened 30 seconds, stood 61 seconds, then pushed out and retracted vomit drops 13 times (total duration 5 minutes 20 seconds), stood motionless 68 seconds, pushed out and retracted vomit drops briefly in 6 seconds, remained motionless 44 seconds, excreted a translucent droplet, stood motionless for 2 minutes and 2 seconds, then flew back to the carcass for another feed.

DISEASE TRANSMISSION IMPLICATIONS

By allowing C. albiceps and C. marginalis to feed on blood inoculated with Bacillus anthracis, De Vos (pers. comm.) established that bacteria pass through the alimentary canal of these flies in large numbers and in a viable form. Epidemiologic evidence during anthrax outbreaks in the K.N.P. since 1959 clearly indicates that the blood-spots deposited by flies after having fed on infected carcasses have a major role in spreading and maintaining an epidemic (Pienaar 1961, De Vos 1973). To gather more data on the distribution of flies having fed at a carcass, and of blood from the carcass, an impala carcass was injected with radioactive material so that the path of these two sources of infection could be followed.

A full-grown male impala, thin due to an injured leg, was immobilised with M99 (Etorphine Hydrochloride **) early in the morning of the 16th November 1983 and placed in an exposed position in the Nwashitsumbe Roan Camp in the southern part of the study area. The vegetation consisted mainly of stunted Mopane (Colophospermum mopane) with interspersed tall Mopane, Marula (Sclerocarya birrea) and Leadwood (Combretum imberbe) trees, with a fairly dense covering of Eragrostis superba, Cenchrus ciliaris, and Schmidtia pappophoroides grass up to 0,67 metres high.

At 08h42, 125 milliCuries of radioactive phosphorous (P^{32}),

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** Reckitt and Coleman (Africa) Ltd.

made up in a 10ml aqueoùs solution, was administered through the jugular vein. After allowing the P^{32} to circulate for an arbitrary period, the impala was euthenased at 08h55. A 30cm incision was made ventrally along the thorax to expose the heart, which was punctured several times for blood to escape so that it would be available to flies. The carcass and surrounding area was then left undisturbed so that flies could feed uninterruptedly in a normal manner.

Early on the 19th November, the fourth day after placement of the impala, a natural sharp decrease (Braack 1981, and elsewhere in this dissertation) in fly-numbers at the carcass was noticed and I commenced examination of the area around the carcass for blood-droplets in the following manner: cardboard squares had been placed in various positions (Fig. 109) on the ground and also at one metre intervals vertically along a pole before placement of the carcass at the site; these were all removed and counts made of the number of blood-droplets per square metre. Additionally, a one metre square metal grid with thin rods spaced 10cm apart was placed over the grass and ground at set sampling distances away from the carcass, and the detector tube of the Geiger-Counter traced along the cross-bars of the grid to determine the number of radioactive droplets deposited along this standardised pathway. Finally, leaves were picked from Mopane shrubs and trees in the vicinity and the number of droplets on these leaves counted. Twenty randomly picked leaves (i.e. 40 leaflets) were taken from each site to standardise the counts.

On the 21st November, 6 days after placement of the carcass, blow-fly traps were placed at various distances (Fig. 110 and Table 26) away from the carcass to capture flies which had fed on the radioactive carcass, thus gaining some estimate of the distance travelled by these flies in the intervening period. Each trap was emptied on the 25th or 26th November and the contents examined for radioactive flies using a Geiger-Counter. As adult flies resulting from eggs having been laid at the carcass only started emerging from their puparia on the 26th, all the radioactive flies captured must have been adults which had fed on blood or other moisture from the carcass.

For the period 16 to 19 November the minimum and maximum temperatures recorded at the site were 21,0^{o} C and 39,0^{o} C, respectively.

FIGURE 109: Radioactively marked impala carcass (in foreground) at Nwashitsumbe Roan Camp, with sampling sites for fly droplets indicated by letters A to Z4 (see also Table 25)

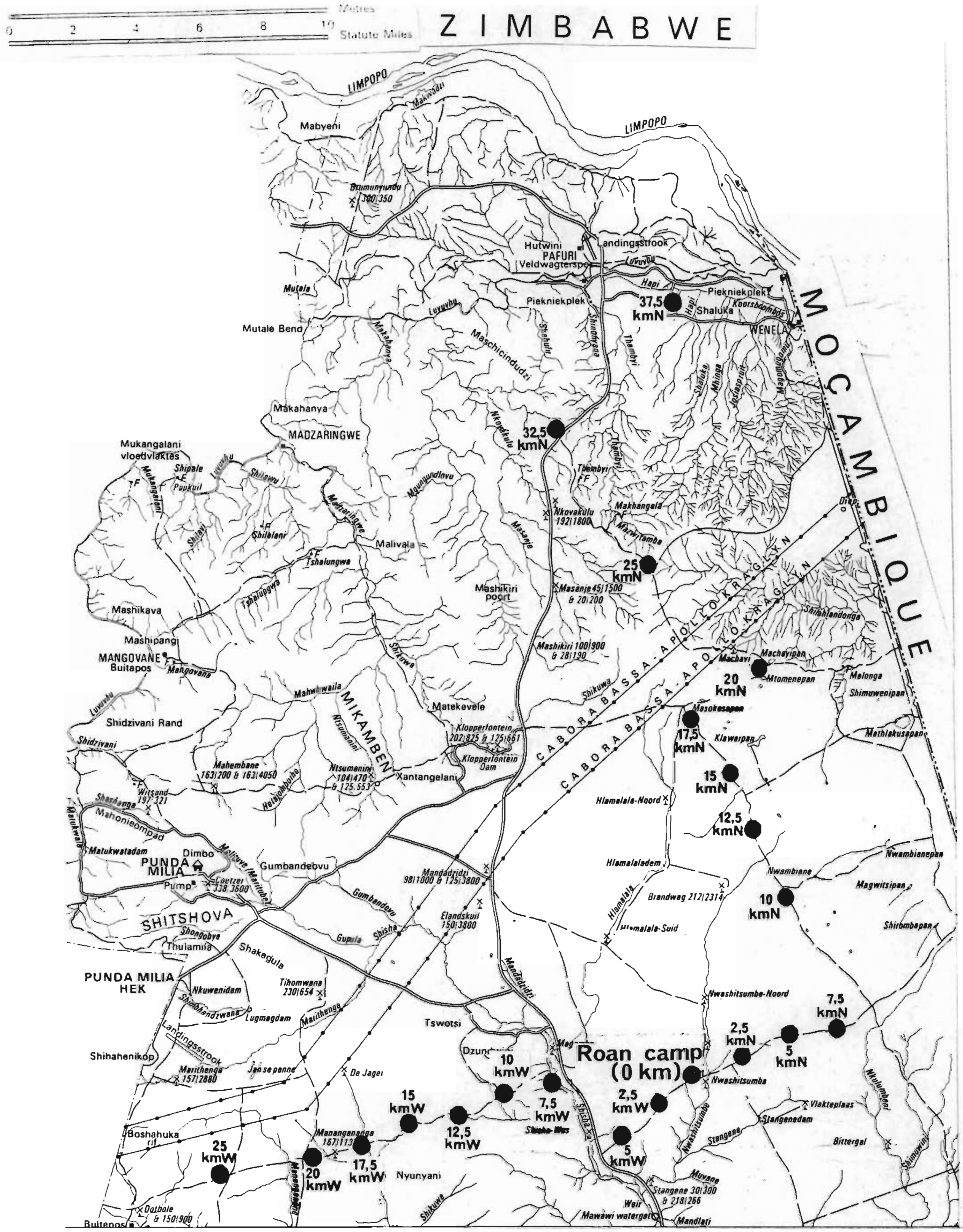

FIGURE 110: Placement of blow-fly traps in the northern K.N.P. for capture of flies having fed on radioactively marked impala carcass at Roan Camp (Nwashitsumbe)

Cloud-cover varied between zero and six-tenths on most days, except during the early morning of the 17th November when overcast weather and a light drizzle (less than 3mm) was recorded. Early mornings were calm, but an intermittent light breeze (4 - 6 knots) usually appeared around mid-morning and lasted until mid-afternoon. During the period 21 November to 26 November the weather over the whole area in which fly-traps had been placed was much the same and no rain fell during this period.

Data are summarised in Tables 25 and 26, giving results. When examining the number of radioactive flies trapped at various distances from the carcass (Table 26), care should be taken not to compare catches from different sites directly as the size of the trap-catch varies according to vegetation type and a number of other factors (see preceding chapter).

ABLE 25: Distribution and density of blood droplets 72 hours after placement of carcass

Sample site	Substrate	Horizontal distance from carcass (m)	Height above ground	Number of blood-droplets per 20 leaves	As measured along rail of grid	Per m²
A	Mopane leaves	1,52	0,60 - 1,04	475	-	-
B	Mopane leaves	2,99	0,61 - 1,21	17	-	-
C	Mopane leaves	2,0	1	306	-	-
D	Mopane leaves	2,0	2	384	-	-
E	Mopane leaves	2,0	3	82	-	-
F	Mopane leaves	2,0	4	8	-	-
G	Mopane leaves	1,93	0,51 - 1,7	126	-	-
H	Mopane leaves	2,46	0,26 - 1,22	7	-	-
I	Mopane leaves	5,0	0,51 - 1,63	0	-	-
J	Mopane leaves	3,0	2	46	-	-
K	Mopane leaves	6,19	0,6 - 1,8	1	-	-
L	Grass & soil	0-1,0	0 - ±0,3	-	*	-
M	Grass & soil	2,5	0 - ±0,3	-	89	-
N	Grass & soil	5,0	0 - ±0,3	-	2	-
O	Grass & soil	10,0	0 - ±0,3	-	0	-
P	Grass & soil	15,0	0 - ±0,3	-	0	-
Q	Grass & soil	20,0	0 - ±0,3	-	0	-
R	Grass & soil	2,5	0 - ±0,3	-	*	-
S	Spoiled due to maggots crawling over cardboard					
T	Cardboard	1,0	0	-	-	2302
U	Cardboard	2,5	0	-	-	3300
V	Cardboard	5,0	0	-	-	1
W	Cardboard	10,0	0	-	-	1
X	Cardboard	15,0	0	-	-	0
Y	Cardboard	20,0	0	-	-	0
Z1	Cardboard	2,5	0	-	-	92
Z2	Cardboard	2,5	1	-	-	86
Z3	Cardboard	2,5	2	-	-	15
Z4	Cardboard	2,5	3	-	-	1

* Continuous chatter (Geiger counter cannot separate droplets)

TABLE 26: Radioactive flies caught in traps placed at various distances from carca

Distance from carcass	*Chrysomyia albiceps* ♂	*Chrysomyia albiceps* ♀	*Chrysomyia marginalis* ♂	*Chrysomyia marginalis* ♀	Other flies
Roan camp (0km)	3	-	12	51	3 *Lucilia* & 3 *Musca*
2,5 km N	-	4	-	6	3 *Lucilia*
2,5 km W	-	-	-	-	2 *Lucilia* & 1 *Sarcophaga*
5,0 km N	-	6	-	11	2 *Lucilia*
5,0 km W	1	-	1	11	-
7,5 km N	-	5	1	19	2 *Lucilia*
7,5 km W	1	3	1	5	-
10,0 km N	Trap damaged by scavenging mammal				
10,0 km W	1	-	-	4	-
12,5 km N	-	2	-	6	-
12,5 km W	-	1	1	4	1 *Musca*
15,0 km N	-	5	-	7	-
15,0 km W	-	-	-	6	-
17,5 km N	-	-	-	9	-
17,5 km W	-	1	-	5	-
20,0 km N	-	1	-	9	-
20,0 km W	-	1	-	-	-
25,0 km N	-	1	-	1	-
25,0 km W	-	1	-	6	-
32,5 km N	-	1	-	-	-
37,5 km N	-	-	-	-	-
TOTAL	6	32	19	163	12 *Lucilia*, 4 *Musca* 1 *Sarcophaga*

Considering first the results obtained by examination of blood-droplets on mopane leaves, there was a definite tendency for blow-flies to settle on trees in the immediate vicinity of the carcass. They fly to the closest tree or shrub, and congregate on that side of the tree or shrub nearest the carcass. This pattern is clearly visible when comparing sampling sites A, G, I and K, where A is the closest shrub, and has the highest density of discard-droplets per leaf, decreasing rapidly to K which is farthest away and has the lowest density per leaf. When comparing results from sites A and B, G and H, and also D and J, it is clearly visible that although the distance between each of the two alternatives is very small, the flies travel the shortest possible distance to rest.

Sample sites C,D, E and F were selected to assess the vertical distribution of discard-droplets, providing some idea of the height preference of the flies. The greatest number of droplets occurred between one and three metres above ground, with a peak at two metres, decreasing thereafter.

Essentially the same pattern as presented by droplets on leaves is provided by examining the results of the counts along the metal grid placed over the grass and soil, and by the cardboard squares placed at various distances. It should be mentioned that the flies appeared to avoid resting on a wide, flat expanse such as presented by the cardboard discs. Similarly, flies were reluctant to settle on the ground to rest, although they readily walked at this level to feed at pools of blood or other moisture. When satiated, however, they flew off to rest on nearby shrubs or a protruding grass stalk well above ground. Many flies often in this manner congregated on a few prominent stalks, twigs, or leaves, whilst broader surfaces such as the trunk of a tree were avoided.

Examination of the trap-catches (Table 26) reveals that flies covered large distances within a relatively short period of time. This supports the findings on flight range as presented in Chapter 6. De Vos (pers. comm.) established in the K.N.P. that C. albiceps and C. marginalis remained infective for at least 28 days after being fed anthrax-inoculated blood, so that these blow-flies have the potential to play a significant role in the dispersal of disease-organisms.

When relating the information gained in this experiment to the transmission of anthrax, it is clear that the habits of these flies greatly increase the risk of bacteria (or their spores) reaching other herbivores. Flies feed on blood at carcasses, settle preferentially on grass stalks but mainly on leaves of nearby shrubs, and any bacteria present pass unchanged through the alimentary canal. The flies void excretory droplets which reach their greatest density at a height between one and three metres which is where animals such as kudu, which are highly susceptible to anthrax, do most of their browsing.

Although nowhere near as abundant as certain other herbivores such as buffalo, kudu are the most vulnerable to anthrax and of 1 054 medium to large-mammal mortalities in the 1960 epizootic, 771 (73,15%) were kudu (Pienaar 1961). Waterbuck and buffalo followed next but with a much reduced incidence of only 7,12% and 5,50%, respectively. Both these species are grazers and the evidence therefore suggests that the exceptionally heavy kudu mortalities must to some extent be correlated with their feeding habits. Examination of cumulative mortality figures for other herbivorous species confirm the disproportionate loss of life by browsers, these animals contributing 79,19% towards the total number of dead herbivores. Witnesses of the 1960 epidemic ascribed the dissemination of anthrax as being effected "chiefly by vultures from dead animals on which they fed to watering places which they visited in order to bathe or drink", and the differential mortality amongst animals as being due to varying tolerances or "inherent resistence" (Pienaar 1961). Blow-flies were allotted a secondary role. The role of resistance may be somewhat over-emphasied as the differential mortality can adequately be explained by the feeding habits of these animals. The potential of blow-flies in increasing the availability and accessibility of disease bacteria must not be underestimated. It is suggested that in the northern K.N.P. vultures are probably the main agents for long-distance dispersal of anthrax, but that blow-flies cause local dissemination with a potential for explosive spread within a region.

From an epidemiological point of view, the fact that blow-flies deposit the majority of discard droplets in the immediate vicinity of a carcass greatly facilitates disease management efforts. This area can then be burnt, a practice which has been applied for some time already during anthrax epizootics in the Kruger National Park (Pienaar 1960, 1961).

CHAPTER 8

CONCLUDING SUMMARY AND RECOMMENDATIONS

A total of 227 arthropod species in 36 families were recorded utilising the carrion habitat, and 98,68% of the species were of the class Insecta. The most abundant and consistent users of the habitat were Histeridae (24 species), Trogidae (6 species), Scarabaeidae (46 species), Dermestidae (1 species), Cleridae (1 species), Piophilidae (2 species), Sphaeroceridae (12 species), Chloropidae (9 species), Milichiidae (5 species), Muscidae (21 species), Calliphoridae (20 species), Tineidae (1 species), Pteromalidae (1 species), Diapriidae (1 species), Formicidae (10 species), and Acarina (3 species), showing a clear predominance of Coleoptera and Diptera.

Resource utilisation by the species enabled them to be grouped as sarcophagous, coprophagous, keratophagous, detritivorous, predaceous, or parasitic, with the immature stages of some species resorting under a differing trophic category to the adults. All species were attracted to particular components of the carcass, or as predators and parasites to a narrow range of insects present at carrion. All species showed definite periods of peak visitation such that a sequential pattern of arrival and departure was exhibited which conformed in many aspects to the traditional concept of succession. Succession at carcasses resulted in destruction of the habitat however, unlike succession as generally interpreted in other habitats where it results in a stable climax community.

Of the resource requirements for the various species, carcass soft-tissues for blow-fly larvae were the most limiting because of competition by vertebrate scavengers such as hyenas and vultures. Between 10 and 20% of medium- to large mammal carcasses in the study area were found to remain undiscovered by vertebrates or retained sufficient soft tissues for a period sufficiently long for blow-fly larvae to complete their development.

The blow-flies <u>Chrysomyia albiceps</u> and <u>Chrysomyia marginalis</u>

were crucial pivotal species in the carrion community because of the ability of the immature stages to consume all carcass soft-tissues within four days in summer and fifteen days in winter, and by their presence and action on the carcass drastically influencing other members of the carrion community. The presence especially of C. marginalis larvae stimulated the arrival of large numbers of histerid and other predatory beetles, and their feeding activities made available nutrient-rich fluids and other resources and influenced the timing of peak arrival of insects such as piophilids, chloropids, milichiids, clerids, dermestids and also scarabs.

Adult Chrysomyia marginalis blow-flies were the first arthropods to arrive at the carcass, within minutes in summer and generally within an hour in cooler months. Peak abundance of this species both in summer and winter occurred during the first 36 hours after death of an animal, with females predominating at first and males becoming more numerous later. C. albiceps showed a slightly delayed pattern of arrival and reached peak abundance on the second and third days after death, females also being more numerous at first.

Adult Chrysomyia albiceps and C. marginalis imbibed considerable quantitities of carcass fluids such as blood, rumen-fluids and lachrymal secretions. Females oviposited in shaded and concealed locations such as in the mouth, nostrils, axil regions, and especially at the soil/carcass interface. Female C. albiceps deposited an average of 260 eggs per laying, whereas the larger C. marginalis females averaged 324. The egg incubation period for C. albiceps varied between 738 minutes and 1 085 minutes at average temperatures of 33,75°C and 24,65°C, respectively. For C. marginalis the egg incubation period varied between 603 minutes and 895 minutes at respective average temperatures of 33,75°C and 24,25°C.

The rates of development of the larvae of blow-flies were greatly influenced by temperature, with a correlation coefficient of 0,89 for C. albiceps and 0,81 for C. marginalis when plotting mean minimum ambient temperatures against time taken from oviposition to reaching the post-feeding third instar stage. In summer C. albiceps larvae pupariated between Days 5 and 7 and C. marginalis between Days 4 and 6, whereas in winter both species generally pupariated between Days 9 and 14. Up to 114 943 *C. albiceps* larvae and 139 086 *C. marginalis* larvae were present at an impala carcass. Experimentation showed that when fed to vultures, larvae of both *C. albiceps* and *C. marginalis* did not survive passage through the gastro-intestinal tract.

Monthly monitoring revealed that *C. albiceps* adults were most numerous from October/November to February, whereas *C. marginalis* adults had a longer abundance period lasting from September to February. Radioactively marked flies released from a central point revealed a potential rate of dispersal of 2,20 km per day for *C. albiceps* and 2,35 km per day for *C. marginalis*. *C. albiceps* were retrieved at a maximum distance of 37,5 km 17 days after release, whereas *C. marginalis* were found capable of travelling 63,5 km within 22 days after release. Both species showed a clear preference for well-wooded environments and were least numerous in arid open areas. Average population densities for the two species over the study area as a whole were computed and yielded estimates of 756 *C. albiceps* adults per km^2 (7,56 per hectare) and 2 903 *C. marginalis* per km^2 (29,03 per hectare).

The feeding behaviour of *C. albiceps* and *C. marginalis* was examined with regard to the potential role of these flies in anthrax transmission. Adults of both species imbibed blood and other liquids at fresh carcasses and deposited large numbers of potentially infective reject droplets on vegetation in the area around a carcass. The droplets were categorised as vomit droplets from the mouth, and discard droplets and faecal droplets from the anus. Discard droplets were the main cause of the speckled appearance of carcasses and surrounding vegetation, caused by the rapid passage of presumed excess fluids through the alimentary canal of the flies and deposition of undigested material. The flies displayed a preference for resting positions between one and three metres in height, resulting in discard droplets being most numerous at the prime feeding height of such browsers as kudu.

By way of conclusion it is appropriate that some suggestions on disease-management and other considerations relating to carrion arthropods be noted.

Recommendation: Despite the potentially important role of blow-flies in the transmission of anthrax during an epidemic, such flies should be regarded as being very beneficial in general and having a positive role.

Motivation: Blow-flies form an integral and essential component of a natural ecosystem, such as exists in the K.N.P., because of their ability to rapidly locate carcasses and effectively dispose of soft tissues in the absence of vertebrate scavengers. During summer conditions, for example, they are capable of reducing a kudu-sized carcass to skin and bone within as little as five days.

At carcasses of anthrax mortalities adult blow-flies are charged with consuming carrion-fluids and discarding infective droplets on surrounding vegetation, but on the positive side the larvae have the potential for consuming all the carcass soft-tissues which contain a far greater magnitude of infective material, and by eventually dispersing they cause dissipation or a great dilution of the spores originally highly concentrated in the carcass.

The population of Chrysomyia albiceps and C. marginalis should therefore be encouraged to remain at a high level and only during an anthrax or other fly-influenced epidemic should measures be considered to temporarily depress blow-fly numbers in the zone of heaviest animal mortality.

Recommendation: Blow-fly traps should be placed in strategic locations throughout the zone of heavy mortality during an anthrax epidemic.

Motivation: Large numbers of blow-flies congregate at fresh and partially decomposed carcasses, and where such carcasses result from anthrax the flies are a potential threat as disseminators of the disease. Blow-fly traps are effective in removing considerable numbers of flies from the environment, and especially when placed in areas of high density and in the vicinity of anthrax-infected carcasses should reduce the potential for anthrax transmission by the actions of these flies.

Recommendation: The present practice of burning the area adjoining anthrax mortalities should be continued.

Motivation: Blow-flies deposit enormous numbers of mainly discard droplets on vegetation and the soil in the area immediately next to a carcass. During anthrax epizootics such droplets may be highly infective, making it advisable to burn such vegetation. Blow-flies settle on vegetation nearest the carcass, so that plants farther away are very low in infectivity.

Recommendation: During culling operations any buffalo carcasses condemned and left in the field should have the skin slashed through in several places so that vultures are allowed easy access to the soft tissues inside.

Motivation: On a number of occasions in the northern K.N.P. it has been found, especially when several carcasses are rejected simultaneously, that large numbers (millions) of blow-fly larvae feed on these carcasses. Vultures are generally unable to penetrate a buffalo carcass without the aid of a stronger scavenger such as hyena, and in the northern K.N.P. where the density of these mammalian scavengers is relatively low and a large number of buffalo are culled with several rejections at times, situations do arise where buffalo carcasses are utilised exclusively by blow-flies. A single buffalo carcass has the potential to sustain more than 500 000 blow-fly larvae. In times of drought, such as during late-1982, buffalo carcasses were also found in the Lower Sabie area which had been exclusively consumed by blow-fly larvae. Slashing the skin of contaminated buffalo carcasses will enable vultures to rapidly enter and utilise soft-tissues without having to wait for hyenas.

Recommendation: Short studies should be undertaken in the southern K.N.P. to determine the species of blow-flies breeding in carcasses especially during winter.

Motivation: From blow-fly traps placed in the Skukuza area for monitoring seasonal fluctuations in blow-fly populations it has emerged that the species composition during winter and the proportionate numerical contribution of some species to overall abundance differs considerably from that present in the northern K.N.P. Chrysomyia chloropyga and C. bezziana, for example, occasionally reach considerable abundance in the Skukuza area and the question arises whether these actually breed in carcasses in the southern K.N.P. or whether they enter from farming areas adjoining the K.N.P.

Recommendation: The taxonomic distinctness of Lucilia cuprina and L. sericata should be investigated to determine whether they are separate species or morphological variants of the same species, and to determine reliable characters for consistent separation of the two populations.

Motivation: Several workers have experienced difficulty in reliably separating the two species and have reservations concerning their distinctness especially when using morphological characteristics traditionally employed in keying out the species.

Recommendation: Field-staff and forensic personnel should be made aware that in critical situations where it is essential to accurately determine the time of death of an animal, it is often possible to obtain an estimate of time elapsed since death of the animal by examination of the insects present at the carcass.

Motivation: The estimation of carcass-age by examination of stage of insect-succession reached and application of known rates of development of some species present at the carcass has long been acceptable in courts-of-law either as corroborating evidence or when more conventional methods of carcass-age estimation have failed or not been possible. There exists a predictable correlation between temperature and rate of development of, for example, blow-fly larvae so that probable time of death can be estimated by examination of maggot-size and a knowledge of the general successional position occupied by the species of fly to which the maggot belongs. Over longer time intervals other species, such as keratophagous beetles and parasites of fly pupae, can provide reasonably accurate estimates of time elapsed since death.

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