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**BIOLOGY AND CONSERVATION OF *CIRCELLIUM BACCHUS*
FABRICIUS (COLEOPTERA: SCARABAEIDAE)**

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**Biology and conservation of
Circellium bacchus Fabricius (Coleoptera: Scarabaeidae)**

by

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A PREAMBLE TO THE PROJECT

"Welcome to the jungle it gets worse here every day" (G N' R)

The last twenty years have seen a dramatic upsurge in environmental awareness. The "Green" movement has, however, only fairly recently become an issue in the hearts and minds of the South African public. Consumer action and the media have forced many changes in the manufacturing and packaging of goods and thus today most products sport the "environment friendly" label.

Conservation of local fauna and flora, however, dates back much further than the last 20 years with the inception of The National Parks Board. The idea behind the establishment of parks in South Africa is to conserve certain areas of land along with the plants and animals inhabiting these areas.

More recently however, organisations such as "The Rhino and Elephant Foundation" have become involved in protection and conservation of threatened species. Although many of these organisations pledge themselves to the protection of all living creatures, it is often the case that much of their time, effort and funds go towards the "big and hairy's".

It is only fairly recently that the spotlight has fallen on insects. The plight of *C. bacchus* and the subsequent media coverage that it has received was one of the major factors leading to the establishment of the Endangered Insect Trust (E.I.T) in July 1991.

The story has its beginnings as early as 1980 when *C. bacchus* was made one of the priority species in the Addo Elephant Park's management plan. One of the aims of the plan is "To promote a viable, genetically uncontaminated population of the flightless dung beetle *Circellium bacchus*". This was a red letter day for entomologists, as never in the R. S. A. had such a small animal been given such priority in any of the National or Regional parks.

In March 1979 Mr Harold Braack, who was to be the new park warden at the Addo National Park, was informed of the beetle by Dr A. Hall-Martin and asked to undertake a research project on it. To quote Mr H. Braack "for a variety of reasons the project was initiated only during 1982, though casual and preliminary observations had been made prior to this". Effectively the project was terminated with the transfer of Mr. Braack in January 1983. Besides a paper concerning thermoregulation in the beetle, no further work was done.

In April 1990 the Department of Entomology at the University of Pretoria was approached by the Parks Board in the person of Dr P. Novellie. Dr. Novellie had received complaints from tourists, as well as the Wildlife Society, in connection with the alarming number of unnatural deaths of this beetle in the Addo Park, caused by cars driving over them on the roads of the Park.

This unnecessary slaughter must have been going on unchecked since the roads inside the park, once closed to tourist traffic, had been opened to the public, approximately 11 years ago. This seems a long time to allow the wholesale slaughter of any species to carry on unabated, let alone one enjoying priority status in the Park.

Mrs J. Burton, who resides on a nearby farm, remembers "Bokamp", an area of the Park, teeming with *C. bacchus* in the days before the inner roads were opened to the public. According

to her, "Bokamp" was thinned out extensively by Mr Sep Leroux, in order to accommodate the tourists who were not seeing any game. This was, according to Mrs Burton, Parks Board policy at the time. "Bokamp" is at the moment (see fig 1) very poorly populated with this dung scarab. The buffalo were, although they had access to the rest of the Park, originally confined to this area of land and in the words of Mrs Burton "far more abundant than they are now".

Professor Clarke Scholtz, Head of the Department of Entomology at the University of Pretoria, accompanied me to Addo in April 1990. We made the preliminary assessment that the elephants preferred walking unhindered in the roads and therefore large quantities of dung littered the roads of the Park. Many of the beetles attracted to the dung were driven over either on their way to or from the dung or were killed *en masse* while lying feeding under the dung's crust.

Some of the beetles which had constructed a brood or food ball could not negotiate the steep sides of many of the roads. The beetles would try in vain to push the heavy ball up the embankments. After a number of attempts, the beetle would invariably abandon the ball or bury it in the soft sand on the sides of the roads. After heavy rains, when the roads were slippery and unmanageable, the grader would be brought in. This would result in some of the balls buried on the side of the road being broken open and the larva killed, as well as the road sides becoming steeper.

Many beetles were also found dead at the side of the roads. They had been desiccated by the sun, unable to climb off the road and find shelter in the shade offered by the dense vegetation. *C. bacchus* beetles are ectothermic and therefore rely on the ambient temperature to warm them up and cool them down. Stranded in the boiling sun, being flightless and thus without the ability to lift their elytra and pass off some of this heat to the atmosphere, many beetles were fried alive.

We decided to tackle the problem on three fronts; the first being an in-depth study of the biology of this little-known insect; secondly a public awareness campaign comprising pamphlets, exhibitions and radio and television coverage and thirdly, based on the biological information obtained, we would propose a management scheme aimed at the reduction of these vehicle-induced deaths in order to benefit the beetle numbers in the long term.

A public awareness campaign was launched early in 1991. It consisted of extensive media coverage mainly in the local newspapers and on the local radio station. Articles concerning the plight of the beetle also featured in literature available nation-wide.

The public awareness campaign in Addo centred around a leaflet which was handed to the driver of each car, containing information concerning the beetle and a strong plea to the driver not to drive over single beetles or any dung lying in the roads.

A large display showing the life cycle of *C. bacchus* and the importance of dung beetles in general was made, and is prominently displayed in the reception area of the restaurant. All talks given by the rangers to the many visiting groups contain relevant information on the beetles.

The remarkable interest in the beetle is fantastic. So far there seems to be an improvement, in that fewer beetles are being driven over and the tyre tracks of cars are seen to be going around the heaps of dung where previously they went over them. The problem is that if 20 cars go around

a pile of dung and the 21st car goes over it, we have achieved nothing. The fact that the beetles are so numerous around the dung on the roads after rains that falling short of climbing out of the vehicle and moving the beetles, there is no way of avoiding them.

The publicity campaign has been a success, but the main problem now lies with the roads. There are approximately 50 km of dirt roads in the park that are open to public traffic. The roads are scraped after rains and this leads to a cliff-like vertical slope on the one side of the road and a more gentle slope on the other side. The gentle slope is negotiable to single beetles seeking refuge in the vegetation next to the road but the cliff-like slope, which varies from a few centimetres to as much as a metre in height, is impossible for single beetles and ball-rollers alike to scale.

Brood balls were constructed using mainly buffalo dung throughout most of the year except after good summer rains when elephant dung was also used extensively. Many of the buffalo originally spread through the park have moved to the newly acquired grassland area called Alva. This area, although well suited to the buffalo, is not conducive to the breeding or survival of the beetles, except in the areas where three valleys extend into Alva. These valleys contain the same dense vegetation that occurs in the rest of the park.

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1. SUMMARY

Activity of the large, flightless, telecoprid dung scarab, *Circellium bacchus*, is governed by precipitation and temperature. Mild to warm temperatures (18-26°C) following rain, or high relative humidity can cause a hundred-fold increase in their visible numbers. Seasonal peaks therefore coincide with the warm and wet months of the year.

In the Addo Elephant National Park and surrounding areas the rainfall, although distributed throughout the year, is characteristically trimodal with peaks in autumn, spring and early summer. Although once widespread this monospecific genus is now restricted to a few small populations in the southern and eastern Cape Province with the largest population enjoying the suitable habitat and protection afforded by the Park.

The females of *C. bacchus* are responsible for rolling and burying the brood ball. The male sometimes joins the female in the final stages of brood ball construction. Elephant dung is preferred for feeding while the more pliable buffalo dung is mainly used for breeding. The large brood balls (43-63 mm diameter) are rolled between 10 and 80 m before being buried in a brood chamber at an average depth of approximately 250 mm.

Mating takes place underground one to four days after burial. The ball is reshaped into a brood pear and a solitary egg is laid in the apex. Three larval instars and the pupal stage follow, lasting approximately 4 - 4.5 months under favourable conditions. The female stays with the brood ball for the duration of the immature stages and thus only produces one or two generations per year. The males leave the brood ball five to seven days after the ball is buried.

The high unnatural mortality of the beetles, caused by cars, in the Park can largely be attributed to the design of the tourist roads and public ignorance. Solutions to these problems include altering the design of the roads, and a public awareness campaign involving pamphlets and the media, highlighting the plight of the beetle.

SAMEVATTING

Aktiwiteit van die groot, nie-vlieënde kopriede miskruier, *Circellium bacchus*, word deur reënval en temperatuur beïnvloed. Matig tot warm temperature (18-26°C) net na reën, of hoër relatiewe humiditeit kan 'n ongeveer honderdmaal vermeerdering in die waarneembare aantal kewers veroorsaak. Seisoenale pieke kom dus in die warm, nat maande van die jaar voor.

In die Addo Olifant Nasionale Park en omliggende gebiede word die reënval, alhoewel dit deur die jaar versprei is, gekenmerk deur trimodale pieke gedurende die lente, herfs en vroeë somer. Alhoewel hierdie monospesifieke genus eers wydverspreid was, is dit tans tot net 'n paar klein bevolkings in die suid- en oostelike Kaapprovinsie beperk, met die grootste bevolking in die Addo Olifant Nasionale Park waar hulle beskerming geniet.

Die wyfie van *C. bacchus* rol en begrawe die broedbal. Die mannetjie sal soms die wyfie bystaan in die finale stadium van broedbal-konstruksie. Olifantmis word verkies vir voeding, terwyl die meer ploeiare buffelmis hoofsaaklik vir broeidoeleindes benut word. Die groot broedballe (43-63mm in deursnee) word tussen 10 en 80m gerol, voordat hulle in 'n broeikamer, wat gemiddeld 250 mm onder grondoppervlakte is, begrawe word.

Paring vind ondergronds plaas een tot vier dae na begrawing. Die bal word in 'n broeipeer hervorm en 'n enkele eier word in die bopunt van die bal gelê. Drie larvale instars en die papie-stadium, wat ongeveer 4-4.5 maande onder goeie omstandighede duur, volg hierna. Die wyfie bly by die broedbal tydens die larvale stadiums, en daarom produseer sy net een of twee generasies per jaar. Die mannetjie verlaat die broedbal vyf tot sewe dae nadat die bal begrawe is.

Die hoë onnatuurlike sterftes onder die kewers veroorsaak deur voertuie in die Park kan hoofsaaklik aan die ontwerp van die toeristepaaie en publieke onkunde toegeskryf word. Oplossings vir hierdie probleme sluit die verandering van die paaie in sowel as 'n publieke bewusmakingsveldtog, wat pamflette en die media insluit, om die verknorsing van die kewer te beklemtoon.

2. INTRODUCTION

2.1. ADDO ELEPHANT PARK

The Addo Elephant National Park is located in the Eastern Cape Province, 72 km from Port Elizabeth and 25 km from the coast at Algoa Bay. It is an island in a sea of increasing agricultural development. The Park is relatively small by National Park standards, comprising approximately 12 000 ha of mildly undulating Valley Bushveld, of which close to 8 600 ha are open to the public (see fig 1) (Grobler & Hall-Martin 1982).

The areas restricted to the public, but open to game, consist of recently-acquired farm land, some of which was used for crop farming and is thus totally disturbed. Four grass species were subsequently planted and this area now supports a number of grazers. The altitude in the Park varies from 76 to 341 metres above sea level (Grobler & Hall-Martin 1982).

HISTORY

The Addo Elephant Reserve was proclaimed a National Park on the 3rd of July 1931. This was due to public pressure, after large numbers of elephants were shot for raiding crops and interfering with farming activities. At this stage there were only 11 elephants left. Warden S. H. Trollope herded the remaining animals into the Park and sunk boreholes to provide water for them as there is no permanent water available in the Park (Grobler & Hall-Martin 1982). In 1954 Graham Armstrong introduced the elephant-proof fence. This had a dramatic effect on elephant numbers in the Park and saw them rise from a mere 18 in 1954 to a very healthy 170 + at present.

CLIMATE (See figure 2)

Rainfall is characteristically trimodal with a major peak in autumn (March/April) and lesser peaks in spring (August), and early summer October/November, although rainfall has been recorded in all months of the year. Precipitation occurs mainly as light showers; thundershowers are rare. The average annual rainfall for the area is 407 mm, although there is geological evidence of former periods of much higher rainfall (Grobler & Hall-Martin 1982).

The prevailing winds usually blow from the south-east or south-west. Mists are common in the early morning especially in the valleys but frost seldom occurs. The average daily maximum temperature is about 29°C in January and 21°C in July. January and February are the hottest months of the year with temperatures sometimes exceeding 40 °C. The average daily minimum temperature is approximately 16 °C in January and 5 °C in July (fig 2) (Grobler & Hall-Martin 1982).

FLORA

The vegetation, known locally as the "Addo Bush" is classified as Valley Bushveld (Acocks 1975). The Valley Bushveld is situated between the Zuurberg and the Sundays River Valley. The height of the bush, when not disturbed, varies between three and four metres but, in the ravines

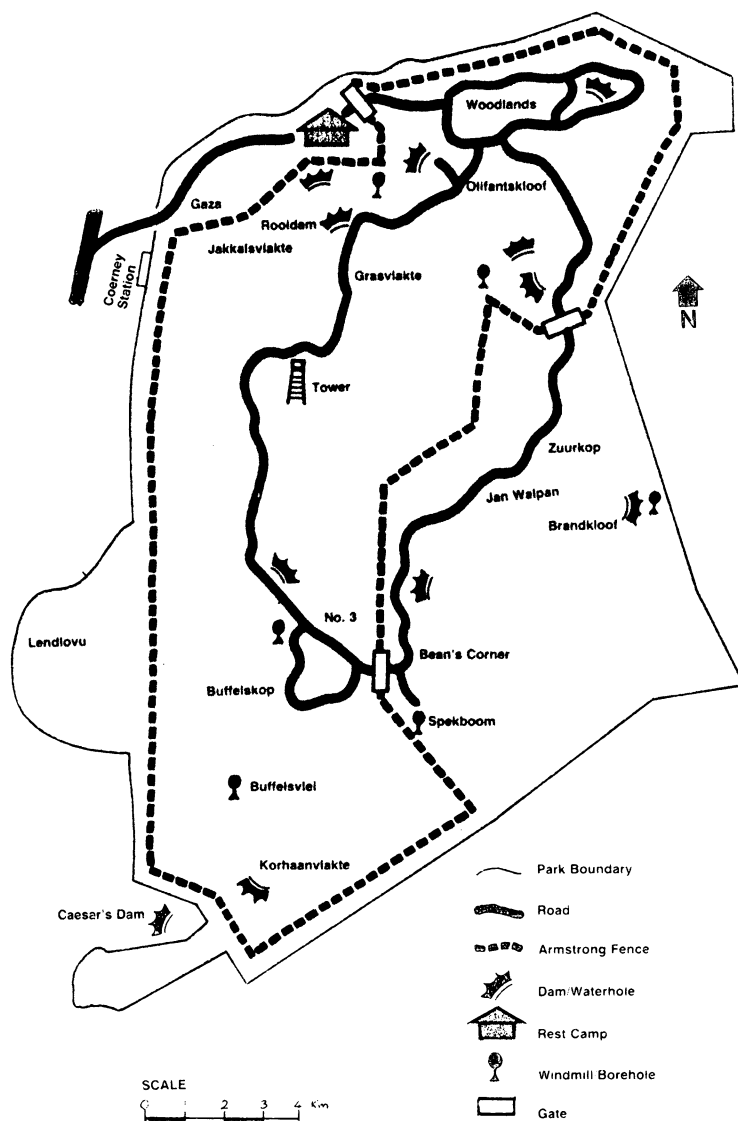


FIGURE 1: Map of the Addo Elephant National Park (Grobler & Hall-Martin 1982).

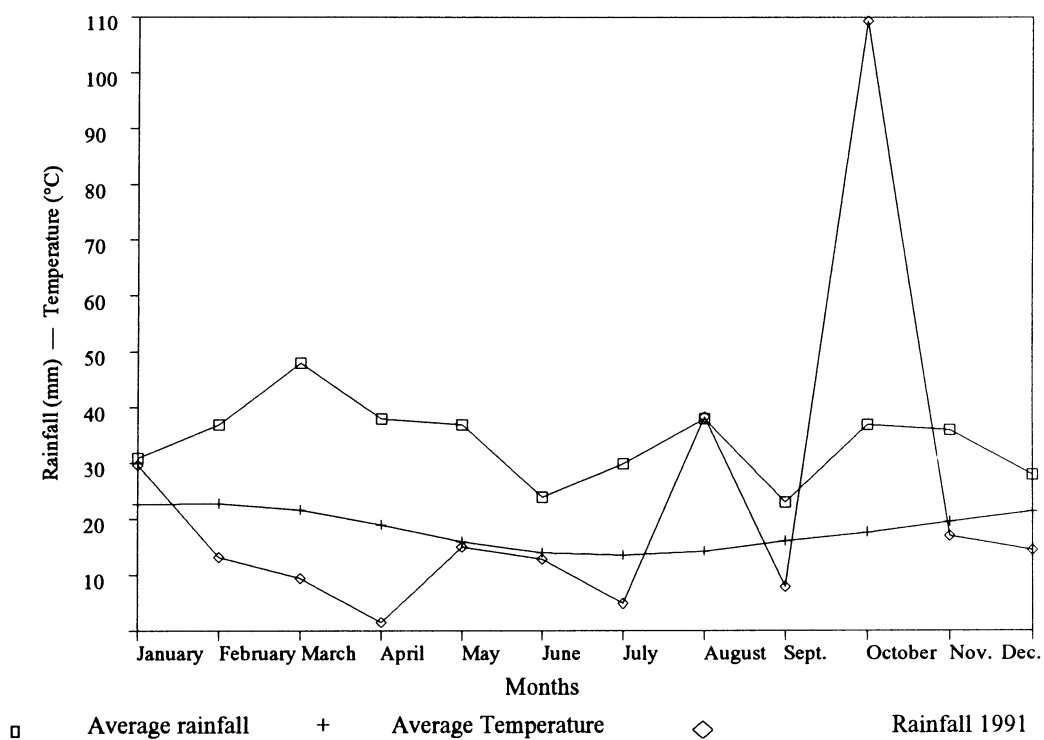


FIGURE 2: Monthly rainfall and average temperatures for the Addo Elephant National Park during 1991 and the average monthly rainfall for the last 30 years.

and on the mountain slopes the growth is more luxuriant and higher. It is characterised by dense, evergreen, semi-succulent shrub thickets (Grobler & Hall-Martin 1982).

The vegetation in the Park can be divided into five main types; Spekboomveld, Karoo Bushveld, Mixed Shrub and Grassveld, Bonteveld and Coastal Bush (see fig 3). Spekboomveld is the dominant vegetation type and covers more than 90% of the Park. It is made up of the succulent spekboom *Portulacaria affra*, the scarlet flowering Karoo boer-bean *Schoria affra*, and the thorny currant *Rhus longispina*. Spekboom is important to the browzers, due to its high moisture content, palatability and rapid regeneration rate.

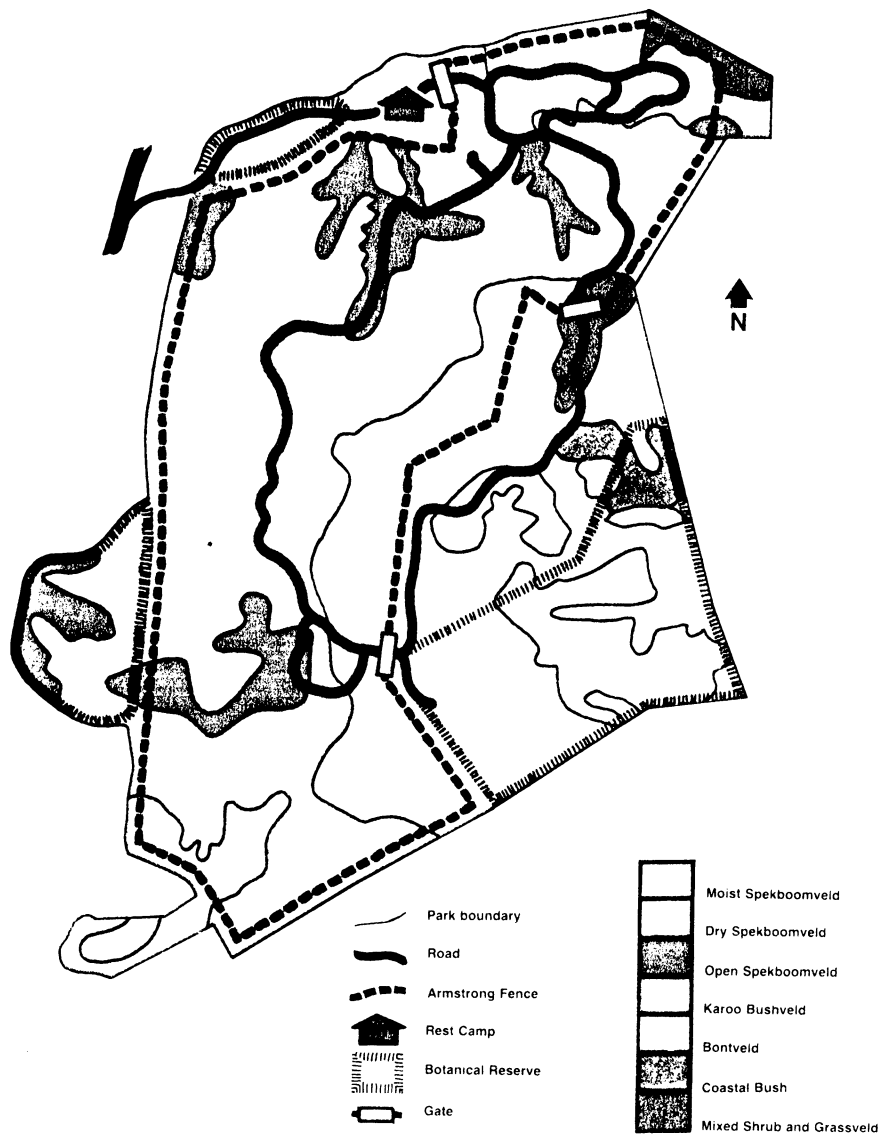


FIGURE 3: Major vegetation types and botanical reserves of the Addo Elephant National Park (Grobler & Hall-Martin 1982).

THE LARGE HERBIVORES

INTRODUCTION

There are a number of herbivore species present in the Park. The three main dung producers suitable for *C. bacchus*'s feeding and breeding habits are the elephant *Loxodonta africana* (Blumenbach), the black rhino *Diceros bicornis michealensis* (L.), and the cape buffalo *Syncerus caffer* (Sparrman).

ELEPHANT

Evidence suggests that elephant populations have shrunk dramatically since the late 1400's. Elephants were plentiful in the Cape Province but have now dwindled to those in the Knysna area and those protected in the Addo National Park see (fig 4a), (Skead 1980 cited in Smithers 1986). During the latest survey (June 1991) 172 elephants were counted in the Park.

The elephants' diet is determined by the habitat they are found in. In the thick evergreen bush of the Addo Park, elephants are mainly browsers, feeding on leaves, buds, twigs and branches. In other parts of southern Africa, such as the Kruger Park, grass makes up a good part of their diet (Hall-Martin 1990). The elephants that have moved into the grassland area called Alva, which was previously the farm Glenmore, have been seen grazing there.

Elephants are bulk feeders, needing up to 200 kg of food per day and can adapt their diet to what is seasonally available. The partly digested food takes approximately 24 hours to pass through the gut. The animal is not a ruminant and only minimal digestion takes place in the stomach. They prefer drinking clean water, sometimes up to 200 litres per day (Hall-Martin 1990).

Elephants have both positive and negative effects or influences on their surroundings. The negative effects include the destruction of their environment, or the changing of areas of woodland into grassland, favourable for some animals, but detrimental to others. The killing of trees also exposes the area to the destructive effects of borers and potential fire damage (Hall-Martin 1990).

A positive effect that elephants have on their surroundings is the dispersal and germination of seeds as some seeds will only germinate after passing through the elephant's gut. The dung itself is a rich seed bed for fungi and other plants, as well as a feeding ground for birds, termites and many species of beetles, including dung beetles. Another positive effect is that the Addo elephants have been instrumental in opening up the thick Addo bush, benefitting grazers like buffalo and mixed feeders like kudu (Hall-Martin 1990).

Elephants defecate between 10 and 17 times per day with a daily dung production of between 140 and 180 kg per animal (Bosman & Hall-Martin 1986). Considering the 172 elephants occurring in Addo, the daily dung production for the elephants in the Park must be in the range of 27 500 kg of dung per day, which works out to over 10 000 tonnes of elephant dung egested per annum in the Addo Elephant Park.

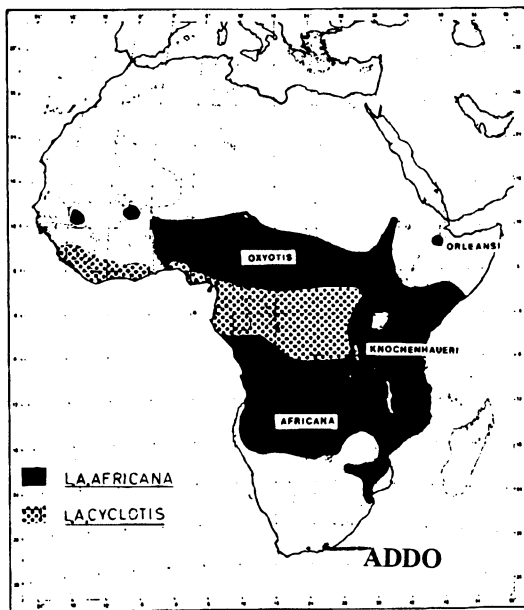


FIGURE 4a: The African distribution of the african elephant (Smithers 1986).

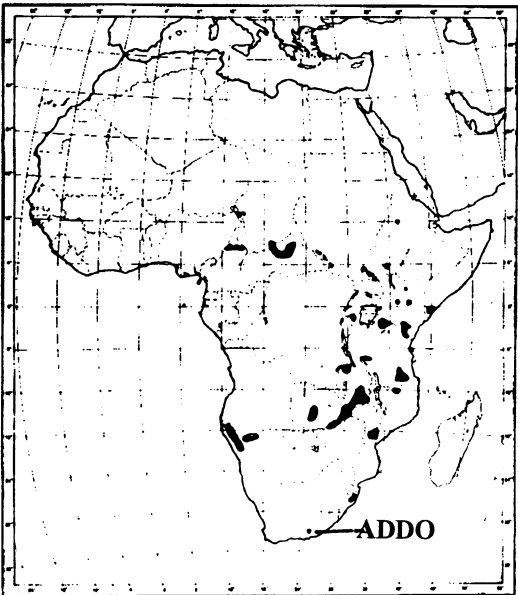


FIGURE 4b: The African distribution of the black rhino (Smithers 1986).

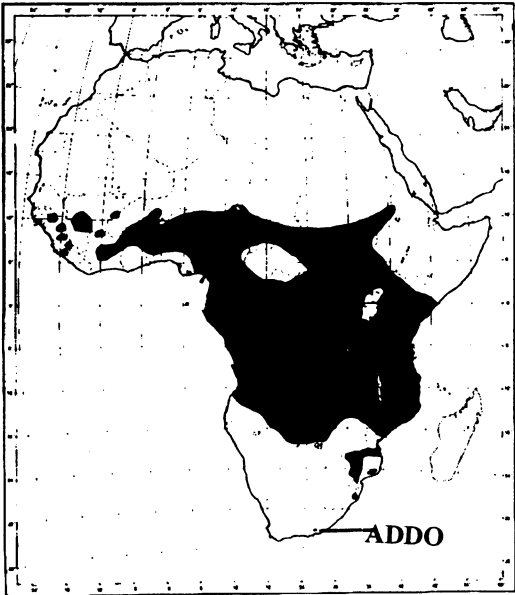


FIGURE 4c: The African distribution of the Cape buffalo (Smithers 1986).

RHINO

The black rhino was reintroduced into Addo from Kenya in 1961/1962 (see fig 4b). Unlike the grazing white rhino, the black rhino browsers on the leaves and stems of shrubs and trees (Grobler & Hall-Martin 1982). Black rhino are not territorial but use communal middens, probably to relate their presence in an area to other rhino. Bulls often scatter their dung using their hind legs in vigorous backward kicks. They prefer shrubby open areas with dense thickets for shelter and an availability of water which they will usually drink on a daily basis (Balfour & Balfour 1991). At the last aerial count there were 21 black rhino in the Park.

Buffalo being grazers are dependent on good rains but in times of drought the grasses suffer and therefore so do the buffalo numbers. The Addo buffalo are reportedly free of foot-and-mouth disease which is prevalent in many of the other African populations.

Historically distribution of buffalo extended along the south coast of the Republic of South Africa. Today, besides the Addo National park, and other parks such as the Andries Vosloo Kudu Reserve, where they are protected, they are absent from the Cape Province (see fig 4c) (Smithers 1986). The buffalo benefited from the opening of the grassland area, Alva where large numbers of buffalo can now be seen grazing.

GEOLOGY AND SOILS

The present topography of the Park can be attributed to a number of rising and falling sea levels over many millions of years. This resulted in periods of deposition followed by periods of exposure to weathering and erosion. These events can be traced back to the Cretaceous period more than 70 million years ago (Grobler & Hall-Martin 1982).

Zuurkop (see fig 5) forms the barrier between the white to greyish calcrete sands to the west and the reddish brown sands to the south and east. Water and wind erosion have exposed the sea bed deposits of the Cretaceous periods in parts of the Park. They are composed mainly of mudstone and sandstone. The mudstone weathers to brightly colored clay. Elsewhere these sediments are covered by a reddish brown soil.

There are patches of river terrace gravel outcrops distributed throughout the Woodlands area. These are evidence of former periods of much higher rainfall than is the case today (Grobler & Hall-Martin 1982).

2.2. GENERAL DUNG BEETLE BIOLOGY

Dung beetles can be divided into three groups or guilds. These are endo-, para- and telecoprids. Endocoprids excavate a chamber in the dung pad and form brood balls within this chamber. They are generally small and are suited to feeding and breeding within dung. Paracoprids construct

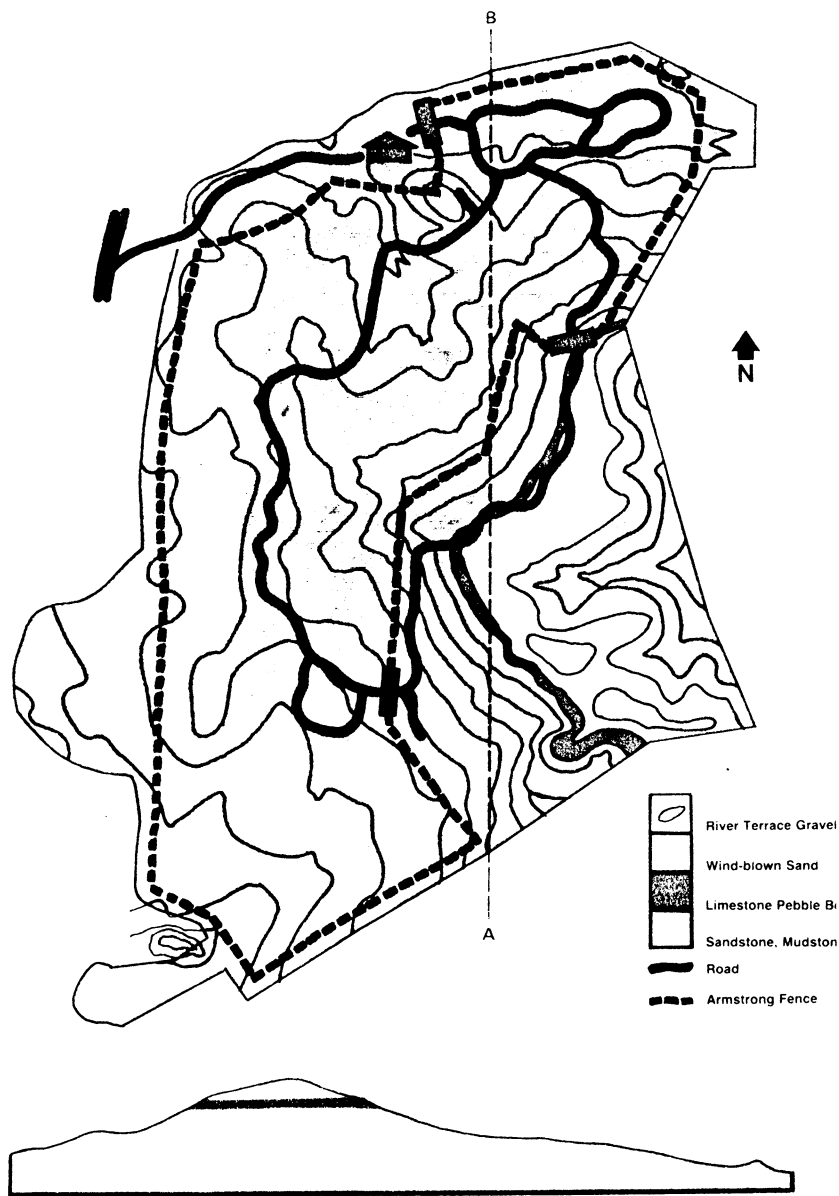


FIGURE 5: The geology of the Addo Elephant National Park (Grobler & Hall-Martin 1982).

chambers under or beside the dung source and are diggers or burrowers. Telecoprids cut off a portion of the dung which is shaped into a ball and rolled some distance before it is buried in the soil (Halffter & Matthews 1966).

Dung beetles are ecologically important as they redistribute the organic material littering the ground surface. They are also economically important in terms of the destruction of the juvenile stages of many vectors of diseases, as well as having an aesthetic value.

The subfamily Scarabaeinae is a highly successful and specialized group. Their evolutionary success can be attributed to a number of major adaptive features. These include the burying of a temporary food supply which is less susceptible to daily extremes underground than on the surface. The beetles also lessen the risk of being seen on the surface by predators and also reduce the risk of competition by feeding away from the dung source.

Enhanced musculo-skeletal features make scarabs excellent diggers, allowing entry into compact soil and the adept ability to mold and roll plastic masses. Other major adaptive features are a de-emphasis on courtship behaviour, increased male-female co-operation and a reduction in fecundity. Adaptations contributing to larval and pupal development within a closed space are modified mouthparts and digestive tract modifications. Most of the major adaptations are concerned with the adult stage which has historically been subjected to a harsher selective regime (Halffter & Edmonds 1982).

Although the tribe Scarabaeini was erected fairly recently by Péringuey (1901), it was more or less defined by Reiche (1842) in his classification of the subfamily Scarabaeinae, when he distinguished Ateuchilides from Coprides by the differences in the hind tibia; those of the latter being distally dilated, while the former has a slender tibia (Mostert & Scholtz 1986).

Ball rollers fall into two of the six subtribes, these being the Scarabaeina and the Canthonina.

GENERAL TELECOPRID BIOLOGY

Most members of the tribe Scarabaeini are telecoprids (for the exceptions see Halffter & Matthews (1966) and Halffter & Edmonds (1982). Ball making and rolling have received much detailed study in various parts of the world (Fabre 1897, Halffter & Matthews 1966 and Halffter & Edmonds 1982). The balls provide food for either the adult beetles (food ball) or the larva (brood ball). In both cases the ball is constructed at the food source and then rolled away and buried or placed intact in a suitable place. Either a single beetle or a male-female combination will roll a ball. The following sequence is always followed: approaching the dung, cutting, shaping, rolling, and burial of the ball (Matthews 1962 cited in Halffter & Matthews 1966).

Tactile perception, as well as the ability to manipulate plastic masses, seems to be highly developed in ball rolling beetles. Ambient temperature is often critical to most species and activity normally takes place between rather narrow limits (Halffter & Matthews 1966).

2.3. DESCRIPTION OF *CIRCELLIUM BACCHUS*

Circellium bacchus is a monospecific genus belonging to the family Scarabaeidae, subfamily Scarabaeinae, and the tribe Scarabaeini. Janssens (1938) and Ferreira (1968) treated it as belonging to the subtribe Scarabaeina, but Cambefort (1978) transferred it to the Canthonina. Mostert & Scholtz (1986) and Scholtz & Howden (1987) followed Cambefort (Scholtz & Coles 1991).

Adults are amongst the largest African dung beetles (22-47mm, $x = 36.3$, $n = 80$). The males are slightly larger than the females, but weigh slightly less (See table 1).

TABLE 1: Length, width and mass of live *Circellium bacchus* adults. Length and width in mm. Mass in grammes.

	LENGTH			WIDTH			MASS		
MALE	N= 40	X= 37.5	S= 5.3	N=37	X=26.6	S=5.3	N=81	X=6.0	S=2.0
FEMALE	N= 40	X= 35.1	S= 4.1	N=35	X=24.8	S=2.8	N=67	X=6.2	S=1.7
TOTAL	N= 80	X= 36.3		N=72	X=25.7		N=148	X=6.04	S=1.9

For larval descriptions see Scholtz & Coles (1991).

2.4. MARKING OF BEETLES

INTRODUCTION

The most important requirement of any marking technique is that it should not affect the behaviour or longevity of the animals. This should be tested thoroughly in the laboratory before field trials (Southwood 1978). Numerous marking methods are suggested by Southwood (1978). These methods must be carefully chosen to suit the type of animal and the life-style it leads. Conspicuous marks on the animal may destroy its camouflage and increase the risk of predation. The durability of the mark can also pose a problem (Southwood 1978). As the waxy outer layer of the insect's cuticle is slowly sloughed off, whatever is painted or stuck onto the beetle can come off over time. This can be seen in dung beetles which spend most of their time either embedded in dung, or under the ground.

The purpose of marking the beetles in this study was twofold. First, short-term marking was used to record the following: time spent at dung, distances walked in a day, the role of the sexes and numerous other behavioural activities. Second, beetles were marked and released for

observation over a longer period. This was to ascertain longevity and determine distances travelled over time.

METHODS AND MATERIALS

The method used for short-term observation involved painting a mark on the beetle's elytra with either "Tipp-Ex", a quick-drying liquid paper, or oil paints. It was not suitable for longer term studies because the paints rubbed off over time.

Beetles were marked for long-term observation, with a yellow heat-shrinking plastic sleeve (used by electricians). The sleeve was placed over the femur of the middle leg. Males were marked on the right leg and females on the left. In addition to the sleeve, bee-markers (small, coloured and numbered disks) were attached to the pronotum with quick-drying glue. Each colour-and number-coded beetle was described in terms of its sex, presence and absence of tarsi as well as any conspicuous dents or markings. This was to ascertain the "wear and tear" on the beetle over time. None of the marking techniques used had any visible detrimental effects on the beetles in the laboratory.

Five hundred beetles were marked using the second technique and released into the Park at different times and locations over a period of a year. Sightings of these beetles were noted along with the date and place of observation.

RESULTS AND DISCUSSION

The use of "Tipp-Ex" and oil paint was successful for short term marking. Depending on the moisture content of the dung and the burrowing intensity of the particular beetles, the "Tipp-Ex" rubbed off one day to a week after marking. Numerous data on the behavioural habits of the beetle were recorded using this method.

Only two beetles, marked for long-term observation, were sighted again after release. The first one was seen one day later, less than 10 metres from the release site. The second one was sighted by a tourist approximately a month after release in the same area in which it had been released. Future sightings of marked beetles will be recorded by the staff at Addo Elephant Park.

3. DISTRIBUTION

3.1. GENERAL INTRODUCTION

Spatial distribution of dung beetles is regionally strongly influenced by climate (Kirk & Ridsdill Smith 1986) and at local level habitat, including vegetation type are important (Davis 1990). Davis (1990) stated that "owing to the strong association with indigenous shrubland shown by some of the endemic species (dung beetles), the widespread clearance of indigenous vegetation is a cause for concern for survival of much of the insect fauna endemic to the south-western Cape." The same principle would therefore apply to any species closely associated with the indigenous flora of any particular area.

Another important contributor to the distribution of dung beetles is history. The Tertiary period saw Africa as the centre of a dramatic period of mammal radiation. From the middle Eocene, forest and bush gradually changed into grassland. Dung beetles specializing in the dung of forest browsers gave rise to scarabs adapted to utilize the dung of grazers. The older dung beetle groups retained their southern Gondwanaland distribution and in periods of contraction were forced into small relictual populations (Cambefort 1991).

Scholtz & Howden (1987) stated that all but one genus of the Canthonini, in Africa, have a typical relictual distribution. This distribution pattern may be as a result of inter alia, competition with the "modern rollers" (Scarabaeini, Gymnopleurini and Sisyphini) (Cambefort 1991).

Since no species exists in isolation, telecoprid ecology can be understood only in the context of the beetles association with co-inhabitants of the same region. One of the primary factors affecting abundance and distribution of coprophagous dung beetles, is the availability of suitable dung (Halfpter & Matthews 1966). The overall distribution of dung beetles is therefore greatly affected by the behaviour and movement of large herbivores. These herbivores often clump together for protection and this results in the clumping of dung. Clumping of dung may also be the result of territorial behaviour, as in rhinoceros which defecate on particular middens.

The fencing-off of large tracts of land for farming purposes has greatly decreased the land available for the migration of large herbivores and therefore game is now concentrated in reserves. This has had a major effect on the distribution of those dung beetles associated with large indigenous herbivores (Halfpter & Matthews 1966 and Tribe 1976).

3.2. DISTRIBUTION OF *CIRCELLIUMBACCHUS*.

Péringuey (1901) stated that *C. bacchus* was distributed throughout the Cape Colony in the areas of Knysna, George, Bredasdorp, Caledon and Paarl. Ferreira (1958) gave the localities as "between Uitenhage and Addo, Gamtoos, Gamtoos River and 20 miles NE of Humansdorp". In 1967 Ferreira gave another locality, that of Lumbo in Mocambique and in 1968 stated that *C. bacchus* previously covered large areas of the Cape, with its distribution extending north into the Transvaal.

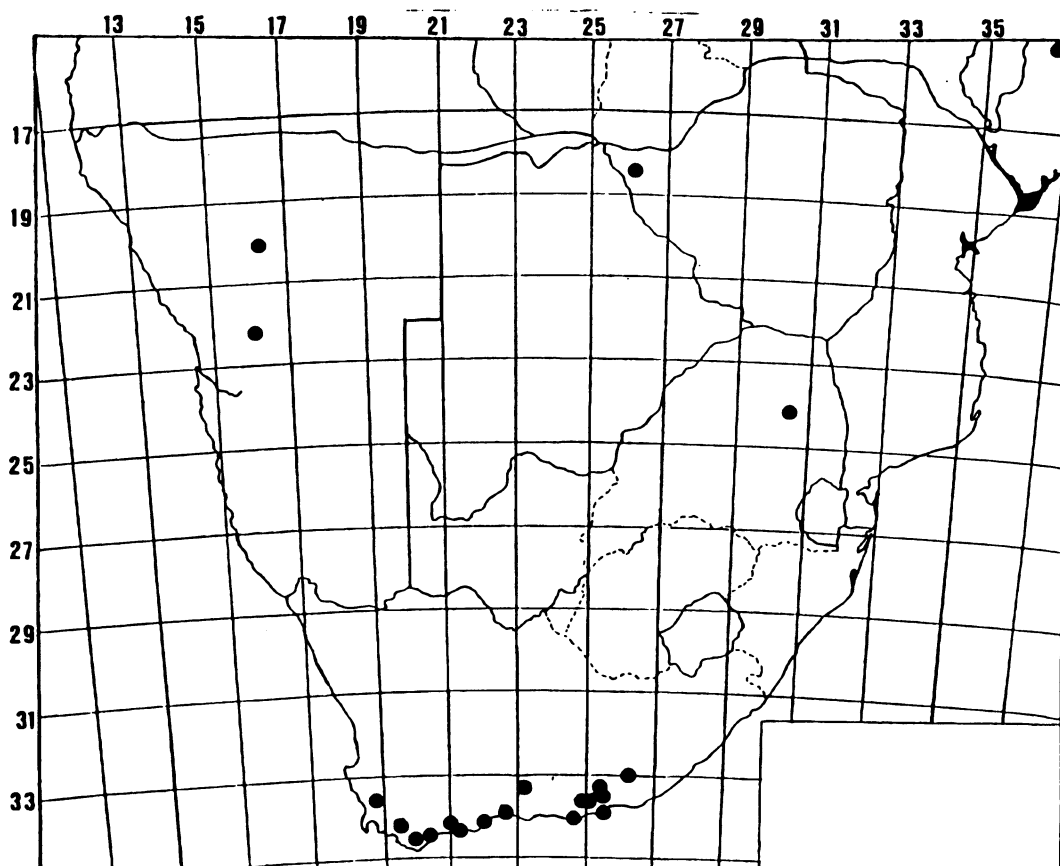


FIGURE 6a: Map showing the museum and literature records of *Circellium bacchus*.

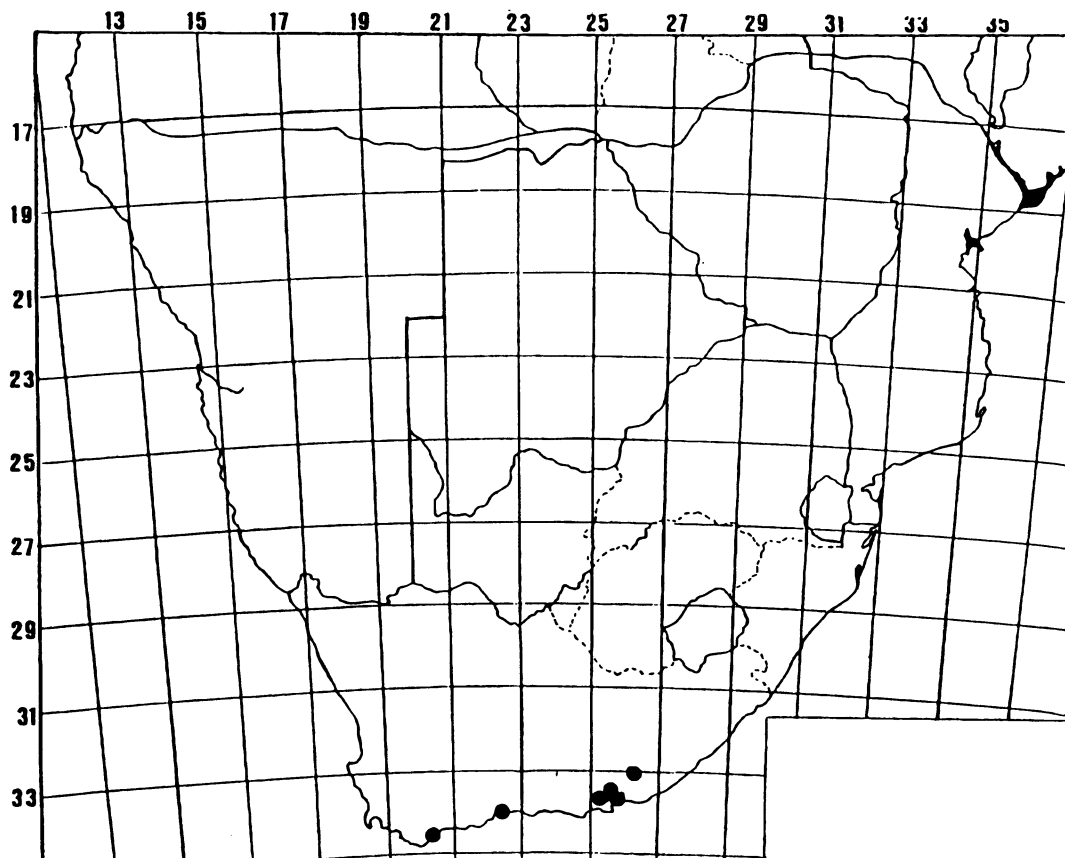


FIGURE 6b: Map showing the recent distribution of *Circellium bacchus*.

In addition to Ferreira's localities, specimens housed in the museums of Paris, London and South Africa were collected at various localities (see fig 6 a & b & table 2). Numerous specimens with incomplete locality data in South Africa, the "Cape" (*sensu latu*) and Kaffraria were also seen.

TABLE 2: localities of *Circellium bacchus* from museum specimens (see map).

CAPE PROVINCE (SOUTH AFRICA)

Albany	National Museum, Bloemfontein, South Africa; Transvaal Museum, Pretoria, South Africa.
Bedford District	Museum National D' Histoire Naturelle, Paris, France.
Brake Kloof Farm	The Natural History Museum, London England.
Brandfontein	National Collection of Insects (N.C.I.), Pretoria, South Africa.
Bredasdorp	N.C.I. Pretoria, South Africa.
De Hoop	N.C.I. Pretoria, South Africa.
George	Transvaal Museum, Pretoria, South Africa.
Grahamstown	The Natural History Museum, London, England.
Knysna	Transvaal Museum, Pretoria, South Africa. N.C.I. Pretoria, South Africa; National Museum, Bloemfontein, South Africa. National D' Histoire Naturelle, Paris, France.
Port Elizabeth	Museum National D' Histoire Naturelle, Paris France; The Natural History Museum, London England.
Riversdal	National Museum, Bloemfontein, South Africa.
Stilbaai	Transvaal Museum Pretoria, South Africa; National Museum, Bloemfontein, South Africa.
Uitenhage	National Museum Bloemfontein, South Africa; Transvaal Museum Pretoria, South Africa; N.C.I. Pretoria, South Africa.
Willowmore	Transvaal Museum, Pretoria, South Africa.

TRANSVAAL (SOUTH AFRICA)

Blyde River	National Museum, Bloemfontein, South Africa.
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NAMIBIA

Kombat	Transvaal Museum, Pretoria South Africa.
Windhoek	Transvaal Museum, Pretoria South Africa.

ZIMBABWE

Victoria Falls	Transvaal Museum, Pretoria, South Africa.
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The records suggest that the past/historical distribution of *C. bacchus* extended from the south western Cape, with Paarl the most western locality, throughout the Transvaal and into Mocambique. There are also isolated records for *C. bacchus* in Namibia and Zimbabwe. According to Acocks (1975) most of these areas were Forest and Subforest vegetation type in 1400 A.D. Thackery (pers. comm.) mentioned that in cooler periods between 18 and 25 thousand years ago, much of the south eastern Cape was covered in grassland, thus supporting large herds of grazers.

3.3. RECENT DISTRIBUTION

Tribe (1976) stated that *C. bacchus* is restricted to the Eastern Cape and that the only sizeable population occurs in the Addo Elephant National Park. While it seems as if the largest population does occur in the Addo National Park, there are a number of other localities where *C. bacchus* has recently been observed (see fig 6b & table 3).

TABLE 3: Recent distribution of *Circellium bacchus*.

Surnames in brackets indicate personal communication by observer.

SOUTH AND EASTERN CAPE PROVINCE OF SOUTH AFRICA

Addo village - (Braack) and (Coles);

Andries Vosloo Kudu Reserve near Grahamstown - (Fike) and (Coles);

Colchester - (Scholtz) and (Joubert);

De Hoop Nature Reserve, east of Bredasdorp - (Scholtz);

Farms surrounding A.E.N.P. Gorraah, van Straaten, Langbos - (Braack) and (Coles);

Kaboega - (Ardendorff) and (Mc Murtery);

Kirkwood - (Braack);

Puntjie, at the mouth of the Duiwenhoks river - (Braack);

Saasveld, near George - (Braack);

30 - 35 km from A.E.N.P. on road to Port Elizabeth - (Coles).

DISCUSSION

The localities shown in fig 6b & table 3 give the present distribution of *C. bacchus* along the Southern and Eastern Cape coastal regions. It is apparent that the recent distribution of this dung beetle is associated with areas where there is minimal disturbance to the natural vegetation. The species is indirectly afforded protection in two provincial nature reserves and a national park.

The lack of substantiated evidence concerning some localities from the Transvaal, Mocambique, Zimbabwe and Namibia, makes it impossible to give the historical distribution of this beetle with any certainty (refer to fig 6a & table 2). However, when comparing the past and present distribution records, it would seem that *C. bacchus*'s range has decreased drastically over the last 20 - 50 years. This is possibly due to man's decimation of large areas of natural vegetation and the herbivore populations that used to roam these areas. These herbivores were replaced, after the bush was cleared, by cattle, small livestock and fields of crops.

The opening up of the natural vegetation may have introduced large numbers of flighted competing species of dung beetles into the area. It is possible that *C. bacchus* beetles have been forced, through competition from generalist species, into the small pockets of pristine, dense and undisturbed vegetation. Here *C. bacchus* would have been isolated from flighted scarabs which may have had difficulty flying and navigating in the dense vegetation. These densely vegetated areas would also provide shelter and protection to various herbivores, thus ensuring abundant dung for the beetles. The importance of dense vegetation can be seen from the absence of *C. bacchus* on large cleared areas of farms adjoining the A.E.N.P., while on undisturbed farms *C. bacchus* is still found.

Other reasons for the association of *C. bacchus* with dense natural vegetation may be protection from its predators and the need to escape from overheating by tunnelling into the humus rich areas under the vegetation (Braack pers. comm.). *C. bacchus*, being ectothermic and flightless, uses this vegetation, as it does piles of coarse dung, apparently to escape extremes in temperature and thus avoids direct sunlight in summer and cold in winter. Beetles which are unable to escape intense heat die from overheating.

Climate may also be important in determining the present range of the beetle. *C. bacchus* are found mainly in arid regions with low rainfall. Although beetle activity is governed by precipitation, low rainfall may prevent the abundance of other scarabs adapted to regions of higher rainfall. The Addo area has relatively low rainfall, with an average of 407 mm annually and great fluctuations in the monthly and annual rainfall. Warm and arid regions would exclude winged dung scarab species as large amounts of moisture are lost in flight. Winged scarabs are also excluded from the cool, wet forest localities. Keeping an optimum thoracic temperature for flight in these areas would mean raising and maintaining the beetles temperature approximately 20 - 25 degrees above ambient.

Many scarab species also need an initial heavy downpour to release the beetles from the soil (Halfpter & Matthews 1966). *C. bacchus* is adapted to a fairly sandy region which places more restraints on its distribution.

3.4 THE DISTRIBUTION WITHIN THE PARK

RESULTS

Within the Park, *C. bacchus* is more common in certain vegetation types than in others. The beetles tend to favour Moist and Dry Spekboomveld above other vegetation types (refer to fig 3). Bonteveld, Coastal Bush and Mixed Shrub and grassveld vegetation types are slightly more densely populated by the beetle than Open Spekboomveld and Karoo Bushveld. Few are present in the antelope and rhino camp areas (refer to fig 3) which are highly disturbed, although elephant and buffalo are often found there.

During the study, elephants moved around extensively in the Park. Dung that was dropped in densely vegetated areas was worked quickly by the beetles while dung dropped in large disturbed areas was hardly utilized.

The Botanical Reserve is approximately 800 hectares of land which was fenced off in 1985 to exclude large mammals. I saw 34 beetles on a route of approximately 5 km in this area after rains. The only game in this area are a few bushbuck, grey duiker and small kudu that are able to get in and out of the elephant-proof fence.

DISCUSSION

The distribution of *C. bacchus* within the park is patchy. There is a distinct preference for areas of denser vegetation and an avoidance of large open areas and disturbed bush around popular water holes.

Braack (pers. comm.) observed high densities of the beetle on Zuurkop (refer to fig 5) which he attributed to the drift sand found there as well as to the speculated higher rainfall than that falling in the lower-lying regions, as well as to the fact that this is the traditional feeding ground of buffalo. He also mentions that he observed the greatest numbers of other scarab species in this area.

In my opinion this would lead to increased competition in this area. *C. bacchus* being a weak competitor due to its flightlessness, would be displaced back to denser bush. My results show the concentration of *C. bacchus* in that area to be lower than areas with denser vegetation.

The fact that beetles permanently inhabit the Botanical Reserve, proves that a population can survive on the faeces of small antelope and that large herbivores are not essential to maintain a population of *C. bacchus*. It must, however, be stressed that there were always far fewer beetles in the Botanical area than were active in the elephant camp where dung was abundant.

To conclude; the densest populations of the beetle in the Park are found where the vegetation is dense, the dung abundant and the soil soft and sandy.

3.5. ANDRIES VOSLOO KUDU RESERVE

There were records (Fike pers. comm.) that small numbers of *C. bacchus* occurred naturally in the Andries Vosloo Kudu Reserve (AVKR) prior to 1988. On 15 April 1988 approximately 200 *C. bacchus* beetles were released into the AVKR. A second reintroduction of 500 beetles was done on 24 November 1988 (D. Joubert pers. comm.). They were released onto black rhino middens in the eastern section of the AVKR to supplement a failing population of the beetle (Fike pers. comm.). The beetles had been randomly collected from the Addo Elephant Park the previous day. As no external method of sexing was known at that time, it was hoped that a representative proportion of both sexes had been captured.

The AVKR (33°20 S, 26°40 E) is situated north-east and approximately 35 km by road from Grahamstown. Since being proclaimed in 1973, its size has increased considerably with the addition of several adjoining farms now known as the Sam Knott Nature Reserve. Bordering on these reserves is the L.L. Sebe Game Reserve in Ciskei. The total conservation area represented by these three reserves exceeds 45 000 ha.

Rainfall is low with an average of approximately 500 mm per annum. The vegetation (Fish River Valley Bushveld - Acocks 1975) consists mainly of very dense, semi-succulent, thorny scrub about 2 m high, although there are patches of forest, Karoo scrub and open grassland. A number of large herbivores, including black rhino and buffalo have been re-introduced (Fike pers. comm.).

On the 27/10/1991, almost three years after the release of the beetles, I visited the reserve to monitor the beetle population. Conditions appeared perfect for beetle activity, as 5mm of rain had fallen the previous night. Temperatures fluctuated between 22 - 26 °C.

We searched the Park for signs of the beetles, concentrating our efforts in the areas frequented by rhino and buffalo. Three beetles, two female and one male, were seen during the morning. One of the females was teneral, proving that although the beetle numbers in the Park appear low, they are breeding. Game guards keep a record of beetles seen, which yield fairly regular sightings, but low numbers.

4. FEEDING

4.1. GENERAL INTRODUCTION

The explosive radiation of mammals and the subsequent abundance of protein-rich dung was probably responsible for the evolution of coprophagy from saprophagy. Mammalian dung is not very different in texture and composition from rich humus and the transition was made from one food source to another (Cambefort 1991).

Adult dung scarabs have a fairly lengthy period of feeding after their emergence from the nest. This is termed maturation feeding or "Reifungsfrass". This is in contrast to the many other types of insects that do most of their feeding in the immature stages (Halffter & Matthews 1966). Larval feeding takes place within the food source which is supplied by one or both of the parents. The larvae have strong crushing and cutting mouthparts, enabling them to ingest compact and solid dung (Halffter & Matthews 1966).

Feeding in dung scarabs can be divided into various stages. The beetles must locate the dung, and then, depending on a number of internal and external factors, either feed at the pat or construct and roll away a food ball. In the tribe Scarabaeini nearly every species feeds at the dung source either before or during the ball making process (Halffter & Matthews 1966). Beetles spend most of the time that they are on the dung-pad feeding, with their mouthparts buried in the dung.

METHODS AND MATERIALS

Most of the following data were obtained by observation in the field and the laboratory. Notes were taken describing the actions of the beetles while approaching, feeding and leaving various types of dung. Time of arrival and departure of beetles, as well as duration of feeding were noted. Times taken to roll food balls of different dung types and consistencies were measured.

Ambient temperatures and relative humidities were also recorded using a Novasina electronic thermohygrometer. Beetle and ball sizes were measured in millimetres with a Mitutoyo calliper.

DUNG TYPES UTILIZED FOR FEEDING

Adult *Circellium bacchus* beetles aggregated around the dung of many herbivore or omnivore species. Elephant, rhino and buffalo dung were most commonly utilized, although *C. bacchus* was observed feeding on antelope, monkey, human, ostrich and hare faeces if sufficiently moist. *C. bacchus* was also seen feeding on the stomach contents flowing from the mouth of a dead eland, as well as the stomach contents of a dead elephant.

LOCATING DUNG

The distances walked by the beetle to a food source ranged from a few millimetres in the case where fresh dung was deposited close by an individual, to over 100 m. In all cases observed the beetles approached the dung upwind. Beetles that were upwind from the dung, no matter how close to it, never found it.

C. bacchus locate and approach the dung, but it is not known whether they cruise continuously in search of dung or wait until they smell it. However, in peak activity periods generally after rain, I found hundreds of them wandering around in what seemed to be an aimless manner.

The direction and force of the wind which spreads the dung's odour is important for locating the dung pad. If *C. bacchus* loses the scent it circles around, antennae extended, until it picks it up again, or loses it completely and goes off in a new direction.

FACTORS AFFECTING FEEDING BEHAVIOUR

Feeding was observed on fresh dung at ambient temperatures between 14°C-38°C. Feeding began at temperatures as low as 14 °C in the morning. As the ambient temperature rose, the number of beetles at the dung increased (see fig 7). Food balls were constructed as the temperatures increased towards late morning and again when it cooled down toward evening.

After arriving at the dung, *C. bacchus* either burrowed directly into or under the dung mass or immediately started to carve out a ball from the dung. The type of behaviour depended on the ambient temperature, the burrowing occurring in response to lower temperatures and the ball-construction as a result of higher temperature. Other factors which played a role in the behaviour exhibited were the type of dung involved, the state of the dung as well as the sex and maturity of the beetle. Teneral adults were never found feeding at the source but always constructed a food ball.

The degree of plasticity of the dung, which in turn is dependent on the coarseness rating (refer to table 12) as well as its moistness, affected the eventual feeding behaviour of the beetle. Feeding on elephant dung occurred most often in the morning, while the ambient relative humidity was high, the temperatures mild and the moisture content of the dung at its highest (see fig 8). Buffalo dung was colonized later in the day (see fig 9), when the moisture in the dung had evaporated and the dung was more pliable and easily rolled away as food or brood balls. It may be that different dung plasticity requirements cause scarabs to come to the dung either as soon as it has been deposited or a while later when it has lost some of its liquid content and is in a more pasty state. This could be one of the factors which explains dung preferences amongst different scarab species, as herbivore dung varies in coarseness and changes in moisture content over time after defecation.

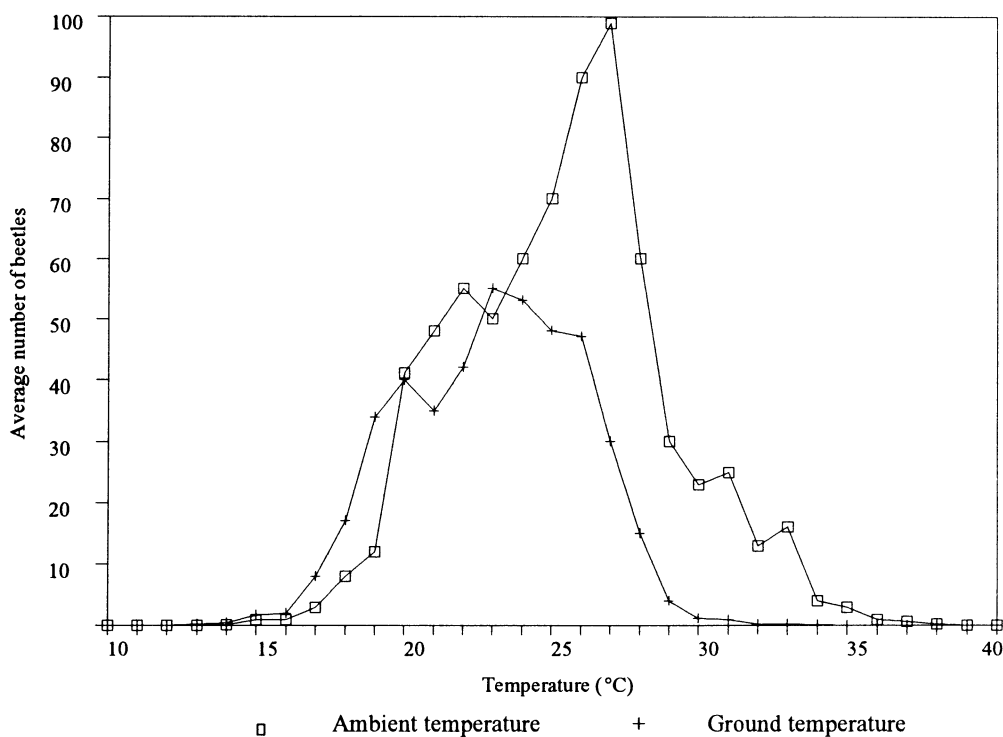


FIGURE 7: Trends in numbers of *Circellium bacchus* feeding on dung, correlated against ambient and ground surface temperatures. (Based on year round observations under diverse conditions).

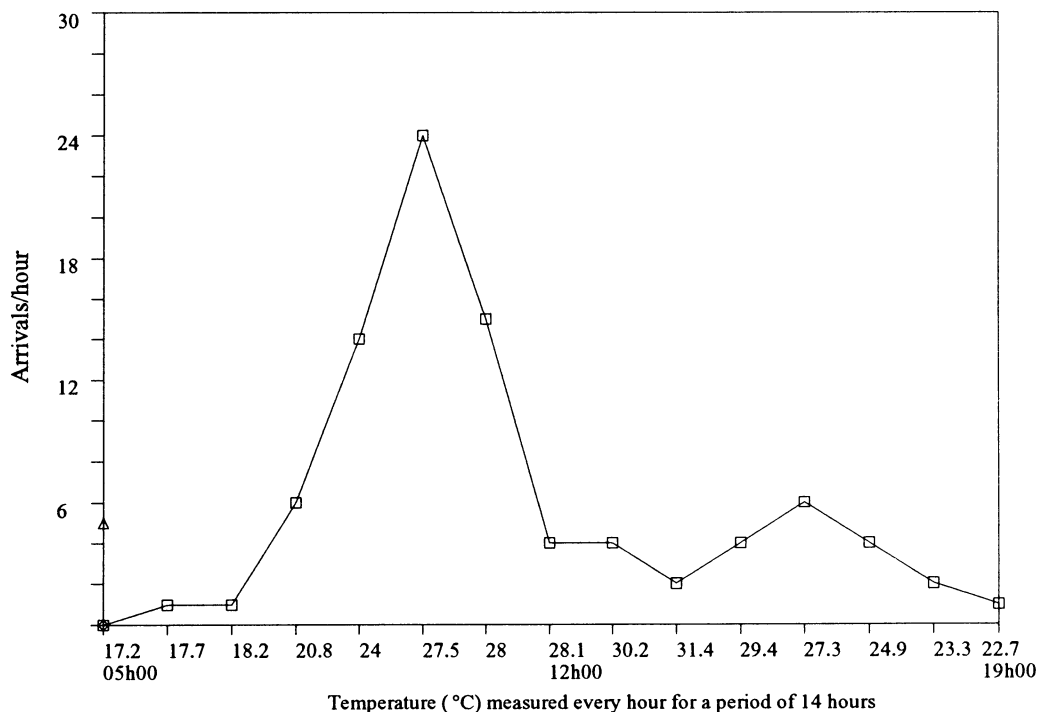


FIGURE 8: The arrival of *Circellium bacchus* at elephant dung per hour - temperature indicated hourly.

4.2. FEEDING AT THE DUNG PAD

Feeding at the pad is the most common feeding method amongst *C. bacchus*. The highest incidence of feeding occurred between 22–28°C, (fig 9). Feeding took place at various times during the day and night. Beetles that were found on or in piles of dung at temperatures below approximately 14°C and above approximately 32°C probably arrived at the dung at more moderate temperatures. When the ambient temperature exceeded 35°C there was little or no feeding observed.

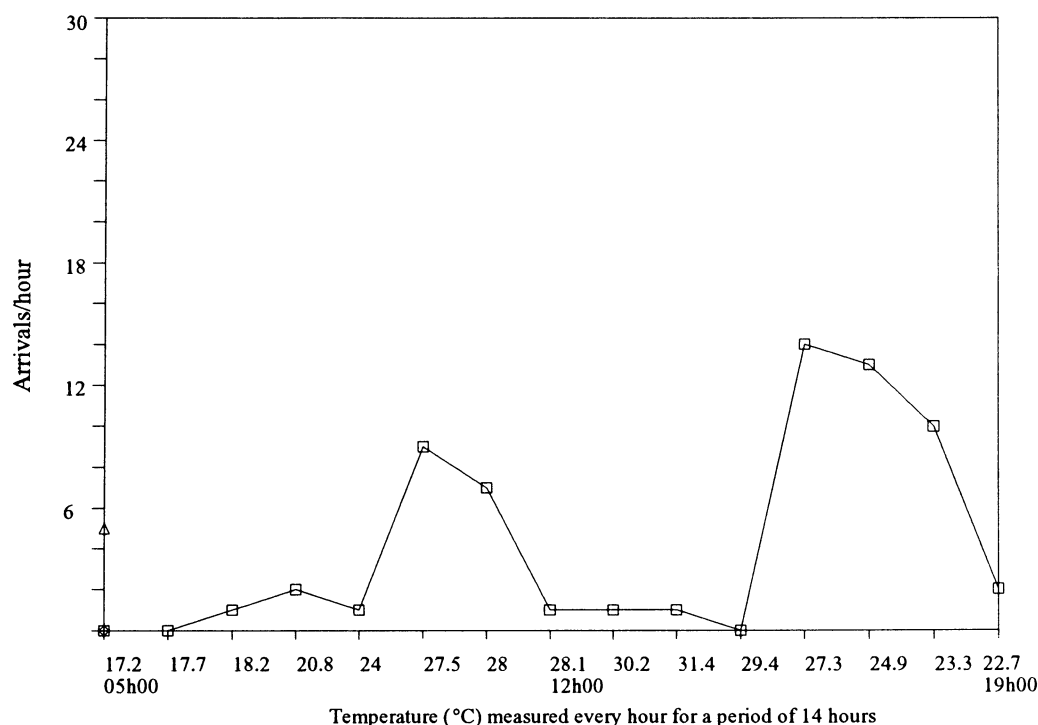


FIGURE 9: The arrival of *Circellium bacchus* at buffalo dung per hour
- temperature indicated hourly.

C. bacchus reduced and flattened a pile of elephant dung within a few days. This is to the beetles' detriment as flattening the pile causes it to dry out more quickly. The beetles fed on the outside of the dung when temperatures were cool to warm (18–26°C). As temperatures rose, the outside of the dung dried out and the beetles either moved inside the dung to continue feeding or left the pad in search of shelter. They returned to the dung when the temperature dropped and the relative humidity increased. When feeding on fresh dung on a warm to hot day, the beetles fed on the shaded side of the dung. They were occasionally observed on the same dung pad for longer than 24 hours.

Buffalo and cattle dung were fed on before a crust formed. The beetles seldom tunnelled into the dung and generally left the pad when it got too warm or a hard crust formed. Beetles that did tunnel, got covered with dung which dried and stuck to their bodies. Beetles that were only

supplied with buffalo or cattle dung in the laboratory sometimes died from starvation because their mouthparts stuck together.

After good rains and during cool to warm periods (18-26°C) large piles of elephant dung were often covered by up to 200 beetles. The beetles lay on top of one ^{another} with only their mouthparts in contact with the dung. Although pads were covered with beetles, aggression was only observed when a food or brood ball was constructed.

4.3. FEEDING AWAY FROM THE DUNG PAD

The second feeding method is the construction of a food ball at the dung pad and its transport to a suitable site. It is rolled away from the dung and either buried or consumed on the surface, usually in the shade.

Food balls, constructed from a variety of dung types, were rolled by both males and females. Their sizes varied between 16,0 and 33,0 mm (mean = 25.3; n = 42; S = 4.5 mm) and weighed between 0.9 and 18,0 g dry (mean 5.2 g; n = 25; s = 3.8). The food ball was fashioned in a relatively short time, between 3,0 and 15,0 minutes (mean 5.7 minutes; n = 30) depending on the temperature and type of dung. Food balls were constructed quickest at ambient temperatures between 24 and 28 °C.

Food balls were constructed throughout the year, with peaks occurring in the warmer, wetter months, when most beetles are active (see fig 10). Very little food ball construction was seen in the colder, drier winter months. Although the beetles usually excavated under the food ball, allowing it to slowly sink below the surface, I did observe beetles pulling chunks of dung backwards into already-made holes. They were also observed rolling irregular pieces of dry buffalo dung.

Food balls were not always buried but were sometimes fed on in a sheltered area such as under a shady bush. When they were buried it was between 20 and 100 mm below the surface but occasionally down to 300 mm. The beetles remained underground with a food ball for 7.6 days on average (n = 20), with a longest stay of 14 days and a shortest stay of 3 days. This does not take into account occasions when the food ball was abandoned.

4.4. ADVANTAGES AND DISADVANTAGES OF A FOOD BALL

The advantages of constructing a food ball are debatable. Beetles leave the dung pile where there is usually little competition and exchange this reliable supply of food for a perilous journey with an uncertain outcome. There must be a trade-off between the benefits at the food source and the energetic hardships and uncertainties experienced away from it. The general advantages and disadvantages of ball rolling *vs* feeding at the dung pad are dealt with in detail by Halffter & Matthews (1966).

Advantages relevant to *C. bacchus* in this scenario, appear to be escape in space and time from adverse climatic conditions and keeping the food ball moist by burying it under the ground. Disadvantages include the energetic expenditure involved in rolling, and competition for the ball

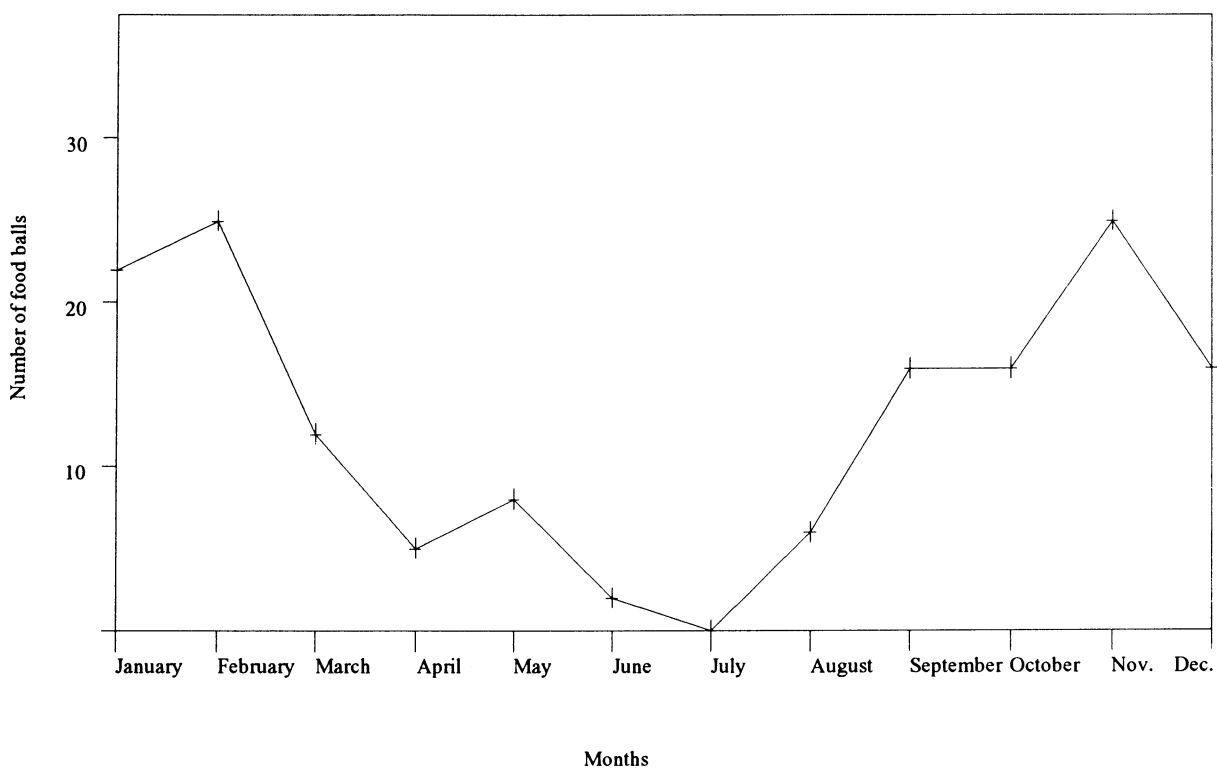


FIGURE10: The number of *Circellium bacchus* food balls being rolled, observed per month during 1991.

by conspecifics. Predation was seldom observed and therefore ignored in this discussion. This leads me to believe that rolling the ball and therefore experiencing biotic hardships (competition) are safer than experiencing the abiotic hardships of desiccation and exposure to the elements, associated with staying at the food source.

Tenerals (recently-emerged adults with incompletely sclerotised cuticles), were not observed feeding at a dung pad and were only found to feed on food balls. They also seemed to be the more aggressive when protecting their food ball than mature adults. Their dependence on food balls and their aggression could be due to the fact that they are less sclerotized and possibly more susceptible to the elements than are mature adults. To escape adverse conditions, teneral spend as little time as possible above ground and only venture out to construct a food ball. This is substantiated by the fact that very few teneral were seen.

4.5. DIFFERENCES BETWEEN FOOD AND BROOD BALLS

Halffter & Matthews (1966) stated that beetles which roll balls for breeding employ the same behavioural patterns as those which roll food balls, except that a food ball is rolled by an individual, while a brood ball is usually rolled by a pair. They continue by saying that there is no difference between the initial structures of a brood and food ball, nor in the manner in which they are formed at the source.

Observers of some European *Gymnopleurus*, *Sisyphus* and *Scarabaeus* spp. have not found any difference in size, shape or consistency between food and brood balls (Halffter & Matthews 1966). Halffter (1961) cited in Halffter & Matthews (1966) observed individuals of *Canthon indigaceus chevrolati* rolling balls of two different types. Some were smooth and regular in shape 10 - 11 mm in diameter, while the others were irregular, roughly made and varied from 12-17 mm in diameter. Halffter & Matthews (1966) speculate that these correspond to brood balls and food balls respectively. Matthews (1963) found that in *Canthon pilularius* (L.) brood balls were much more carefully made, more regularly spherical and smoother surfaced than food balls.

In *C. bacchus* there are two important differences between food and brood balls; the size of the ball and the type of dung used. Food balls are much smaller than brood balls (see chapter 4.3); and are constructed from various types of dung (coarse or smooth), although mainly from elephant dung (coarse). The overwhelming majority of brood balls are constructed from the smoother buffalo dung, but after rains or when the dung is very moist, *C. bacchus* will use elephant, rhino or antelope dung for brood purposes. Food balls are rolled by both sexes of mature or immature adults while brood balls are only rolled by mature females.

C. bacchus therefore not only has a size distinction with regard to their two kinds of balls, but a different preference in ball construction materials.

5. BREEDING

5.1. GENERAL INTRODUCTION

Intensive competition amongst dung scarab species to secure and make effective use of dung, an ephemeral food-source, both for themselves and their offspring, has led to a variety of breeding strategies (Halffter & Edmonds 1982). In the ball-rollers, although there are many subtle differences and variations among the species, the main processes remain the same. These are: construction of the brood ball, recognition of the sexes, overland transport, burial, copulation, some form of brood care, larval and pupal development and adult emergence.

METHODS AND MATERIALS

Methods used to record breeding and brooding data are similar to those used in obtaining feeding data. Data concerning all aspects of breeding were recorded at different times, temperatures and relative humidities.

Temperature and relative humidities were measured with a Novasina electronic hygrometer and ball-rolling distances and ball sizes with a tape measure and a Mitutoyo calliper respectively.

Life cycle data were obtained from colonies of captive beetles. They were kept in glass terraria measuring 600 x 300 x 300 mm which were approximately three-quarters filled with fine sand. The sand was moistened weekly. Pairs of beetles found rolling balls were removed with the ball and placed in breeding containers. Female beetles found rolling balls in the field were also placed with their balls in these containers to breed.

Nests were excavated and balls were removed and opened periodically. The number of days since burial, as well as life cycle stages, were noted. The larvae needed for study were killed in PAAD (1: Paraffin, 8: Isopropyl alcohol, 2: Glacial Acetic acid & 1: Dioxane) and preserved in 96% ethyl alcohol. They were subsequently described and illustrated.

The beetles were sexed by examining the abdominal sternites. The seventh sternite is approximately twice the width of the sixth in females, while they are of a similar width in males (see fig 11). In males the anterior margin of the pygidium is pointed medially and intrudes into the penultimate segment.

Accurate sexing was assured by regular examination and dissection of dead beetles found along the roads. There was 100 % accuracy in all the beetles sexed in this way.

5.2. CONSTRUCTION OF THE BROOD BALL

In the Park *C. bacchus* constructed brood balls, from (in order of preference) buffalo, elephant, and rhino dung. Bushbuck, kudu, Cape hare and ostrich dung, if sufficiently moist, was also occasionally used. Cattle are the major source of dung for beetles outside the Park.

Moist antelope dung-pellets were sometimes scraped together to form a ball. The half-formed ball was not left behind while fetching new material, but was dragged along as described in *Scarabaeus sacer* (L.) by Puzanova-Malysheva (1956) cited in Halffter & Matthews (1966).

Halffter & Matthews (1966) stated that no canthonine species has been observed doing this.

When the adult female is ready for breeding and the climatic conditions are favourable and she is also in possession of an adequate amount of suitable dung, she will initiate brood ball construction. This process was observed during both the day and at night. Comignan (1928) cited in Halffter & Matthews (1966) investigated the stimuli present which induced ball-making in scarabs and concluded that a combination of olfactory and/or tactile stimuli is necessary once the ambient (or the dung) temperature is at a required level.

The diameter of brood balls constructed by *C. bacchus* ranged from 43.52 - 64.2 mm (mean = 53.08 mm; n = 50; s = 5.54). The dry mass ranged from 22.0 - 85.0 g (mean 41.16 g; n = 40; s = 14.3) depending on the type of dung and how compact the ball was. Generally brood balls were close to spherical, although occasionally with very wet buffalo or cattle dung, balls became cylindrical or flat during rolling. They were buried nevertheless.

Construction of the ball is divided into cutting and shaping phases. The clypeus and fore tibiae were used extensively while cutting the dung mass into a manageable size and the middle and hind legs shaped it. The middle and hind legs gauged the size of the dung (thus smaller beetles ultimately give rise to smaller balls and possibly to smaller offspring).

The crude dung mass was shaped and patted into a sphere, usually with the fore tibiae. The ball was most often completed without the help of the male. The male occasionally fed on the incomplete ball. Ball-making took 47 minutes on average (n = 15; s = 20 min) and the patting process another 16 minutes (n = 15; s = 6.1 min). Temperature greatly influenced speed of construction. Balls constructed at temperatures in the high teens and low twenties took two to three times longer than those in the higher twenties.

The construction of the brood ball took place on the dung pad and the patting process 10-100 mm away. When the dung ball became distinguishable from the mass from which it was hewn, it also became attractive to other females who tried to wrest it from the original female. Three females were observed co-operating and co-constructing one ball. This co-operation came to an abrupt and violent end at the completion of the ball as the females challenged each other for the completed product.

Heymons & von Lengerken (1929) cited in Halffter & Matthews (1966) gave the lower limit for ball-making in *Scarabaeus semipunctatus* (Fabricius) as 21 °C and the optimal range between 25 and 30°C. *C. bacchus* were observed constructing brood balls between 16°C and 32°C. The optimal range in ground temperature was between 22 and 29 °C and in ambient temperature between 20 and 27°C (see fig 12).

Along with ambient temperature, substrate temperature is an important factor in brood ball construction, as reported by Halffter & Matthews (1966) for *Canthon indigaceus chevrolati* (Harold). While the temperature was between 28-34 °C, the beetles fed inside the dung but did not initiate ball-making. When the temperature exceeded 34 °C, after receiving intermittent sunshine, ball-making started. Actual substrate temperature may also be important for *C. bacchus*, as they are flightless and subjected to temperatures at ground level which in most cases, during the day, are a few degrees higher than ambient temperature.

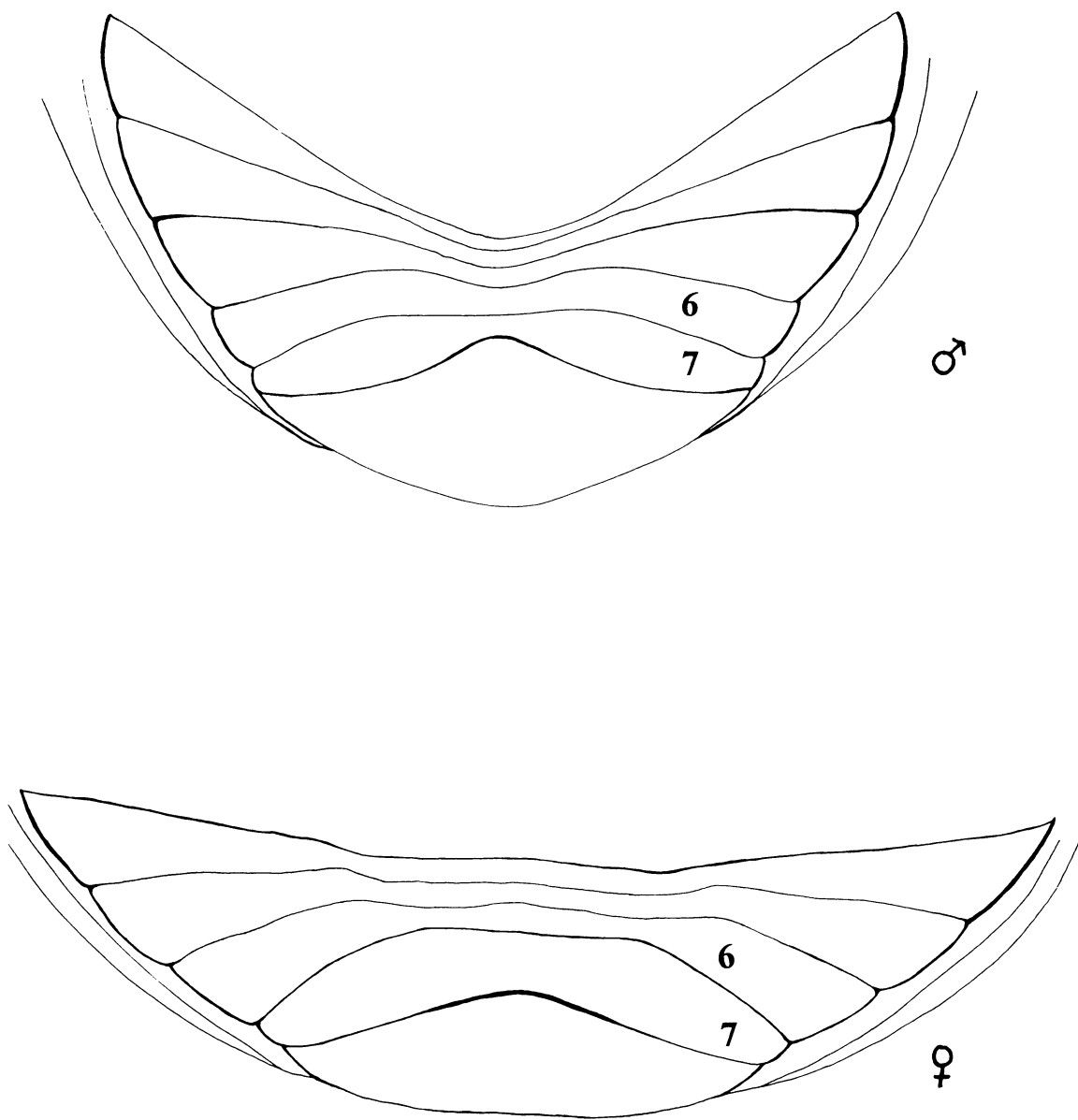


FIGURE 11: Ventral view of the abdomen of male and female *Cirrellium bacchus* showing last segments.

On warm nights in the laboratory, brood ball construction and rolling continued throughout the night.

Pairs of beetles found rolling balls in the field were taken to the laboratory and supplied with dung. These beetles started to roll brood balls more readily than those that were merely sexed and placed together in the container. It may be that the latter females were not receptive for breeding.

5.3. ENCOUNTER AND RECOGNITION OF THE SEXES

The dung pat was not only where *C. bacchus* adults aggregated for feeding, it was also the meeting place of the sexes. Recognition in *C. bacchus*, as in other ball-rollers, was effected by head to head contact. This recognition in certain scarabs is the product of contact between the antennae and palpi and is therefore chemotactic in nature (Halffter & Matthews 1966).

No characteristic stance that would seem to indicate long-range pheromone emission, was observed. The smell of fresh dung seemed to be all that was needed to attract beetles. If a beetle was recognised as a member of the opposite sex it was almost always accepted and the pair carried out their rolling and burial rituals.

5.4. OVERLAND TRANSPORT

INTRODUCTION

The active partner in the process of ball-rolling is that beetle which at least initiates the making of the ball (sometimes making it entirely), rolls it in the backwards pushing position and buries it. The passive partner joins the active one during or after ball rolling and plays a passive role in rolling and burying the brood ball (Halffter & Matthews 1966). Rolling is important for two reasons: it diminishes aggregation and, subsequently, competition around the dung source; and it establishes a bond between the male and female. The rolling process is a powerful visual stimulant for the attraction of a mate (Halffter & Matthews 1966).

Halffter & Matthews (1966) and Tribe (1976) named three basic positions adopted by co-operative ball rollers.

- 1) Male rolls the brood ball and the female clings to it.
- 2) Male rolls the brood ball while the female follows.
- 3) "Pushing" and "pulling" behaviour involving both sexes.

Tribe (1976) stated that Method 1 is employed by all African *Kheper* species, *Circellium bacchus* and a number of *Scarabaeus* species.

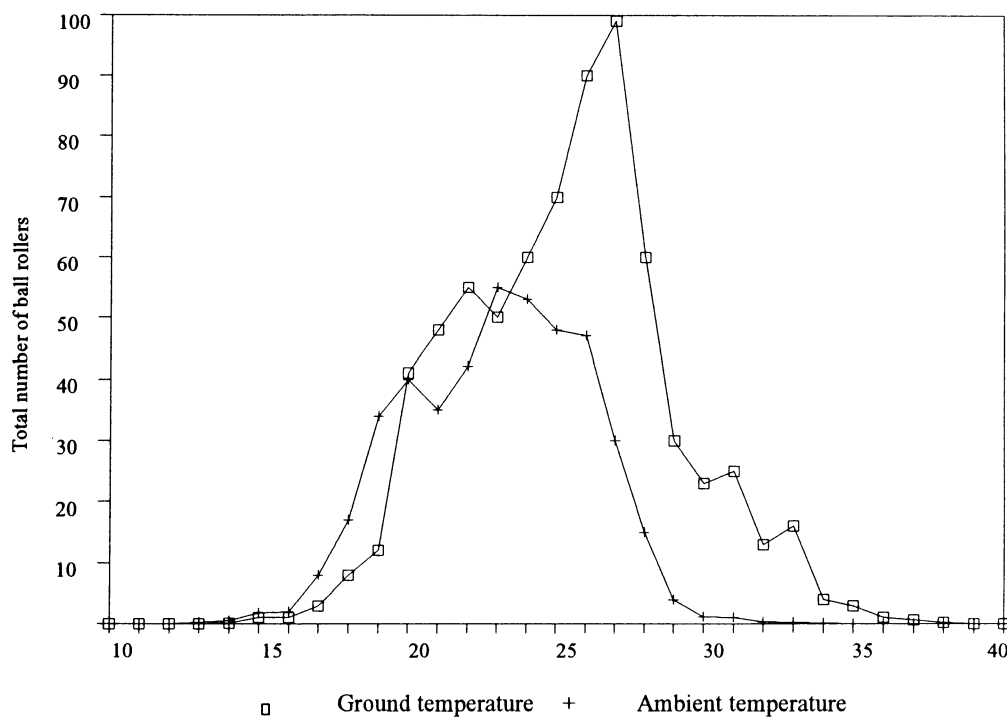


FIG 12: Number of brood balls rolled by *Circellium bacchus* at various ground and ambient temperatures. (n = 189)

RESULTS AND DISCUSSION

The males were most probably attracted to the female and dung ball by the dung itself. The female rolled the ball away and if a male was in attendance it was usually between 10 - 30 mm behind her. The journey was hardly ever uneventful, and often other males and females contested for the female or the ball respectively. Encounter, acceptance and rejection occurred at various stages while ball construction and rolling were taking place.

Females of *C. bacchus* roll the ball backwards with their second and third pairs of legs gripping and controlling the ball while their fore legs remain on the ground. They roll the ball for a few centimetres, then climb on top of the ball where they do a complete circle with their antennae flared. They then descend and as their fore legs touch the ground, their middle and hind legs grip the ball and they continue rolling. This pattern is always followed and thus a consistent direction is maintained.

The brood ball is rolled until a suitable site is reached. The journey can be brought to a temporary halt by an abortive attempt at burying the ball. Rolling occurred most often in a straight line and most obstructions encountered by the female were overcome by going over or through them instead of around them. This leads one to believe that the stimulus for directional rolling must be fairly constant throughout the journey.

A serious obstacle such as the steep road sides with their relatively soft sand, often forced ball abandonment or burial at the base of the obstacle. Besides apparently obvious factors such

as a suitable site, other unknown factors contribute to the choice of burial site. These factors may be one of, or a combination of, ambient temperature, some physiological factor associated with sexual readiness or energetic trade-offs.

Brood ball-rolling was most often seen after rain when temperatures rose above 13-14 °C. It was observed at ground temperatures between 13°C and 37°C with an optimum between 21-28 °C (refer to fig 12).

C. bacchus were observed rolling ready-made balls at temperatures lower than they would normally have constructed them. This was also found in *Scarabaeus semipunctatus* (Fabricius), in Italy, where the beetle would not begin to make balls until the air temperature reached 21 °C, but would roll ready-made balls at 19°C (Heymons and Lengerken 1929:543 cited in Halffter & Matthews 1966) . The rapidity and "skill" of brood ball-rolling in *C. bacchus* increased proportionally to the increase in ambient temperature. In Germany this was also found (Prasse 1957b:592) to be true for *Sisyphus schaefferi* (L.) and for *Gymnopleurus geoffroyi* (Fuessly).

Ready-made balls, according to Halffter & Matthews (1966), are accepted by ball-rollers without hesitation. In *C. bacchus* ready-made balls were usually accepted, rolled away and buried. Interchanging of balls or beetles of either sex in *Kheper nigroaeneus* (Boheman) did not result in any behavioural changes, the new partner or ball was most often immediately accepted (Tribe 1976). *C. bacchus* females also accepted new partners or balls if human interference was kept to minimum. If the female beetle was in any way disturbed, she left the ball or her mate.

Halffter & Matthews (1966) report that in all the canthonines they briefly observed, except for *Canthonella parva* (Chapin) in which pushing and pulling-positions were assumed, one beetle, generally the male, was in the pushing position while the other clung to the ball, never aiding in rolling. Of all the hundreds of cases of ball-rolling in *C. bacchus* I observed, a male was never seen rolling a brood ball, nor a beetle clinging to the ball while it was being rolled, as was reported by Tribe (1975).

To explain this unusual behaviour I propose another category to supplement those used by Halffter & Matthews (1966) and Tribe (1975): one in which the female rolls the ball with the male following close behind.

In most telecoprid scarabs the male is the active partner, while the female usually assumes this role in paracoprids (Halffter & Edmonds 1982). It is generally accepted that the female telecoprid is passive in the rolling and construction of the ball, in order to conserve energy for breeding and brooding. The telecoprid male, who has little to do with breeding and brooding, uses energy on construction and rolling of the ball, thus indirectly saving the female energy.

A possible reason why *C. bacchus* females roll the brood ball is that as a result of their flightlessness, they can energetically afford to do so. The females have the most to gain by forming the brood ball to their satisfaction and choosing a suitable burial site, as they will be spending months caring for their brood. Energy saved due to flightlessness has allowed females to initiate and carry out breeding and brooding with the minimal male help.

CHALLENGES

Challenges, related to breeding, usually occurred only between members of the same sex, although minor fights were observed between opposite sexes before recognition occurred.

If a beetle came into contact with a member of the same sex during construction or rolling of a brood ball, a brief but fierce battle ensued with the victor keeping or claiming the prize, whether it was the ball or the female with ball. The loser usually left the area, but occasionally returned to challenge again.

In many endothermic dung beetles, where the flight muscles are used to raise the body temperature above ambient, the victor of combat is the beetle with the warmest thoracic temperature (Heinrich & Bartholomew 1979a & b). *C. bacchus*, being ectothermic (Nicolson 1987), rely on size and position on the ball to give them a competitive advantage.

Challenges between *C. bacchus* individuals were frequent in peak season. When a female was challenged by another female, the original female climbed on top of the ball from where she most often was able to defend it. This she did by flicking the challenger to the ground. Female challenges lasted between 3 and 95 seconds (mean = 18 seconds, $n = 20$). During all observed conflicts none of the beetles was damaged. The original female was the victor in 70 % of the fights ($N = 20$). The challenger was only victorious if she could dislodge the original female from the top of the ball.

When a male was challenged for his position following a female and a ball, the battle was slightly longer, (7-200 seconds; mean=55 seconds; $n = 15$) and fiercer. With no ball to climb onto and therefore no height advantage, the males came together grasping each other with their legs and producing audible clicks as they flung each other away. The larger of the two males was most often the victor when the ambient temperature was above 22°C, while the smaller individuals seemed to be better suited to the temperatures below 22°C ($n = 15$). As with females, no serious combat injuries were observed. Beetles were encountered in the field missing limbs and dented, but it is doubtful that these injuries arose from fighting.

Prasse (1958) recorded combat in *Gymnopleurus geoffroyi* (Fuessly) and *Sisyphus schaefferi* (L.) and found that fights were always only between two beetles and always between beetles of the same sex. Sometimes more than two *C. bacchus* males contested for a female and her ball. While the males were fighting, the females continued to roll oblivious of their surroundings. Other males could start following her at this stage. Females accepted whichever male followed her.

DIRECTIONS IN WHICH BALLS WERE ROLLED

Hingston (1923) noted that *Gymnopleurus miliaris* (Fabricius) rolled balls in a straight line, directly away from a source of dung and that the beetles strictly adhered to this course if possible, going over and not around obstacles. Matthews (1963) stated that the initial direction chosen by

Canthon pilularius (L.) was influenced by the slope of the ground, the wind direction and the position of the sun, in that order. He maintained that the beetle would tend to roll uphill, with the wind and towards or away from the sun.

These three factors were also highly instrumental in the direction of rolling chosen by *C. bacchus* females. Seventy-four percent of the females rolled their brood balls toward the sun ($n = 27$), 69 % of the time with the wind ($n = 20$) and 88% ($n = 25$) of the time uphill. Females of *C. bacchus* therefore, usually, roll the balls uphill, toward the sun and with the wind.

DISTANCES ROLLED

There can be no doubt that the difficulty of the terrain and the ambient temperature influence the distances that balls are rolled by different species. Average distances rolled by species were reported by Halfpter & Matthews (1966); they ranged from 300 mm in some species of *Scarabaeus* to over 10 m in some species of *Canthon*.

C. bacchus rolled brood balls from 7 m to about 80 m. The average distance was 28 m ($n = 22$) and the average rolling time was 65 minutes ($n = 19$). The longest journey took over five hours in a more or less straight line with two aborted attempts at burial.

5.5. BURIAL AND NIDIFICATION BEHAVIOUR

INTRODUCTION

Very few insects provide nests for their progeny. Nesting involves the creation of a place which functions as a site for oviposition and postembryonic development and in some cases a residence for the adults. An integral part of this process is the provision of a sufficient amount of food to allow development of the organism from egg to adult (Halfpter & Edmonds 1982).

BURIAL OF THE BALL

After rolling the ball a distance, the female excavates under the ball and buries it. The purpose of rolling does not seem to be primarily that of searching for a burial site, as seemingly appropriate burial sites are often passed over before the ball is buried.

When a suitable site was found burial commenced. The ball is buried as the female excavates under it. As the ball and female sink slowly below the surface the male climbs onto the ball and disappears with it. Occasionally, for unknown reasons, the ball was only partially buried and then brought to the surface again.

Burial was much faster at warmer temperatures (22-28°C) and/or in softer soil. However, in cool conditions and/or on hard ground, this process often took longer. Times taken to bury brood balls in the field ranged from 35-65 minutes (mean = 45.6 min; $n = 13$). Burial speed was quicker in the laboratory where the soil was less compact. Here the time necessary to bury a ball ranged from 15-51 minutes (mean = 26.4; $n = 10$; $s = 13.1$).

During cool weather when the ball was being rolled in the late afternoon, the female buried the brood ball a few centimetres below the surface. The brood pair spent the night with the ball. The next morning when the ambient temperature rose above approximately 18 °C, the ball was dug up and rolling continued.

The ball's final position, where a chamber is excavated around it, is not always directly below where it disappeared, but up to 500 mm to one side of the entrance hole. The soil directly surrounding the chamber was compacted and harder than that between the surface and the chamber. The brood chamber was excavated between 170-370 mm (mean = 250 mm; n = 25) below the surface. It was round and 10 - 30 mm larger than the ball itself. The female was usually positioned directly under or to the side of the ball. The male was to the side, 10-50 mm from the ball, often buried in soil.

NIDIFICATION BEHAVIOUR

Halffter & Matthews (1966) provided a summary of four nidification categories in Scarabaeinae. In group I scarabs, egg (s) is (are) laid directly in a food mass which is packed into a tunnel near or under the dung. In group II species, the egg is laid underground in a dung ball. It is provided with an outer shell of soil. The brood ball is found near or under the dung pat. Usually only one brood ball is found in each burrow but there may be several. No brooding occurs. Members of group III construct spacious underground chambers under or near the dung pat. The dung cake (a large mass of dung) is divided into many brood ovoids each containing an egg. There is no clay shell. Brooding occurs, part or full time, by one or both parents .

C. bacchus falls into Group IV, which is characterized by the ball being fashioned on the surface at the food source and then rolled away, to be provided with an egg at a later stage and at some distance from the dung. The species placed in group IV are mostly in the tribe Scarabaeini.

Group IV behaviour can be sub-divided into three variations. Variation I is where the brood ball is covered with a clay shell in a burrow. Variation II is when the ball is not buried but is coated with a clay shell. *C. bacchus* have the characteristics of variation III. Beetles in this category bury the brood ball, which is not coated with a clay shell, but which often has a thin outer layer of soil or dung and soil mixed. Other species which exhibit this variation in brooding behaviour are the genera *Canthon*, *Scarabaeus*, *Gymnopleurus* and *Sisyphus*. According to Halffter & Matthews (1966) the soil is deliberately placed on the ball by the females of *Scarabaeus*, *Gymnopleurus* and *Sisyphus*. *Canthon* brood balls have a thin layer of sand particles that may or may not have been placed there by the female (Halffter & Matthews 1966).

C. bacchus brood balls pick up a thin layer of fine sand during rolling and the ball is buried with this sandy layer. When balls were dug up, any time after the brood pear had been formed, the sand layer is less prominent. This would suggest that during the refashioning of the brood ball, the sand either falls off or is removed by the female and thus may be a product of the rolling operation and not a deliberate protection mechanism.

BROOD PEAR FORMATION

The process of brood pear formation was described in detail by Prasse (1957b) for *Gymnopleurus geoffryi* (L.) and *Sisyphus schaefferi* (Fuessly). In these species as soon as the male departs from the nest, the female begins to reconstruct the brood ball by pulling it apart and putting it together in a denser and more compact form.

In *C. bacchus*, the male, returned to the surface after the pear was formed and the egg laid. Small amounts of dung could sometimes be found on the floor of the brood chamber. This could have been left over after the reconstruction of the ball or could serve as food for the female's impending vigil with her offspring.

Oviposition and egg chamber construction were not observed in *C. bacchus*.

The apex of the brood pear always pointed upwards and the projections averaged 10.5 mm ($n = 10$; $s = 4.5$; range = 6.24-19.5 mm) higher. The apex of the ball became less conspicuous as the larva developed.

5.6. COPULATION

Halffter & Matthews (1966) stated that it is unusual to observe a pair of Scarabaeinae *in coitu*. In many genera, even those as common as *Copris*, *Phanaeus* and *Dichotomius*, copulation has never been witnessed.

I observed copulation twice in *C. bacchus*; once 6 hours after burial commenced and once 4 days after burial. It was similar to that described by Prasse (1957a). The male straddles the female, stroking her elytra with his fore legs and palpi while the middle legs encircled her elytra. The hind legs steadied the copulating beetles. On both occasions mating ceased as a result of the disturbance. Copulation took place on top of the ball. In one of the cases the ball was buried at a depth of 80 mm and after copulation it was moved down to 170 mm.

On another occasion I watched a male stroking the thorax and elytra of his mate with his fore-legs, antennae and palpi before submerging totally. This "precopulatory behaviour" lasted about six minutes but did not end in copulation.

5.7. BROOD CARE

Social behaviour in insects has its essence in a beneficial contact between the offspring and one or both of the parents (Halffter & Matthews 1966). They define the continued presence of the parent(s) during early stages of brood development, without actual beneficial contact, as "subsocial behaviour".

RESULTS

The reason for the female parent remaining in the nest has not been satisfactorily determined (Halffter & Matthews 1966). One noticeable effect of removing the female is the growth of fungi on the brood ovoids as the microclimate in which the brood ball is found is ideal ^{for} this.

Only one of the balls constantly attended by a female parent showed any signs of fungal growth (n = 35). Balls that had been abandoned by the female parent before or just after the brood pear was constructed, became covered with fungi. In the absence of a female only 33% of the balls containing eggs and first instar larvae produced mature larvae or healthy adults. Removing the female, while her brood were 2nd and 3rd instar larvae had a less detrimental effect. Only 10 % of larvae abandoned in the third instar failed to become adults (see table 4). When the outside of abandoned balls of 1st and 2nd larval instars was cleaned by hand, a high percentage (90%) of healthy offspring was produced (see table 4).

TABLE 4: Percentage of individuals surviving the removal of the female at various life cycle stages.

STAGE FEMALE WAS REMOVED	NO. BALLS EXAMINED	% SURVIVAL
FEMALE NOT REMOVED (Control)	35	94
EGG	6	33
FIRST INSTAR	6	33
SECOND INSTAR	8	75
THIRD INSTAR	10	90
FEMALES ROLE FULFILLED * (1ST/2ND INSTAR)	10	90

* In this case I fulfilled the role of the female by regularly cleaning the outside of the brood ball.

I have not ascertained whether the female merely feeds on the outer layer of the ball, as seen in *Kheper nigroaeneus*, Tribe (1976), keeping it free from fungi; or whether she adds an antibiotic of sorts, to curb fungal infection. This was suggested by Halffter & Matthews (1966) for *Copris* species.

On more than one occasion, a first instar larva, without a brooding female, was found parasitised by other Coleoptera larvae. Many of the balls abandoned in the field had tiny holes in them, and the eggs or larvae were found dead.

5.8. THE EGG

Brood balls were cut open to reveal conical eggs (mean = 9.035×5.115 mm; $n = 3$). The creamy coloured eggs were not cemented to the chamber as in *Garreta* and *Allogymnopleurus* (Tribe 1976), but lay loosely in a chamber inside the cone of the brood pear. The egg was positioned perpendicular to the base of the brood pear. As in *Kheper nigroaeneus* (Tribe 1976) the conical projection also disappeared in *C. bacchus* soon after the egg hatched and the larva began feeding.

5.9. LARVAL DEVELOPMENT

The Scarabaeinae immature stages always consists of an egg, three larval instars and an inactive pupal stage. The transition between the third instar and the pupal stage is termed a prepupa (Halffter & Matthews 1966).

The embryonic and larval stages are usually spent underground in the dung prepared by one or both parents. Within this dung mass, the immature stages are relatively free from predators and disease, and are subjected to fairly constant humidity and temperature (Halffter & Edmonds 1982).

C. bacchus larvae display the characteristic features of Scarabaeinae larvae. These include *inter alia* fully developed mouthparts with strong mandibles. The consistency of the larval food differs greatly from that which the adult must ingest. The larva needs strong mandibles for biting off and feeding on the insides of the compact dung ball. Another common feature is the “coprine hump” - an enlargement of the dorsal portions of some or all of the first six abdominal segments, enclosing coils of the mid and hind gut (Halffter & Matthews 1966). This hump is important in aiding the movement of the larva inside the cavity it forms within the dung ball, as well as serving as a storage place for most of the ingested dung.

DURATION OF DEVELOPMENT

There are few studies giving the exact developmental period in Scarabaeinae (Halffter & Matthews 1966). The normal timespan from egg to adult appears to be between 30 and 50 days, (for examples see Halffter & Matthews 1966).

Large species seem to need longer periods of development, ranging from four months in the case of *Copris hispanus* (L.) to two years for *Onitis caffer* (Boheman). Unfavourable climatic conditions are generally responsible for the delay in development.

Even in cases where development is rapid, as in some species of *Onthophagus*, the complete life-cycle (egg-egg) can still take a full year in temperate climates. This is because the young adult must undergo a period of “maturation feeding” (“Reifungsfrass”), during which the young adult’s gonads ripen and it becomes sexually mature. This period of feeding takes over a month on average and in some cases up to four months, usually bringing the adult to winter (Halffter & Matthews 1966). The “Reifungsfrass” period measured by Prasse (1957a) for species of *Gymnopleurus* and *Sisyphus* averaged between 3.0 and 3.5 months.

RESULTS

The average length of undisturbed immature development in *C. bacchus* is approximately 4 - 4.5 months. The average adult life-span is estimated at between 3-5 years.

TABLE 5: Duration of immature stages, and head capsule widths of *Circellium bacchus* larvae.

STAGE	DURATION (DAYS)			HEAD CAPSULE WIDTH (mm)		
EGG	N = 6	X = 7.8	(7-9)			
1ST INSTAR	N = 6	X = 11.1	(9-12)	N = 4	X = 4.17	(3.8 - 4.4)
2ND INSTAR	N = 4	X = 12.8	(11-14)	N = 5	X = 5.91	(5.6 - 6.2)
3RD INSTAR	N = 4 (70 - *)			N = 12	X = 8.25	(7.6 - 8.8)

STAGE DURATION (days)			
PUPA	N = 4	X = 14	(13-17)
CALLOW**	N = 5	X = 3	(2-5)
ADULT	N = 8 (120 -)		

TABLE 6: *Circellium bacchus* stage duration in days from burial.

0	- 4	DAY — COPULATION
4	- 6	DAY — EGG LAID
5	- 7	DAY — MALE RETURNS TO SURFACE
12	- 14	DAY — EGG HATCHES (1ST INSTAR)
21	- 25	DAY — 2ND INSTAR
28	- 32	DAY — 3RD INSTAR
105	- *	DAY — PUPA

* Some larvae remained in the third instar for 5 months. This is possibly as a result of them being moved from the mild climate in Addo to the colder winter of Pretoria. All these specimens died before pupating.

** Teneral still in brood ball.

LARVAL BEHAVIOUR

Halfpter & Matthews (1966) state that the newly emerged scarab larva derives its nourishment from the yolk that fills the midgut, and so does not feed externally for a few days after hatching. On completion of this period, it begins feeding on the side walls of the egg chamber and also

perhaps on the egg shell. After some days, the larva begins to eat into the floor of its chamber and from then on continues to eat its way downward.

Halffter & Matthews (1966) explain that by rotating as it eats, the larva creates a spherical space around itself. The diameter of the space correlates with the size of the larva. The larva wedges itself into this space by applying the flattened anal area to one surface and the dorsum of its hump to the opposite surface. The forebody is now able to move freely up and down for feeding. The legs play no role in locomotion at this stage, but, as in *Scarabaeus affinis* (Brulle) (Ronchetti 1949 cited in Halffter & Matthews 1966) the anterior pair is directed forwards and may aid in feeding. As the larva eats, it leaves behind some of its own faeces mixed with a certain amount of inedible frass. This mixture is deposited evenly on the inner walls of the cavity and is subsequently eaten again and again by the developing larva. The exuviae are not eaten, but usually only the head capsules of the last two moults can be found afterwards, and then only with difficulty (Halffter & Matthews 1966).

RESULTS AND DISCUSSION

The larval feeding habits of *C. bacchus* show little or no variation from the above description by Halffter & Matthews (1966).

Upon opening brood balls containing third instar larvae of *C. bacchus* that were soon to pupate, a coating of faecal material on the walls of the chamber was found; at this stage it appeared that the larvae had ceased feeding.

Fabre (1897) describes the behaviour of Scarabaeinae larva repairing a breach in the brood ball using a mixture of oral and anal secretions. The larva patched up a hole on exposure to the air, which Fabre stated is detected not by the light entering the hole, but by the different physico-chemical properties of the air entering the hole.

Thus it would seem that the larva has a remarkable ability to maintain the integrity of the ball and to seal itself off completely from the outside world. It is thought that the major agent causing breaks or cracks in the ball is the movement of the larva itself as it grows inside the ball and in the process thins out the walls.

When brood balls of mature larvae of *C. bacchus* were opened, the larvae excreted a large amount of faeces and then resumed eating without attempting to repair the damage done to the ball. On inspection a few days later, the larvae had repaired or attempted to repair the damage, depending on the extent of damage to the ball.

Three brood balls examined approximately 80 days after burial had many small projections protruding from a number of places on the outer surface of the ball. It looked as if they were the result of restoring and repairing the breaches made in the ball by feeding. All the balls with these projections were smaller than average and it may have been that the larvae, in trying to feed as optimally as possible had breached and repaired the balls in a number of places.

PUPAL DEVELOPMENT

The function of a pupal chamber is to protect the larvae as they pupate and develop into young adults. The walls of the chamber provide an excellent barrier to the influences of the outside world. In Scarabaeinae which produce brood balls, larvae do not make pupation chambers, but pupate within the confines of the hardened walls of the brood ball (Halffter & Matthews 1966). *C. bacchus* also exhibits this behaviour.

ADULT EMERGENCE

Halffter & Edmonds (1982) state that the fact that development must continue after eclosion, is likely to be the result of a limited food source provided to the developing larva. Thus a period of time devoted to adult feeding, varying among species, is necessary for gonad maturation.

The young adults emerged from their pupal chamber after approximately 4.0 - 4.5 months (see tables 5 & 6). Maturation feeding lasts approximately 50-65 days. *C. bacchus* produce only one or two progeny a year.

6. DAILY ACTIVITY AND DUNG COLONISATION

6.1. DAILY ACTIVITY

INTRODUCTION

Ambient temperature directly influences the daily activity patterns of ball-rolling scarabs and is also one of the most important factors limiting the geographic distribution of telecoprid beetles (Tribe 1976).

Halffter & Edmonds (1982) state that the Scarabaeinae tend to be fairly exact in the timing of their daily activities. In most communities, there is a sharp distinction between diurnal and nocturnal species. Furthermore, while there is often a certain amount of activity-overlap among species, most diurnal species tend to concentrate their activities to specific daylight hours. This seems likely to be in response to the prevailing temperatures. Species exhibiting bimodal, diurnal activity patterns tend to be active in the early morning and again in the late afternoon, after an inactive period at midday. Unimodal species concentrate their efforts into a single activity period of a few hours.

METHODS AND MATERIALS

Based on preliminary data during which minimum and maximum temperatures for activity were determined, daily activity was investigated by regularly driving a designated route of 9 or 13 km. Transects were driven at selected times and ambient temperatures to try to cover the complete activity spectrum. Beetles encountered en route were counted and sexed. Those found on or within 5 m of fresh dung were ignored. This was done to standardize the data, as occasionally elephants voided large quantities of dung along the route. Later the number of beetles encountered per km was calculated and plotted against time, ambient temperature and relative humidity.

Because conditions on the morning of the 22/10/91 seemed ideal for beetle activity, 11 nine kilometre transects were driven instead of the usual two. This particular day was chosen for the experiment as it had rained less than 48 hours previously and looked as if it was going to be a morning with a high range in temperatures from cool to very hot. The number of beetles per km was recorded, as were the temperature and corresponding relative humidity for each transect.

RESULTS

Transect data that were analysed and plotted against ambient temperature are given in figure 13.

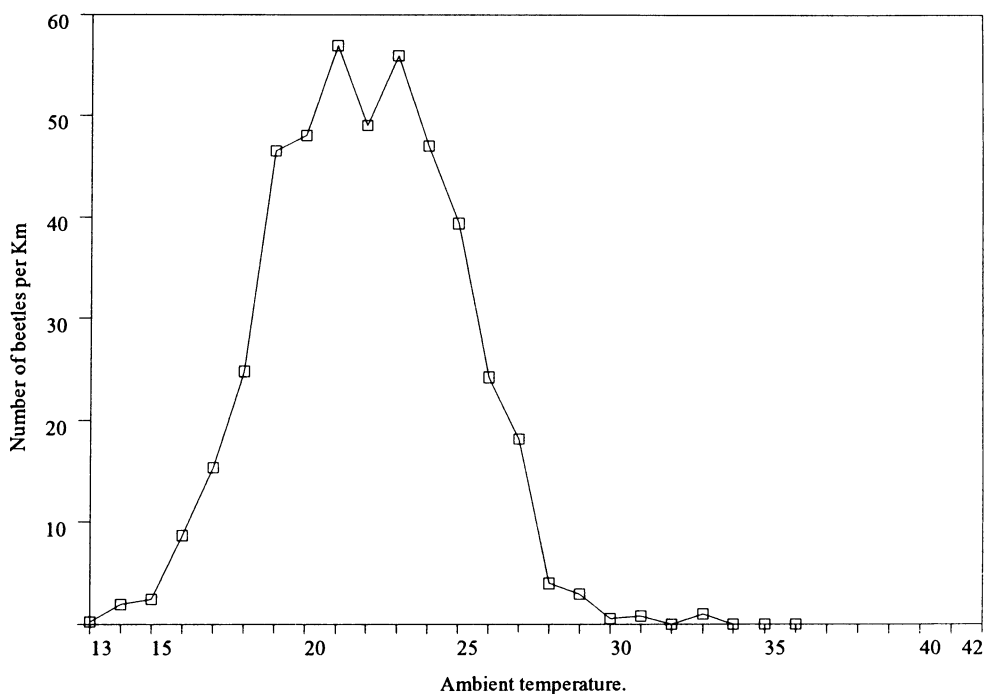


FIGURE 13: Number of *Circellium bacchus* sighted per km plotted against ambient temperature.

The data recorded during the transects driven on 22/10/91 are given in table 7.

TABLE 7: *Circellium bacchus* activity reflected in numbers of beetles per km on a day with optimum conditions at different ambient temperatures and relative humidities.

TEMPERATURE		RH	BEETLE NUMBERS	BEETLES PER KM
Ta	Ts			
15°C	15.0°C	90%	42	4.6
17°C	18.5°C	80%	81	9.0
19°C	22.0°C	80%	129	14.3
20°C	24.0°C	70%	160	17.7
23°C	27.0°C	60%	185	20.5
24°C	29°C	58%	190	21.1
25°C	32.5°C	55%	175	19.4
27°C	34.0°C	45%	25	2.7
29°C	35.5°C	40%	17	1.9
31°C	36°C	39%	4	0.4
33°C	37°C	36%	0	0

Ta = Temperature ambient (shade)

Ts = Temperature ambient (sun)

6.2. DUNG COLONISATION

INTRODUCTION

Paschalidis (1974) found that different species of *Sisyrphus* colonized different areas of the dung pat. She also observed a preference amongst certain species for dung lying in the shade, while other species preferred dung in the sun. There was also a distinct difference in the peak colonization periods of some species.

Experiments were carried out during the first part of April 1991 to observe *C. bacchus*'s colonization of four types of herbivore dung.

METHODS AND MATERIALS

Two experiments were carried out to determine dung colonisation of fresh elephant, buffalo, rhino and cow dung by *C. bacchus*. The quantity used in each case was that of one animal's defecation. The dung was collected the night before or early on the morning of the experiment. It was kept in air-tight plastic bags and removed 30 minutes before the start of the experiment. Each dung type was placed separately on the ground (Experiment 1) or in separate plastic buckets buried flush with the ground (Experiments 2a & b). The colonisation of each dung type as well as that of the all the dung used in the experiment was recorded.

In Experiment 1 carried out on the 13/02/91, the four types of dung were placed on the ground in a straight line 15 m apart. This left the beetles free to come and go as they wished.

Temperature, relative humidity, numbers and sexes of beetles arriving at and departing from dung were recorded every hour on the hour between 06h00 and 18h00. All ambient temperatures, unless otherwise stated, were taken in the shade.

The dung was not disturbed, firstly, because the beetles leave the pat if it is disturbed and, secondly, to recreate the exact conditions of dung which is voided in the morning and is influenced by the elements throughout the day.

Experiment 2 (a) and (b) took place in the first half of April 1991. The containers used for these experiments were round, 300 mm deep with a 300 mm diameter across the top. The four containers were buried in a straight line 15 m apart and filled with fresh dung.

Temperature, relative humidity and numbers and sexes of beetles arriving at the dung, were recorded every hour on the hour from sunrise to sunset. The first occasion was a typical summer's day (Experiment 2 a), i.e. cool and humid in the morning, becoming hot and dry at midday and cooling off again in the late afternoon. The second day was atypical (Experiment 2 b) i.e. cold with drizzle in the morning, overcast and cool with the temperature and humidity fluctuating for most of the day.

RESULTS

Results obtained from the dung colonization experiments are tabulated (see tables 8 - 11) or plotted against environmental parameters (also see figures 14 a & b, 15 a & b and 16).

TABLE 8 : Time (minutes) after start of experiment of arrival of first *Circellium bacchus* and its sex at different dung types during two colonisation experiments.

EXP 2a					EXP 2b			
Dung type	Sex	Time	Ta	RH	Sex	Time	Ta	RH
Elephant	F	55	17.7	80%	F	130	19.6	72%
Cow	F	95	18.0	82%	F	50	16.3	80%
Buffalo	M	110	18.2	82%	F	135	19.8	70%
Rhino	F	150	20.8	80%	F	200	22.0	53%

Ta = Ambient temperature.

EXPERIMENT 1

TABLE 9: Arrivals, departures and ball making by *Circellium bacchus* at four different types of dung on a typical summer day.

TIME	6H00	7H00	8H00	9H00	10H00	11H00	12H00	13H00	14H00	15H00	16H00	17H00	18H00	19H00	20H00	TOT
TEMP.	21.0	22.2	23.5	27.8	28.9	31.8	32.1	32.2	33.6	32.1	29.1	27.1	25.7	23.8	21.5	
RH	63.0	68.6	70.5	60.2	52.0	46.9	39.5	36.4	34.2	35.4	42.4	47.3	48.6	51.0	65.7	
ELEPHANT																
ARRIVE	1	20	52	40	2	0	0	0	0	0	0	4	5	0	124	
LEAVE	0	0	1	5	25	43	0	10	0	0	0	0	0	0	84	
TOT	1	21	72	107	84	41	41	31	31	31	31	35	40	40		
FBALLS	0	0	3	3	1	0	0	0	0	0	1	0	1	0	9	
BBALLS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
BUFFALO																
ARRIVE	1	5	6	7	0	0	0	0	0	0	8	7	13	22	69	
LEAVE	0	1	2	0	13	0	2	0	0	0	0	0	0	0	18	
TOT	1	5	9	16	3	3	1	1	1	1	9	16	29	51		
FBALLS	0	0	0	0	0	1	0	0	0	0	0	1	1	0	3	
BBALLS	0	0	1	2	1	1	1	0	0	0	1	1	1	1	10	
RHINO																
ARRIVE	1	3	7	2	0	0	0	0	0	0	1	4	6	12	36	
LEAVE	0	0	3	5	3	0	0	0	0	0	0	0	0	0	11	
TOT	1	4	8	5	2	2	2	2	2	2	3	7	13	25		
FBALLS	0	0	0	1	1	0	0	0	0	0	0	0	1	1	4	
BBALLS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
COW																
ARRIVE	1	3	5	3	0	0	0	0	0	0	7	9	3	11	42	
LEAVE	0	2	6	0	4	0	0	0	0	0	0	1	0	1	14	
TOT	1	2	1	4	0	0	0	0	0	0	7	15	18	28		
FBALLS	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
BBALLS	0	0	0	1	1	0	0	0	0	0	1	2	0	0	5	
TOTAL																
ARRIVE	4	31	70	52	2	0	0	0	0	0	16	24	27	45	271	
LEAVE	0	3	12	10	45	43	2	10	0	0	0	1	0	1	116	
TOT	4	32	90	132	89	46	44	34	34	34	50	73	100	145		
FBALLS	0	0	3	4	2	1	0	0	0	0	1	1	3	2	17	
BBALLS	0	0	1	3	2	1	1	0	0	0	2	3	1	1	15	

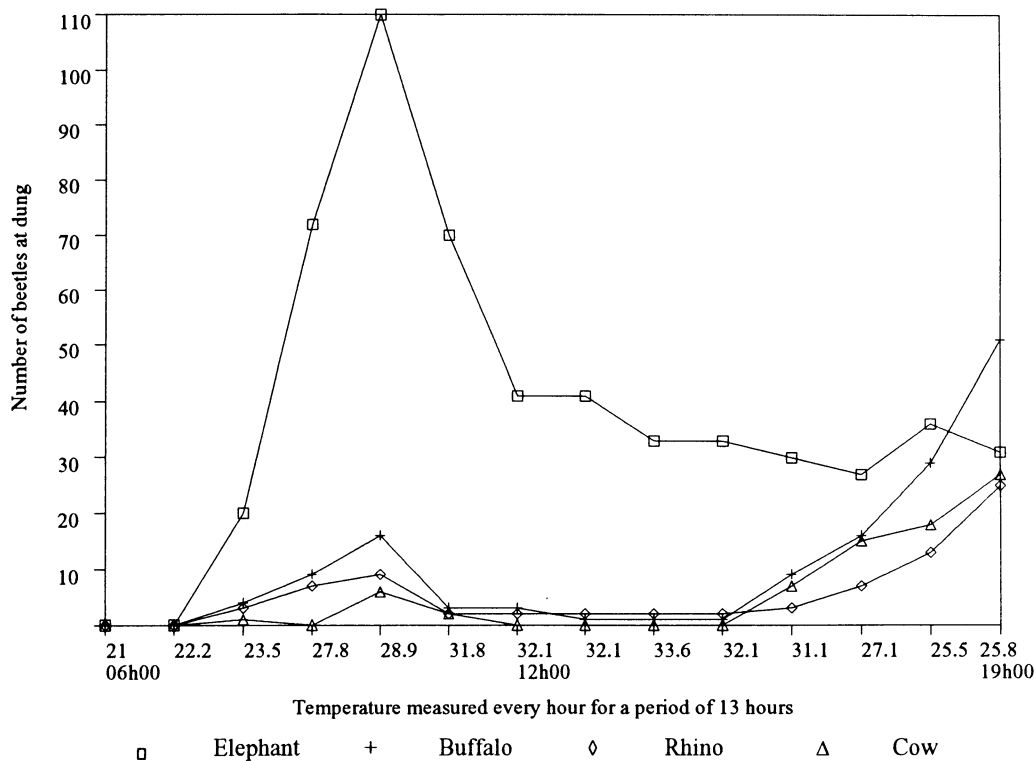


FIGURE 14a: The number of *Circellium bacchus* arriving at four types of dung (indicated separately) on a typical summer day - temperature (°C) indicated hourly. (Exp. 1)

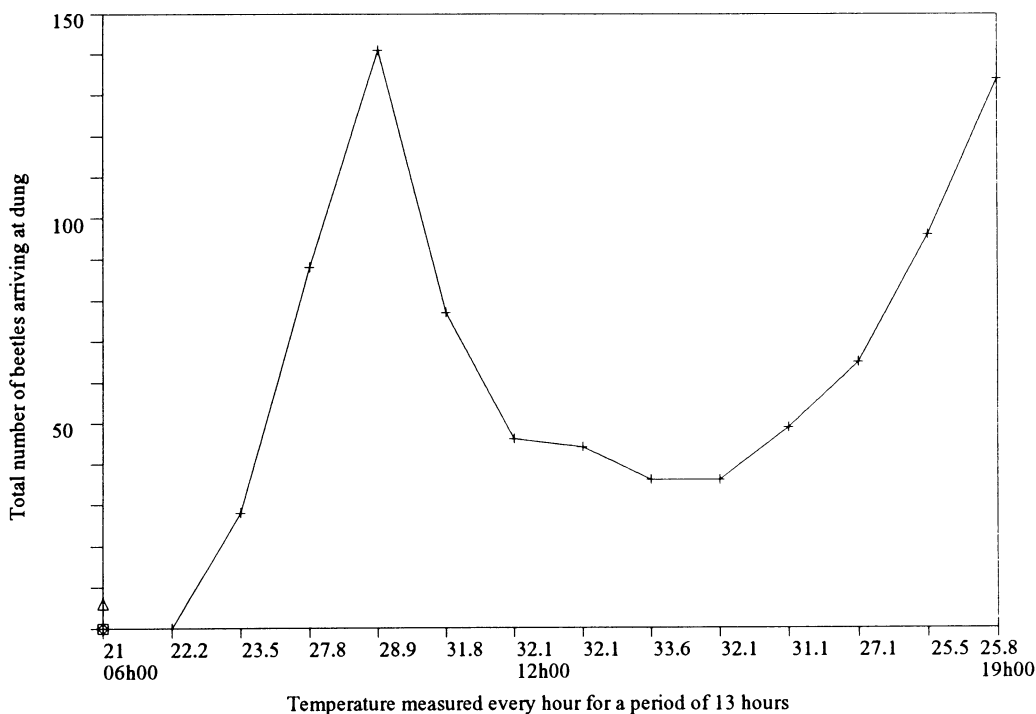


FIGURE 14b: The total number of *Circellium bacchus* arriving at all the dung types on a typical summer day - temperature (°C) indicated hourly. (Exp. 1)

TABLE 10: Number of *Circellium bacchus* arriving per hour on a typical summer day at four types of dung (Exp. 2a)

TIME	5H00	6H00	7H00	8H00	9H00	10H00	11H0	12H00	13H00	14H00	15H00	16H00	17H00	18H00	19H00
TEMP	17.2	17.7	18.2	20.8	24.0	27.5	28.0	28.0	30.2	31.4	29.4	27.3	24.9	23.3	22.7
RH	78.2	80.0	82.4	80.8	70.8	55.2	52.9	50.4	46.3	43.5	46.6	51.3	60.6	66.9	71.1
ELEPHANT	1	1	6	14	24	15	4	4	2	4	6	4	2	1	
BUFFALO	0	1	2	1	9	7	1	1	1	0	14	13	10	2	
COW	0	2	6	16	9	9	4	1	0	2	4	2	5	1	
RHINO	0	0	3	4	10	8	2	3	2	0	7	3	5	1	
TOTAL	1	4	17	35	52	39	11	9	5	6	31	22	22	5	

TABLE 11: Number of *Circellium bacchus* arriving per hour, on an atypical summer day at four types of dung (Exp. 2b)

TIME	6H00	7H00	8H00	9H00	10H00	11H00	12H00	13H00	14H00	15H00	16H00	17H00
TEMP	14.7	16.4	18.7	19.6	22.0	27.3	26.1	26.1	26.2	26.5	23.5	21.7
RH	68.0	80.1	72.5	61.2	53.8	41.1	44.5	46.1	45.6	44.9	53.2	60.6
ELEPHANT	0	0	0	1	10	6	2	0	1	0	1	1
BUFFALO	0	0	0	2	4	5	2	1	2	1	1	1
COW	0	1	0	0	0	7	1	1	0	0	1	0
RHINO	0	0	0	0	13	6	3	1	1	0	0	0
TOTAL	0	1	0	3	17	24	8	3	4	1	3	2

6.3. GENERAL DISCUSSION

C. bacchus responded to fluctuations in temperature and relative humidity. The highest activity was seen at cool to warm ambient temperatures (22-28 °C) and medium to high relative humidities (55 % and above). Activity was divided into that which took place before encountering dung and that which occurred afterwards.

It was evident from Experiments 1 & 2a, as well as the transect data, that there were two peaks in the activity of *C. bacchus* on a typical summer's day (refer to fig 14a and b). The morning increase in activity coincided with increasing temperature and decreasing, albeit relatively high relative humidity. The afternoon activity was initiated by the temperature cooling down after high midday temperatures, and an increase in relative humidity.

The high temperatures and low relative humidities at midday were unsuitable for beetle activity. Beetles were, however, still active but in very low numbers during these periods. Activity was low in the cold, dry winter months (see chapter on seasonal rhythms).

In summary, the daily activity of *C. bacchus* can be divided up as follows:

In the early morning when temperatures were low, the only beetles visible were those that had used the dung to overnight in. In this dung, feeding as well as ball construction was observed if the ambient temperature was above 12 - 14°C. After sunrise, as temperatures rose, and while the relative humidity was still high, the beetles left their shelters in search of fresh dung. This searching began when the temperature was approximately 14-16°C, after a night when the temperature did not fall below approximately 8 °C. After a colder night searching began at warmer temperatures between 18 - 20 °C. The searching activity increased and reached a peak at temperatures between 22-24 °C. By the time the temperature had risen to 26-28°C, most visible beetles were feeding. Beetles fed on the first dung they encountered after becoming active and continued feeding until temperatures reached the high 20's and low 30's (ambient temperature) (see chapter on feeding). The ground temperature was usually a few degrees higher than the ambient temperature. Feeding transcended all relative humidities whether high or low.

When the ambient temperature increased to over 30 °C, beetles left the dung heap for nearby vegetation or crawled into the dung. Feeding and dung colonisation began again as soon as the temperature started dropping, and at temperatures of approximately 26-24 °C, ball-making resumed. In the evening when the temperature fell below optimum (usually about 18 °C, but sometimes as low as 12°C) the beetles that did not burrow into the dung left the dung for the shelter of nearby vegetation or soil.

This cycle was repeated the following morning. There were, however, many variations in the cycle. Rainfall or high relative humidity enabled the beetles to be active for longer periods of time. Higher than normal activity occurred for a few days after a substantial downpour and warm evening temperatures enabled the beetles to be active after dark.

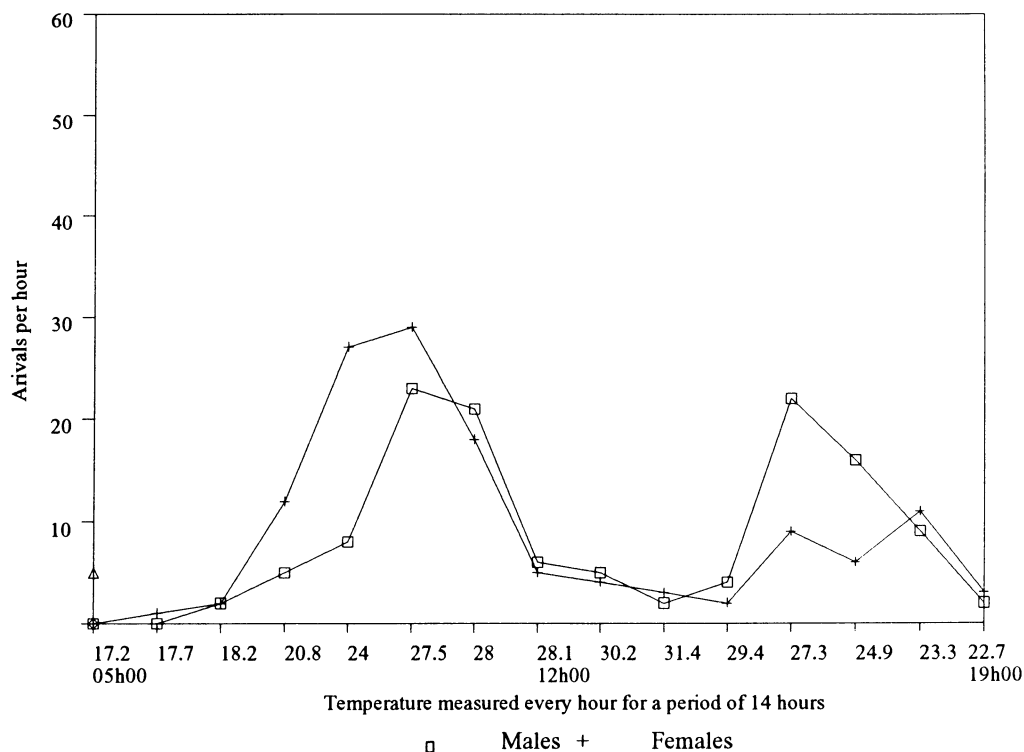


FIGURE 15a. Number of male and female *Circellium bacchus* arriving at dung per hour during a typical day - temperature (°C) indicated hourly.

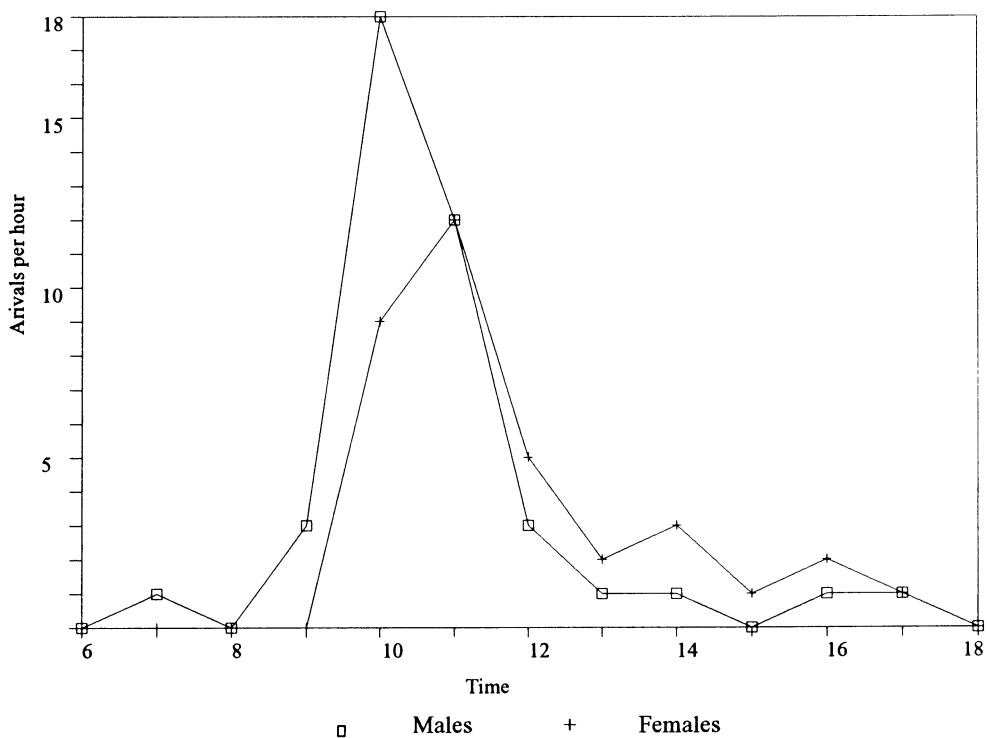


FIGURE 15b. Number of male and female *Circellium bacchus* arriving at dung per hour during an atypical day.

Food and brood balls were constructed and rolled throughout this activity period, but most were rolled at the higher end of the temperature spectrum. However, beetles rolled already-made balls at temperatures lower than those at which a ball would normally be constructed. On a number of occasions females were observed rolling brood balls at temperatures of about 17 °C. At these temperatures, no males followed. When the temperature reached approximately 20°C, males began to join the females.

Observations by Tribe (1976) of *K. nigroaeneus* at dung showed that during early periods more males were present than females. The females arrived at the dung pat only after male flying activity had decreased. He attributed this to the possibility that males are active at slightly cooler temperatures than females. He speculated that the males in possession of dung are known to produce sex pheromones and thus attract females as soon as they arrive. He also stated, as a possibility, that the males that arrived earlier at the dung were physiologically ready for mating and those that arrived later were just there to feed.

In *C. bacchus*, the females which are the active partners, were found at the dung pat earlier and in greater numbers than males (see table 8 & figures 15 a & b). These females may have been ready for breeding and therefore arrived before the males to feed and begin ball-making and rolling. When the males arrived they either found the females ready to construct the ball or already in the process of doing so.

7. DUNG PREFERENCE

7.1 GENERAL INTRODUCTION

Most dung scarab species feed with a low degree of preference, but some are more specific in the dung they feed on (Halffter & Matthews 1966, Edwards 1991). Tribe (1976) stated that preference depends on the coarseness (see table 12), volume and characteristic odour of the dung (Halffter & Edmonds 1982). Added to this is its moisture content (Halffter & Matthews 1966) as well as the time of day or night it is voided. As the dung dries out and forms a crust, it becomes less attractive and less suitable for feeding.

When conditions are optimal for beetle activity, fresh dung does not stay intact and exposed for more than 24 hours, since by that time the dung has been ingested, carried off or buried by various dung beetle species (Tribe 1976; Heinrich & Bartholomew 1979b). During the off-season or during drought, when few beetles are active, the dung lies on the surface and becomes dry and hard (Tribe 1976).

Tribe (1976) suggested that *Kheper* species are attracted to any herbivore dung in the morning, but only to coarser dung as the temperature rises. From sunrise *Kheper* species fed and rolled balls from most types of dung, but as the day progressed they showed an increasing preference for rhino dung. By midday there were few left flying and most beetles had burrowed into the dung and only appeared again in the late afternoon when the temperature had dropped.

Selection for nocturnal, diurnal or crepuscular behaviour in dung beetles may have been in response to the timing of herbivore defecations. *Canthon pilularius* (L.) was recorded by Matthews (1963) to prefer cow dung with more than a day of exposure to the elements, in which case the surface was hardened although the interior remained plastic. *Phanaeus vindex* (Macleay), and probably most other Coprini, come to semi-liquid cow dung and are able to utilize it immediately, since in this group food balls are not made (Matthews 1963).

TABLE 12: Comparative coarsness rating of mammal dung (From Tribe 1976)

SPECIES	RATING OUT OF FIVE	FOOD TYPE
Black Rhino	+++++	Twigs and bark
Elephant	++++	Twigs, bark and leaves/grass
Cow	++	Grass
Buffalo	++	Grass
Monkey	+	Vegetable matter
Human	+	Animal and vegetable matter

During dung preference tests, one must take into consideration the quantity and quality of the dung that the particular beetle would come into contact with under normal circumstances. Factors such as temperature, the volume of dung, the amount of shade or sun it is exposed to as well as its age are important if one wishes to recreate approximately natural conditions. To test dung preference of *C. bacchus* under different environmental conditions, three similar experiments were designed.

METHODS AND MATERIALS

Three dung preference experiments were carried out and the data were compared with many observations of dung preference in the field. These experiments took place in the first half of April 1991, a month of relatively high beetle activity. There had been no rain in the three days prior to each repetition. All dung preference tests were carried out in areas of high beetle activity.

Experiment 1 was designed to test the preference of *C. bacchus* for four different types of herbivore dung. In Experiment 2, the dung types were placed closer together, allowing the beetles more of a "choice". In Experiment 3 the dung was placed in buckets buried with the lip flush with the ground, to capture the visiting beetles. Water was added to the dung every hour to simulate the odour of fresh dung.

7.2. EXPERIMENT 1

This experiment ran from 6h00 -18h00 on a typical summer's day. The temperature was 17.7 °C and the relative humidity 80 % at the start of the experiment. The temperature peaked at 31.4 °C, while, at the same time, the relative humidity dropped to 43%. At the end of the experiment the temperature was 23.3 °C and the relative humidity was 66.9 %.

Elephant, rhino, buffalo and cow dung pats (one defecation) were placed on the ground 12 m apart in the semi-shade. (A preliminary experiment recorded the total numbers of beetles arriving at dung positioned in the sun, shade and semi-shade. The experiment showed 31 beetles arriving at dung in semi-shade as opposed to the 15 and 10 arriving at the shaded and sun-exposed dung respectively).

Numbers of beetles arriving and leaving the dung, as well as those switching dung pats, were noted. In this experiment the dung was not disturbed, firstly as the beetles tend to leave the pad when disturbed and secondly to simulate the conditions of dung being voided in the morning and influenced by the elements throughout the day.

RESULTS

Elephant dung attracted most *C. bacchus*, namely 124. The buffalo, cow and rhino dung attracted 69, 42 and 36 beetles respectively.

It was noticeable that as the temperature increased above approximately 30°C, the beetles sought shelter under the crust of the coarser elephant and rhino dung. Those that were feeding on the cow and buffalo dung either left with food or brood balls, or sought shelter. As the temperature

dropped in the middle to late afternoon the beetles returned, but this time the buffalo and cow dung were the most popular. The total number of beetles at the dung in the afternoon was less than the morning numbers (see fig 16).

Some of the beetles arriving at the elephant dung both in the morning and afternoon, fed for a short time and then left the elephant dung for the undergrowth or for the buffalo dung a few metres away. In the event of reaching the dung, they commenced brood-ball construction.

A total of 9, 3, 4 and 1, food balls was rolled on the elephant, buffalo, rhino and cow dung respectively. Ten brood balls were formed from buffalo dung and five from cow dung. None was formed with elephant or rhino dung.

7.3. EXPERIMENT 2

Experiment 2 began at 9h00 and ended at 15h00 when the small quantities of dung had dried up (a quarter the amount of dung used in experiment one was used in experiment 2). This experiment was carried out on the same day as Experiment 1, but over a shorter period of time. The temperature at the beginning of the experiment was 27.5 °C and the relative humidity 55% and at the end of the experiment the conditions were approximately the same at 27.3 °C and 51% relative humidity.

The same four dung types as above were placed 200 mm apart in the same area as in Experiment 1. This was to allow the beetles to receive a mixed aroma of the dung types and to make a "choice". The possibility existed that the dung placed further apart, in the previous experiment, would only attract the beetles from the area around it.

RESULTS

The elephant dung in Experiment 2 again attracted the most beetles in the initial stages (see table 13). As the dung dried out, the beetles left the elephant dung and started feeding on the cow and buffalo dung and making brood balls from it as it became more pliable. Two food balls were constructed from the elephant dung and one from the rhino dung. No food balls were constructed from buffalo or cow dung. Five brood balls were rolled from buffalo and cow dung while none was constructed from the other dung types. Only one beetle was seen on the rhino dung.

TABLE 13: Number of *Circellium bacchus* arriving at four dung types over 6 hours (9h00 - 15h00).

DUNG TYPE	1 HOUR	2 HOURS	3-5 HOURS	6 HOURS	TOTAL
ELEPHANT	10	10	0	0	20
BUFFALO	3	2	0	6	11
COW	3	6	0	8	17
RHINO	0	1	0	0	1

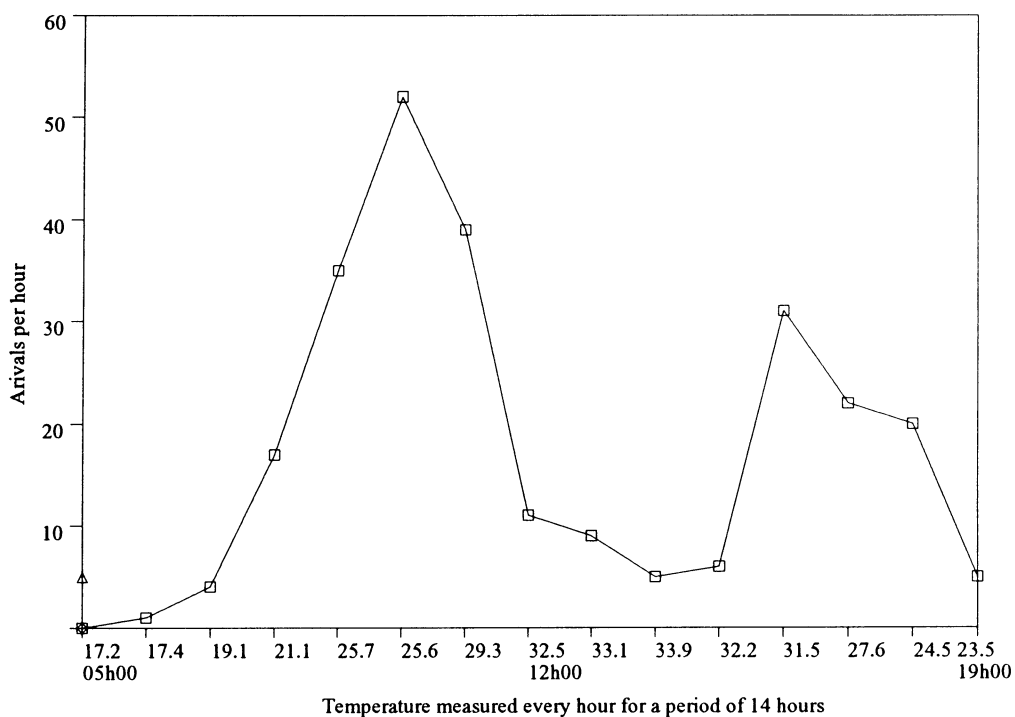


FIGURE 16: Total number of *Circellium bacchus* arriving at all types of dung per hour - temperature indicated hourly.

7.4 EXPERIMENT 3

Experiment 3 was carried out between 5h00 and 19h00 on two typical summer days, as well as between 6h00 and 18h00 on an atypical summer day. The temperature ranged, on the typical days, from approximately 18°C to 32°C and the relative humidity ranged from approximately 80% to 40%. On the atypical day, which was overcast, the temperatures were much lower, ranging between 14.7°C to 27.3 °C and the relative humidity between 80.1 and 41.1 %.

In this experiment the same four types of dung were placed the same distance apart as in Experiment 1. This time they were placed in buckets buried with the rims flush with the ground and approximately half filled with the dung. In this experiment the dung was disturbed every hour on the hour by breaking the crust, adding water and stirring it. This was to simulate the odour of fresh dung. The beetles were collected from each bucket on the hour and sexed. Temperature and relative humidity were also measured at these times. The captured beetles were only released on completion of the experiment.

RESULTS

The experiments carried out on the typical summer days showed that *C. bacchus* had a distinct feeding preference for elephant dung (see table 14). As buffalo and cattle are both grazers, they have similar dung consistency and attracted similar numbers of beetles. Because the beetles were removed from the dung during the experiment, and the dung was kept moist, very little brood ball construction was observed. On the atypical day (see table 15), far fewer beetles were attracted to the dung and these beetles spread themselves fairly evenly among the different dung types.

If water was continually added to the elephant and buffalo dung, the elephant dung attracted more beetles in the afternoon than it previously had, although still not as many as in the morning. As long as the buffalo dung was kept wet it was not as attractive to the beetles.

TABLE 14 : Number of *Circellium bacchus* arriving and feeding at four different dung types over a period of 14 hours (5h00-19h00) on two typical summer days.

	DAY 1	DAY 2
ELEPHANT	88	110
BUFFALO	62	54
COW	61	30
RHINO	46	24
TOTAL	257	218

TABLE 15: Number of *Circellium bacchus* arriving at four different dung types over a period of 12 hours on an atypical, cool summer's day.

DUNG TYPE	NUMBER OF BEETLES
ELEPHANT	22
BUFFALO	19
COW	20
RHINO	24
TOTAL	85

7.5 GENERAL DISCUSSION

In experiments 1, 2 & 3, the trends were the same. Elephant dung is preferred for feeding (see table 14) and the construction of food balls as seen in table 9. Buffalo, and to a lesser extent cow dung, is preferred for the construction of brood balls. Rhino dung attracted relatively few beetles. Elephant dung is more attractive in the mornings, while buffalo is best utilized a few hours after it has been deposited, usually in the mid-morning and late afternoon.

8. SEASONAL RHYTHMS

8.1. GENERAL INTRODUCTION

The south-eastern Cape has a climate intermediate between a summer and winter rainfall region with the possibility of rainfall, albeit very little, all year round. This allows dung beetles to be active to some extent throughout the year.

Annual rainfall between 200 and 1000 mm per annum is necessary for scarab activity, since most dung beetle species are found in areas that receive rainfall within this range. Not only is the annual rainfall of importance, but the period over which it falls must coincide with temperatures that are warm enough for beetle activity. The climate of the south-eastern Cape sometimes results in the temperatures being too low for activity during the periods when adequate rains fall.

Rainfall is important for releasing aestivating beetles from the hard-packed surface soil. Thus, the greater part of telecoprid distribution occurs in areas which have soil types described under the major headings as "sands or weakly developed soils on rock" (according to the Soil Map of S.A. 1973, cited in Tribe 1976). If the soil does not cement into a hard crust, as is the case with some of the littoral and near littoral sands, then high rainfall is not necessary for loosening the soil and allowing the beetles to escape (Tribe 1976). Summer rainfall is, however, not always essential to the emergence of certain species of telecoprids found in winter or "even" rainfall regions where the effective temperature is above 15°C (Tribe 1976).

Scarab activity patterns in the northern Transvaal are closely correlated with prevailing climatic conditions, with surface activity extremely low in the winter months. There is a distinct activity peak in mid-December, although the different species may peak at any time between October and March. Some species show two or even three peaks of activity in one season (Endrödy-Younga 1982). In the Nylsvley area, it was found that 56% of fresh dung was removed, during the eight summer months, while almost nothing was removed over the four winter months (Endrödy-Younga 1982). Dung beetle activity is also strongly influenced by short-term weather conditions. A cold windy spell even in mid-summer can cause a cessation of activity until conditions improve. Experiment were carried out to determine the effects of seasonal changes on the abundance and biology of *C. bacchus*.

METHODS AND MATERIALS

The same transects used for observing daily activity, (see chapter 6) were travelled frequently every month. The transects used to record seasonal abundance were always at the time of day most favourable for beetle activity i.e. early to mid morning and middle to late afternoon. Times were chosen when the temperature was cool to warm and the relative humidity high. This was in order to observe seasonal fluctuations in activity at uniform optimal daily temperatures and humidities.

Numbers of beetles observed per kilometre were recorded. This included beetles resting, walking, constructing and rolling food and brood balls. Teneral were easily distinguished from

mature adults by their characteristic shiny and soft exoskeleton. Monthly averages were obtained and plotted against rainfall and temperature for that period.

These data show peaks in seasonal abundance and are used as the basis for deriving the annual life history of *C. bacchus*.

8.2. RESULTS AND GENERAL DISCUSSION

The numbers of beetles per kilometre seen per month in the Park (see fig 17 and table 16) indicate much higher beetle activity in the warmer and wetter months of the year. There were two peaks in the seasonal abundance of *C. bacchus*; a small one in February/March and a larger one between August and November. These two peaks were separated by periods of low activity over the cold, dry, winter months and the hot, dry summer months.

The number of beetles active before rain was lower than after rain (see fig 18 and table 18). The amount of rain that fell as well as the temperature had a marked effect on the number of active beetles. Even precipitation as low as 1-2 mm caused a dramatic increase in activity. In table 18 and figure 18 the effect of rainfall is obvious, as activity before and after rainfall is clearly different. On average there was an eight-fold increase in the activity of *C. bacchus* after rain. December and January were extremely dry and therefore the beetle numbers were very low. After rain in these dry months the increase in beetle numbers seen was 20-fold. In November, after the good rains in October, the increase was only just over 3-fold. This was because beetle numbers were already high due to the wet conditions.

Brood and food ball construction and rolling, also coincided with the high activity periods experienced in the wetter, warmer months of the year (see table 17 and fig 19). Rain not only caused a substantial increase in the numbers of beetles, but in the summer months it also transformed the Park from a dry, brown dusty expanse to a lush green habitat with a carpet of grass and leafy forbs.

The elephants fed on these forbs as well as their normal diet of spekboom which was now even more moist and succulent than usual. This was seen in the very moist and fine dung produced by the elephants at this time. The texture of the dung resembled that of buffalo dung and was utilized by the beetles in the same way. The number of brood balls formed from elephant dung increased over this period from under 10 %, of the total brood balls constructed, to approximately 50 %.

Considering the abundance of smooth moist elephant dung available, as well as that of buffalo, and the high beetle activity, it is clear why the highest numbers of brood balls were rolled at this time. Edwards (1991) states that the periods following rain supply the dung beetles with high quality dung for feeding and breeding. This ensures a high quality resource for their offspring. This leads to the possible conclusion that the beetle's activity patterns are adapted to rainfall, not only to allow them to escape from the ground but also to take advantage of the abundant, moist, high quality dung of various sorts for breeding purposes.

Teneral were seen throughout the year, although the numbers were low (table 17). The low numbers seen could possibly be attributed to the fact that teneral hardly ever feed at the dung pat but feed on food balls underground.

The following figures and tables depict observational data collected throughout the year.

TABLE 16: The average number of *Circellium bacchus* per km, the average rainfall and temperature for the past 30 years, as well as rainfall and average maximum and minimum temperature each month in 1991. Rain in mm, temperature in °C.

MONTH	RAIN '91	AVE RAIN	AVE TEMP. '91	AVE TEMP.	NO/KM
JANUARY	29.7	31	30.7/16.7	29.0/ 16.3	1.7
FEBRUARY	13.3	37	30.0/17.6	29.2/16.5	2.6
MARCH	9.4	48	30.1/15.5	28.1/15.3	2.5
APRIL	1.5	38	26.0/12/0	*	0.74
MAY	15.1	37	23.5/8.5	*	1.0
JUNE	12.9	34	20.3/8.2	21.9/5.9	0.5
JULY	4.9	30	21.9/9.1	21.9/5.2	0.04
AUGUST	38.3	28	20.2/7.4	22.4/6.2	3.1
SEPTEMBER	8.0	23	24.7/8.1	23.5/8.7	3.5
OCTOBER	109.3	37	24.4/12.3	24.7/10.7	8.24
NOVEMBER	17.0	36	25.7/13.6	26.1/12.8	6.6
DECEMBER	15.5	28	28.1/14.7	*	2.9
TOTAL	274.9	407			

*** - Data unavailable**

TABLE 17: Total numbers of *Circellium bacchus* brood and food balls and tenerals counted during transects each month.

MONTH	FOOD BALLS	BROOD BALLS	TENERALS
JANUARY	22	18	4
FEBRUARY	25	38	0
MARCH	12	45	0
APRIL	5	2	8
MAY	8	2	6
JUNE	2	3	4
JULY	0	0	0
AUGUST	15	6	4
SEPTEMBER	16	25	3
OCTOBER	16	38	3
NOVEMBER	25	78	0
DECEMBER	17	20	4
TOTAL	163	275	36

TABLE 18: Average number of *Circellium bacchus* counted per km three days before and three days after rain.

MONTH	BEFORE	AFTER
JANUARY	0.22	4.4
FEBRUARY	1.44	10.0
MARCH	0.6	5.1
APRIL	0.14	2.8
MAY	0.48	2.8
JUNE	0	1.4
JULY	0	0.07
AUGUST	0.9	12.0
SEPTEMBER	0.9	16.0
OCTOBER	1.9	17.0
NOVEMBER	3.2	10.6
DECEMBER	1.1	3.7
TOTAL	10.88	85.87
AVERAGE	0.9	7.2

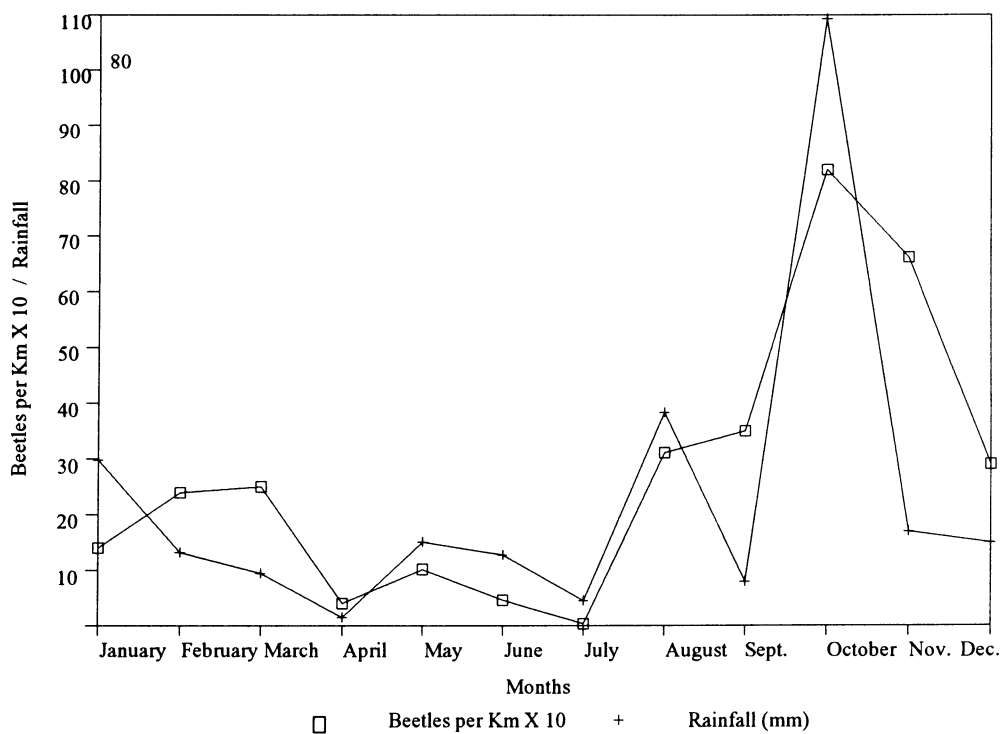


FIGURE 17: The number of *Circellium bacchus* per km per month, correlated against monthly rainfall.

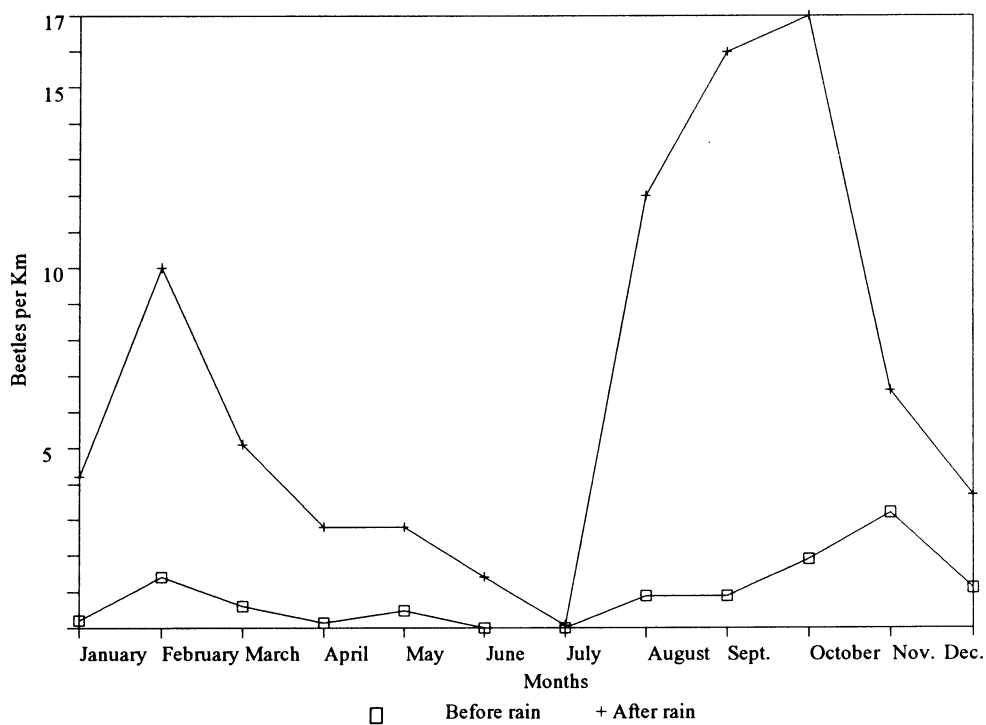


FIGURE 18: The number of *Circellium bacchus* per km seen three days before and after rain.

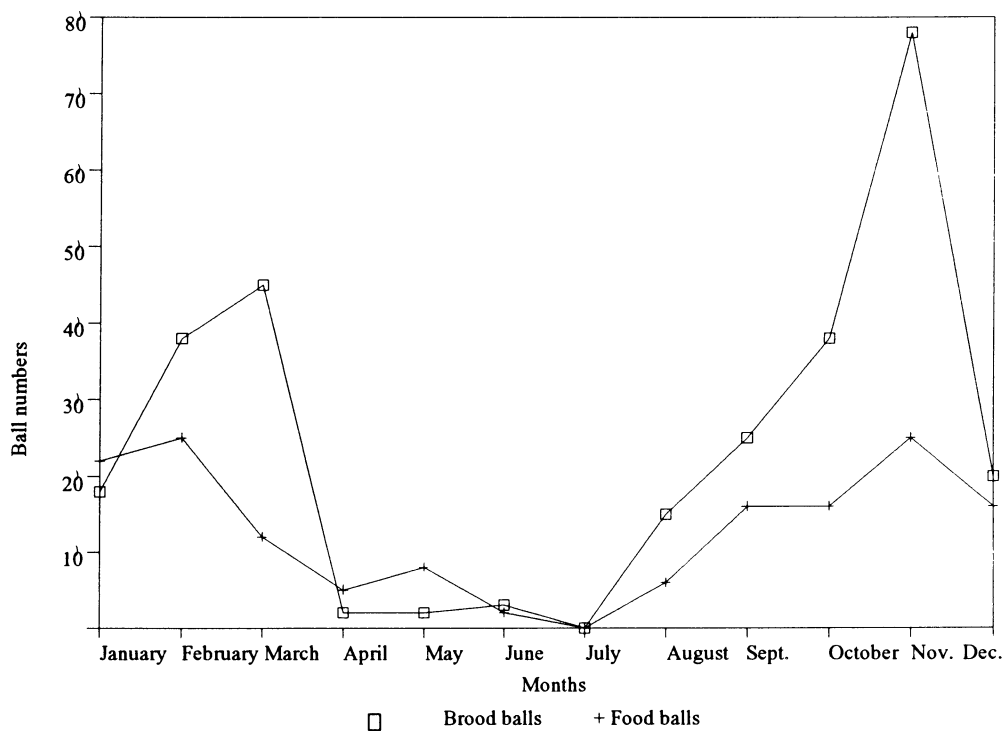


FIGURE 19: The number of food and brood balls rolled by *Circellium bacchus* per month during 1991.

9. CONSERVATION

"The road to extinction must pass through rarity" (Ferrar 1989)

Man has been the main cause of the modification and degradation of virtually all the ecosystems of southern Africa. It seems as if these changes are most significant in the inability of these affected ecosystems to support the populations they once did. Drastic reductions in the distribution of many species indicate that man's negative influence must be kept to a minimum if the biotic diversity of southern Africa is to be preserved (Macdonald 1989). Conservative estimates state that 20-25% of existing species will be destroyed by man within the next quarter of a century (Lovejoy 1986).

Some of the benefits proposed for the preservation of biotic diversity include: the interdependence of nature (each species being an integral part of the holistic ecosystem); the resilience of diversity to perturbation; the usefulness of species either now or in the future; the scientific and cultural value of species; and the aesthetic or collector's urge to preserve all rarities (Bond 1989).

Management objectives that aim to preserve genetic diversity as opposed to species diversity are often too general to be workable. It is not uncommon to find large morphological, but negligible genetic changes, in closely related species (King & Wilson 1975). The taxonomist's view of diversity does not always coincide with the view of other disciplines and interests (Raven, Berlin & Breedlove 1971). Diversity, like beauty, lies in the eye of the beholder (Bond 1989).

Conservation biologists consider species to be rare in terms of three fundamental attributes. These are: habitat specificity (specialization); geographic range (distribution); and local population (abundance). These attributes provide a means of ranking levels of rarity in species (Ferrar 1989).

The International Union for the Conservation of Nature (IUCN) provides a list of categories of threat ranging from endangered to threatened. Ferrar (1989) suggests a more refined order of the different categories of rarity by considering the ability of conservation management to influence these attributes. **Category one** includes the organisms most vulnerable to extinction pressure. These include highly specialized and restricted endemics, with markedly reduced abundance. The **second category** consists of highly specialized and restricted endemics, with local populations that are not critically reduced. **Category three** contains highly specialized species with reduced populations not restricted in their distribution. **Category four** includes species that are less specialized or non-specialized, but have limited distribution and reduced abundance. Species in the **fifth category** are localized endemics that are neither habitat specialists nor critically reduced in numbers. Category six consists of specialized species with wide distribution and populations not reduced to levels that pose any threat. Species in category seven are generalist species of wide distribution but with markedly reduced populations.

Norton (1986) supplies a number of characteristics which increase the likelihood of endangerment and/or extinction. They are:

- 1) rarity
- 2) large individual size
- 3) relative height in the trophic level
- 4) low dispersability, low fecundity and long individual lifespan
- 5) specialization of habitat
- 6) mutualism and coevolution
- 7) existence in ecosystems of high diversity.

9.1. DISCUSSION

According to Ferrar (1986), most conservation biologists use specialization, distribution and population abundance as the most important criteria for determining the rarity of a species. To ascertain to which of Ferrar's seven categories *C. bacchus* belongs, we must evaluate the beetle in terms of each of these criteria.

Specialization

— *C. bacchus* is a habitat specialist as it is most often found in areas of relatively low rainfall (even though its activity is governed by rainfall), sandy soils and dense bush. It seems unable to survive in areas where the bush has been cleared or in areas of higher rainfall which often support many more flying species, capable of outcompeting *C. bacchus* for food.

— *C. bacchus* has been seen feeding on almost any available dung type in the Addo Elephant National Park, but has a definite feeding preference for the coarser elephant dung. It seems as if *C. bacchus* is an opportunist, feeding on whatever dung is available, but if given the choice, specializes on moist elephant dung for feeding, and buffalo dung for breeding.

— The daily and seasonal activity patterns of *C. bacchus* are determined by temperature and rainfall and thus *C. bacchus*'s activity is greatly influenced by climatic changes. This specialised behavioural trait allows *C. bacchus* to be active in mild to warm temperatures and also allows escape from extremes in hot and cold.

— *C. bacchus* is a breeding specialist producing only a single offspring at a time and, at most, two per year, and exercising intensive brood care. The role played by the sexes, where the female is entirely responsible for the construction and rolling of brood balls is something no other scarab does.

— Another specialized characteristic is the loss of flight in the beetle. This may be due to a constant and abundant food source, the dense vegetation and the lack of predation and competition from other species. This loss of flight may be important in the conservation of energy and moisture.

Distribution

— The distribution of *C. bacchus*'s is restricted to national parks and reserves within the south-eastern Cape. Evidence from literature and specimens in museums suggest that this distribution has shrunk dramatically over the last 20 - 50 years.

Population abundance

— *C. bacchus* can be found in large numbers, in the Addo Elephant National Park, especially after rain.

From the above discussion it is evident that *C. bacchus* is specialized in many aspects of its biology. It has a reduced distribution, is endemic to the south-eastern Cape with an abundant local population in the Addo Elephant National Park. This suggests that *C. bacchus* would fall into Ferrar's second rarity category.

C. bacchus complies with five of the seven characteristic which increase the likelihood of endangerment or extinction, supplied by Norton (1986). *C. bacchus* is rare: it has a large individual size relative to other scarabs; is reasonably high in the trophic level considering the fact that it feeds on the dung of large herbivores; it has very low dispersability and fecundity; they have an extended life-span and are habitat specific. These characteristics make *C. bacchus* an extremely good candidate for endangerment and therefore it should receive priority in conservation programmes and management plans.

Recent conservation efforts have been largely restricted to conserving the big or the beautiful. Enlisting support to save a large mammal is far easier than for some rare spider or worm (Kellert 1986). The attitude of most people is that of "vertebrate chauvinists". Invertebrates are not perceived to be experiencing beings and therefore people feel no obligation to safeguard their welfare (Kellert 1986).

There has been much debate as to whether one should conserve diversity at the genetic, species or habitat level. The plight of *C. bacchus* is somewhat unique if not ironic, as not only was it indirectly preserved along with the Addo elephants in their Valley Bushveld habitat, but it is now being killed off in large numbers, in the very area which resulted in its preservation.

9.2. MANAGEMENT AIMS

Although the Addo Elephant National Park supports a large and seemingly healthy population of *C. bacchus*, it should remain a priority-species in the park. This assessment is based on the limited number of healthy populations found at other localities. It is imperative that other populations of *C. bacchus* thrive in areas such as the Andries Vosloo Kudu Reserve and the De Hoop Nature Reserve. These populations can be used as a reserve genetic pool if a population crash was to occur in the Addo Elephant National Park.

C. bacchus needs to remain a priority species in the Park as it falls into Ferrar's (1986) second category of rarity. It also complies with many of Norton's (1986) characteristics which increase the likelihood of endangerment or extinction, as well as being vulnerable to habitat modification and the decimation of large herbivores.

The leaflets and other publicity drives should be continued by the staff in the Park. Monitoring should also continue to ascertain fluctuations in the numbers of *C. bacchus* beetles in the Park, as well as the number of road fatalities.

Of paramount importance is a new or revised system of road scraping or grading. Firstly an assessment of the condition of the roads after rain should be done to ascertain whether it is indeed necessary to scrape them. Secondly, the method of scraping needs some careful thought. Mention has been made of an attachment to the grader's blade that can circumvent the construction of a steep cliff-like side to the road. Alternatively, a heavy roller could be used to flatten the sides. Flattening the sides of the road would be to the advantage of not only the beetles, but also to the fairly large tortoise population in the park. Thirdly bush clearing such as was done in the "Bokamp" area should be kept to an absolute minimum, as the beetles rely heavily on the vegetation for protection against the elements, and are seldom found in areas denuded of vegetation. Lastly, due to the dependence of the beetle on buffalo dung for breeding purposes, the buffalo population should be kept at its highest safe carrying capacity without affecting any of the other priority species in the Park.

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