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Biology and ecology of *Circellium bacchus* (Fabricius 1781) (Coleoptera Scarabaeidae), a South African dung beetle of conservation concern

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The dung beetle *Circellium bacchus* (Fabricius 1781) was once widespread in southern Africa but is now restricted to a few isolated fragments in the south of the Western and Eastern Cape Provinces of South Africa, with the largest population present in the Addo Elephant National Park (AENP). The beetles' activity is governed by precipitation and temperature; 18-26 ºC and high relative humidity favour activity. The beetles are generalist dung feeders and breeders but have clear preferences for elephant dung for feeding, and buffalo dung for breeding. Fecundity is the lowest recorded for a dung beetle, with a maximum of two but on average only one progeny produced per year. The species is unique amongst ball-rolling (telecoprid) dung beetles in that females initiate, form and roll brood balls, something carried out exclusively by males in other species. The beetles are habitat specialists preferring dense undisturbed vegetation to more open, disturbed vegetation. The species should be considered rare because of its narrow geographical range, restricted biotope specificity and biological attributes. Furthermore, it complies with most of the characteristics that increase its likelihood of endangerment or extinction and qualifies as "vulnerable" according to IUCN criteria of threatened species.

KEY WORDS: *Circellium bacchus*, conservation, ecology, scarab, vulnerable.

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INTRODUCTION

Circellium bacchus (Fabricius 1781) was among the earliest beetles described from southern Africa. Despite this and the fact that it is large and conspicuous and was formerly widespread in southern Africa (Ferreira 1968), relatively little is known of its biology (but see Chown et al. 1995). It is currently restricted to small, isolated, densely vegetated areas in the south of the Eastern and Western Cape Provinces of South Africa, with a relatively large population present in the Addo Elephant National Park (AENP). At 22-47 mm long, they are among the largest dung beetles in Africa, and globally. They are flightless, diurnal ball-rollers (telecoprids) that feed mostly on the dung of various large native herbivores and cattle.

Circellium bacchus has been something of an entomological and conservation enigma in South Africa for years. A considerable body of anecdotal evidence has accumulated in scientific papers, conservation officials' reports, the media, student theses and museum collections about their putative range contraction, their low reproductive rate and their probable dependence on elephant (*Loxodonta africana* Blumenbach 1797) dung for survival (Ferreira 1968, Tribe 1976, Nicolson 1987). The beetle's range contraction was thought to be linked to the decrease in elephant distribution because of the purported association between *C. bacchus* and elephants. Because few specimens have been recorded outside the AENP in recent times, it was thought to be restricted to the AENP which added to the contentions about the beetles' dependence on elephant dung.

Ferreira (1968) commented on its distribution, and Tribe (1976), in an unpublished thesis, briefly mentioned its supposed feeding preferences, commented on brood ball formation and speculated on its likely fecundity. Nicolson (1987) determined that *C. bacchus* is an ectotherm and that this dependence on external heat sources would reduce its ability to compete against large and active endothermic ball-rolling scarabs, consequently limiting its distribution to areas where no or few endothermic telecoprids occur.

Because of its once widespread but now localized distribution, *C. bacchus* has been perceived to be endangered. In 1992 legislation was passed in the Cape Province (Proclamation no. 24/1992) to protect it from exploitation. The species was already protected in the AENP, but the provincial legislation was apparently intended to supplement this and protect individuals that occur outside of the Park.

The population in the AENP was apparently healthy. However, with increasing numbers of tourists visiting the park a problem in the form of beetle road fatalities from vehicles has arisen. Because of the dense bush in the park, elephants frequently walk along the roads which leads to an accumulation of dung there and a consequent concentration of the beetles where large numbers are sometimes killed. Concern by Park's Board officials about the effect that this may be having on the beetle population precipitated a request to us to study the biology of *C. bacchus* so that its ecological needs could be considered and accommodated in park management programmes.

The principal aim of this project was consequently to study the biology of *C. bacchus* in the AENP. The emphasis of the study was on the beetles' daily and seasonal activity, breeding behaviour and success, and the environmental factors that regulate or control its behaviour and possible survival. Furthermore, we investigated habitat and dung preferences of *C. bacchus* in AENP as well as in Buffalo Valley Game Farm, a privately owned game farm near Knysna where another stable population of this beetle is found. The information obtained would then be used to make inferences about the factors that determine the distribution and abundance of this dung beetle inside and outside the park and to allow speculation on its conservation status.

MATERIALS AND METHODS

The beetles

Circellium is a monotypic genus and has no known close relatives. Janssens (1938) and Ferreira (1968) treated it as belonging to the subtribe Scarabaeina of the tribe Scarabaeini, but Cambefort (1978) transferred it to the Canthonini. Mostert & Scholtz (1986) and Scholtz & Howden (1987) followed Cambefort.

Distribution

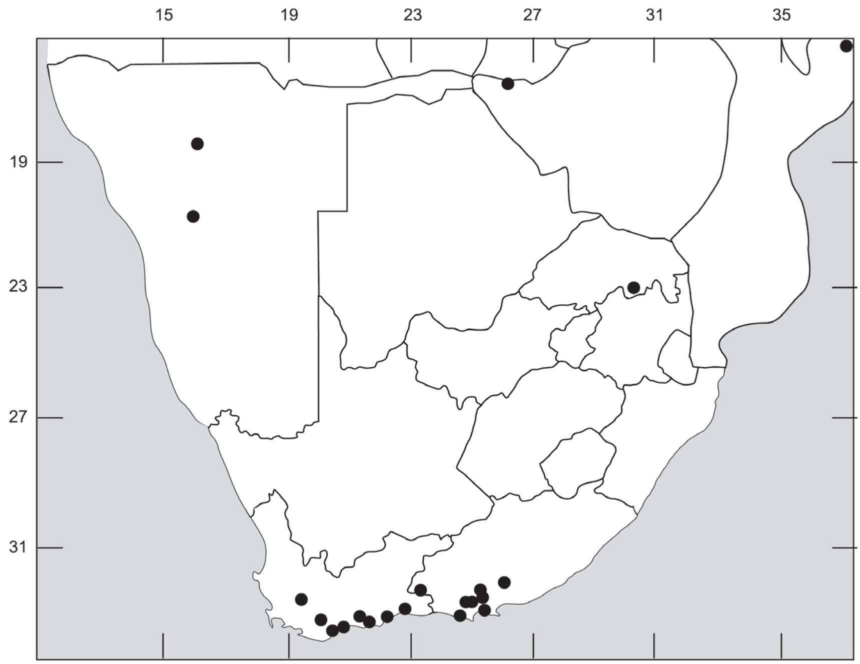
Most *C. bacchus* locality records from the literature as well as those on specimens housed in the local and major European natural history museums were plotted on a map of southern Africa (Fig. 1). The record cited by Ferreira (1967) from Lumbo (Zambesia, northern Mozambique) was out of range of the plotted map. A distinction was made between those records collected prior to 1968 (Fig. 1A) and those collected subsequently (Fig. 1B). The records from before 1968 were treated as representing "past" distribution whereas those from after 1968 were considered to represent "present" distribution. During the course of this study many of the sites where beetles had previously been found were visited and beetles sought.

Study areas

This study was conducted between January 1991 and January 1997 in the following localities:

(a) The Addo Elephant National Park, located in the Eastern Cape Province of South Africa (33°28'S 25°45'E). The core of the park is a relatively small pristine area comprising more than 12 000 ha of mostly Xeric Succulent Thicket vegetation (Low & Rebelo 1996), one of the geographically small vegetation types that make up the Thicket Biome of southern Africa (Lubke et al. 1986), in an otherwise greatly disturbed farming region. The park was established in 1931 to conserve the few remaining individuals of the fast-dwindling local elephant population. Their numbers have increased steadily over the years (to over 250) resulting in a high density of elephants in the park. By 2003 the total size of the AENP including contractual areas had increased to 150000 ha.

A



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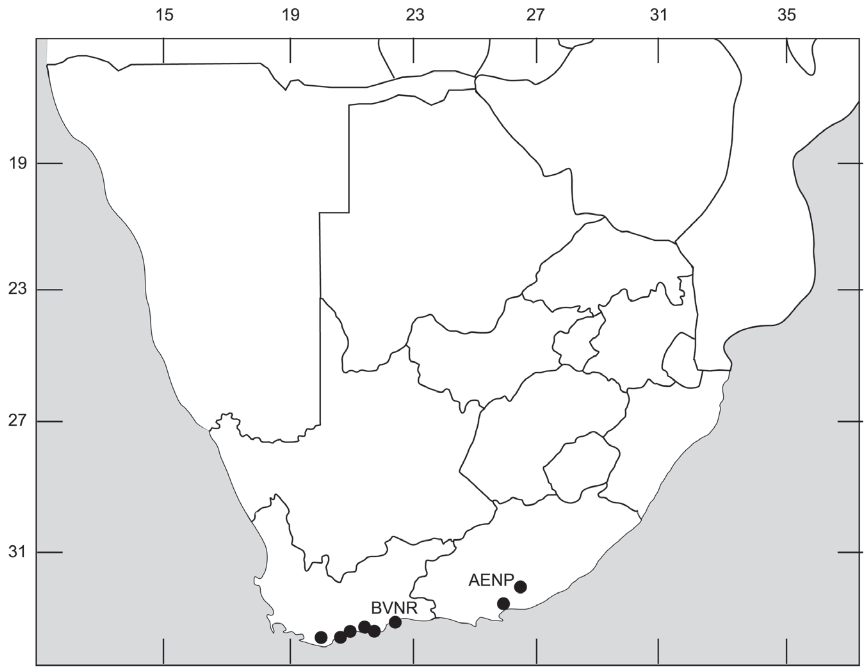

Fig. 1. — A, Map showing distribution of *Circellium bacchus* based on specimens collected before 1968. B, Present distribution of *Circellium bacchus*, AENP marks the Addo Elephant National Park, BVNR marks the Buffalo Valley Nature Reserve.

The park lies in a semi-arid area with mean annual rainfall of about 400 mm. Although rain may occur throughout the year, rainfall is characteristically trimodal, with a major peak in autumn (March/April) and smaller peaks in late winter (August) and early summer (October/November). Rain is mainly in the form of light showers. The mean daily maximum temperature is about 29 ºC in January (but temperatures often exceed 40 ºC in summer) and about 21 ºC in July. The mean daily minimum temperatures are about 16 ºC in January and about 5 ºC in July.

Vegetation in the park is characterised by dense, evergreen, semi-succulent shrub thickets that vary between 3-4 m in height. Spekboom (*Portulacaria affra*) is the dominant woody plant species and the elephants' main food item (GROBLER & HALL-MARTIN 1982).

Besides elephant, the park also hosts black rhinoceros (*Diceros bicornis* Linnaeus 1758), buffalo (*Syncerus caffer* Sparrman 1779) and various large and small antelope species. Elephant and rhino are mainly browsers, buffalo are almost exclusively grazers and the other antelope species consist of browsers and grazers.

Three different habitat types within the AENP were identified, representing the most divergent combinations of herbivore presence and different plant communities, for the trials on habitat and dung preferences:

(I) Pristine Xeric Succulent Thicket — this area was flat, northeast facing without any sign of erosion and supposedly represented the natural habitat for *C. bacchus* with exposure to mega-herbivores.

(II) Botanical Reserve — this area was characterized by pristine xeric succulent thicket where only herbivores up to the size of kudu (*Tragelaphus strepsiceros* Pallas 1766, 200 kg) have access (the mega-herbivores were excluded from this area and therefore trampling was less pronounced).

(III) Alva — this area used to be a privately owned cattle farm where the natural bush had almost entirely been transformed into artificial pastures for grazing. In 1991 it was added to the AENP and by the time of this study various large herbivores including elephant and buffalo were grazing on the lush grasses growing in this area.

(b) Buffalo Valley Game Farm. This privately owned 175 ha game farm is situated 12 km from Knysna (34º05'S 22º45'E) in a fynbos and dune forest area on the south coast of the Western Cape. It falls within the winter rainfall area with precipitation peaks in midwinter around June and July (DAVIS 1987). This specific fynbos region has not been rigorously described in terms of floristics and structure (COWLING & RICHARDSON 1995). Between the shallow limestone and the deeper neutral sands the communities vary considerably in species composition. Dominant vegetation types are *Protea obtusifolia* (limestone sugarbush), *Chrysanthemoides monilifera* (bietou), *Leucadendron coniferum* (dune conebush) and *L. galpinii* (COWLING 1992).

The once abundant wildlife that occurred in the surrounding areas included big herbivores such as buffalo (*Syncerus caffer* Sparrman 1779), but the only natural remnants of this today are bushbuck (*Tragelaphus scriptus* Pallas 1766), grysbok (*Raphicerus sharpei* Thomas 1897) and grey rhebok (*Pelea capreolus* Forster 1790). Bontebok (*Damaliscus pygargus* Pallas 1767), Burchell's zebra (*Equus burchellii* Gray 1824) and black wildebeest (*Connochaetes gnou* Zimmerman 1780) have been re-introduced in the recent past.

Three different areas were identified for the trials on habitat and dung preferences with respect to the herbivorous plant layer; none showed signs of erosion:

(I) A north-east facing concave grassveld with dense covering by *Stenotaphrum secundatum* (coastal buffalo grass), *Cynodon dactylus* (couch grass), *Setaria verticillata* (bur bristle grass) and *Sporobolus africanus* (ratstail dropseed). In this area a fair amount of trampling was evident.

(II) Dense fynbos on the periphery of sandy dunes with a slight slope leading up the dune side that led to the beach. In this area the canopy cover consisted mainly of *Acacia saligna*(golden wreath wattle), *Rhus crenata*(dune crow-berry), *Hakea suaveolens* (sweet hakea) and *Asclepias fruticosa* (milkwood); a thick layer of litter and decomposing detritus covered the ground.

(III) An open, clear-cut area with secondary regrowth of the natural fynbos (herbaceous cover) along one of the roads.

Activity pattern

Based on preliminary data which indicated approximate activity periods, the minimum temperature before beetles became active and maximum temperature above which no activity took place, the beetles' activity was monitored during slow daily drives from January 1991 until December 1991 along a designated 9 km route. Transects were driven at various times and at different ambient temperatures and relative humidities (RH) during the activity cycle, to try to cover the complete cycle. Data were recorded as the number of beetles encountered per kilometre en route.

Furthermore, the same transects were travelled on selected mornings or afternoons every month when the temperature was uniformly cool to warm and the relative humidity high. The purpose of the selection of transect samples from comparable days through out the year was to assess the amount of seasonal fluctuation in activity.

Feeding biology

Whenever beetles were encountered at dung in the field it was recorded how many were feeding on the dung, or forming food or brood balls. Furthermore, the dung type as well as ambient temperature and humidity were documented.

Breeding biology

Breeding behaviour was observed in the field and in the laboratory. Life cycle data were obtained from captive beetles that were maintained in large drums with moist soil and a plentiful supply of fresh dung. As soon as pairs of beetles formed and started to roll balls, they were placed in terraria measuring 60 × 30 × 30 cm and 3/4 filled with moist soil. Pairs of beetles found rolling balls in the field were also placed in breeding containers. Nests were excavated and balls were removed and opened periodically. The number of days elapsed since burial, and the life cycle stage present were recorded.

Habitat preferences

Six transects consisting of six 1-litre bucket pitfall traps each were placed at 20 m intervals in each of the three identified habitats in AENP as well as in Buffalo Valley Game Farm. The traps were baited with 200 g of either fresh elephant dung (in AENP) or cattle dung (in Buffalo Valley Game Farm). The trapping was done from 19-23 December 1996 in AENP and from 21-26 January 1997 in Buffalo Valley Game Farm. The traps were checked hourly starting at sunrise and the number and sex of *C. bacchus* specimens captured in each pitfall trap was documented. The beetles were kept overnight and released at the end of the experiment.

Dung preferences

(a) Breeding

Trials to determine possible preferences in dung utilization for brood ball construction were conducted on 18 and 19 December 1996 and 11-13 March 1998 in the Botanical Reserve in AENP. At 16 different sites spaced apart by at least 5 m, four different dung types were placed in 2 × 2 m square grids. Per grid one litre of fresh elephant, rhinoceros, buffalo and cattle dung was used and the dung types were positioned in randomised order relative to each other. The 16 sites were checked half-hourly and the number of formed brood balls was noted. Statistical analysis of these data was carried out using the non-parametric Tukey Type multiple comparison.

(b) Feeding

During the above-described trial conducted on 11-13 March 1998, beetles feeding on the dung were collected on the half-hourly checks; and after counting and sexing them they were released at the end of the experiment. These data were analysed using the Friedman two-way analysis of variance test. To determine whether significant differences occurred between samples the Friedman test was implemented.

RESULTS

The beetles

Adults vary greatly in length (range 22-47 mm, $\bar{x}$ = 36.3 mm, n = 80). Males ($\bar{x}$ = 37.5 mm, ± 5.3 mm, n = 40) are slightly larger than females ($\bar{x}$ = 35.1 ± 4.1 mm, n = 40) but weigh slightly less (males: $\bar{x}$ = 6 ± 2.0 g, n = 81; females: $\bar{x}$ = 6.2 ± 1.7 g, n = 67). Males and females can be distinguished by the width of the sixth and seventh abdominal sternites; the seventh is twice the width of the sixth in females whereas they are of similar width in males. The sizes of the different larval instars were given by Scholtz & Coles (1991).

Distribution

Circellium bacchus is currently only known from a few isolated localities in the Western and Eastern Cape Province of South Africa (Fig. 1B). Besides the large population in the AENP there are small, apparently healthy, but widely separated populations present in the Grootbos Private Nature Reserve (34°25'S 19°18'E), Bredasdorp (34°32'S 20°02'E), De Hoop Nature Reserve (34°29'S 20°29'E), Riversdale (34°06'S 21°16'E), Stilbaai (34°21'S 21°23'E), Buffalo Valley Game Farm (34°02'S 23°02'E) in the southern part of the Western Cape Province and the Andries Vosloo Kudu Reserve (33°07'S 26°40'E) in the Eastern Cape Province.

Activity pattern

The beetles were seasonally most active during the warm to hot months and after rain (Tables 1 and 2). Daily activity also reflected this dependence on moderately high ambient temperatures and relative humidity (Fig. 2, Table 3).

Feeding biology

The beetles either fed at a dung source or formed and rolled food balls away to be eaten in a protected location. Elephant, buffalo (and cattle dung, when avail-

Table 1.

Mean number of *Circellium bacchus* specimens (per km, of two daily 9 km-transects), the average rainfall and temperature for the past 30 years, as well as rainfall and average maximum and minimum temperature each month in 1991; rainfall in mm and temperature in ºC. * = data unavailable.

Month	Rain 1991	Average Rain	Temp. 1991	Average Temp.	n / km
January	29.7	31	30.7 / 16.7	29.0 / 16.3	1.70
February	13.3	37	30.0 / 17.6	29.2 / 16.5	2.60
March	9.4	48	30.1 / 15.5	28.1 / 15.3	2.50
April	1.5	38	26.0 / 12.0	*	0.74
May	15.1	37	23.5 / 8.5	*	1.00
June	12.9	34	20.3 / 8.2	21.9 / 5.9	0.50
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	3.10
September	8.0	23	24.7 / 8.1	23.5 / 8.7	3.50
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	6.60
December	15.5	28	28.1 / 14.7	*	2.90
Total	274.9	407			

Table 2.

Mean number of active *Circellium bacchus* specimens (per km, of two daily 9 km-transects) 3 days before and 3 days after rain.

Month	Before Rain	After Rain
January	0.22	4.40
February	1.44	10.00
March	0.60	5.10
April	0.14	2.80
May	0.48	2.80
June	0.00	1.40
July	0.00	0.07
August	0.90	12.00
September	0.90	16.00
October	1.90	17.00
November	3.20	10.60
December	1.10	3.70
Total	10.88	85.87
Average	0.90	7.20

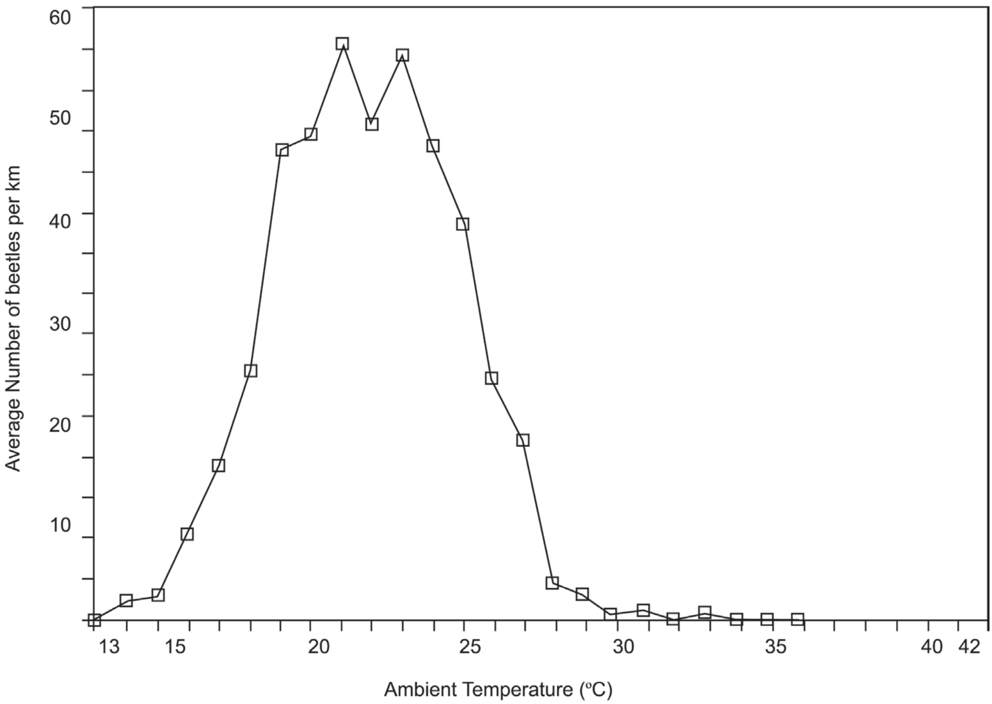

Fig. 2. — Activity of *Circellium bacchus* (measured in mean number of beetles per km transect, based on observations over 12 months) in dependence on ambient temperatures (measured in degree Celsius).

able) and rhino dung were most commonly utilized, although various antelope droppings, if sufficiently moist, as well as monkey, human, hare and ostrich faeces were fed on. Under optimal conditions beetles wander around in an apparently aimless manner until dung or its scent is located. Beetles approached a dung source upwind from distances of up to about 100 m.

Beetles began feeding at temperatures as low as 14 °C and ceased when the temperature reached about 38 °C (Fig. 3). As the ambient temperature rose, the number of beetles at dung increased. Food balls were constructed as temperatures rose during late morning and again when it was cooling down in late afternoon. Immediately after arriving at dung the beetles burrowed into it or started forming a ball from it. The type of behaviour depended on the ambient temperature, the burrowing occurring in response to the lower temperatures and the ball-construction as a result of higher temperatures. Other factors that played a role in the behaviour exhibited were the type and state of the dung as well as the sex and maturity of the beetle. Teneral (not yet fully matured) adults never fed at the dung but always constructed and rolled a food ball that was eaten in a protected location.

The plasticity and the moistness of the dung affected the beetles' behaviour towards it; for example, feeding on elephant dung occurred most often in the morning while the ambient relative humidity was high, the temperatures cool and the moisture content of the dung at its highest (Fig. 4). Buffalo dung, on the other

Table 3.

Circellium bacchus activity reflected in total numbers of beetles (total n) and mean numbers of beetles ($n\ km^{-1}$) observed along eleven 9-km transects on a day with optimum conditions (22 October 1991) at different ambient temperatures (Ta = in the shade, Ts = in the sun) and relative humidities (RH).

Temperature (°C)		RH (%)	Total n	$n\ km^{-1}$
Ta	Ts			
15.0	15.0	90	42	4.6
17.0	18.5	80	81	9.0
19.0	22.0	80	129	14.3
20.0	24.0	70	160	17.7
23.0	27.0	60	185	20.5
24.0	29.0	58	190	21.1
25.0	32.5	55	175	19.4
27.0	34.0	45	25	2.7
29.0	35.5	40	17	1.9
31.0	36.0	39	4	0.4
33.0	37.0	36	0	0.0

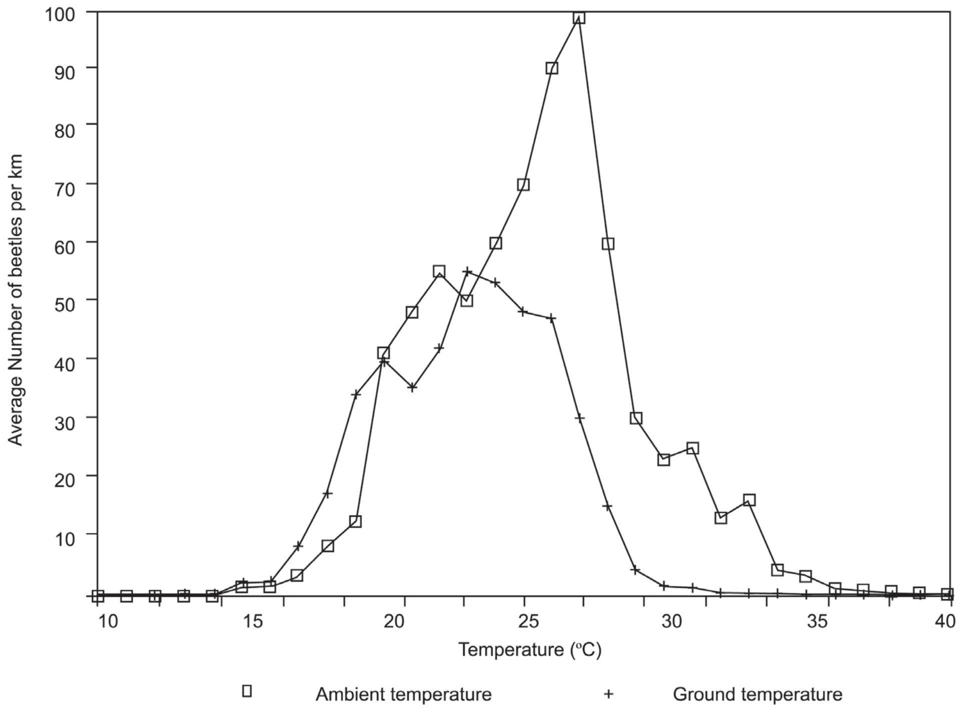

Fig. 3. — General feeding activity of *Circellium bacchus* (mean number of beetles per km transect, based on observations over 12 months) plotted against the ambient and ground temperature (in degree Celsius).

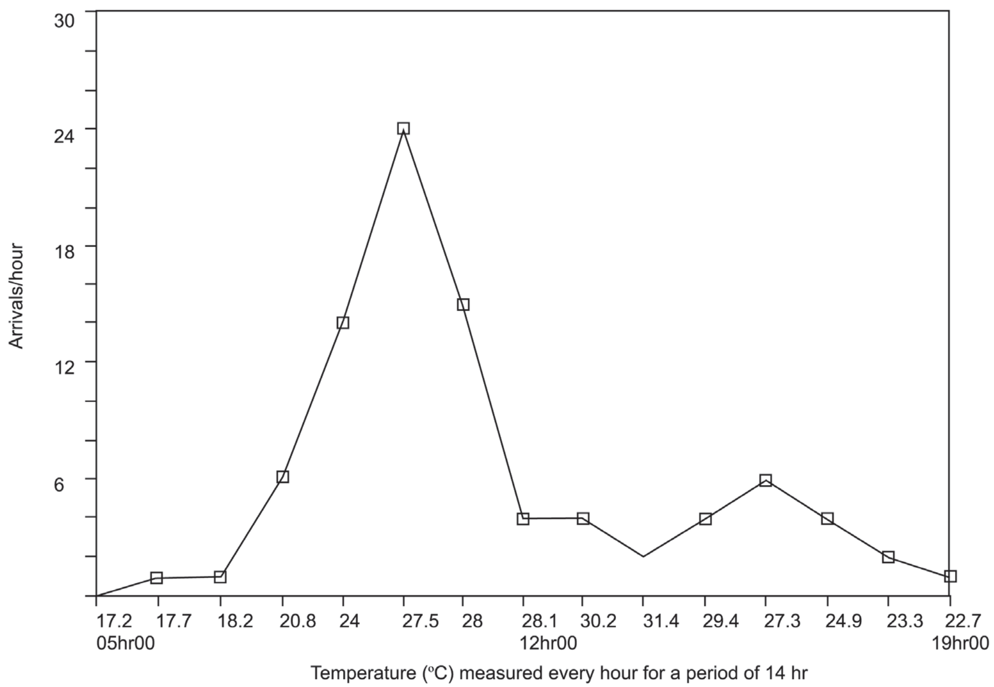

Fig. 4. — Mean number of *Circellium bacchus* specimens arriving at elephant dung pads per hour (based on observations over 12 months) plotted against ambient temperature (in degree Celsius).

hand, was colonised later in the day (Fig. 5), when the dung had dried a little and become more pliable and thus easier to roll into balls.

Food balls, constructed from various dung types, were rolled by males and females. They varied in diameter between 16-33 mm ($\bar{x}$ = 25.3 ± 4.5 mm, n = 42) and weighed between 0.9-18 g dry ($\bar{x}$ = 5.2 ± 3.8 g, n = 25). The balls were fashioned in from 3-15 min ($\bar{x}$ = 5.7 min, n = 30), depending on the temperature and the type of dung. They were fashioned most quickly at temperatures of between 24 and 28 ºC. The food balls were either fed on in a protected place such as under a bush, or were buried at between 2-10 cm below the soil surface where they were fed on. The beetles remained underground with a food ball for 7.6 days on average (range 3-14 days, n = 20).

Breeding biology

All breeding behaviour revolves around the possession of a dung ball. Only females constructed brood balls. When a female was (presumably) ready to breed, climatic conditions were favourable and she was in possession of an adequate amount of suitable dung, she would initiate brood ball construction. The diameter of brood balls ranged between 43.5-64.2 mm ($\bar{x}$ = 53 mm, s = 5.5 mm, n = 50). Their dry mass ranged from 22-85 g ($\bar{x}$ = 41.2 g, s = 14.3 g, n = 40).

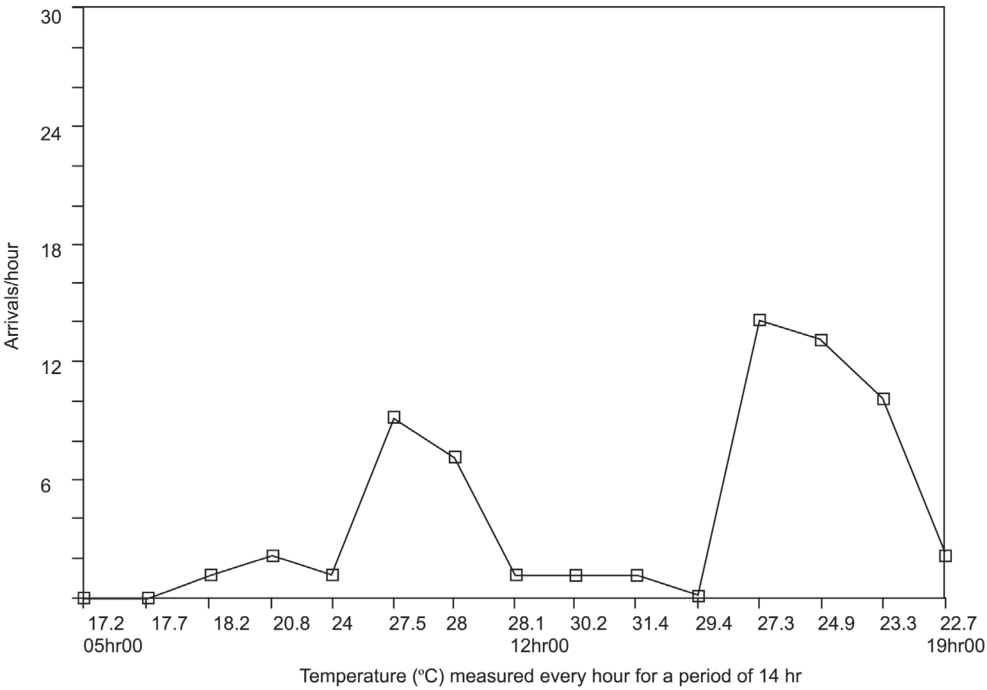

Fig. 5. — Mean number of *Circellium bacchus* specimens arriving at buffalo dung pads per hour (based on observations over 12 months) plotted against ambient temperature (in degree Celsius).

Construction of the ball was divided into cutting and shaping phases. The clypeus and fore tibia were used extensively while cutting the dung mass into a manageable size, and the middle and hind legs were used to shape it. The middle and hind legs gauged the size of the ball (thus small beetles formed small balls and ultimately gave rise to small progeny). The crude dung mass was shaped and patted into a sphere, usually with the fore tibiae. Ball-making took 47 min on average (s = 20 min, n = 20) and the patting process another 16 min (s = 6.1 min, n = 15). The construction of the brood ball took place on the dung pad and the patting process 1-10 cm away. Temperature greatly influenced speed of ball construction; those constructed at temperatures in the high teens and low twenties took 2 to 3 times longer than those in the high twenties. When a dung ball became distinguishable from the mass from which it was hewn it became attractive to other females, which led to challenges and conflict between them. These challenges lasted between 3-95 sec ($\bar{x}$ = 18 sec, n = 20). The female on top of the ball (usually the maker of the ball) was the victor in 70% of the fights observed. Males approached females in the process of forming, or while rolling a ball, and after brief head to head contact the pair carried out their rolling and burying rituals. In all cases the male followed 1-3 cm behind the female and did not participate in ball rolling. Conflict between males vying for the same female was common. Male conflicts lasted between 7-200 sec ($\bar{x}$ = 55 sec, n = 15).

The females roll the balls backward by pushing with the fore legs and holding and controlling the ball with the middle and hind legs. They roll the ball a short distance, then climb on top of it where they do a complete circle with their antennae flared, whereafter they climb down and continue pushing in the original direction. The ball is rolled until a suitable site is found although there may be several attempts at burial along the way. Balls were always rolled in a more or less straight line with attempts to overcome rather than avoid obstacles.

Brood ball-rolling was seen most often after rain at temperatures between 13 and 37 °C, with a peak in ball-rolling activity at temperatures between 21 and 28 °C. The beetles rolled balls distances of between about 7-80 m ($\bar{x}$ = 27.6 m, n = 22) over an average rolling time of about 65 min (n = 19). The longest journey took over 5 hr in a more or less straight line, with two aborted attempts at burial.

When a suitable site was found the ball was buried by the female excavating under it. As the ball and female sunk below the surface the male climbed onto the ball and disappeared with it. Times taken to bury the brood balls ranged from 35-65 min ($\bar{x}$ = 45.6 min, n = 13).

The ball's final position in the soil was usually up to about 50 cm to one side of the position where excavation started. A chamber was then excavated around the ball (17-37 cm below the surface; $\bar{x}$ = 25 cm, n = 25). It was round, with a diameter 1-3 cm larger than the ball itself. The female was usually under or to the side of the ball whereas the male was always 1-5 cm to the side, often buried in soil.

On two occasions beetles were observed mating; once 6 hr after burial and on the other occasion 4 days after burial. The male straddled the female, stroking her elytra with his fore legs and palpi while the middle legs encircled her elytra. His hind legs steadied the copulating beetles.

After mating and deposition of the egg the males returned to the surface (5-7 days after burial). The females remained with the brood throughout the immature development. Brood attended by the female had high survival rates whereas those abandoned by the female (or where the female was removed experimentally), particularly in the early stages of development, suffered high mortality. Where the female was removed in an advanced stage of larval development, or where she was removed during early developmental stages but her role of cleaning the outside of the ball of enveloping fungus was mechanically fulfilled, survival was high (Table 4).

The duration of immature development (from egg to adult) was a minimum of 120 days under optimum conditions and without disturbance but under suboptimal conditions or if the immatures were disturbed the total developmental time doubled

Table 4.

Percentage of *Circellium bacchus* instar survival after removal of the attending female at various life cycle stages, n = number of broodballs examined. The last case refers to a situation where the female was removed, but the broodballs were cleaned by the investigators.

Stage at which female was removed	n	% survival
Female not removed	35	94
Egg	6	33
First Instar	6	33
Second Instar	8	75
Third Instar	10	90
Broodball cleaned by investigator (1st and 2nd instar)	10	90

and mortality increased greatly (see Tables 5 and 6). The young adults emerged 120-140 days after the eggs were laid. Thereafter they underwent a maturation feeding period of 50-65 days before becoming sexually mature. Under optimal conditions females bred twice per year but once appeared to be the norm. Consequently, at best, females produced two offspring per year.

Habitat preferences

(a) AENP

In general *Circellium bacchus* tended to favour dense, undisturbed vegetation growing on sandy soil over the more open and disturbed areas even when dung was abundant in the disturbed areas. Dung dropped in densely vegetated areas was quickly colonised whereas dung dropped in adjacent disturbed areas was hardly utilized. Consequently, beetle distribution in the park is patchy.

A total of 509 *C. bacchus* specimens was collected in AENP, 193 males and 316 females with a mean mass of 6.23 g. The Kruskall-Wallis one way analysis by

Table 5.

Stage durations in *Circellium bacchus* in days from burial.

Stage	Duration
Copulation	day 0-4
Egg laid	day 4-6
Male returns to surface	day 5-7
Egg hatches (First Instar)	day 12-14
Second Instar	day 21-25
Third Instar	day 28-32
Pupa	day 105-120

Table 6.

Mean duration (in days) of immature stages in *Circellium bacchus*, n = number of observations, n.a. = not available (some larvae remained in the third instar for 5 months, possibly due to the transfer from the mild climate in Addo Elephant National Park to the colder winter in Pretoria, * = all these specimens died before pupating.

Stage	n	Duration
Egg	6	7.8 (7-9)
First Instar	6	11.1 (9-12)
Second Instar	4	12.8 (11-14)
Third Instar	4	n.a. (70-*)
Pupa	4	14 (13-17)
Callow	5	3 (2-5)
Adult	8	? (120-?)

ranks of *C. bacchus* density retrieved a significant difference among the three habitats ($H_{(2;108)} = 59.73$, $P = 0.00$). The average ranks in declining order were: Botanical Reserve = 73.32, Pristine Area = 68.17, Alva = 22.01. The non-parametric Tukey type multiple comparisons further showed that the density of beetles in the area called Alva was significantly lower than in the other two habitats ($P < 0.01$) while densities in the Pristine Area and the Botanical Reserve did not differ significantly from each other.

(b) Buffalo Valley Game Farm

The pitfall traps in Buffalo Valley yielded a total of 343 *C. bacchus* specimens, 76 males and 267 females with a mean mass of 4.19 g. The Kruskall-Wallis one way analysis by ranks resulted in highly significant differences across the three habitat types ($H_{(2,108)} = 24.26$, $P = 0.00$). In declining order the average ranks were: Fynbos = 70.97, Dunes = 57.17, Grass = 35.36. The density of *C. bacchus* was significantly greater in the Fynbos and Dune areas than in the Grass area (non-parametric Tukey type multiple comparisons, $P < 0.01$).

Dung preferences

(a) Breeding

Totalling both trial dates, 40 brood balls were constructed from buffalo dung, 31 from cattle dung, seven from rhino dung and five from elephant dung. Table 7 shows the number of brood balls constructed from the different dung types separated for the two trials. A Kruskall-Wallis non-parametric multiple comparison rejected the null hypothesis (test statistic $H_{(3,46)} = 21.43$, $P = 0.001$) and Table 8 indicates the significance of the differences between the four dung types as inferred from non-parametric Tukey Type multiple comparisons.

Table 7.

Number of brood balls constructed by *Circellium bacchus* from different dung types during the dung preference trial for brood ball formation as well as brood balls constructed during the dung feeding preference trials.

Date	Dung type	Total number of brood balls
18-19 December 1996	Buffalo	25
	Elephant	3
	Rhino	7
	Cattle	20
11-13 March 1998	Dung type	Total number of brood balls
	Buffalo	15
	Elephant	2
	Rhino	0
	Cattle	11

Table 8.

Results of a non-parametric Tukey Type multiple comparison of the number of brood balls constructed by *Circellium bacchus* from the four different dung types. * denotes significant differences at $P < 0.05$ and ** denotes significant differences at $P < 0.01$.

Dung Type	Buffalo	Elephant	Rhino	Cattle
Buffalo	—	3.95*	4.12*	0.56
Elephant		—	0.17	4.51**
Rhino			—	4.68**
Cattle				

(b) Feeding

A total of 284 *C. bacchus* fed on the dung pads over the three trial days. The first sampling day revealed significant differences in dung colonization between cattle and elephant dung (Z-stat = 2.59, overall alpha = 0.1), cattle and rhino dung (Z-stat = 3.12, overall alpha = 0.05), and rhino and buffalo dung (Z-stat = 2.46, overall alpha = 0.1). On the second sampling day no significant differences were found between any combination of dung types (Friedman test statistic = 4.62, $P = 0.2016$, ZC = 2.39 for overall alpha = 0.10). On the third sampling day the rate of colonization of rhino dung was significantly lower than that of buffalo (Z-stat = 3.65, overall alpha = 0.05) and elephant dung (Z-stat = 3.39, overall alpha = 0.05).

Competition with other dung beetles

The areas where *C. bacchus* still occurs in any numbers are either fairly arid or densely vegetated and potential scarab competitors appear restricted. None of the large active savanna telecoprids occurs sympatrically with *C. bacchus* with the result that dung piles consist of virtually monospecific assemblages of *C. bacchus* individuals. The low numbers of small scarab species sometimes present are clearly not significant competitors.

DISCUSSION

Distribution and habitat preferences

The distribution of *C. bacchus* is now restricted to tiny fragments of its putative original range. It only occurs in remnant patches of near-pristine bush surrounded by an unfavourable agricultural matrix. The increasing insularization and biotope changes have caused a massive decline in the species' range. With the exception of the populations inside protected areas the species appears to be under extreme pressure.

Early records indicate that *C. bacchus* was historically quite widely distributed in southern Africa but apparently only occurred in small localized populations. Its current distribution in small undisturbed, localized, and mostly protected, areas may reflect, but on a greatly reduced scale, the original distribution type. Within these reserves it is restricted to areas of dense, undisturbed vegetation.

The lack of substantiated evidence concerning some recorded localities from the former Transvaal in South Africa, Mozambique, Zimbabwe and Namibia, makes it impossible to give the historical distribution of the beetle with any certainty (but see CHOWN et al. 1995). However, when comparing the apparent past and the present distribution of the species, it appears that the range of *C. bacchus* has decreased greatly over the past 50 years. This was probably due to man's transformation of large areas of natural vegetation and decrease of the mammalian herbivore populations. The land was transformed into fields for growing crops and the native herbivores were replaced with livestock. Burkey's stochastic simulation model points to time being critical to how the risk of extinction changes with fragmentation (SAMWAYS 1994). For short to moderate time spans the probability of extinction increases exponentially with degree of fragmentation. The model shows that a species is more likely to survive in a continuous tract of natural habitat than in a fragmented one of isolated patches. If the predictions of the model are widely applicable the implications for the survival of *C. bacchus* are serious.

The transformation of the natural vegetation and the abundance of livestock (mainly cattle) dung may have admitted large numbers of mobile competing species into the areas. *C. bacchus* may have been forced through competition with aggressive generalist feeders into the remaining small pockets of pristine dense bush where they would have had an advantage over flighted species which would have had difficulty flying and navigating in dense vegetation (STEENKAMP & CHOWN 1996). The densely vegetated areas would also have provided shelter and refuges for various herbivores such as black rhinos that would have provided the dung necessary for the beetles' survival (CHOWN et al. 1995). Other reasons for *C. bacchus*'s association with dense vegetation may be for protection from predators and climatic extremes since they readily find refuge in thick undergrowth and under leaf litter.

Feeding biology

The facts about *C. bacchus*' apparent feeding preferences may give a false impression about their original feeding patterns. The AENP (where this research was done) is clearly a very artificial environment when compared with what it was before it was proclaimed a park and elephants and other large herbivores were fenced in or re-introduced. Given that the use of an ephemeral and patchy resource such as dung tends to promote the maintenance of flight capability (SOUTHWOOD 1962), a flightless beetle of the size of *C. bacchus* could only have survived in the presence of a constant, readily available source of food. There can be little doubt that there was migratory movement of elephants and buffalo in and out of the valley bushveld areas where *C. bacchus* mostly occurs. This irregular abundance of food in the form of dung deposited by herds of large herbivores moving through an area would have been offset by the availability of dung from resident populations of smaller antelope, zebras and black rhinos.

Circellium bacchus indicated a distinct preference for feeding on elephant dung in the early morning (while cattle/buffalo dung was preferred later in the day after the sun had dried these dung piles enough to make them pliable for the beetles). A pile of elephant dung is clearly much more than just a food source. The beetles shelter in it when it becomes hot and there can be little doubt that the dung is also an important source of free water in a fairly arid environment.

They either feed at the dung source (usually) or roll food balls away and feed on them in a protected location. The only specific feeding pattern that emerged was that teneral beetles always roll food balls while older beetles usually feed at the dung source and only occasionally roll food balls.

The advantages of constructing a food ball are debatable. Beetles leave the dung pile where there is usually little competition and exchange this reliable food supply for an energetically costly and potentially hazardous journey with an uncertain outcome. There must, consequently, be a trade-off between these benefits and the energetic costs of forming, rolling and burying the ball and the risks associated with these behaviours. Some of the advantages, particularly for the weakly-sclerotized tenerals, appear to be: avoidance of adverse climatic conditions which may be experienced while feeding at the dung source; avoidance of injury by other individuals during feeding; provision of a protected environment in which to feed while sclerotization proceeds; predator-avoidance; food dependability, once acquired; and moisture retention of the food source in a protected environment. The main consequence of food-ball construction is that the vulnerable tenerals spend a minimum of time exposed above ground, which may also explain the fact that few tenerals are ever encountered.

Halffter & Matthews (1966) stated that dung beetles that roll food balls employ the same behavioural patterns as they do when they roll brood balls, except that a food ball is rolled by an individual and a brood ball is usually rolled by a pair. They claimed 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. Most published records indicate no difference in size, shape or consistency between food and brood balls. Halffter & Matthews (1966) reported that *Canthon indigaceus chevrolati* rolls balls of two different shapes and sizes and speculated that these two types of balls correspond to brood and food balls respectively. Matthews (1963) reported that in *Canthon pilularius* brood balls were much more carefully made, more regularly spherical and smoother surfaced than were food balls.

In *C. bacchus* there are two important differences between food and brood balls; food balls are much smaller than brood balls; and food balls are constructed from various types of dung (coarse or smooth), although mainly from coarse elephant dung, while the overwhelming majority of brood balls are constructed from the smoother buffalo dung. Food balls are constructed by both sexes of mature and immature adults, while brood balls are only rolled by mature females. Consequently, *C. bacchus* is exceptional in that it rolls balls of different sizes for feeding and breeding, and unique in its preference for different types of dung for the different balls.

Breeding biology

Intensive competition among dung scarabs 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 the main processes remain the same: 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.

Circellium bacchus constructed brood balls in the AENP, in order of preference, from buffalo, elephant and rhino dung. However, moist antelope and hare pellets as well as ostrich dung were sometimes used. The dung pellets were scraped together to form a ball, the partially-formed ball being dragged along as more pellets were added. This is the first canthonine species in which this phenomenon has been observed.

If the female is ready for breeding, the climatic conditions are favourable and she is in possession of an adequate amount of suitable dung she initiates brood ball construction. In *C. bacchus* this occurred during day- and night-time.

The brood balls were constructed at the dung source and shaped and smoothed some distance away. Up to several females often co-operated during the early stages of ball-formation but as soon as the ball was recognisable as such it became intensely desirable to the females involved (and others) and the co-operation ended in violent conflict.

The dung pad 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 affected by brief head to head contact. If the other beetle was recognized as a member of the opposite sex after a brief encounter it was almost always accepted and the pair carried out their rolling and burial rituals.

The active partner in the ball-rolling process is that beetle which at least initiates the ball-making (sometimes making it entirely), rolls it in the 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. To date there have been three basic positions described for co-operative ball-rolling (Halffter & Matthews 1966, Tribe 1976):

(i) male rolls the brood ball and female clings to it;

(ii) male rolls the brood ball while the female follows;

(iii) "pushing" and "pulling" behaviour involving both sexes.

Tribe (1976) claimed that position (i) is employed by all African *Kheper* species, *C. bacchus* and a number of *Scarabaeus* species.

In most telecoprid species the male is the active partner, while the female usually assumes this role in paracoprids. It is generally accepted that female telecoprids are passive during the rolling and construction of the ball in order to conserve energy for breeding and the often long underground vigil, during which time the female barely feeds, that is associated with brooding. The male, on the other hand, plays no part in brood care and leaves the brood chamber after mating and can thus soon resume feeding.

In *C. bacchus*, however, only females form and roll brood balls. The males typically follow some distance behind, taking no active part in forming, rolling or burying the brood ball. This unusual behaviour has not been unequivocally documented in any other ball-rolling species. We were unable to confirm Tribe's (1976) claims that *C. bacchus* males roll and the females cling to the brood balls. The only other recorded canthonine species in which the female is at all in contact with the ball during ball-rolling is in the New World species *Canthonella parva* (Chapin 1930) in which the female clings to the ball while it is being rolled by the male (Halffter & Matthews 1966).

The unusual behaviour of *C. bacchus* justifies adding another category to those mentioned above; one in which the female initiates, forms and rolls the brood ball while the male follows behind, without participating in the process in any way.

Dung beetles are among the relatively few insects that provide nests for their progeny. Halffter & Matthews (1966) provided a summary of four nidification categories in Scarabaeinae. *Circellium 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 some distance from the dung source. In species such as *C. bacchus*, which exhibit variation III of group IV behaviour, the brood ball is buried without a clay layer (also in some *Canthon* Hoffmansegg 1817, *Scarabaeus* Linnaeus 1758, *Gymnopleurus* Illiger 1803, *Sisyphus* Latreille 1807). This could account for the fact that the female remains in the nest. One noticeable effect of removing female *C. bacchus* from the nest is the growth of fungi on the brood balls, which, if it occurs during the early stages of immature development causes fairly high mortality. *Circellium bacchus* is probably the most K-adapted scarab species ever studied, producing probably only one but at most two progeny per year; so the strategy of caring for the brood for the duration of its development clearly maximises fitness in this species.

Conservation

One traditional approach to conservation of invertebrates has been to follow the usual "vertebrate procedure" (New 1993) and orientate conservation programmes around notable species. For "charismatic" species such as butterflies this approach has fostered goodwill and public interest in the species. *Circellium bacchus* is one of only a few invertebrate species in South Africa which could be considered to have a sufficiently high individual profile to be regarded as a flagship species (New 1993). It conforms to most of New's functionally significant criteria for a flagship species, the most important of which are probably that its taxonomy be well known, it be accessible to study/sampling (and readily visible), it should respond to changes in its environment and that it should engender public sympathy. Within this framework *Circellium bacchus* has a high profile in South Africa as a flagship species because it is large and conspicuous, it has long been thought by entomologists to be endangered, it has been well publicized in the popular media and in the Addo Elephant National Park. The research on the beetle has come at a time of growing public awareness of the importance of insects in natural ecosystems as well as their intrinsic value as conservation objects.

Circellium bacchus undoubtedly qualifies as rare in the language of conservation biologists. It is considered rare because populations are mostly small and are restricted to isolated, but probably environmentally constant, relict fragments of particular habitat-types with probably little or no gene flow between the populations. Species such as this that are adapted to evenness of surrounding conditions and are genetically remote, are particularly threatened. They are among the species physiologically least able to adjust to man-induced changes, whether local landscape modification or global climatic change. Yet they are also among the most intrinsically valuable species because of the uniqueness of much of their active genome (Samways 1994).

Circellium bacchus falls into Rabinowitz et al. (1986) sixth rarity category, namely species with narrow geographical range, restricted biotope specificity and some large (Addo) and some small (elsewhere) local populations.

Norton (1986) provided a number of characteristics that increase the likelihood of endangerment and/or extinction. They are: rarity, large individual size, relative height in the trophic level, low dispersability, low fecundity and long individual lifespan, specialization of habitat, mutualism and co-evolution, and existence in ecosystems of high diversity. *Circellium bacchus* complies with five of these seven characteristics which increase the likelihood of endangerment or extinction. It is rare; it has large individual size relative to other related species; it has very low dispersability and fecundity; individuals are long-lived and are habitat-specific. These characteristics put *C. bacchus* extremely at risk to endangerment and it should therefore receive priority in conservation programmes and management plans.

According to IUCN criteria on threatened species (Wells et al. 1983) *C. bacchus* can be considered to be "Vulnerable" (taxa of which most or all populations are decreasing or being lost to habitat disturbance and fragmentation; and taxa whose biogeographical range is decreasing through loss of peripheral populations).

Ferrar (1989) elaborated on the basic attributes of rarity and suggested a more refined ordering of the different categories of rarity proposed by Rabinowitz et al. (1986). Ferrar (1989) ranked vulnerability to extinction pressure in seven categories (from most to least vulnerable) depending on habitat specificity, geographic range and local population size. This study has confirmed that *Circellium bacchus* is extremely specialized to arid and undisturbed habitat and Chown et al. (1995) have speculated on possible reasons for this. Local population sizes of *C. bacchus* vary from locally abundant to rare. However, concerns have been raised that populations of *C. bacchus* are unnaturally high in AENP due to the restriction of a large number of elephants to a small area and the consequent virtually unlimited availability of dung. Under natural circumstances the beetles would have had to depend on smaller quantities of much more ephemeral food sources and, food would clearly have been a limiting factor. The present situation in the De Hoop Nature Reserve probably most nearly approximates the original conditions under which the beetles lived — resident populations of smaller antelope and zebra on which the beetles in all probability relied on for a regular dung supply with the likely seasonal increase in food availability provided by transient herds of large herbivores. *Circellium bacchus*' eclectic and opportunistic use of virtually any available dung allows it to maintain a viable, yet fluctuating population size under such circumstances.

It probably has the lowest fecundity of any scarab (possibly among the lowest of any insect) and is one of the most K-selected insect species known. Based on the fact that they probably spend long periods in a quiescent state or in diapause it can safely be assumed that they live for several years. Although they have low fecundity, the production of one or two progeny per year over a few years obviously results in a net population increase under the artificially favourable conditions that they experience in the AENP.

Within Ferrar's (1989) system, *C. bacchus* would consequently fall into category one (organisms most vulnerable to extinction pressure, including highly specialized and restricted endemics, with markedly reduced abundance) or category two (highly specialized and restricted endemics, with local populations that are not critically reduced). The results of this study therefore clearly demonstrate the urgent need to install adequate conservation measures in order to protect this enigmatic species and its habitat.

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