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# DESICCATION RESISTANCE IN DUNG-FEEDING SCARABAEINAE

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# Desiccation resistance in dung-feeding Scarabaeinae

by

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*'I suppose you are an entomologist?'*
*'Not quite so ambitious as that, sir. I should like to put my eyes on the individual entitled to that name. No man can truly be called an entomologist, sir; the subject is too vast for any single human intelligence to grasp.'*

Oliver Wendell Holmes.

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# INTRODUCTION

*As far as I can conjecture the art consists in habitually searching for the causes and meaning of everything which occurs. This implies sharp observation, and requires as much knowledge of the subject as possible.*

Charles Darwin, in a letter to his youngest son Horace, congratulating him on passing his exam, 1872.

## *THE IMPORTANCE OF WATER FOR LIFE*

*Water, alone or in conjunction with temperature, is probably the most important physical factor affecting the ecology of terrestrial organisms.*

Charles J. Krebs, 1985.

*Body water contents and reserves in insects*

Because most of the molecules in animals are water molecules, water is one of the most important chemical compounds necessary for life. Non-aqueous molecules, expressed as a percentage of total mass, rarely exceed 40% of the total mass in animals not under physiological stress. However, water contents in different arthropod structures are very different. Internally, water contents are uniformly high (70 to 80% of total mass), but in the dense and hardened cuticle water contents vary from 13 to 70% (Filshie 1982, Machin and Lampert 1987, 1989).

The physiological state of an insect also gives rise to differences in water contents. Under very favourable conditions, *Tenebrio molitor* has large lipid reserves which in turn reduce the total water content of the beetle (Wharton 1985). Habitat also influences body water content and insects in drier areas maintain higher body water contents than those in more mesic areas (Edney 1977, Wharton 1985). For example, the Subantarctic - *Perimylops antarcticus* occurs in drier areas than *Hydromedion sparsutum*, and maintains a higher body

water content than the latter species (70 - 83% of fresh mass compared to 68 - 73%) (Ring *et al.* 1990).

Tolerances of the minimum amount of water to maintain physiological functioning are very uniform among insects. Most insects can tolerate 25 to 30% loss of their total mass before they die (Edney 1977, Fielding and Nicolson 1980, Naidu and Hattingh 1988, Ring *et al.* 1990). Most xeric arthropods do not have significantly higher tolerances than mesic arthropods. Sublethal dehydration affects various biological processes such as food consumption, growth, oxygen consumption and activity (Wharton 1985, Juliano 1985). A few exceptions exist, where species have evolved tolerances of extremely low water levels in order to survive severely desiccating conditions. Cryptobiosis, *sensu* Hinton (1968), is the reversible cessation of metabolic activity during extreme environmental conditions. Anhydrobiosis, *sensu* Crowe (1971), is the reversible cessation of metabolic activity brought about by extreme desiccating conditions. Anhydrobiosis is usually accompanied by high levels of water loss. Species capable of anhydrobiosis can tolerate almost complete dehydration, and this dry state also ensures resistance to extreme temperatures.

Death as a result of desiccation depends on the site of water loss. Certain regions act as buffers showing no effects of water loss, whereas even slight decreases in water contents from other regions have adverse effects. The buffer areas are usually the major locations of water storage. The most prominent location is the body cavity containing the haemolymph. From the haemolymph, water is transported into and out of tissues. This allows for close regulation of water contents and osmotic concentrations in these tissues. The haemolymph can withstand major changes in volume and osmotic concentrations (Edney 1977, Wharton 1985, Bradley 1985) and most water lost during desiccation is lost from haemolymph (Nicolson *et al.* 1974). Water is also stored in the digestive tract, specifically in the hindgut. In this compartment, hypo-osmotic urine accumulates, of which its water can then be reabsorbed through the rectal wall and into the haemolymph when required. Most water in the hindgut is stored in the rectum (Bradley 1985, Wharton 1985). Salivary glands also act as reservoirs in the larvae and pupae of certain blowfly species and in certain termite species (Wharton 1985).

In general, species from more xeric areas have increased water reserves. To promote desiccation tolerance these insects apply a wider range of physiological strategies to extract water from various storage locations that are not affected by large variations in water levels, than insects from more mesic habitats (Edney 1977, Wharton 1985, Bradley 1985, Ring *et al.* 1990).

## WATER FLOW BETWEEN ANIMALS AND THEIR ENVIRONMENT

*Physical laws*

The forces regulating the rates of movement of water between an organism and its environment are adequately described by Fick's law of diffusion. Water movements in a terrestrial environment usually occur in the vapour phase. According to Fick's law, the criteria that determine water movements between the environment and organisms across the cuticular barrier are the saturation vapour density at the temperature of the organism, the actual vapour density of the air (which is the fraction of the saturation vapour density at air temperature, indicated by the relative humidity), the rate of water loss per unit area of the barrier, and the added resistance of the boundary layer of air adhering to the surface of the cuticular barrier (Gates 1980). When body fluids evaporate at the cuticular interface the vapour density of the organism is regarded as saturated. The osmotic concentration of insect body fluids would not markedly influence transpiration because of the extremely steep concentration gradients which exist between insects and their terrestrial environments (Edney 1977, Wharton 1985).

*Functional water loss*

Functional water losses are those losses associated with life processes, such as respiration, excretion, secretion, growth and reproduction. The steep gradients in water vapour densities between the air and the moist membrane interfaces in the respiratory system of insects, and the higher permeabilities of the membranes to water than to the respiratory gasses, cause rapid outward movements of water. The rate of respiration is very closely linked to the rate of desiccation. Two carabid species studied by Juliano (1985) showed decreased rates of water loss caused by lowered respiratory rates brought about by starvation and desiccation. One of the species, *Brachinus mexicanus*, occurs at temporary ponds and had a lower overall respiration rate than *B. lateralis*, which occurs at permanent water bodies. Insects have a variety of adaptations which contribute to a reduction in water loss through the respiratory system. Spiracular valves reduce water loss at low respiratory activity levels. Increased respiratory activity can increase the respiratory water loss by 40% (Hadley and Quinlan 1982, Wharton 1985), but during rest cyclical release of $CO_2$ greatly reduces respiratory water loss (Lighton 1994). Constructions around the spiracular openings such as pits, hairs, scales and the subelytral cavity of beetles create a static body of air which reduces

evaporative water loss but does not impair oxygen transfer (Edney 1977, Slobodchikof and Wismann 1981, Wharton 1985, Scholtz and Caveney 1988, Zachariassen 1991).

Excretion of metabolic and digestive wastes is accompanied by some water loss. However, insects are capable of re-absorbing water through the hindgut. The extent of absorption depends on the physiological state of the insect. Insects under desiccating conditions and insects from xeric habitats usually lose little water via their excretions (Wharton 1985, Bradley 1985, Reynolds and Bellward 1989, Chu *et al.* 1992).

Insects also lose water during reproduction (eg. egg laying) (Hinton 1981, Wharton 1985), growth (especially during ecdysis prior to cuticular hardening) (Wharton 1985, Hadley 1986) and defense. During defensive reflex bleeding, meloid beetles lose substantial amounts of water (Nicolson 1994) and defensive behaviour involving secretions usually ceases in water-stressed insects.

The thermal properties of water are utilised by certain insects in the regulation of their body temperature. Forced transpiration, through pores located on the dorsal side of the abdominal and thoracic cuticle, to regulate temperature by evaporative cooling, has been observed in the desert cicada, *Diceraprocta apache,* and in the Mexican cicada, *Okangodes gracilis*. Evaporative cooling is further facilitated by behavioural responses to excess temperatures such as microclimate selection (Hadley *et al.* 1989, Sanborn *et al.* 1992). This physiological adaptation is possible because of the high water content of the food ingested by these homopterans. In a similar way, the locust species *Schistocerca nitens, Locusta migratoria* and *Tmethis pulchripennis* make use of respiratory evaporation to lower body temperature. These species are able to maintain body temperatures 8°C lower than ambient temperature by means of evaporative cooling (Prange 1990). Thermoregulation via evaporative cooling is only possible for species which have reliable sources of water. Species in xeric habitats usually make use of behavioural thermoregulation.

*Incidental water loss*

Incidental water loss cannot be accounted for by specific biological functions. It is determined by the physical laws of water movements and mostly comprises water lost by diffusion through the insect cuticle and from the openings of the digestive tract. Diffusion rate is determined by the concentration gradient over the transcuticular vapour-liquid interface, by the resistance of the cuticular barrier, by changes in internal pressure through muscular action in the insect body, and by selection of suitable humidities and temperatures (Edney 1977, Gates 1980, Wharton 1985, Corbet 1988, Unwin and Corbet 1991).

Incidental water loss is one of the more important aspects in the study of the desiccation resistance of insects. Specimens can be standardized to eliminate most functional routes of water loss. Because of inherent experimental limitations, respiratory water loss has to be included among the other incidental water loss routes for accurate observations on the water balance of living insects to be made. If insects are housed in containers that exclude the exchange of any other volatile components, except respiratory gasses, most other environmental factors are eliminated. Behavioural reactions are ineffectual and the insects have to rely on physiology alone. Changes in water content during the periods of observation can then be determined gravimetrically (Wharton 1985).

*The components of water gain*

Food sources and free water are the primary sources from which lost body water is replenished (Edney 1977, Scriber and Slansky 1981, Wheeler and Slansky 1991). Atmospheric water is another source of water from the environment. All species are capable of passive absorption. This is a purely physical occurrence brought about by the physical properties of water at the difference in concentrations and temperatures between insects and their environments (Gates 1980, Gelman *et al.* 1988). Active absorbtion, through locations in the cuticle and against concentration gradients necessitates highly specialised mechanisms of water uptake. These adaptations are restricted to some specialised groups of insects living in extremely xeric habitats, and rarely occur in adult insects (Wharton 1985).

A combination of hygroscopic condensation sites together with muscular manipulations of the internal pressures in the insect body can facilitate absorbtion by creating a zero saturation deficit over the cuticular vapour-liquid interface. This eliminates the necessity of selecting microclimates where temperatures and humidities optimally conducive to water vapour absorbtion exist (Machin 1980, Corbet 1988, Unwin and Corbet 1991).

Metabolic water is produced as a by-product of the aerobic catabolism of stored organic materials. Lipids and certain stored carbohydrate compounds such as glycogen are the primary sources of metabolic water. For every gram of carbohydrate metabolized 0.5 g of water are produced together with 4.2 kcal of energy, and for each gram of lipids metabolized more than one gram of water is produced together with 9.6 kcal of energy (Wharton 1985). Species living in xeric habitats, but where food sources are reliable, abundant and of a high nutrient quality, such as those in the genera *Dermestes* (Coleoptera) and *Ephestia* (Lepidoptera) are known to increase their food consumption rates to produce water. The excess energy produced in this process is channelled into reproduction or

dissipated as heat (Wharton 1985). In the Namib desert tenebrionid, *Physadesmia globosa,* stored lipids are metabolised to replace water lost during periods of desiccation (Naidu and Hattingh 1988).

The production of free water through the above avenues is the result of catabolic reactions. Certain anabolic reactions, involving amino acids and sugars are also a source of water, although this strategy for producing metabolic water is less common. Lowering the haemolymph concentration metabolically also releases water for other functions (Wharton 1985).

*Osmotic regulation*

Osmolalities of insect haemolymph range from 300 - 600 mOsmol. This is equivalent to 99.5 - 99.9% relative humidity (Wharton 1985). This means that water movement over the cuticular barrier and through the spiracles is usually outwards, except in water-saturated microclimates. When insects are exposed to desiccating conditions their haemolymph concentration rises. This lowers the concentration gradient across the cuticular barrier and the rates of evaporative water loss decline (Punzo 1989). Most of the water in the haemolymph is transferred to the tissues from where it is lost. If the osmolality in the haemolymph and the tissues becomes too high, muscular contraction, activities of the nervous system, and the structural integrity of membranes and macromolecules are adversely affected (Kohn 1965, Gates 1980). Water extracted from the haemolymph can be replaced by water contained in the digestive tract and by metabolic water (Bradley 1985, Wharton 1985, Reynolds and Bellward 1989).

# *RESISTANCE ADAPTATIONS AND THE ENVIRONMENT*

*For instance, in a dry country , animals and plants work to maintain the fluid content of their cells, work against a natural tendency for water to flow from them into the dry outside world. If they fail they die. More generally, if living things didn't work actively to prevent it, they would eventually merge into their surroundings, and cease to exist as autonomous beings. That is what happens when they die.*

Richard Dawkins, The blind Watchmaker, 1986.

*Desiccation resistance, transpiration and cuticle structure*

Edney (1977) defined resistance to desiccation in arthropods as a combination of the ability to tolerate large losses of body water and the restriction of these losses by a variety of means. The actual resistance to desiccation, which is a result of the combination of both of these factors, can be illustrated by the length of time a species can survive desiccating conditions. The habitat of arthropods seems to dictate to what extent species will utilise either of these adaptations to achieve the necessary levels of desiccation resistance. Most evidence indicates that species from arid areas are more likely to restrict the loss of water than to tolerate high water losses (Edney 1977, Naidu and Hattingh 1988, Ring *et al.* 1990).

The major route of incidental water loss is transcuticular transpiratory water loss. Apart from giving structural integrity to the organisms, the arthropod cuticle is also the primary adaptation to the prevention of water loss from these organisms, which have a large surface area:volume ratio. The epicuticle is the major barrier to water loss in the arthropod integument and contributes little to the structure and strength of the cuticle as a whole (Hadley 1986, Filshie 1982).

Insects living in xeric environments exhibit very different cuticular chemical compositions to those from more mesic environments. In xeric insects, large quantities of epicuticular lipids and a high diversity of hydrocarbons and lipids composed of long chain saturated molecules are present (Hadley 1986).

Thin, unstirred layers of air immediately surrounding the cuticular surface supplement resistance to water loss (Gates 1980). A boundary layer of this nature can be maintained

either by structural modifications of the cuticle and/or by behavioural selection of microclimates. Structural modifications include increasingly complex sculpturing, setae and scales. One of the largest structural modifications which has facilitated maintenance of a boundary layer is the hardening of the mesothoracic wings in the Coleoptera. The elytra completely enclose the dorsal thoracic and abdominal areas and the subelytral cavity provides a static layer of air which surrounds the spiracles. In so doing it decreases respiratory water loss (Slobodchikof and Wismann 1981, Scholtz and Caveney 1988, Zachariassen 1991).

Microclimates selected by insects include burrows, small spaces underneath various objects, moist surfaces, humid spaces in or near plants, and constructions built by the insects themselves. In these microclimates, temperature and humidity are very constant and ventilation of the air in these areas is kept to a minimum (Gates 1980, Willmer 1982, Unwin and Corbet 1991), thus minimizing transcuticular water movements between insects and their environment.

Soil insects such as certain Scarabaeidae species have fewer problems in controlling transcuticular water movements because of the characteristics of the soil microclimate. Soil humidity is very constant, although the water potential may fluctuate significantly. However, the range of fluctuation is very low compared to that in the atmosphere above ground and the common assumption is that the air in soil is saturated (Galbreath 1975, Campbell 1977). In addition, the static layer of air surrounding soil insects further restricts diffusion across the cuticle (Galbreath 1975, Gates 1980). The effects of structural damage i.e. abrasion of the cuticle, or resistance to the abrasive qualities of soil on the soil insects' cuticle is unknown. In *Periplaneta americana,* abrasion damage to the cuticle caused permeabilities an order of magnitude higher than in undamaged cuticles. Damage of this kind can be repaired within three days by the insects (Machin and Lampert 1987).

*The ecological significance of insects' water relations*

The abiotic conditions in the environment influence organisms at every stage of their life histories (Kennedy 1993). Seasonal and daily activities are influenced by abiotic factors such as temperature and the availability of water. To survive both sub- and supralethal abiotic conditions, organisms must be able to mediate these conditions through their morphological, biochemical, behavioural and physiological attributes (Willmer 1982, Kennedy 1993). The extent to which these attributes can mediate environmental conditions determines the distributions of species in their various environments. Therefore studies of the effects of abiotic factors and their actions on interactive associations is liable to increase the

understanding of community structure (Dunson and Travis 1991). Changes in the abiotic factors can change the whole structure of interspecific interactions from the level of primary producers right through to the decomposers in that community (Kingsolver 1989). Comparative studies of species resorting in one of these trophic levels therefore stands to increase our knowledge on how communities are spatially and temporally structured, especially during changing abiotic conditions (Kingsolver 1989).

Most studies of the effects of abiotic factors on insects have been focussed on the effects of temperature (Heinrich 1993). This emphasis is understandable because many insects depend critically on temperature for the onset of activity. For example, for muscular action to be maintained at an optimal level, body temperatures in a range of 30 to 45°C are necessary. In contrast, few studies have explored the effects of humidity and water availability on insects. This is because temperature is both easier to measure than water content and availability, and easier to control in laboratory studies (Winston and Bates 1960, Unwin and Corbet 1991). Despite optimal temperature regimes, long term survival of individual insects, in a specific environment, requires water availability above lower lethal thresholds. Long term survival of an insect population, on the other hand, requires considerably greater concentrations of available water since the maintenance of populations entails reproduction at sufficient rates (Edney 1977, Kennedy 1993). Insects may inhabit areas where the water availability is just above the lethal threshold but will select more appropriate areas in order to reproduce. These suitable areas can be separated either spatially or temporally.

From the above discussion it is clear that the availability of water, whether in liquid or in vapour phase, is a key limiting factor to animals (Edney 1977, Willmer 1982, Currie 1991, Kennedy 1993). Closely related organisms from different areas, or from the same area but operating at different spatial and temporal scales, usually have different behavioral and physiological adaptations to facilitate resistance to desiccation. Identification and quantification of this information stands to contribute greatly to our understanding of physiological adaptations of insects to their environments and to our knowledge of the influence of abiotic factors on insect assemblage structure (Edney 1977, Juliano 1985, Chown *et al.* in press). This is one of the major aims of this study.

# *DUNG BEETLES AS PRACTICAL MODELS ILLUSTRATING WATER RELATIONS BETWEEN ORGANISMS AND THEIR ENVIRONMENTS*

In southern Africa, approximately 55 herbivorous mammal species, ranging in size from the riverine rabbit to the elephant (Smithers 1983), contribute large quantities of dung to the terrestrial ecosystem. As a result, a great diversity of Scarabaeinae beetles which utilise this dung has evolved in Africa (Heinrich & Bartholomew 1979, Scholtz & Holm 1985, Hanski & Cambefort 1991).

Dung beetles employ a number of different strategies for locating and utilising dung (Hanski and Cambefort 1991), and this results in their exposure to a variety of abiotic conditions. They are therefore ideally suited for the study of physiological adaptations to the abiotic environment. Recently, the Ecological Society of America recommended that research efforts should address the role that ecological processes play in shaping patterns of diversity at different temporal and spatial scales, and the ways in which individual species interact with and are modified by the abiotic environment (Lubchenco *et al.* 1991). The former community ecological approach has enjoyed high priority in the Scarabaeinae, and a considerable body of knowledge concerning the natural history (Halffter & Mathews 1966), breeding biology (Halffter & Edmonds 1982) and community structure (Hanski & Cambefort 1991) of dung beetles is available. However, little is known concerning the physiological adaptations of these beetles to their abiotic environments (Hanski and Cambefort 1991, Chown *et al.* in press). In addition, almost no information is available concerning the contribution of different physiological tolerances and tactics to dung beetle assemblage structure (Bartholomew and Heinrich 1978, Heinrich and Bartholomew 1979). The aim of this study was therefore to examine the water relations and the physiological tolerances of a variety of dung beetle species from different habitats, and which have different ecological strategies, in order to address gaps in our knowledge of the ecophysiology of these beetles and to gain further insights into the processes structuring dung beetle assemblages.

*Before the sun becomes too hot, they are there in their hundreds, large and small, of every sort, shape and, size, hastening to carve themselves a slice of the common cake. There are some that labour in the open air and scrape the surface; there are others that dig themselves galleries in the thick of the heap, in search of choice veins; some work the lower stratum and bury their spoil without delay in the ground just below; others again, the smallest, keep on one side and crumble a morsel that has slipped their way during the mighty excavations of their more powerful fellows. Some, newcomers and doubtless the hungriest, consume their meal on the spot; but the greater number dream of accumulating stocks that will allow them to spend long days in affluence, down in some safe retreat...*

*The Beetle has his provisions. The next thing is to withdraw from the fray and transport the victuals to a suitable place.*

Jean Henri Fabre, 1918. The Sacred Beetle

*Basic dung beetle ecology*

Dung beetles live in and feed on dung, which has a high nutrient content ( Hanski and Cambefort 1991). Due to its constitution, dung also creates a favourable microhabitat for animals the size of dung beetles and is very similar to moist soil habitats. Water in its free form is abundant in dung, and the relative humidity in and under a dung pad is close to 100% (Campbell 1977). In addition, the temperatures in and under the dung pad, and in the surrounding soil remain very stable (Hanski 1991, Unwin & Corbett 1991). In relation to the macro-habitat, dung micro-habitats form small, patchy, favourable 'islands' in an unfavourable environment. These 'islands' are ephemeral due to the high numbers of dung beetles and other dung-dwelling invertebrates that utilise dung pads. Hence, dung beetles are forced to move between 'islands' and must be able to survive these bouts of foraging. During these foraging bouts, dung beetles are subject to environmental challenges. Although activity periods and the general ecological strategies of the taxa influence the nature and extent of the environmental challenges facing these beetles, a physiological equilibrium between the beetles, their habitats and their ecological strategies can be expected (Feder 1987).

Halffter and Matthews (1966) and Bornemissza (1969) divided the Scarabaeinae into three groups based on their nesting behaviour. These are the paracoprids, endocoprids and telecoprids. Paracoprids construct their nests underneath or beside the dung pad after arrival at the pad. Tunnels are constructed perpendicular to and below the dung pad or at an angle

to the pad starting at the periphery. Following the construction of the burrow, the feeding or breeding chamber is packed with dung. Endocoprids construct their breeding chambers within the pads on the soil surface. Davis (1977, p.54), after detailed field and laboratory observations, extended the definition to include the construction of the breeding chamber within or directly beneath the pad so that the base of the pad forms the roof of the chamber. In a few cases some endocoprid species construct short tunnels ($\pm$2.5 cm) directly beneath the pad. Telecoprids, after arrival at the pad, allocate a portion of dung to themselves which they either butt away from the pad unaltered, or which they construct into a ball which is then rolled some distance before it is buried. This behaviour, in contrast to that of the endo- and paracoprids, further exposes telecoprids to the stresses of the macro-habitat.

Doube (1991) refined the above behavioural classification by further subdividing the three groups into seven functional groups (Fgs), based on the sizes and more specific behaviours of the various taxa. Doube (1991) also discussed diel activities but did not base group divisions on this criterion. His seven functional groups are:

Functional group I (Fg I) - Large telecoprids.

These are ball rollers with a dry mass greater than 400 mg. They spend approximately 2 - 3 hours at a dung pad during which time they remove 5 - 20 times their own mass from the pad to simple and compound subterranean chambers dug at some distance from the pad. Dung removal is rapid and complete. Maturation feeding on and construction of brood balls with the allocated dung occurs in these chambers. Most species are diurnal.

Functional group II (Fg II) - Small telecoprids.

Ball rollers in this group have a dry mass of less than 400 mg. They spend 2 - 24 hours at a pad removing 5 - 20 times their own mass from the pad to simple subterranean chambers dug at some distance from the pad. Dung removal is completed over several days. Maturation feeding on and construction of brood balls with the allocated dung occurs in these chambers. Most species are diurnal.

Functional group III (Fg III) - Fast burrowing paracoprids.

These are tunnellers which spend 6 - 24 hours at a pad removing up to 500 times their own mass from the pad to simple subterranean chambers dug directly beneath or from the periphery of the pad. Dung removal is complete within 24 hours. Maturation feeding on and construction of brood balls with the allocated dung occurs in these chambers. These species

are mostly nocturnal/crepuscular.

Functional group IV (Fg IV) - Large, slow-burrowing paracoprids.

Tunnellers in this group have a dry mass larger than 10 mg. They spend up to six weeks at a pad removing up to 1000 times their own mass from the pad to compound chambers. Maturation feeding occurs on the surface and in these chambers. Dung allocated for breeding is constructed into brood masses within the compound chambers. Dung removal is complete in some species and in others it is partial; the remaining surface dung is shredded. The species are diurnal, nocturnal or crepuscular.

Functional group V (Fg V) - Small, slow-burrowing paracoprids.

The tunnelling species in this group have a dry mass of less than 10 mg. They spend several weeks in the pad removing unknown quantities of dung to shallow chambers. Depending on the species, the construction of these shallow chambers can be simple or compound. Maturation feeding occurs on surface and on buried dung. Most of the surface dung is shredded after partial dung removal. Species are diurnal, nocturnal and crepuscular.

Functional group VI (Fg VI) - Kleptocoprids

Species of this group are usually very small and utilise dung buried by species of the other groups, shredding it and inhibiting the breeding of these groups.

Functional group VII (Fg VII) - Endocoprids

These small species spend many weeks inside undisturbed dung pads where they feed and breed in compound nests. The species are diurnal.

*I am a firm believer that without speculation there is no good and original observation...*

Charles Darwin in a letter to Alfred Russell Wallace, 22 December 1857.

One of the most important challenges facing dung beetles, i.e. organisms with relatively high body surface to volume ratios, is likely to be the conservation and effective utilization of body water. The Fg scheme provided by Doube (1991), used in conjunction with information on the diel and seasonal activity patterns of particular taxa, can provide preliminary hypotheses concerning the physiological adaptations of these taxa to water stress (Dunson and Travis 1991).

When telecoprids are processing dung and rolling it to secluded places they are exposed for long periods to an inimical abiotic environment. The Fg II species will, because of their large volume to body surface ratios, be more prone to desiccation than the larger Fg I species. However, selection of humid activity periods can reduce the abiotic stresses. Therefore, it is expected that the telecoprid species will show considerable adaptation to desiccation resistance.

The para- and endocoprid groups burrow directly into the dung and/or soil after arrival at a pad and are thus not exposed for such extended periods to adverse abiotic factors as are telecoprids. They are expected not to show considerable adaptations to desiccation resistance. The Fg III species, which frequently move between dung sources, and some of the diurnal Fg IV species may, however, also show considerable physiological adaptation to desiccation.

Species with diurnal activity periods, during which time temperatures are high and humidities are low, are expected to be better adapted to resisting desiccation than species with nocturnal/crepuscular activity periods, during which time temperatures are low and humidities are higher.

Habitats also vary in the extent to which they place dung beetles under water stress and thus certain adaptations may be habitat specific. For example, habitats such as the Namib desert are consistently xeric and only beetles with specific physiological adaptations to xeric conditions can survive there. However, abiotic factors in habitats such as savanna show

larger seasonal and daily variations in temperature and humidity. This enables more species, with various combinations of physiological adaptations, diel rhythms, seasonal rhythms and behavioural strategies to coexist (see also Stevens 1989, 1992). The main goals of this study are, therefore, not only to provide information on desiccation resistance in dung beetles, but also to test these hypotheses.

# MATERIALS & METHODS

*The discovery of scientific method required genius, but its utilization requires only talent. An intelligent young scientist, if he gets a job giving access to a good laboratory, can be pretty certain of finding out something of interest, and may stumble upon some new fact of immense importance.*

Bertrand Russell, The Science to Save Us from Science, 1950.

## *THE EXPERIMENTAL ANIMALS*

The study was carried out during the austral summers of 1991-92 and 1992-93. Live specimens of seventeen dung beetle species were collected with pitfall traps baited with fresh homogenised dung of bovine, equine and/or human origins. The specimens were returned to the laboratory where they were kept in plastic containers, partially filled with soil from their original habitats. These were housed in a in a climate controlled room at 27°C and ±60% relative humidity with 12:12 hour light/dark cycle. Prior to the experiments, the beetles were given fresh dung and water *ad libitum* for 24 hours, but for the next 24 hours only water was provided to allow beetles to clear their digestive tracts.

### *The species and their habitats*

*The principal features of Scarabaeinae relate directly to the facts that these beetles are coprophagous (or something much like it) and that they are soil insects. An examination of the group shows clearly that its evolution has been characterized by a heavy phenotypic investment in adaptations for the efficient exploitation of excrement, a highly perishable food source vulnerable to strong biological and physical disturbances . ...*

Gonzalo Halffter and W.D. Edmonds, 1982.

Only species of which more than twenty specimens were available at any one

collecting locality were used in the experimental studies. The species are organised in the functional groups (Fgs) discussed above and according to descending size within the Fgs.

*Circellium bacchus* (Fabricius), Fg I, occurs in large numbers in the Addo Elephant National Park (33.30S 25.41E) in the Cape Province. It is a large, diurnal, apterous beetle preferring elephant dung for feeding purposes and buffalo dung for breeding. *C.bacchus* has a bimodal activity period regulated by temperature (Coles 1994). It forages on foot for dung in scrub dominated Valley Bushveld (Acocks 1988).

*Pachylomerus femoralis* Kirby, Fg I, was collected in large numbers (over 500 in thirty minutes) at the farm Ubique (24.37S 29.10E) in the Transvaal. It is a large, diurnal, macropterous beetle attracted to most dung types. Its peak activity period is in the early morning ceasing at *c.* 10:00 am when temperatures reach about 30°C (personal observation). It forages on the wing in semi-open bushveld, dominated by *Terminalia sericea, Burkea africana* and *Eragrostis* spp. (Acocks 1988), preferring sandy soils for burrowing.

*Kheper subaeneus* (Harold), Fg I, was collected in moderate numbers at the Maré farm 30 km west of Pretoria (25.44S 28.00E). It is a large, diurnal, macropterous beetle attracted primarily to equine dung. Peak activity is in the morning from 9 - 11 am (personal observation). Seasonal activity is during November-February. It forages on the wing in mixed bushveld.

*Kheper cupreus* (Castelnau), Fg I, was collected at Skukuza in the Kruger National Park (24.59S 31.36E). It is a large, macropterous beetle. The specimens were active during a period of very low rainfall when few other dung beetles were seen (C.H. Scholtz, personal communication). It forages on the wing in lowveld areas.

*Pachysoma gariepinus* Ferreira, Fg I, was collected at Hohenfels in the southern Namib desert on the banks of the Orange river (28.30S 16.37E) and in the Obib dunes (28.03S 16.36E). It is a large, diurnal, apterous beetle. The beetles were active in large numbers in the morning, from 8h00-10h00, and in much lower numbers late in the afternoon, from 17h00-19h00 (pers. obs. and see Scholtz 1989). They forage on foot for dried Gemsbok dung pellets which they drag using their hind legs to pre-constructed burrows. These burrows are from 25-40cm deep and penetrate the moist layer of sand beneath the dune surface

(personal observation). In this layer the dung pellets are rehydrated and used as food or for breeding. At the end of their activity period the beetles retreat into their burrows.

*Scarabaeus zambesianus* Péringuey, Fg I, was collected in moderate numbers at the farm Ubique in the Transvaal. It is a large, nocturnal, macropterous beetle attracted to bovine dung. It forages on the wing in semi-open bushveld dominated by *Terminalia sericea, Burkea africana* and *Eragrostis* spp., preferring sandy soils for burrowing.

*Anachalcos convexus* Boheman, Fg I, was collected in moderate numbers at Marloth Park (25.21S 31.47E) on the Crocodile river south of the Kruger National Park. It is a large, nocturnal, macropterous beetle attracted primarily to carrion but visits dung in low numbers. It forages on the wing in thornveld.

*Pachysoma striatum* Castelnau, Fg I, was collected in low numbers at Port Nolloth (29.14S 16.52E). It is a large, diurnal, apterous beetle. It forages on foot for dried dung pellets which it drags by its hind legs to pre-constructed burrows. In these burrows the dung pellets are rehydrated and the used as food or for breeding. At the end of their activity periods the beetles retreat into these burrows (Scholtz 1989, and personal communication).

*Garetta nitens* Olivier, Fg II, was collected in moderate numbers at Marloth Park on the Crocodile river south of the Kruger National Park. It is a small, diurnal, macropterous beetle attracted to bovine dung. The beetles forage on the wing in thornveld during very humid periods after rains.

*Scarabaeus rubripennis* Boheman, Fg II, was collected at Hohenfels in the southern Namib desert on the banks of the Orange river. It is a small, diurnal, macropterous beetle. The beetles were active in large numbers early in the morning, 7h00-9h00, and in much lower numbers late in the afternoon 17h00- 19h00 (personal observation). They forage on the wing for fresh dung, rotten fruit and carrion which they construct into balls, roll away and bury. In contrast with the sympatric, apterous *P. gariepinus* (see above), their food sources are rich in water and nutrients

*Sisyphus impressipennis* Lansberg, Fg II, was collected in moderate numbers at Pafuri in the Kruger National Park (22.26S 31.20E). It is a small, diurnal, macropterous beetle

attracted to bovine dung. It forages on the wing in tropical riverine vegetation during very humid periods after rains (C.H. Scholtz, personal communication)

*Catharsius tricornutus* De Geer, Fg III, was collected in moderate numbers at the farm Ubique in the Transvaal. It is a large, nocturnal, macropterous beetle attracted to bovine dung. It forages on the wing in semi-open bushveld.

*Copris amyntor* Klug, Fg III, was collected in moderate numbers on the farm Abel (26.54S 27.35E) in the Parys district of the Orange Free State. It is a nocturnal, macropterous beetle attracted to bovine dung. It is active in late summer from April to June (Davis 1977). Most specimens were dug out from underneath relatively fresh dung pads. It forages on the wing in *Cymbopogon-Themeda* veld (C.H. Scholtz, personal communication).

*Onitis caffer* (Boheman), Fg IV, was collected in moderate numbers on the farm Abel in the Parys district of the Orange Free State. It is a nocturnal, macropterous beetle attracted to bovine dung. It is active in late summer from April to June (Davis 1977). These specimens were dug out from underneath dung pads of varying ages. It forages on the wing in *Cymbopogon-Themeda* veld (C.H. Scholtz, personal communication).

*Phalops ardea* Klug, Fg IV, was collected in large numbers at Marloth Park on the Crocodile river south of the Kruger National Park. It is a small, diurnal, macropterous beetle attracted to bovine dung. It forages on the wing in thornveld during very humid periods after rains.

*Onthophagus sapphirinus* Fahraeus, Fg V, was collected in moderate numbers at the Maré farm 30 km west of Pretoria. It is a small, diurnal, macropterous beetle attracted to bovine dung. Peak activity occurs in the morning from 9 - 11 am (personal observation). It is active from November to February. It forages on the wing in mixed bushveld.

*Liatongus militaris* (Castelnau), Fg VII, was collected in moderate numbers at the Maré farm 30 km west of Pretoria. It is a small, diurnal, macropterous beetle attracted to older undisturbed bovine dung pads where a crust has already formed (Davis 1977, personal observation). It forages on the wing in mixed bushveld.

## *DESICCATION RESISTANCE*

*I may be on the trail in this matter, or I may be following a will-o'-the-wisp, but I shall soon know which it is.*

Sherlock Holmes in The Beryl Coronet, Sir Arthur Conan Doyle, 1892.

To determine desiccation resistance, twenty individuals of each species were numbered, weighed and placed in groups of five in desiccation chambers containing silica gel. The desiccation chambers were kept in a climate controlled room at 27°C with a 12:12 light/dark cycle. Temperature and the relative humidity inside the desiccators were monitored regularly with a Novasina thermohygrometer. Beetles were weighed with a Sartorius electronic balance to the nearest 0,1mg at regular intervals (three hours to 24 hours, depending on the endurance of the species involved) until 100% mortality.

Maximum tolerable water loss, expressed as the percentage fresh mass lost (%FM) and as mass loss (g), time to maximum tolerable water loss (hr) and to 50% ($LT_{50}$) and 100% ($LT_{100}$) mortality of the experimental group, and rate of water loss expressed as $\%FM.hr^{-1}$ and $g.hr^{-1}$ were determined. These values were calculated from the mass recorded in the time interval directly prior to death in each individual, except for the LT values which were calculated from the time of death of each individual. Analysis of covariance was used to eliminate the confounding effects of body size on the measured variables. The data were adjusted using a grand mean of fresh mass of all the species and the slope of the line fitted in regression analyses of the variable in question on body mass (Packard and Boardman 1987, 1988). Body size was considered to have a significant effect on the measured variables when an $r^2$ of $\geq 30\%$ was found in the regression analyses. Variance checks indicated that the data were heteroscedastic, which would result in invalid results if the species were to be compared using a parametric ANOVA. Thus the data were subjected to a non-parametric Kruskal-Wallis one way analysis by ranks to determine the extent of differences between the species. The Kruskal-Wallis test was done with STATGRAPHICS Ver.6 statistical package. This program automatically awards average ranks, a significance value ($\alpha$) to each test, and calculates the test statistic (H). Critical values for the Kruskal-Wallis test are approximated by the chi-square distribution with $k$ - 1 degrees of freedom ($k$ = number of species within each group) If H > $\text{Chi-square}_{(k-1)}$ definite differences exist between the species in the

particular group, if H < Chi-square$_{(k-1)}$ no differences are present (Sokal and Rohlf 1981).

Differences or similarities between the species were determined by a pairwise non-parametric multiple comparison test based on the sample sizes and Kruskal-Wallis average ranks for each species with a 95% significance level (Zar 1984: 199). These pairwise comparisons were presented in Punnet diagrams. If a species did not differ significantly from the highest ranked species, it was placed in the high rank group, and inversely, if a species a species did not differ significantly from the lowest ranked species it was placed in the low rank group. If a species did not differ from the higher or lower ranked species it was placed in the intermediate group. This gives a good indication of which species either have a high, low or an intermediate tolerance for the particular parameter analysed. In the first analysis (17 species), a number of different factors, such as aptery vs. macroptery, were expected to contribute to desiccation resistance. Within each of these groups, in turn, other factors (such as activity period) are liable to be important. By repeating the analyses on subgroups identified in each previous analysis, greater resolution of factors contributing to variation in desiccation resistance is expected. This is partly a consequence of the statistical technique that is being used. The Kruskal-Wallis analyses were thus repeated on the subgroups.

## *THE EFFECT OF TEMPERATURE ON DESICCATION RESISTANCE*

*The Experimental Animals*

For comparative studies of the influence of temperature on desiccation resistance, four species were chosen. These species were also selected to compare desiccation resistance in winged vs apterous dung beetles. The apterous species were *Pachysoma gariepinus* (Desert biome) and *Circellium bacchus* (Savanna biome), and the winged species were *Scarabaeus rubripennis* (Desert biome) and *Pachylomerus femoralis* (Savanna biome). These species were also used to study water balance and osmoregulation in more detail. This work is reported in the next section.

*The effect of temperature on desiccation resistance*

Methods used here are identical to those discussed in the previous section. A randomly selected group of individuals (7 - 10) of a species were numbered, weighed and placed in desiccation chambers containing silica gel. The desiccation chambers were kept in temperature controlled cabinets at 15°C, 20°C, 27°C and 35°C, each with a 12 : 12 light/dark cycle. Temperature and relative humidity inside the desiccation chambers were

monitored regularly with a Novasina thermohygrometer. Beetles were weighed with a Sartorius Research electronic balance to the nearest 0.1mg at regular intervals ranging from every three hours to every 24 hours, depending on the endurance of the species involved, until 100% mortality.

Maximum tolerable water loss, expressed as the percentage fresh mass lost (% FM) and as water loss (g), time to maximum water loss (hr) of the experimental group and rate of water loss expressed as $\%FM.hr^{-1}$ and $g.hr^{-1}$ were determined separately at each temperature. These values were calculated from the mass recorded in the time interval directly prior to death in each individual. The data were adjusted to compensate for differences in body mass using Packard and Boardman's methods (1987, 1988)(see previous section). Body size was considered to have a significant effect on the measured variables when an $r^2$ of $\geq 30\%$ was found in the regression analyses. Both the raw and adjusted data were subjected to a non-parametric Kruskal-Wallis one way analysis by ranks to determine the extent of differences between the species at each temperature (Sokal and Rohlf 1981).

Differences or similarities between the four species at the four temperatures were determined by a pairwise non-parametric multiple comparison test with a 95% significance level (Zar 1984: 199). Species identified as similar to the two extreme ranked species were clustered into two groups.

*Activation energies*

Activation energies ($E_a$) were obtained from the slope of the linear regression of the natural logarithm of the rate of water loss, on the reciprocal of the absolute temperatures, $(°C+273)^{-1}$. The $E_a$s were calculated by multiplying the slope of the regression with the universal gas constant R, ($8.3\ J.K^{-1}.mol^{-1}$) (Cossins and Bowler 1987, Yoder and Denlinger 1991).

## *WATER BALANCE AND OSMOREGULATION*

Forty-six individuals were randomly selected and given fresh dung and water *ad lib.* for 24 hours. For the following 24 hours, only water was given to allow the beetles to clear their digestive tracts. Thereafter, individuals were numbered, weighed, and placed in groups of ten in desiccation chambers containing silica gel. The desiccation chambers were kept in a climate controlled room at 27°C with a 12 : 12 light/dark cycle. Temperature and relative humidity inside the desiccators were monitored regularly with a Novasina thermohygrometer. Beetles were weighed with a Sartorius Research electronic balance to the nearest 0.1mg at five regular intervals. These intervals were determined by halving the $LT_{50}$ value for a species, attained during the desiccation resistance at 27°C, and dividing it into five equal intervals. At the start and after each interval, five randomly chosen individuals were removed and haemolymph was extracted with haematocrit capillaries, after removal of the left mesocoxa. Haemolymph was placed in 1.5ml ependorf vials and frozen in liquid nitrogen for subsequent analysis. After the fifth interval, the remaining individuals were divided in two groups, one group was given access to free water on one side of the plastic container and moist sand on the other side. The other group was given acces to high atmospheric humidity (93-97% RH) in a desiccator. These beetles were regularly weighed until such time as their body mass stabilized or attained their original value. At this stage, haemolymph was extracted from another five individuals.

Bodywater contents were determined by drying the beetles at 60°C to constant mass and weighing them to the nearest 0.1mg. Lipid contents were determined by breaking up the dried beetles and extracting the lipids with three changes (one change every 24 hours) of a 2:1 methanol-chloroform solution. The beetles were dried to constant mass and subsequently weighed to determine the lipid free dry mass. Water loss (g) was also monitored during the trial. The original data were corrected for body mass using Packard and Boardman's methods (1987, 1988) (see previous section).

The efficacy of lipid metabolism, to provide metabolic water can be estimated by examining a regression of lipid content, expressed as a percentage of lipid free dry mass, on percentage water loss (Method 1). A high $r^2$ value indicates lipid metabolism (Naidu and Hattingh 1988). Chown *et al.* (in press) calculated the effect of lipid metabolism using a regression of lipid content, expressed as a percentage of dry mass, on percentage water loss (Method 2).

Osmolality of the extracted haemolymph was determined using a Wescor 5120 B

vapour pressure osmometer. Osmotic responses to dehydration were described by a regression line relating water content (g water/g dry mass), and haemolymph osmolality (Riddle 1986). In this approach, the slope of the regression equation provides a single estimate of the osmoregulatory capacity of the beetles over a range of water contents. Comparatively low slope values denote a large capacity for haemolymph osmoregulation, whereas steeper slopes indicate poorer osmoregulatory ability. Linear regression equations were examined by analysis of variance to determine if slopes differed significantly from zero and from each other (Sokal & Rohlf 1981).

# RESULTS

*In a way, science might be described as paranoid thinking applied to Nature: we are looking for natural conspiracies, for connections among apparently disparate data.*

Carl Sagan, The Dragons of Eden, 1977.

## *BODY WATER LOSS, SURVIVAL TIME & RATE OF WATER LOSS*

Table 1 summarizes the results of the 27°C desiccation trial. Based on percentages, few meaningful comparisons could be made. However, *S. rubripennis*, *C. amyntor* and the three apterous species, *C. bacchus, P. gariepinus* and *P. striatum* had greater maximum tolerable mass losses and the lowest rates of water loss. The nocturnal species, with the exception of *C. amyntor*, as well as the other paracoprid species had the highest rates of water loss. The apterous species and *S. rubripennis* had the longest survival times indicating high resistances to desiccation.

The regressions of survival time, rate of water loss and maximum tolerable water loss on body mass were all significant with $r^2$'s greater than 30% (Table 2). The effects of body size were removed using Packard and Boardman's (1987, 1988) method and the summary statistics of the unadjusted and adjusted variables of each species are given in Table 1.

**Table 1.** Summary statistics of the results of the desiccation experiments at 27°C, 5 - 15% RH and 12L:12D photoperiod for the seventeen species.

| Species | Initial mass, g. | | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 6.4887 | 1.2418 | 5.0970-8.9410 |
| *P. femoralis* | 16 | 4.2668 | 1.0899 | 2.3830-5.9140 |
| *K. subaeneus* | 20 | 2.1138 | 0.5476 | 1.4559-3.3698 |
| *K. cupreus* | 20 | 1.7906 | 0.3214 | 1.0640-2.3256 |
| *P. gariepinus* | 20 | 1.7444 | 0.3472 | 1.0256-2.3869 |
| *S. zambesianus* | 20 | 1.2477 | 0.3101 | 0.8156-1.8491 |
| *A. convexus* | 20 | 1.1902 | 0.2663 | 0.6532-1.6275 |
| *P. striatum* | 20 | 0.7949 | 0.1457 | 0.4280-1.0710 |
| *G. nitens* | 20 | 0.3581 | 0.1074 | 0.2041-0.6199 |
| *S. rubripennis* | 20 | 0.1579 | 0.0329 | 0.1056-0.2466 |
| *S. impressipennis* | 20 | 0.0987 | 0.0162 | 0.0761-0.1320 |
| *C. tricornutus* | 20 | 1.3142 | 0.2766 | 0.6547-1.7228 |
| *C. amyntor* | 20 | 0.3006 | 0.0714 | 0.1563-0.3951 |
| *O. caffer* | 20 | 0.5233 | 0.1233 | 0.3216-0.7784 |
| *P. ardea* | 20 | 0.1075 | 0.0168 | 0.0776-0.1374 |
| *O. sapphirinus* | 20 | 0.1252 | 0.0297 | 0.0753-0.1867 |
| *L. militaris* | 40 | 0.0846 | 0.0106 | 0.0558-0.1055 |

| Species | Maximum tolerable mass loss, g. | | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 2.6264 | 0.5905 | 1.8630-3.8680 |
| *P. femoralis* | 16 | 1.2675 | 0.3782 | 0.4530-1.6770 |
| *K. subaeneus* | 20 | 0.5607 | 0.1579 | 0.3857-1.0619 |
| *K. cupreus* | 20 | 0.5599 | 0.1125 | 0.2816-0.7475 |
| *P. gariepinus* | 20 | 0.5971 | 0.2759 | 0.1622-1.1368 |
| *S. zambesianus* | 20 | 0.3206 | 0.1148 | 0.1092-0.5311 |
| *A. convexus* | 20 | 0.3078 | 0.0854 | 0.1847-0.5008 |
| *P. striatum* | 20 | 0.3044 | 0.0887 | 0.1074-0.4999 |
| *G. nitens* | 20 | 0.0893 | 0.0317 | 0.0449-0.1481 |
| *S. rubripennis* | 20 | 0.0683 | 0.0171 | 0.0391-0.1017 |
| *S. impressipennis* | 20 | 0.0259 | 0.0088 | 0.0064-0.0419 |
| *C. tricornutus* | 20 | 0.3924 | 0.1243 | 0.1299-0.6249 |
| *C. amyntor* | 20 | 0.1153 | 0.0286 | 0.0581-0.1790 |
| *O. caffer* | 20 | 0.1767 | 0.0461 | 0.0930-0.2995 |
| *P. ardea* | 20 | 0.0242 | 0.0150 | 0.0066-0.0613 |
| *O. sapphirinus* | 20 | 0.0345 | 0.0075 | 0.0104-0.0505 |
| *L. militaris* | 40 | 0.0264 | 0.0046 | 0.0173-0.0361 |

**(Table 1 continued)**

| Species | Percentage maximum tolerable mass loss | | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 40.31 | 3.08 | 35.51-46.01 |
| *P. femoralis* | 16 | 29.60 | 5.73 | 19.01-39.22 |
| *K. subaeneus* | 20 | 26.83 | 4.55 | 17.68-34.38 |
| *K. cupreus* | 20 | 31.32 | 3.64 | 22.25-37.90 |
| *P. gariepinus* | 20 | 33.03 | 10.99 | 9.96-47.63 |
| *S. zambesianus* | 20 | 25.13 | 4.47 | 13.39-30.59 |
| *A. convexus* | 20 | 26.06 | 5.08 | 17.97-36.80 |
| *P. striatum* | 20 | 37.70 | 6.03 | 25.09-46.68 |
| *G. nitens* | 20 | 25.22 | 5.62 | 14.47-37.82 |
| *S. rubripennis* | 20 | 42.98 | 4.34 | 34.86-52.53 |
| *S. impressipennis* | 20 | 25.93 | 6.93 | 7.25-34.77 |
| *C. tricornutus* | 20 | 29.76 | 6.53 | 10.53-42.13 |
| *C. amyntor* | 20 | 38.53 | 4.52 | 33.02-48.10 |
| *O. caffer* | 20 | 33.71 | 3.08 | 28.92-39.13 |
| *P. ardea* | 20 | 22.19 | 11.97 | 5.77-44.61 |
| *O. sapphirinus* | 20 | 28.85 | 7.12 | 5.57-40.47 |
| *L. militaris* | 40 | 31.42 | 5.06 | 20.55-41.68 |

| Species | Adjusted maximum tolerable mass loss, g. | | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 0.4429 | 0.0333 | 0.3919-0.5057 |
| *P. femoralis* | 16 | 0.3284 | 0.0634 | 0.2136-0.4353 |
| *K. subaeneus* | 20 | 0.3026 | 0.0518 | 0.1990-0.3889 |
| *K. cupreus* | 20 | 0.3543 | 0.0413 | 0.2507-0.4302 |
| *P. gariepinus* | 20 | 0.3735 | 0.1235 | 0.1128-0.5364 |
| *S. zambesianus* | 20 | 0.2866 | 0.0503 | 0.1541-0.3500 |
| *A. convexus* | 20 | 0.2977 | 0.0584 | 0.2037-0.4213 |
| *P. striatum* | 20 | 0.4342 | 0.0685 | 0.2931-0.5340 |
| *G. nitens* | 20 | 0.2962 | 0.0664 | 0.1689-0.4427 |
| *S. rubripennis* | 20 | 0.5136 | 0.0512 | 0.4187-0.6247 |
| *S. impressipennis* | 20 | 0.3131 | 0.0835 | 0.0877-0.4179 |
| *C. tricornutus* | 20 | 0.3391 | 0.0745 | 0.1201-0.4804 |
| *C. amyntor* | 20 | 0.4540 | 0.0538 | 0.3876-0.5706 |
| *O. caffer* | 20 | 0.3922 | 0.0357 | 0.3386-0.4555 |
| *P. ardea* | 20 | 0.2674 | 0.1439 | 0.0695-0.5347 |
| *O. sapphirinus* | 20 | 0.3471 | 0.0867 | 0.0663-0.4901 |
| *L. militaris* | 40 | 0.3809 | 0.0617 | 0.2490-0.5058 |

**(Table 1 continued)**

| Species | Survival time, hr. | | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 211.6 | 66.3 | 96.0-280.0 |
| *P. femoralis* | 16 | 106.2 | 45.5 | 29.5-189.5 |
| *K. subaeneus* | 20 | 61.4 | 8.7 | 38.0-67.0 |
| *K. cupreus* | 20 | 101.3 | 23.1 | 73.0-140.0 |
| *P. gariepinus* | 20 | 392.7 | 287.2 | 27.5-1107.5 |
| *S. zambesianus* | 20 | 32.8 | 15.9 | 10.3-63.0 |
| *A. convexus* | 20 | 64.4 | 26.9 | 25.0-103.0 |
| *P. striatum* | 20 | 235.3 | 69.9 | 102.0-358.0 |
| *G. nitens* | 20 | 15.8 | 9.0 | 5.0-30.0 |
| *S. rubripennis* | 20 | 126.0 | 35.3 | 51.5-181.5 |
| *S. impressipennis* | 20 | 21.2 | 10.8 | 6.0-50.0 |
| *C. tricornutus* | 20 | 27.6 | 4.9 | 16.0-34.0 |
| *C. amyntor* | 20 | 79.2 | 37.7 | 29.0-159.0 |
| *O. caffer* | 20 | 18.8 | 3.4 | 10.0-24.0 |
| *P. ardea* | 20 | 9.5 | 7.4 | 3.0-24.0 |
| *O. sapphirinus* | 20 | 52.0 | 19.4 | 9.0-70.0 |
| *L. militaris* | 40 | 18.0 | 3.3 | 12.0-24.0 |

| Species | Adjusted survival time, hr. | | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 94.1 | 31.2 | 41.9-131.2 |
| *P. femoralis* | 16 | 56.4 | 22.6 | 20.5-102.2 |
| *K. subaeneus* | 20 | 46.5 | 7.3 | 31.2-57.9 |
| *K. cupreus* | 20 | 82.9 | 21.9 | 53.2-144.8 |
| *P. gariepinus* | 20 | 309.5 | 208.4 | 26.6-781.0 |
| *S. zambesianus* | 20 | 30.8 | 12.9 | 10.9-50.7 |
| *A. convexus* | 20 | 62.4 | 23.4 | 29.9-107.9 |
| *P. striatum* | 20 | 278.1 | 72.3 | 162.4-398.3 |
| *G. nitens* | 20 | 26.5 | 13.6 | 7.8-48.6 |
| *S. rubripennis* | 20 | 321.7 | 79.9 | 147.2-433.5 |
| *S. impressipennis* | 20 | 68.6 | 35.9 | 19.6-159.8 |
| *C. tricornutus* | 20 | 26.0 | 4.5 | 15.4-32.5 |
| *C. amyntor* | 20 | 148.1 | 61.2 | 60.3-263.2 |
| *O. caffer* | 20 | 27.4 | 4.5 | 16.2-34.7 |
| *P. ardea* | 20 | 28.5 | 21.0 | 8.6-71.6 |
| *O. sapphirinus* | 20 | 149.4 | 53.5 | 21.2-220.7 |
| *L. militaris* | 40 | 61.9 | 10.8 | 40.2-78.5 |

**(Table 1 continued)**

| Species | | LT50 | LT100 |
|---|---|---|---|
| | n | | |
| *C. bacchus* | 14 | 207.00 | 280.00 |
| *P. femoralis* | 16 | 101.50 | 189.50 |
| *K. subaeneus* | 20 | 65.00 | 67.00 |
| *K. cupreus* | 20 | 94.50 | 140.00 |
| *P. gariepinus* | 20 | 276.00 | 1107.50 |
| *S. zambesianus* | 20 | 27.00 | 63.00 |
| *A. convexus* | 20 | 55.00 | 103.00 |
| *P. striatum* | 20 | 221.00 | 358.00 |
| *G. nitens* | 20 | 15.00 | 30.00 |
| *S. rubripennis* | 20 | 132.50 | 181.50 |
| *S. impressipennis* | 20 | 18.00 | 50.00 |
| *C. tricornutus* | 20 | 28.00 | 34.00 |
| *C. amyntor* | 20 | 67.00 | 159.00 |
| *O. caffer* | 20 | 19.00 | 24.00 |
| *P. ardea* | 20 | 7.00 | 24.00 |
| *O. sapphirinus* | 20 | 58.00 | 70.00 |
| *L. militaris* | 40 | 20.00 | 24.00 |

| Species | | Rate of mass loss, g/hr | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 0.0141 | 0.0072 | 0.0081-0.0348 |
| *P. femoralis* | 16 | 0.0133 | 0.0048 | 0.0075-0.0220 |
| *K. subaeneus* | 20 | 0.0093 | 0.0028 | 0.0058-0.0158 |
| *K. cupreus* | 20 | 0.0058 | 0.0017 | 0.0020-0.0087 |
| *P. gariepinus* | 20 | 0.0022 | 0.0013 | 0.0010-0.0064 |
| *S. zambesianus* | 20 | 0.0109 | 0.0037 | 0.0062-0.0221 |
| *A. convexus* | 20 | 0.0053 | 0.0016 | 0.0027-0.0089 |
| *P. striatum* | 20 | 0.0013 | 0.0003 | 0.0009-0.0020 |
| *G. nitens* | 20 | 0.0072 | 0.0034 | 0.0032-0.0138 |
| *S. rubripennis* | 20 | 0.0006 | 0.0002 | 0.0004-0.0012 |
| *S. impressipennis* | 20 | 0.0014 | 0.0005 | 0.0005-0.0025 |
| *C. tricornutus* | 20 | 0.0114 | 0.0037 | 0.0081-0.0215 |
| *C. amyntor* | 20 | 0.0017 | 0.0007 | 0.0010-0.0035 |
| *O. caffer* | 20 | 0.0096 | 0.0024 | 0.0062-0.0158 |
| *P. ardea* | 20 | 0.0031 | 0.0013 | 0.0011-0.0063 |
| *O. sapphirinus* | 20 | 0.0008 | 0.0004 | 0.0005-0.0019 |
| *L. militaris* | 40 | 0.0015 | 0.0003 | 0.0010-0.0021 |

**(Table 1 continued)**

| Species | Percentage rate of mass loss, %mass loss/hr. | | |
|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 0.22 | 0.09 | 0.13-0.39 |
| *P. femoralis* | 16 | 0.34 | 0.19 | 0.18-0.90 |
| *K. subaeneus* | 20 | 0.37 | 0.08 | 0.21-0.52 |
| *K. cupreus* | 20 | 0.33 | 0.09 | 0.18-0.47 |
| *P. gariepinus* | 20 | 0.53 | 0.24 | 0.11-0.91 |
| *S. zambesianus* | 20 | 0.34 | 0.08 | 0.15-0.44 |
| *A. convexus* | 20 | 0.48 | 0.26 | 0.26-1.12 |
| *P. striatum* | 20 | 0.17 | 0.044 | 0.11-0.25 |
| *G. nitens* | 20 | 2.41 | 1.76 | 0.90-6.32 |
| *S. rubripennis* | 20 | 0.76 | 0.14 | 0.54-1.11 |
| *S. impressipennis* | 20 | 0.36 | 0.12 | 0.08-0.53 |
| *C. tricornutus* | 20 | 1.09 | 0.23 | 0.66-1.52 |
| *C. amyntor* | 20 | 0.59 | 0.27 | 0.26-1.43 |
| *O. caffer* | 20 | 1.86 | 0.41 | 1.35-3.02 |
| *P. ardea* | 20 | 0.32 | 0.22 | 0.06-0.81 |
| *O. sapphirinus* | 20 | 0.42 | 0.13 | 0.06-0.68 |
| *L. militaris* | 40 | 1.80 | 0.41 | 1.13-2.90 |

| Species | Adjusted rate of mass loss, g/hr | | | |
|---|---|---|---|---|
| | n | Mean | SD | Range |
| *C. bacchus* | 14 | 0.0054 | 0.0024 | 0.0032-0.0113 |
| *P. femoralis* | 16 | 0.0067 | 0.0030 | 0.0037-0.0145 |
| *K. subaeneus* | 20 | 0.0067 | 0.0017 | 0.0040-0.0115 |
| *K. cupreus* | 20 | 0.0046 | 0.0012 | 0.0021-0.0065 |
| *P. gariepinus* | 20 | 0.0018 | 0.0013 | 0.0007-0.0061 |
| *S. zambesianus* | 20 | 0.0108 | 0.0044 | 0.0057-0.0237 |
| *A. convexus* | 20 | 0.0054 | 0.0022 | 0.0029-0.0102 |
| *P. striatum* | 20 | 0.0016 | 0.0003 | 0.0011-0.0023 |
| *G. nitens* | 20 | 0.0149 | 0.0089 | 0.0061-0.0342 |
| *S. rubripennis* | 20 | 0.0017 | 0.0006 | 0.0012-0.0036 |
| *S. impressipennis* | 20 | 0.0053 | 0.0019 | 0.0024-0.0098 |
| *C. tricornutus* | 20 | 0.0131 | 0.0026 | 0.0078-0.0190 |
| *C. amyntor* | 20 | 0.0036 | 0.0015 | 0.0018-0.0081 |
| *O. caffer* | 20 | 0.0147 | 0.0030 | 0.0111-0.0218 |
| *P. ardea* | 20 | 0.0116 | 0.0049 | 0.0038-0.0244 |
| *O. sapphirinus* | 20 | 0.0028 | 0.0012 | 0.0015-0.0076 |
| *L. militaris* | 40 | 0.0063 | 0.0012 | 0.0042-0.0085 |

**Table 2:** Regression of the maximum tolerable mass loss, rate of mass loss and survival times on the wet mass of the seventeen Scarabaeinae species obtained from desiccation experiments at 27± 1°C and 5 - 15% RH. The regressions are in the form logY = b logX + a

| Variable | n | Slope±SE | Intercept±SE | $r^2$ | p |
|---|---|---|---|---|---|
| Mass loss | 350 | 1.0226±0.0131 | -1.2023±0.0197 | 94.62% | $<1x10^{-5}$ |
| Rate of mass loss | 350 | 0.5487±0.0313 | -5.3399±0.0473 | 46.84% | $<1x10^{-5}$ |
| Survival time | 350 | 0.4739±0.0375 | 4.1376±0.0566 | 31.45% | $<1x10^{-5}$ |

## *MULTIPLE COMPARISONS OF DESICCATION RESISTANCE*

*Statistics were just as much a fantasy in their original version as in their rectified version. A great deal of time you were expected to make them up out of your head.*

George Orwell, Nineteen Eighty-Four.

*The seventeen species*

The Kruskal-Wallis non-parametric analyses of unadjusted and adjusted data indicated large differences between the seventeen species (Table 3a-f). In the tables and in the pairwise analyses diagrams the species are organised according to the descending average ranks given to each by the Kruskal-Wallis test.

In the analyses maximum tolerable water loss, where the effects of body sizes were not corrected for (Table 3a and Diagram 1a) none of the species in functional group I differed from each other in maximum tolerable water loss. *Circellium bacchus* (highest ranked), *P. femoralis, K. cupreus, K. subaeneus, P. gariepinus, C. tricornutus, S. zambesianus, A. convexus* and *P. striatum* formed the high rank group with large tolerance of water loss. The smaller and medium-sized species, *P. ardea* (lowest ranked), *L. militaris, S. impressipennis, O. sapphirinus, S. rubripennis, G nitens* and *C. amyntor* formed the group with low tolerance of water loss. *Onitis caffer,* overlapped both groups, and did not differ from any of the species. This species is therefore intermediate with regards to unadjusted tolerance of the maximum amount of water lost.

The results of the comparisons of unadjusted rate of mass loss, (Table 3b and Diagram 1b), are different to the results obtained from the data on maximum tolerable mass loss. Here size played less of a role than in the previous analysis. *Catharsius tricornutus* (highest ranked), *P. femoralis, C. bacchus, S. zambesianus, O. caffer, K. subaeneus, G. nitens, K. cupreus* and *A. convexus* formed the high rank group with the fastest rate of water loss. Those species with the slowest rate of water loss were *S. rubripennis* (lowest ranked), *O. sapphirinus, P. striatum, S. impressipennis, L. militaris, C. amyntor* and *P. gariepinus. Phalops ardea* was intermediate and overlapped with both groups.

In the analysis of unadjusted survival time (Table 3c and Diagram 1c), *P. striatum* (highest ranked), *C. bacchus, P. gariepinus, S. rubripennis, K. cupreus, P. femoralis, C.*

*amyntor, K. subaeneus* and *A. convexus* formed the high rank group comprising species that have a high resistance to desiccation. The less resistant species that form the low rank group are *P. ardea* (lowest ranked), *G. nitens, L. militaris, O. caffer, S. impressipennis, S. zambesianus,* and *C. tricornutus. Onthophagus sapphirinus* was intermediate.

In all three analyses, the three brachypterous species, *C. bacchus*, *P. gariepinus* and *P. striatum*, were included in the groups with high resistance to desiccation. Similarly tolerant species were *S. rubripennis*, the larger Fg I species, and *C. amyntor*. In the unadjusted analyses large and/or apterous species emerged as those most resistant to desiccation.

**Table 3a.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted maximum tolerable mass loss of seventeen Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 324.808 Significance level $\alpha$ = $<0.0001$ $Chi^2$ approximation = 45.9249 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average ranks |
|---|---|---|---|
| | ▲*C. bacchus* | 14 | 343.5000 |
| | ▲*P. femoralis* | 16 | 323.0310 |
| | ▲*K. cupreus* | 20 | 286.0750 |
| | ▲*K. subaeneus* | 20 | 282.6000 |
| ***HR*** | ▲*P. gariepinus* | 20 | 276.2000 |
| | ▲*C. tricornutus* | 20 | 243.9500 |
| | ▲*S. zambesianus* | 20 | 221.9250 |
| | ▲*A. convexus* | 20 | 219.3250 |
| | ▲*P. striatum* | 20 | 217.4000 |
| ***IR*** | ⇕*O. caffer* | 20 | 175.0000 |
| | ▼*C. amyntor* | 20 | 147.0000 |
| | ▼*G. nitens* | 20 | 130.9750 |
| | ▼*S. rubripennis* | 20 | 117.8000 |
| ***LR*** | ▼*O. sapphirinus* | 20 | 77.5250 |
| | ▼*S. impressipennis* | 20 | 46.0250 |
| | ▼*L. militaris* | 40 | 44.7250 |
| | ▼*P. ardea* | 20 | 40.1250 |

**Table 3b.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted rate of mass loss of seventeen Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 301.611 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 45.9249 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average ranks |
|---|---|---|---|
| | ▲*C. tricornutus* | 20 | 315.6500 |
| | ▲*P. femoralis* | 16 | 304.3750 |
| | ▲*C. bacchus* | 14 | 302.2860 |
| | ▲*S. zambesianus* | 20 | 285.8500 |
| ***HR*** | ▲*O. caffer* | 20 | 271.3500 |
| | ▲*K. subaeneus* | 20 | 266.4000 |
| | ▲*G. nitens* | 20 | 233.7500 |
| | ▲*K. cupreus* | 20 | 214.4000 |
| | ▲*A. convexus* | 20 | 203.9500 |
| ***IR*** | ⇕*P. ardea* | 20 | 161.1750 |
| | ▼*P. gariepinus* | 20 | 125.5500 |
| | ▼*C. amyntor* | 20 | 104.3500 |
| | ▼*L. militaris* | 40 | 102.4000 |
| ***LR*** | ▼*S. impressipennis* | 20 | 89.3250 |
| | ▼*P. striatum* | 20 | 82.8000 |
| | ▼*O. sapphirinus* | 20 | 38.2000 |
| | ▼*S. rubripennis* | 20 | 18.5000 |

**Table 3c.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted survival time of seventeen Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 295.429 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 45.9249 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average ranks |
|---|---|---|---|
| | ▲*P. striatum* | 20 | 319.0500 |
| | ▲*C. bacchus* | 14 | 312.2860 |
| | ▲*P. gariepinus* | 20 | 307.9500 |
| | ▲*S. rubripennis* | 20 | 273.9250 |
| ***HR*** | ▲*K. cupreus* | 20 | 257.7500 |
| | ▲*P. femoralis* | 16 | 252.9690 |
| | ▲*C. amyntor* | 20 | 224.4000 |
| | ▲*K. subaeneus* | 20 | 206.7000 |
| | ▲*A. convexus* | 20 | 205.1000 |
| ***IR*** | ⇕*O. sapphirinus* | 20 | 178.4750 |
| | ▼*C. tricornutus* | 20 | 134.6750 |
| | ▼*S. zambesianus* | 20 | 133.6000 |
| | ▼*S. impressipennis* | 20 | 88.0000 |
| ***LR*** | ▼*O. caffer* | 20 | 73.4000 |
| | ▼*L. militaris* | 40 | 72.6375 |
| | ▼*G. nitens* | 20 | 69.5000 |
| | ▼*P. ardea* | 20 | 32.4750 |

**Diagram 1a.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted maximum tolerable mass loss of seventeen Scarabaeinae species. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$

Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Pg = Pachysoma gariepinus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Ps = Pachysoma striatum, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Cb* | *Pf* | *Kc* | *Ks* | *Pg* | *Ct* | *Sz* | *Ac* | *Ps* | *Oc* | *Ca* | *Gn* | *Sr* | *Os* | *Si* | *Lm* | *Pa* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cb* I | | - | - | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Pf* I | - | | - | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Kc* I | - | - | | - | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Ks* I | - | - | - | | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Pg* I | - | - | - | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Ct* III | - | - | - | - | - | | - | - | - | - | - | - | - | + | + | + | + |
| *Sz* I | - | - | - | - | - | - | | - | - | - | - | - | - | - | + | + | + |
| *Ac* I | - | - | - | - | - | - | - | | - | - | - | - | - | - | + | + | + |
| *Ps* I | - | - | - | - | - | - | - | - | | - | - | - | - | - | + | + | + |
| *Oc* IV | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Ca* III | + | + | - | - | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Gn* II | + | + | - | - | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Sr* II | + | + | + | + | + | - | - | - | - | - | - | - | | - | - | - | - |
| *Os* V | + | + | + | + | + | + | - | - | - | - | - | - | - | | - | - | - |
| *Si* II | + | + | + | + | + | + | + | + | + | - | - | - | - | - | | - | - |
| *Lm* VII | + | + | + | + | + | + | + | + | + | - | - | - | - | - | - | | - |
| *Pa* IV | + | + | + | + | + | + | + | + | + | - | - | - | - | - | - | - | |

**Diagram 1b.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted rate of mass loss of seventeen Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Pg = Pachysoma gariepinus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Ps = Pachysoma striatum, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Ct* | *Pf* | *Cb* | *Sz* | *Oc* | *Ks* | *Gn* | *Kc* | *Ac* | *Pa* | *Pg* | *Ca* | *Lm* | *Si* | *Ps* | *Os* | *Sr* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ct* III | | - | - | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Pf* I | - | | - | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Cb* I | - | - | | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Sz* I | - | - | - | | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Oc* IV | - | - | - | - | | - | - | - | - | - | - | + | + | + | + | + | + |
| *Ks* I | - | - | - | - | - | | - | - | - | - | - | + | + | + | + | + | + |
| *Gn* II | - | - | - | - | - | - | | - | - | - | - | - | - | - | - | + | + |
| *Kc* I | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | + | + |
| *Ac* I | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | + | + |
| *Pa* IV | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Pg* I | + | + | + | + | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Ca* III | + | + | + | + | + | + | - | - | - | - | - | | - | - | - | - | - |
| *Lm* VII | + | + | + | + | + | + | - | - | - | - | - | - | | - | - | - | - |
| *Si* II | + | + | + | + | + | + | - | - | - | - | - | - | - | | - | - | - |
| *Ps* I | + | + | + | + | + | + | - | - | - | - | - | - | - | - | | - | - |
| *Os* V | + | + | + | + | + | + | + | + | + | - | - | - | - | - | - | | - |
| *Sr* II | + | + | + | + | + | + | + | + | + | - | - | - | - | - | - | - | |

**Diagram 1c.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted survival time of seventeen Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Pg = Pachysoma gariepinus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Ps = Pachysoma striatum, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Ps* | *Cb* | *Pg* | *Sr* | *Kc* | *Pf* | *Ca* | *Ks* | *Ac* | *Os* | *Ct* | *Sz* | *Si* | *Oc* | *Lm* | *Gn* | *Pa* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ps* I | | - | - | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Cb* I | - | | - | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Pg* I | - | - | | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Sr* II | - | - | - | | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Kc* I | - | - | - | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Pf* I | - | - | - | - | - | | - | - | - | - | - | - | - | + | + | + | + |
| *Ca* III | - | - | - | - | - | - | | - | - | - | - | - | - | - | + | - | + |
| *Ks* I | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | - | + |
| *Ac* I | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | + |
| *Os* V | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Ct* III | + | + | + | - | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Sz* I | + | + | + | - | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Si* II | + | + | + | + | + | - | - | - | - | - | - | - | | - | - | - | - |
| *Oc* IV | + | + | + | + | + | + | - | - | - | - | - | - | - | | - | - | - |
| *Lm* VII | + | + | + | + | + | + | + | - | - | - | - | - | - | - | | - | - |
| *Gn* II | + | + | + | + | + | + | - | - | - | - | - | - | - | - | - | | - |
| *Pa* IV | + | + | + | + | + | + | + | + | + | - | - | - | - | - | - | - | |

When the effects of body size were removed, patterns changed substantially. In the adjusted maximum tolerable mass loss analysis, *S. rubripennis* (highest ranked), *C. amyntor*, *C. bacchus* and *P. striatum* formed the high rank group of species which could tolerate the highest mass loss (Table 3d and Diagram 1d). *Scarabaeus zambesianus* (lowest ranked), *A. convexus, G. nitens, K. subaeneus, P. ardea, S. impressipennis, P. femoralis, C. tricornutus* and *O. sapphirinus* form the low rank group with the lowest tolerance of water loss (Table 3d and Diagram 1d). *Onitis caffer, L. militaris, P. gariepinus* and *K. cupreus* were intermediate (Table 3d and Diagram 1d). The grouping of species in the high and low rank groups much more uneven than that in the unadjusted analysis, with the low rank group containing most of the species. More species were also considered intermediate.

The analysis of adjusted rate of mass loss (Table 3e and Diagram 1e) showed a more symmetrical grouping of species in the high and low rank groups, although there were more species included in the intermediate group than in the unadjusted rate of mass loss analysis. *Onitis caffer* (highest ranked), *C. tricornutus, G. nitens, P. adrea, S. zambesianus, K. subaeneus* and *L. militaris* formed the group with the highest rates of water loss. Species with the lowest rates of water loss were *P. striatum* (lowest ranked), *S. rubripennis*, *P. gariepinus*, *O. sapphirinus, C. amyntor*, *K. cupreus* and *A. convexus. Pachylomerus femoralis, S. impressipennis* and *C. bacchus* were intermediate.

Finally, the analysis of adjusted survival time (Table 3f and Diagram 1f) also showed a more asymmetrical grouping in the high and low rank groups than that found in the unadjusted analysis. *Scarabaeus rubripennis* (highest rank), *P. striatum*, *P. gariepinus*, *C. amyntor* and *O. sapphirinus* formed the group with the longest survival time i.e. most desiccation resistance. *Catharsius tricornutus* (lowest ranked), *G. nitens, O. caffer, P. adrea, S. zambesianus, K. subaeneus* and *P. femoralis* formed the group that showed a much lower survival time. *Circellium bacchus, K. cupreus, L. militaris, S, impressipennis* and *A. convexus* were intermediate. The seemingly unusual results shown by *L. militaris* and *K. cupreus* (see Diagram 1f) were partly due to the nature of the formula used to calculate the pairwise comparisons.

In this trial the most important factor influencing resistance to desiccation was aptery. The three apterous species were either included in the groups representing high resistance to desiccation, (*P. gariepinus* and *P. striatum*) or were intermediate, (*C. bacchus*). Other highly resistant species were the desert species, *S. rubripennis*, the Orange Free State grassland species *C. amyntor,* and the savanna species *O. sapphirinus* and *K. cupreus.*

**Table 3d.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted maximum tolerable mass loss of seventeen Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 171.466 Significance level $\alpha$ = <0.0001 Chi$^2$ approximation = 45.9249 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average ranks |
|---|---|---|---|
| | ▲*S. rubripennis* | 20 | 323.7500 |
| ***HR*** | ▲*C. amyntor* | 20 | 283.1500 |
| | ▲*C. bacchus* | 14 | 279.0710 |
| | ▲*P. striatum* | 20 | 258.5000 |
| | ⇕*O. caffer* | 20 | 218.5500 |
| ***IR*** | ⇕*L. militaris* | 40 | 199.5500 |
| | ⇕*P. gariepinus* | 20 | 196.4000 |
| | ⇕*K. cupreus* | 20 | 165.8500 |
| | ▼*O. sapphirinus* | 20 | 163.9000 |
| | ▼*C. tricornutus* | 20 | 150.4500 |
| | ▼*P. femoralis* | 16 | 135.3130 |
| | ▼*S. impressipennis* | 20 | 129.1000 |
| ***LR*** | ▼*P. ardea* | 20 | 103.8500 |
| | ▼*K. subaeneus* | 20 | 100.2000 |
| | ▼*G. nitens* | 20 | 97.4000 |
| | ▼*A. convexus* | 20 | 95.6000 |
| | ▼*S. zambesianus* | 20 | 81.8500 |

**Table 3e.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted rate of mass loss of seventeen Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 276.959 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 45.9249 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average ranks |
|---|---|---|---|
| | ▲*O. caffer* | 20 | 316.6500 |
| | ▲*C. tricornutus* | 20 | 303.4500 |
| | ▲*G. nitens* | 20 | 287.2500 |
| ***HR*** | ▲*P. ardea* | 20 | 274.1000 |
| | ▲*S. zambesianus* | 20 | 269.6000 |
| | ▲*K. subaeneus* | 20 | 204.6500 |
| | ▲*L. militaris* | 40 | 195.8500 |
| | ⇕*P. femoralis* | 16 | 193.5000 |
| ***IR*** | ⇕*S. impressipennis* | 20 | 160.9000 |
| | ⇕*C. bacchus* | 14 | 158.3570 |
| | ▼*A. convexus* | 20 | 157.0000 |
| | ▼*K. cupreus* | 20 | 139.0500 |
| | ▼*C. amyntor* | 20 | 105.3500 |
| ***LR*** | ▼*O. sapphirinus* | 20 | 81.3500 |
| | ▼*P. gariepinus* | 20 | 42.4500 |
| | ▼*S. rubripennis* | 20 | 37.1000 |
| | ▼*P. striatum* | 20 | 35.0000 |

**Table 3f.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted survival time of seventeen Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 271.041 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 45.9249 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average ranks |
|---|---|---|---|
| | ▲*S. rubripennis* | 20 | 322.4500 |
| | ▲*P. striatum* | 20 | 314.0000 |
| ***HR*** | ▲*P. gariepinus* | 20 | 286.3500 |
| | ▲*C. amyntor* | 20 | 265.9500 |
| | ▲*O. sapphirinus* | 20 | 258.6500 |
| | ⇕*C. bacchus* | 14 | 224.1430 |
| | ⇕*K. cupreus* | 20 | 217.0500 |
| ***IR*** | ⇕*L. militaris* | 40 | 174.8250 |
| | ⇕*S. impressipennis* | 20 | 173.1500 |
| | ⇕*A. convexus* | 20 | 167.4500 |
| | ▼*P. femoralis* | 16 | 150.8750 |
| | ▼*K. subaeneus* | 20 | 127.9000 |
| | ▼*S. zambesianus* | 20 | 71.8000 |
| ***LR*** | ▼*P. ardea* | 20 | 66.6000 |
| | ▼*O. caffer* | 20 | 59.6500 |
| | ▼*G. nitens* | 20 | 59.5500 |
| | ▼*C. tricornutus* | 20 | 53.4500 |

**Diagram 1d.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted maximum tolerable mass loss of seventeen Scarabaeinae species. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Pg = Pachysoma gariepinus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Ps = Pachysoma striatum, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Sr* | *Ca* | *Cb* | *Ps* | *Oc* | *Lm* | *Pg* | *Kc* | *Os* | *Ct* | *Pf* | *Si* | *Pa* | *Ks* | *Gn* | *Ac* | *Sz* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sr* II | | - | - | - | - | - | - | + | + | + | + | + | + | + | + | + | + |
| *Ca* III | - | | - | - | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Cb* I | - | - | | - | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Ps* I | - | - | - | | - | - | - | - | - | - | - | - | - | + | + | + | + |
| *Oc* IV | - | - | - | - | | - | - | - | - | - | - | - | - | - | - | - | - |
| *Lm* VII | - | - | - | - | - | | - | - | - | - | - | - | - | - | - | - | - |
| *Pg* I | - | - | - | - | - | - | | - | - | - | - | - | - | - | - | - | - |
| *Kc* I | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | - | - |
| *Os* V | + | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | - |
| *Ct* III | + | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Pf* I | + | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Si* II | + | - | - | - | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Pa* IV | + | + | + | - | - | - | - | - | - | - | - | - | | - | - | - | - |
| *Ks* I | + | + | + | + | - | - | - | - | - | - | - | - | - | | - | - | - |
| *Gn* II | + | + | + | + | - | - | - | - | - | - | - | - | - | - | | - | - |
| *Ac* I | + | + | + | + | - | - | - | - | - | - | - | - | - | - | - | | - |
| *Sz* I | + | + | + | + | - | - | - | - | - | - | - | - | - | - | - | - | |

**Diagram 1e.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted rate of mass loss of seventeen Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Pg = Pachysoma gariepinus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Ps = Pachysoma striatum, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Oc* | *Ct* | *Gn* | *Pa* | *Sz* | *Ks* | *Lm* | *Pf* | *Si* | *Cb* | *Ac* | *Kc* | *Ca* | *Os* | *Pg* | *Sr* | *Ps* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Oc* IV | | - | - | - | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Ct* III | - | | - | - | - | - | - | - | - | - | - | + | + | + | + | + | + |
| *Gn* II | - | - | | - | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Pa* IV | - | - | - | | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Sz* I | - | - | - | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Ks* I | - | - | - | - | - | | - | - | - | - | - | - | - | - | + | + | + |
| *Lm* VII | - | - | - | - | - | - | | - | - | - | - | - | - | - | + | + | + |
| *Pf* I | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | - | - |
| *Si* II | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | - |
| *Cb* I | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Ac* I | + | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Kc* I | + | + | - | - | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Ca* III | + | + | + | + | + | - | - | - | - | - | - | - | | - | - | - | - |
| *Os* V | + | + | + | + | + | - | - | - | - | - | - | - | - | | - | - | - |
| *Pg* I | + | + | + | + | + | + | + | - | - | - | - | - | - | - | | - | - |
| *Sr* II | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - | | - |
| *Ps* I | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - | - | |

**Diagram 1f.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted survival time of seventeen Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Pg = Pachysoma gariepinus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Ps = Pachysoma striatum, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Sr* | *Ps* | *Pg* | *Ca* | *Os* | *Cb* | *Kc* | *Lm* | *Si* | *Ac* | *Pf* | *Ks* | *Sz* | *Pa* | *Oc* | *Gn* | *Ct* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sr* II | | - | - | - | - | - | - | + | - | - | + | + | + | + | + | + | + |
| *Ps* I | - | | - | - | - | - | - | + | - | - | - | + | + | + | + | + | + |
| *Pg* I | - | - | | - | - | - | - | - | - | - | - | + | + | + | + | + | + |
| *Ca* III | - | - | - | | - | - | - | - | - | - | - | - | + | + | + | + | + |
| *Os* V | - | - | - | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Cb* I | - | - | - | - | - | | - | - | - | - | - | - | - | - | - | - | - |
| *Kc* I | - | - | - | - | - | - | | - | - | - | - | - | - | - | + | + | + |
| *Lm* VII | + | + | - | - | - | - | - | | - | - | - | - | - | - | - | - | - |
| *Si* II | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | - |
| *Ac* I | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Pf* I | + | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Ks* I | + | + | + | - | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Sz* I | + | + | + | + | + | - | - | - | - | - | - | - | | - | - | - | - |
| *Pa* IV | + | + | + | + | + | - | - | - | - | - | - | - | - | | - | - | - |
| *Oc* IV | + | + | + | + | + | - | + | - | - | - | - | - | - | - | | - | - |
| *Gn* II | + | + | + | + | + | - | + | - | - | - | - | - | - | - | - | | - |
| *Ct* III | + | + | + | + | + | - | + | - | - | - | - | - | - | - | - | - | |

*The macropterous species*

The Kruskal-Wallis non-parametric analyses of unadjusted and adjusted data again indicated large differences between the macropterous species. (Table 4a-f). However, with the exclusion of the apterous species, the unadjusted maximum tolerable mass loss analysis (Table 4a and Diagram 2a) differed from the previous analyses in that the group of macropterous species were evenly divided into high and low rank groups with no intermediate species. The high rank group consisted of *P. femoralis* (highest ranked), *K. cupreus, K. subaeneus, C. tricornutus, S. zambesianus, A. convexus* and *O. caffer*. All the Fg I species and the larger species from Fg III and Fg IV resort in the high rank group. The smaller and medium-sized macropterous species, *P. ardea* (lowest ranked), *L. militaris, S. impressipennis, O. sapphirinus, S. rubripennis, G nitens* and *C. amyntor* formed the low rank group.

As in the previous analyses, the results of the comparisons of unadjusted rate of mass loss (Table 4b and Diagram 2b), showed no clear pattern with regard to the sizes of the species. In addition, no intermediate species were found and the separation into groups was asymmetrical. The low rank group contained only *S. rubripennis* (lowest ranked), *O. sapphirinus, S. impressipennis, L. militaris, C. amyntor* and *P. ardea. Catharsius tricornutus* (highest ranked), *P. femoralis, S. zambesianus, O. caffer, K. subaeneus, G. nitens, K. cupreus* and *A. convexus* formed the high rank group i.e. species with comparatively high rates of mass loss.

In the analysis of the survival times (Table 4c and Diagram 2c), size did not emerge as an important factor, and species were evenly divided into high and low rank groups with no intermediates. *Scarabaeus rubripennis* (highest ranked), *K. cupreus, P. femoralis, C. amyntor, K. subaeneus*, *A. convexus* and *O. sapphirinus* formed the high rank group containing the macropterous species that have a comparatively high resistance to desiccation. The less resistant species that formed the low rank group were *P. ardea* (lowest ranked), *G. nitens, L. militaris, O. caffer, S. impressipennis, S. zambesianus,* and *C. tricornutus*.

**Table 4a.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted maximum tolerable mass loss of fourteen macropterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 275.288 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 40.8707 ***HR*** ▲ = High rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| | ▲*P. femoralis* | 16 | 285.0310 |
| | ▲*K. cupreus* | 20 | 257.5750 |
| | ▲*K. cupreus* | 20 | 254.1000 |
| ***HR*** | ▲*C. tricornutus* | 20 | 224.1500 |
| | ▲*S. zambesianus* | 20 | 207.4250 |
| | ▲*A. convexus* | 20 | 205.7250 |
| | ▲*O. caffer* | 20 | 172.1000 |
| | ▼*C. amyntor* | 20 | 146.3000 |
| | ▼*G. nitens* | 20 | 130.6750 |
| | ▼*S. rubripennis* | 20 | 117.8000 |
| ***LR*** | ▼*O. sapphirinus* | 20 | 77.5250 |
| | ▼*S. impressipennis* | 20 | 46.0250 |
| | ▼*L. militaris* | 40 | 44.7250 |
| | ▼*P. ardea* | 20 | 40.1250 |

**Table 4b.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted rate of mass lost of fourteen macropterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 262.359 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 40.8707 ***HR*** ▲ = High rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| | ▲*C. tricornutus* | 20 | 267.6500 |
| | ▲*P. femoralis* | 16 | 257.1250 |
| | ▲*S. zambesianus* | 20 | 240.3500 |
| | ▲*O. caffer* | 20 | 227.5500 |
| ***HR*** | ▲*K. cupreus* | 20 | 223.3000 |
| | ▲*G. nitens* | 20 | 192.6000 |
| | ▲*K. cupreus* | 20 | 175.3500 |
| | ▲*A. convexus* | 20 | 164.9000 |
| | ▼*P. ardea* | 20 | 127.7250 |
| | ▼*C. amyntor* | 20 | 84.1500 |
| ***LR*** | ▼*L. militaris* | 40 | 81.4250 |
| | ▼*S. impressipennis* | 20 | 73.0250 |
| | ▼*O. sapphirinus* | 20 | 34.5000 |
| | ▼*S. rubripennis* | 20 | 18.0500 |

**Table 4c.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted survival time of fourteen macropterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 234.935 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 40.8707 ***HR*** ▲ = High rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average range |
|---|---|---|---|
| | ▲*S. rubripennis* | 20 | 267.2000 |
| | ▲*K. cupreus* | 20 | 253.3000 |
| | ▲*P. femoralis* | 16 | 247.5310 |
| ***HR*** | ▲*C. amyntor* | 20 | 220.7500 |
| | ▲*K. cupreus* | 20 | 204.0250 |
| | ▲*A. convexus* | 20 | 202.7000 |
| | ▲*O. sapphirinus* | 20 | 176.6250 |
| | ▼*C. tricornutus* | 20 | 133.9750 |
| | ▼*S. zambesianus* | 20 | 132.7500 |
| | ▼*S. impressipennis* | 20 | 87.8500 |
| ***LR*** | ▼*O. caffer* | 20 | 73.4000 |
| | ▼*L. militaris* | 40 | 72.6375 |
| | ▼*G. nitens* | 20 | 69.4500 |
| | ▼*P. ardea* | 20 | 32.4750 |

**Diagram 2a.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted maximum tolerable mass loss of fourteen macropterous Scarabaeinae species. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris*. The Roman numerals in the vertical axis represent the functional group of each species.

| | *Pf* | *Kc* | *Ks* | *Ct* | *Sz* | *Ac* | *Oc* | *Ca* | *Gn* | *Sr* | *Os* | *Si* | *Lm* | *Pa* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pf* I | | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Kc* I | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Ks* I | - | - | | - | - | - | - | - | - | + | + | + | + | + |
| *Ct* III | - | - | - | | - | - | - | - | - | - | + | + | + | + |
| *Sz* I | - | - | - | - | | - | - | - | - | - | + | + | + | + |
| *Ac* I | - | - | - | - | - | | - | - | - | - | - | + | + | + |
| *Oc* IV | - | - | - | - | - | - | | - | - | - | - | - | + | + |
| *Ca* III | + | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Gn* II | + | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Sr* II | + | + | + | - | - | - | - | - | - | | - | - | - | - |
| *Os* V | + | + | + | + | + | - | - | - | - | - | | - | - | - |
| *Si* II | + | + | + | + | + | + | - | - | - | - | - | | - | - |
| *Lm* VII | + | + | + | + | + | + | + | - | - | - | - | - | | - |
| *Pa* IV | + | + | + | + | + | + | + | - | - | - | - | - | - | |

**Diagram 2b.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted rate of mass loss of fourteen macropterous Scarabaeinae species. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$

Mnemonics for the species: *Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Ct* | *Pf* | *Sz* | *Oc* | *Ks* | *Gn* | *Kc* | *Ac* | *Pa* | *Ca* | *Lm* | *Si* | *Os* | *Sr* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ct* III | | - | - | - | - | - | - | - | + | + | + | + | + | + |
| *Pf* I | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Sz* I | - | - | | - | - | - | - | - | - | + | + | + | + | + |
| *Oc* IV | - | - | - | | - | - | - | - | - | + | + | + | + | + |
| *Ks* I | - | - | - | - | | - | - | - | - | + | + | + | + | + |
| *Gn* II | - | - | - | - | - | | - | - | - | - | - | - | + | + |
| *Kc* I | - | - | - | - | - | - | | - | - | - | - | - | + | + |
| *Ac* I | - | - | - | - | - | - | - | | - | - | - | - | + | + |
| *Pa* IV | + | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Ca* III | + | + | + | + | + | - | - | - | - | | - | - | - | - |
| *Lm* VII | + | + | + | + | + | - | - | - | - | - | | - | - | - |
| *Si* II | + | + | + | + | + | - | - | - | - | - | - | | - | - |
| *Os* V | + | + | + | + | + | + | + | + | - | - | - | - | | - |
| *Sr* II | + | + | + | + | + | + | + | + | - | - | - | - | - | |

**Diagram 2c.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted survival time of fourteen macropterous Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Sr* | *Kc* | *Pf* | *Ca* | *Ks* | *Ac* | *Os* | *Ct* | *Sz* | *Si* | *Oc* | *Lm* | *Gn* | *Pa* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sr* II | | - | - | - | - | - | - | + | + | + | + | + | + | + |
| *Kc* I | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Pf* I | - | - | | - | - | - | - | - | - | + | + | + | + | + |
| *Ca* III | - | - | - | | - | - | - | - | - | + | + | + | + | + |
| *Ks* I | - | - | - | - | | - | - | - | - | - | + | + | + | + |
| *Ac* I | - | - | - | - | - | | - | - | - | - | + | + | + | + |
| *Os* V | - | - | - | - | - | - | | - | - | - | - | - | - | + |
| *Ct* III | + | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Sz* I | + | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Si* II | + | + | + | + | - | - | - | - | - | | - | - | - | - |
| *Oc* IV | + | + | + | + | + | + | - | - | - | - | | - | - | - |
| *Lm* VII | + | + | + | + | + | + | - | - | - | - | - | | - | - |
| *Gn* II | + | + | + | + | + | + | - | - | - | - | - | - | | - |
| *Pa* IV | + | + | + | + | + | + | + | - | - | - | - | - | - | |

When the effects of body size were removed, patterns changed substantially. No even divisions between high and low rank groups were found and intermediate groups appeared. In the adjusted maximum tolerable mass loss analysis, only *S. rubripennis* (highest ranked) and *C. amyntor* formed the high rank group of species which could tolerate the highest mass loss (Table 4d and Diagram 2d). *Scarabaeus zambesianus* (lowest ranked), *A. convexus, G. nitens, P. adrea, K. subaeneus, S. impressipennis, P. femoralis,* and *C. tricornutus* formed the low rank group. *Onitis caffer, L. militaris, P. K. cupreus* and *O. sapphirinus* were intermediate. The grouping of species into the high and low rank groups in the adjusted analysis of maximum tolerable mass loss was much more asymmetrical than in the unadjusted analysis, with the low rank group containing most of the species.

The adjusted rate of mass loss analysis (Table 4e and Diagram 2e) showed a more symmetrical grouping of species in the high and low rank groups and included only one intermediate species. *Onitis caffer* (highest ranked), *C. tricornutus, G. nitens, P. adrea, S. zambesianus, K. subaeneus* and *L. militaris* formed the high rank group. Species in the low rank group were *S. rubripennis* (lowest ranked), *O. sapphirinus, C. amyntor, K. cupreus, A. convexus* and *S. impressipennis. Pachylomerus femoralis* was intermediate.

The adjusted survival time analysis (Table 4f and Diagram 2f) of the macropterous species also showed an asymmetrical grouping in the high and low rank groups and also contained an intermediate group. *Scarabaeus rubripennis* (highest rank), *C. amyntor, O. sapphirinus, K. cupreus* and *L. militaris* formed the high rank group as the most desiccation resistant macropterous scarabs. *Catharsius tricornutus* (lowest ranked), *G. nitens, O. caffer, P. adrea, S. zambesianus, K. subaeneus* and *P. femoralis* formed the low rank group. *Sisyphus impressipennis* and *A. convexus* were intermediate. The unusual results shown by *L. militaris* in the adjusted rate of mass loss and adjusted survival time analyses are partly due to the statistical quirks of the formula used to calculate the pairwise comparisons brought about by the large sample size of *L. militaris* ($n = 40$).

In this trial the two most important factors influencing resistance to desiccation appeared to be the diel activities and the strategies of the macropterous species. Most of the nocturnal species, except *C. amyntor* and *A. convexus*, were either included in the groups representing low resistance to desiccation, or were ranked lowest in the intermediate groups. Most telecoprids exhibited high resistance to desiccation.

**Table 4d.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted maximum tolerable mass loss of fourteen macropterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 141.095 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 40.8707 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| | ▲*S. rubripennis* | 20 | 277.8000 |
| ***HR*** | ▲*C. amyntor* | 20 | 250.6000 |
| | ⇕*O. caffer* | 20 | 200.5500 |
| | ⇕*L. militaris* | 40 | 181.4750 |
| ***IR*** | ⇕*K. cupreus* | 20 | 154.3000 |
| | ⇕*O. sapphirinus* | 20 | 150.7500 |
| | ▼*C. tricornutus* | 20 | 138.6000 |
| | ▼*P. femoralis* | 16 | 125.4380 |
| | ▼*S. impressipennis* | 20 | 120.2500 |
| ***LR*** | ▼*K. cupreus* | 20 | 93.4000 |
| | ▼*P. ardea* | 20 | 92.9500 |
| | ▼*G. nitens* | 20 | 90.1000 |
| | ▼*A. convexus* | 20 | 88.8500 |
| | ▼*S. zambesianus* | 20 | 76.3500 |

**Table 4e.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted rate of mass loss of fourteen macropterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 221.032 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 40.8707 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| | ▲*O. caffer* | 20 | 262.7000 |
| | ▲*C. tricornutus* | 20 | 249.7500 |
| | ▲*G. nitens* | 20 | 234.4000 |
| ***HR*** | ▲*P. ardea* | 20 | 221.9500 |
| | ▲*S. zambesianus* | 20 | 216.8500 |
| | ▲*K. cupreus* | 20 | 154.8500 |
| | ▲*L. militaris* | 40 | 146.2750 |
| ***IR*** | ⇕*P. femoralis* | 16 | 144.7500 |
| | ▼*S. impressipennis* | 20 | 114.6000 |
| | ▼*A. convexus* | 20 | 111.0000 |
| | ▼*K. cupreus* | 20 | 94.5500 |
| ***LR*** | ▼*C. amyntor* | 20 | 65.5500 |
| | ▼*O. sapphirinus* | 20 | 47.4000 |
| | ▼*S. rubripennis* | 20 | 15.8500 |

**Table 4f.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted survival time of fourteen macropterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 220.112 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 40.8707 ***HR*** ▲ = High rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| | ▲*S. rubripennis* | 20 | 284.2500 |
| | ▲*C. amyntor* | 20 | 248.6000 |
| ***HR*** | ▲*O. sapphirinus* | 20 | 239.9000 |
| | ▲*K. cupreus* | 20 | 208.9000 |
| | ▲*L. militaris* | 40 | 169.6750 |
| ***IR*** | ⇕*S. impressipennis* | 20 | 166.4000 |
| | ⇕*A. convexus* | 20 | 162.1500 |
| | ▼*P. femoralis* | 16 | 146.5000 |
| | ▼*K. cupreus* | 20 | 124.5000 |
| | ▼*S. zambesianus* | 20 | 70.6500 |
| ***LR*** | ▼*P. ardea* | 20 | 65.1500 |
| | ▼*O. caffer* | 20 | 59.0500 |
| | ▼*G. nitens* | 20 | 58.7500 |
| | ▼*C. tricornutus* | 20 | 52.9500 |

**Diagram 2d.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted maximum tolerable mass loss of fourteen macropterous Scarabaeinae species. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Sr* | *Ca* | *Oc* | *Lm* | *Kc* | *Os* | *Ct* | *Pf* | *Si* | *Ks* | *Pa* | *Gn* | *Ac* | *Sz* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sr* II | | - | - | - | - | - | + | + | + | + | + | + | + | + |
| *Ca* III | - | | - | - | - | - | - | - | + | + | + | + | + | + |
| *Oc* IV | - | - | | - | - | - | - | - | - | - | - | - | - | - |
| *Lm* VII | - | - | - | | - | - | - | - | - | - | - | - | - | - |
| *Kc* I | - | - | - | - | | - | - | - | - | - | - | - | - | - |
| *Os* V | - | - | - | - | - | | - | - | - | - | - | - | - | - |
| *Ct* III | + | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Pf* I | + | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Si* II | + | + | - | - | - | - | - | - | | - | - | - | - | - |
| *Ks* I | + | + | - | - | - | - | - | - | - | | - | - | - | - |
| *Pa* IV | + | + | - | - | - | - | - | - | - | - | | - | - | - |
| *Gn* II | + | + | - | - | - | - | - | - | - | - | - | | - | - |
| *Ac* I | + | + | - | - | - | - | - | - | - | - | - | - | | - |
| *Sz* I | + | + | - | - | - | - | - | - | - | - | - | - | - | |

**Diagram 2e.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted rate of mass loss of fourteen macropterous Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris.* The Roman numerals in the vertical axis represent the functional group of each species.

| | *Oc* | *Ct* | *Gn* | *Pa* | *Sz* | *Ks* | *Lm* | *Pf* | *Si* | *Ac* | *Kc* | *Ca* | *Os* | *Sr* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Oc* IV | | - | - | - | - | - | + | - | + | + | + | + | + | + |
| *Ct* III | - | | - | - | - | - | - | - | + | + | + | + | + | + |
| *Gn* II | - | - | | - | - | - | - | - | - | - | + | + | + | + |
| *Pa* IV | - | - | - | | - | - | - | - | - | - | - | + | + | + |
| *Sz* I | - | - | - | - | | - | - | - | - | - | - | + | + | + |
| *Ks* I | - | - | - | - | - | | - | - | - | - | - | - | - | + |
| *Lm* VII | + | - | - | - | - | - | | - | - | - | - | - | - | + |
| *Pf* I | - | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Si* II | + | + | - | - | - | - | - | - | | - | - | - | - | - |
| *Ac* I | + | + | - | - | - | - | - | - | - | | - | - | - | - |
| *Kc* I | + | + | + | - | - | - | - | - | - | - | | - | - | - |
| *Ca* III | + | + | + | + | + | - | - | - | - | - | - | | - | - |
| *Os* V | + | + | + | + | + | - | - | - | - | - | - | - | | - |
| *Sr* II | + | + | + | + | + | + | + | - | - | - | - | - | - | |

**Diagram 2f.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted survival time of fourteen macropterous Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Pf = Pachylomerus femoralis, Ks = Kheper subaeneus, Kc = Kheper cupreus, Sz = Scarabaeus zambesianus, Ac = Anachalcos convexus, Gn = Garetta nitens, Sr = Scarabaeus rubripennis, Si = Sisyphus impressipennis, Ct = Catharsius tricornutus, Ca = Copris amyntor, Oc = Onitis caffer, Pa = Phalops ardea, Os = Onthophagus sapphirinus, Lm = Liatongus militaris*. The Roman numerals in the vertical axis represent the functional group of each species.

| | *Sr* | *Ca* | *Os* | *Kc* | *Lm* | *Si* | *Ac* | *Pf* | *Ks* | *Sz* | *Pa* | *Oc* | *Gn* | *Ct* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sr* II | | - | - | - | + | - | - | + | + | + | + | + | + | + |
| *Ca* III | - | | - | - | - | - | - | - | - | + | + | + | + | + |
| *Os* V | - | - | | - | - | - | - | - | - | + | + | + | + | + |
| *Kc* I | - | - | - | | - | - | - | - | - | + | + | + | + | + |
| *Lm* VII | + | - | - | - | | - | - | - | - | - | - | - | - | + |
| *Si* II | - | - | - | - | - | | - | - | - | - | - | - | - | - |
| *Ac* I | - | - | - | - | - | - | | - | - | - | - | - | - | - |
| *Pf* I | + | - | - | - | - | - | - | | - | - | - | - | - | - |
| *Ks* I | + | - | - | - | - | - | - | - | | - | - | - | - | - |
| *Sz* I | + | + | + | + | - | - | - | - | - | | - | - | - | - |
| *Pa* IV | + | + | + | + | - | - | - | - | - | - | | - | - | - |
| *Oc* IV | + | + | + | + | - | - | - | - | - | - | - | | - | - |
| *Gn* II | + | + | + | + | - | - | - | - | - | - | - | - | | - |
| *Ct* III | + | + | + | + | + | - | - | - | - | - | - | - | - | |

*The apterous species*

> *Flightlessness among the holometabolous insects is a relatively rare phenomenon []. This may be a consequence of the rarity with which holometabolous insects occupy niches that favour the evolution of flightlessness and/or the frequency with which flightless morphs arise in populations of winged holometabolous insects. Providing the ecologies of species within a taxon are reasonably diverse, these two factors should favour the evolution of flightlessness primarily in taxa containing large numbers of species.*
>
> Derek A. Roff, 1990.

The comparative analyses of the group of seventeen species did not point directly to any differences in desiccation resistance among the three apterous species. When the statistical analyses were repeated on the three species, noticable differences, particularly between the two genera, became clear.

Among the three apterous species, the two *Pachysoma spp.* differed markedly from *C. bacchus* in terms of maximum tolerable water loss (Table 5a and Diagram 3a). The rates of water loss also differed between *C. bacchus* and the *Pachysoma spp.* In this analysis, *C. bacchus* had a much higher rate of loss than the other two species (Table 5b and Diagram 3b). However, the survival times of the three species did not differ significantly.

When the effects of body size were removed, no statistical differences in tolerance to the amount of body water lost were found, although *C. bacchus* still had the highest average ranking (Table 5d and Diagram 3d). In contrast to this, *C. bacchus* showed a more rapid rate of water loss when the effects of body size were removed (Table 5e & Diagram 3e). The adjusted survival times of the three apterous beetles show that *P. gariepinus* and *P. striatum* differ significantly from *C. bacchus* (Table 5f and Diagram 3f). These results indicate that the *Pachysoma spp.* are more desiccation tolerant than *C. bacchus* and that it is *C. bacchus'* large size that promotes its resistance to desiccation.

**Table 5a.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted maximum tolerable mass loss of the three apterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 37.693 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 18.4207 ***HR*** ▲ = High rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 14 | 47.5000 |
| | ▼*P. gariepinus* | 20 | 27.1500 |
| ***LR*** | ▼*P. striatum* | 20 | 13.8500 |

**Table 5b.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted rate of mass loss of the three apterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 35.085 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 18.4207 ***HR*** ▲ = High rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 14 | 47.5000 |
| | ▼*P. gariepinus* | 20 | 25.8000 |
| ***LR*** | ▼*P. striatum* | 20 | 15.2000 |

**Table 5c.** Kruskal-Wallis nonparametric one way analysis by ranks of unadjusted survival time of the three apterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 2.274 Significance level $\alpha$ = <0.5 $Chi^2$ approximation = 18.4207

| Species | n | Average rank |
|---|---|---|
| *P. gariepinus* | 20 | 31.5000 |
| *P. striatum* | 20 | 26.2000 |
| *C. bacchus* | 14 | 23.6429 |

**Diagram 3a.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted maximum tolerable mass loss of the three apterous Scarabaeinae species. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pg = Pachysoma gariepinus, Ps = Pachysoma striatum,*
The Roman numerals in the vertical axis represent the functional group of each species.

| | | *Cb* | *Pg* | *Ps* |
|---|---|---|---|---|
| *Cb* | I | | + | + |
| *Pg* | I | + | | - |
| *Ps* | I | + | - | |

**Diagram 3b.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted rate of mass loss of the three apterous Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pg = Pachysoma gariepinus, Ps = Pachysoma striatum,*
The Roman numerals in the vertical axis represent the functional group of each species.

| | | *Cb* | *Pg* | *Ps* |
|---|---|---|---|---|
| *Cb* | I | | + | + |
| *Pg* | I | + | | - |
| *Ps* | I | + | - | |

**Diagram 3c.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted survival time of the three apterous Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pg = Pachysoma gariepinus, Ps = Pachysoma striatum,*
The Roman numerals in the vertical axis represent the functional group of each species.

| | | *Cb* | *Pg* | *Ps* |
|---|---|---|---|---|
| *Cb* | I | | - | - |
| *Pg* | I | - | | - |
| *Ps* | I | - | - | |

**Table 5d.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted maximum tolerable mass loss of the three apterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 3.911 Significance level $\alpha$ = <0.5 $Chi^2$ approximation = 18.4207

| | Species | n | Average rank |
|---|---|---|---|
| | *C. bacchus* | 14 | 31.2857 |
| | *P. striatum* | 20 | 30.3500 |
| | *P. gariepinus* | 20 | 22.0000 |

**Table 5e.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted rate of mass loss of the three apterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 26.7933 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 18.4207 ***HR*** ▲ = High rank group, ***IR*** ↕ = Intermediate rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 14 | 46.2143 |
| | ▼*P. striatum* | 20 | 21.5000 |
| ***LR*** | ▼*P. gariepinus* | 20 | 20.4000 |

**Table 5f.** Kruskal-Wallis nonparametric one way analysis by ranks of adjusted survival time of the three apterous Scarabaeinae species. The average ranks calculated for each species are sorted in descending order. Test statistic H = 22.6197 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 18.4207 ***HR*** ▲ = High rank group, ***LR*** ▼ = Low rank group.

| | Species | n | Average rank |
|---|---|---|---|
| ***HR*** | ▲*P. striatum* | 20 | 34.5500 |
| | ▲*P. gariepinus* | 20 | 32.4500 |
| ***LR*** | ▼*C. bacchus* | 14 | 10.3571 |

**Diagram 3d.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted maximum tolerable mass loss of the three apterous Scarabaeinae species. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pg = Pachysoma gariepinus, Ps = Pachysoma striatum,*
The Roman numerals in the vertical axis represent the functional group of each species.

| | *Cb* | *Pg* | *Ps* |
|---|---|---|---|
| *Cb* I | | - | - |
| *Pg* I | - | | - |
| *Ps* I | - | - | |

**Diagram 3e.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted rate of mass loss of the three apterous Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pg = Pachysoma gariepinus, Ps = Pachysoma striatum,*
The Roman numerals in the vertical axis represent the functional group of each species.

| | *Cb* | *Ps* | *Pg* |
|---|---|---|---|
| *Cb* I | | + | + |
| *Ps* I | + | | - |
| *Pg* I | + | - | |

**Diagram 3f.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted survival time of the three apterous Scarabaeinae species.
+ = Species are different, - = Species are similar. Significance level $\alpha = 0.05$
Mnemonics for the species: *Cb = Circellium bacchus, Pg = Pachysoma gariepinus, Ps = Pachysoma striatum,*
The Roman numerals in the vertical axis represent the functional group of each species.

| | *Ps* | *Pg* | *Cb* |
|---|---|---|---|
| *Ps* I | | - | + |
| *Pg* I | - | | + |
| *Cb* I | + | + | |

## THE EFFECT OF TEMPERATURE ON DESICCATION RESISTANCE

Table 6 summarises the results of the desiccation trials, and in Table 7 the regressions of maximum tolerable mass loss, rate of mass loss, and the survival times on wet mass at the four temperatures are given. All variables, with the exception of survival time at all four temperatures and maximum tolerable mass loss at 15°C were significantly correlated with the sizes of the species.

**Table 6.** Summary statistics of the results of the desiccation experiments at 15, 20, 27 and 35°C, 5-15% RH and 12L:12D photoperiod of *C. bacchus, P. femoralis, P. gariepinus* and *S. rubripennis*.

| Species | | Initial mass, g. | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | 6.1449 | 1.1921 | 4.5571-8.1966 |
| *C. bacchus* | 20°C | 10 | 5.6173 | 2.1530 | 2.6495-9.3066 |
| *C. bacchus* | 27°C | 14 | 6.4887 | 1.2418 | 5.0970-8.8410 |
| *C. bacchus* | 35°C | 10 | 5.8879 | 1.6957 | 3.8629-8.7917 |
| *P. femoralis* | 15°C | 10 | 4.1398 | 0.8653 | 2.6706-5.5580 |
| *P. femoralis* | 20°C | 10 | 4.5111 | 1.2030 | 2.3048-6.3127 |
| *P. femoralis* | 27°C | 16 | 4.2668 | 1.0899 | 2.3830-5.9140 |
| *P. femoralis* | 35°C | 10 | 4.1418 | 0.8154 | 2.6917-5.4845 |
| *P. gariepinus* | 15°C | 7 | 2.1831 | 0.4193 | 1.6530-2.8689 |
| *P. gariepinus* | 20°C | 7 | 2.1565 | 0.2146 | 1.8240-2.4829 |
| *P. gariepinus* | 27°C | 20 | 1.7444 | 0.3472 | 1.0256-2.3869 |
| *P. gariepinus* | 35°C | 7 | 1.9358 | 0.3843 | 1.2125-2.3165 |
| *S. rubripennis* | 15°C | 7 | 0.1861 | 0.0542 | 0.1101-0.2863 |
| *S. rubripennis* | 20°C | 7 | 0.1968 | 0.0413 | 0.1284-0.2421 |
| *S. rubripennis* | 27°C | 20 | 0.1579 | 0.0329 | 0.1056-0.2466 |
| *S. rubripennis* | 35°C | 7 | 0.2277 | 0.0604 | 0.1433-0.3290 |

**(Table 6 continued)**

| Species | | Maximum tolerable mass loss, g. | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | 2.4440 | 0.5078 | 1.8060-3.1371 |
| *C. bacchus* | 20°C | 10 | 2.3205 | 0.0902 | 0.9779-3.6129 |
| *C. bacchus* | 27°C | 14 | 2.6264 | 0.5905 | 1.8630-3.8680 |
| *C. bacchus* | 35°C | 10 | 2.2418 | 0.7274 | 1.4756-3.6578 |
| *P. femoralis* | 15°C | 10 | 1.2440 | 0.3179 | 0.7420-1.8690 |
| *P. femoralis* | 20°C | 10 | 1.8489 | 0.5619 | 1.0460-2.8156 |
| *P. femoralis* | 27°C | 16 | 1.2675 | 0.3782 | 0.4530-1.6770 |
| *P. femoralis* | 35°C | 10 | 1.5722 | 0.4425 | 1.0515-2.4953 |
| *P. gariepinus* | 15°C | 7 | 0.8861 | 0.2708 | 0.4245-1.2559 |
| *P. gariepinus* | 20°C | 7 | 0.8566 | 0.2096 | 0.5995-1.1389 |
| *P. gariepinus* | 27°C | 20 | 0.5971 | 0.2759 | 0.1622-1.1368 |
| *P. gariepinus* | 35°C | 7 | 0.4897 | 0.1944 | 0.2593-0.7702 |
| *S. rubripennis* | 15°C | 7 | 0.0735 | 0.0288 | 0.0396-0.1286 |
| *S. rubripennis* | 20°C | 7 | 0.0843 | 0.0190 | 0.0561-0.1037 |
| *S. rubripennis* | 27°C | 20 | 0.0683 | 0.0171 | 0.0391-0.1017 |
| *S. rubripennis* | 15°C | 7 | 0.0767 | 0.0318 | 0.0482-0.1353 |

**(Table 6 continued)**

| Species | | Percentage maximum tolerable mass loss | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | 39.87 | 4.10 | 30.86-45.19 |
| *C. bacchus* | 20°C | 10 | 41.16 | 4.43 | 35.59-47.41 |
| *C. bacchus* | 27°C | 14 | 40.31 | 3.08 | 35.51-46.01 |
| *C. bacchus* | 35°C | 10 | 37.91 | 3.25 | 33.32-42.24 |
| *P. femoralis* | 15°C | 10 | 30.54 | 6.23 | 14.99-38.48 |
| *P. femoralis* | 20°C | 10 | 40.92 | 3.48 | 35.97-46.56 |
| *P. femoralis* | 27°C | 16 | 29.60 | 5.73 | 19.01-39.22 |
| *P. femoralis* | 35°C | 10 | 37.80 | 5.90 | 25.51-45.50 |
| *P. gariepinus* | 15°C | 7 | 39.85 | 6.65 | 25.46-44.97 |
| *P. gariepinus* | 20°C | 7 | 39.50 | 7.79 | 28.74-49.40 |
| *P. gariepinus* | 27°C | 20 | 33.03 | 10.99 | 9.96-47.63 |
| *P. gariepinus* | 35°C | 7 | 24.86 | 7.07 | 18.62-37.78 |
| *S. rubripennis* | 15°C | 7 | 38.75 | 4.87 | 32.78-44.92 |
| *S. rubripennis* | 20°C | 7 | 42.78 | 2.23 | 37.98-44.55 |
| *S. rubripennis* | 27°C | 20 | 42.98 | 4.34 | 34.86-52.53 |
| *S. rubripennis* | 35°C | 7 | 33.02 | 5.89 | 24.27-41.12 |

**(Table 6 continued)**

| Species | | Adjusted maximum tolerable mass loss, g. | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | ****** | ****** | ******-****** |
| *C. bacchus* | 20°C | 10 | 1.3278 | 0.1451 | 1.1599-1.5352 |
| *C. bacchus* | 27°C | 14 | 1.3051 | 0.1010 | 1.1452-1.4891 |
| *C. bacchus* | 35°C | 10 | 1.2245 | 0.1065 | 1.0715-1.3209 |
| *P. femoralis* | 15°C | 10 | ****** | ****** | ******-****** |
| *P. femoralis* | 20°C | 10 | 1.3154 | 0.1118 | 1.1538-1.5057 |
| *P. femoralis* | 27°C | 16 | 0.9507 | 0.1844 | 0.6044-1.2590 |
| *P. femoralis* | 35°C | 10 | 1.2138 | 0.1901 | 0.8201-1.4687 |
| *P. gariepinus* | 15°C | 7 | ****** | ****** | ******-****** |
| *P. gariepinus* | 20°C | 7 | 1.2537 | 0.2480 | 0.9114-1.5695 |
| *P. gariepinus* | 27°C | 20 | 1.0443 | 0.3494 | 0.3144-1.5142 |
| *P. gariepinus* | 35°C | 7 | 0.7872 | 0.2251 | 0.5890-1.1977 |
| *S. rubripennis* | 15°C | 7 | ****** | ****** | ******-****** |
| *S. rubripennis* | 20°C | 7 | 1.2990 | 0.0687 | 1.1498-1.3537 |
| *S. rubripennis* | 27°C | 20 | 1.3000 | 0.1329 | 1.0500-1.5951 |
| *S. rubripennis* | 35°C | 7 | 1.0054 | 0.1818 | 0.7397-1.2609 |

**(Table 6 continued)**

| Species | | Survival time, hr. | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | 410.9 | 155.6 | 257.5-809.0 |
| *C. bacchus* | 20°C | 10 | 260.3 | 79.8 | 137.5-378.0 |
| *C. bacchus* | 27°C | 14 | 211.6 | 66.3 | 96.0-280.0 |
| *C. bacchus* | 35°C | 10 | 98.6 | 29.1 | 62.5-142.5 |
| *P. femoralis* | 15°C | 10 | 174.2 | 101.2 | 50.0-334.0 |
| *P. femoralis* | 20°C | 10 | 235.3 | 85.8 | 57.7-358.3 |
| *P. femoralis* | 27°C | 16 | 106.2 | 45.5 | 29.5-189.5 |
| *P. femoralis* | 35°C | 10 | 57.8 | 18.2 | 26.0-92.5 |
| *P. gariepinus* | 15°C | 7 | 1617.8 | 491.0 | 957.0-2208.8 |
| *P. gariepinus* | 20°C | 7 | 976.0 | 316.6 | 596.5-1511.8 |
| *P. gariepinus* | 27°C | 20 | 392.7 | 287.2 | 27.5-1107.5 |
| *P. gariepinus* | 35°C | 7 | 90.6 | 51.5 | 45.0-165.0 |
| *S. rubripennis* | 15°C | 7 | 370.6 | 133.0 | 192.0-548.0 |
| *S. rubripennis* | 20°C | 7 | 288.3 | 49.9 | 213.7-356.0 |
| *S. rubripennis* | 27°C | 20 | 126.0 | 35.3 | 51.5-181.5 |
| *S. rubripennis* | 35°C | 7 | 47.5 | 16.6 | 20.0-48.0 |

**(Table 6 continued)**

| Species | | Rate of mass loss, g/hr | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | 0.00658 | 0.00226 | 0.00245-0.00912 |
| *C. bacchus* | 20°C | 10 | 0.00915 | 0.00355 | 0.00414-0.01785 |
| *C. bacchus* | 27°C | 14 | 0.01413 | 0.00721 | 0.00813-0.03485 |
| *C. bacchus* | 35°C | 10 | 0.02489 | 0.01164 | 0.01237-0.04288 |
| *P. femoralis* | 15°C | 10 | 0.00995 | 0.00652 | 0.00355-0.02500 |
| *P. femoralis* | 20°C | 10 | 0.00893 | 0.00388 | 0.00478-0.01814 |
| *P. femoralis* | 27°C | 16 | 0.01334 | 0.00475 | 0.00749-0.02203 |
| *P. femoralis* | 35°C | 10 | 0.02898 | 0.00906 | 0.01508-0.04257 |
| *P. gariepinus* | 15°C | 7 | 0.00057 | 0.00016 | 0.00029-0.00078 |
| *P. gariepinus* | 20°C | 7 | 0.00093 | 0.00033 | 0.00075-0.00167 |
| *P. gariepinus* | 27°C | 20 | 0.00217 | 0.00129 | 0.00102-0.00640 |
| *P. gariepinus* | 35°C | 7 | 0.00610 | 0.00196 | 0.00340-0.00960 |
| *S. rubripennis* | 15°C | 7 | 0.00020 | 0.00005 | 0.00013-0.00025 |
| *S. rubripennis* | 20°C | 7 | 0.00029 | 0.00005 | 0.00023-0.00036 |
| *S. rubripennis* | 27°C | 20 | 0.00057 | 0.00019 | 0.00037-0.00120 |
| *S. rubripennis* | 35°C | 7 | 0.00169 | 0.00060 | 0.00110-0.00290 |

**(Table 6 continued)**

| Species | | Percentage rate of mass loss, %mass loss/hr. | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | 0.11 | 0.03 | 0.05-0.16 |
| *C. bacchus* | 20°C | 10 | 0.17 | 0.05 | 0.11-0.27 |
| *C. bacchus* | 27°C | 14 | 0.22 | 0.09 | 0.13-0.39 |
| *C. bacchus* | 35°C | 10 | 0.41 | 0.12 | 0.25-0.63 |
| *P. femoralis* | 15°C | 10 | 0.27 | 0.23 | 0.10-0.77 |
| *P. femoralis* | 20°C | 10 | 0.23 | 0.20 | 0.12-0.79 |
| *P. femoralis* | 27°C | 16 | 0.34 | 0.19 | 0.18-0.90 |
| *P. femoralis* | 35°C | 10 | 0.70 | 0.17 | 0.45-0.98 |
| *P. gariepinus* | 15°C | 7 | 0.03 | 0.01 | 0.02-0.04 |
| *P. gariepinus* | 20°C | 7 | 0.04 | 0.01 | 0.03-0.07 |
| *P. gariepinus* | 27°C | 20 | 0.14 | 0.11 | 0.04-0.52 |
| *P. gariepinus* | 35°C | 7 | 0.33 | 0.12 | 0.16-0.48 |
| *S. rubripennis* | 15°C | 7 | 0.12 | 0.04 | 0.08-0.19 |
| *S. rubripennis* | 20°C | 7 | 0.15 | 0.02 | 0.12-0.18 |
| *S. rubripennis* | 27°C | 20 | 0.37 | 0.14 | 0.25-0.77 |
| *S. rubripennis* | 35°C | 7 | 0.75 | 0.22 | 0.58-1.21 |

**(Table 6 continued)**

| Species | | Adjusted rate of mass loss, g/hr | | | |
|---|---|---|---|---|---|
| | | n | Mean | SD | Range |
| *C. bacchus* | 15°C | 10 | 0.00359 | 0.00110 | 0.00175-0.00527 |
| *C. bacchus* | 20°C | 10 | 0.00567 | 0.00152 | 0.00365-0.00844 |
| *C. bacchus* | 27°C | 14 | 0.00731 | 0.00306 | 0.00446-0.01359 |
| *C. bacchus* | 35°C | 10 | 0.01392 | 0.00435 | 0.00831-0.02123 |
| *P. femoralis* | 15°C | 10 | 0.00864 | 0.00721 | 0.00320-0.02463 |
| *P. femoralis* | 20°C | 10 | 0.00737 | 0.00611 | 0.00385-0.02447 |
| *P. femoralis* | 27°C | 16 | 0.01107 | 0.00596 | 0.00583-0.02799 |
| *P. femoralis* | 35°C | 10 | 0.02279 | 0.00562 | 0.01446-0.03219 |
| *P. gariepinus* | 15°C | 7 | 0.00056 | 0.00019 | 0.00037-0.00089 |
| *P. gariepinus* | 20°C | 7 | 0.00132 | 0.00036 | 0.00102-0.00210 |
| *P. gariepinus* | 27°C | 20 | 0.00418 | 0.00334 | 0.00134-0.01542 |
| *P. gariepinus* | 35°C | 7 | 0.00996 | 0.00340 | 0.00484-0.01399 |
| *S. rubripennis* | 15°C | 7 | 0.00290 | 0.00100 | 0.00191-0.00450 |
| *S. rubripennis* | 20°C | 7 | 0.00381 | 0.00051 | 0.00309-0.00442 |
| *S. rubripennis* | 27°C | 20 | 0.00922 | 0.00332 | 0.00614-0.01914 |
| *S. rubripennis* | 35°C | 7 | 0.01918 | 0.00553 | 0.01484-0.03112 |

**Table 7:** Regressions of the maximum tolerable mass loss, rate of mass loss and survival times on the wet mass of the beetles at 15, 20, 27 and 35°C and 5 - 15% RH. The regressions are in the form $\log Y = b \log X + a$.

| Variable | n | Slope ± SE | Intercept ± SE | $r^2$ | p |
|---|---|---|---|---|---|
| **15°C** | | | | | |
| Mass loss | 34 | 0.1954 ± 0.2072 | -0.6823 ± 0.3726 | 2.62% | 0.3526 |
| Rate of mass loss | 34 | 1.0312 ± 0.1154 | -6.9740 ± 0.1750 | 71.38% | $< 1x10^{-5}$ |
| Survival time | 34 | -0.5688 ± 0.1706 | 6.1829 ± 0.3068 | 25.19% | 0.0021 |
| **20°C** | | | | | |
| Mass loss | 34 | 0.9889 ± 0.0159 | -0.8880 ± 0.0236 | 99.18% | $< 1x10^{-5}$ |
| Rate of mass loss | 34 | 1.0136 ± 0.0913 | -6.6794 ± 0.1354 | 79.38% | $< 1x10^{-5}$ |
| Survival time | 34 | -0.0248 ± 0.0897 | 5.7914 ± 0.1329 | 0.24% | 0.7841 |
| **27°C** | | | | | |
| Mass loss | 70 | 0.9447 ± 0.0237 | -1.0271 ± 0.0358 | 95.88% | $< 1x10^{-5}$ |
| Rate of mass loss | 70 | 0.8434 ± 0.0503 | -6.0680 ± 0.0758 | 80.53% | $< 1x10^{-5}$ |
| Survival time | 70 | 0.1013 ± 0.0606 | 5.0409 ± 0.0913 | 3.94% | 0.0994 |
| **35°C** | | | | | |
| Mass loss | 34 | 1.0559 ± 0.0330 | -1.1416 ± 0.0476 | 96.96% | $< 1x10^{-5}$ |
| Rate of mass loss | 34 | 0.8832 ± 0.0603 | -5.2095 ± 0.0868 | 87.03% | $< 1x10^{-5}$ |
| Survival time | 34 | 0.1727 ± 0.0617 | 4.0679 ± 0.0889 | 19.66% | 0.0086 |

*Multiple comparisons of desiccation resistance at four temperatures*

*Desiccation resistance at 15°C*

At 15°C, the small desert scarab, *S. rubripennis*, differed only from the large *C. bacchus* in the unadjusted mass loss analysis (Table 8a and Diagram 4a). In the unadjusted rate of mass loss analysis, *P. femoralis* had the highest rate of water loss and differed from the two desert species, while *C. bachhus* was intermediate (Table 8b and Diagram 4b). In the adjusted rate of mass loss analysis, *C. bacchus* and *S. rubripennis* formed the low rank group, and *P. gariepinus* was intermediate (Table 8c and Diagram 4c). The two apterous species, *P. gariepinus* and *C. bacchus,* were the most desiccation resistant at 15°C (Table 4d and Diagram 4d), i.e. they survived for the longest time, and *S. rubripennis* was intermediate.

**Table 8a.** Kruskal-wallis non-parametric one way analysis by ranks of unadjusted maximum tolerable mass loss at 15°c The average ranks are sorted in descending order. Test statistic H = 28.7309 Significance level $\alpha$ = <0.0001 Chi$^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 15 | 10 | 29.4000 |
| ***IR*** | ⇕*P. gariepinus* | 15 | 7 | 18.3000 |
| | ⇕*P. femoralis* | 15 | 10 | 12.8571 |
| ***LR*** | ▼*S. rubripennis* | 15 | 7 | 4.0000 |

**Table 8b.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted rate of mass loss at 15°C. The average ranks are sorted in descending order. Test statistic H = 26.0198 Significance level $\alpha$ = <0.0001 Chi$^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 15 | 10 | 25.7000 |
| ***IR*** | ⇕*C. bacchus* | 15 | 10 | 23.3000 |
| | ▼*P. gariepinus* | 15 | 7 | 11.0000 |
| ***LR*** | ▼*S. rubripennis* | 15 | 7 | 4.0000 |

**Diagram 4a.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted maximum tolerable mass loss at 15°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Cb* | *PF* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Cb* | | - | - | + |
| *Pf* | - | | - | - |
| *Pg* | - | - | | - |
| *Sr* | + | - | - | |

**Diagram 4b.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted rate of mass loss at 15°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Cb* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Pf* | | - | + | + |
| *Cb* | - | | - | - |
| *Pg* | + | - | | - |
| *Sr* | + | - | - | |

**Table 8c.** Kruskal-Wallis non-parametric one way analysis by ranks of adjusted rate of mass loss at 15°C. The average ranks are sorted in descending order. Test statistic H = 21.1668 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 15 | 10 | 26.3000 |
| ***IR*** | ⇕*P. gariepinus* | 15 | 7 | 19.8571 |
| | ▼*C. bacchus* | 15 | 10 | 16.5000 |
| ***LR*** | ▼*S. rubripennis* | 15 | 7 | 4.0000 |

**Table 8d.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted survival time at 15°C. The average ranks are sorted in descending order. Test statistic H = 24.6647 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. gariepinus* | 15 | 7 | 31.0000 |
| ***IR*** | ⇕*C. bacchus* | 15 | 10 | 19.0000 |
| | ▼*S. rubripennis* | 15 | 7 | 17.1429 |
| ***LR*** | ▼*P. femoralis* | 15 | 10 | 6.8000 |

**Diagram 4c.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted rate of mass loss at 15°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Pg* | *Cb* | *Sr* |
|---|---|---|---|---|
| *Pf* | | - | + | + |
| *Pg* | - | | - | - |
| *Cb* | + | - | | - |
| *Sr* | + | - | - | |

**Diagram 4d.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted survival time at 15°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pg* | *Cb* | *Sr* | *Pf* |
|---|---|---|---|---|
| *Pg* | | - | - | + |
| *Cb* | - | | - | + |
| *Sr* | - | - | | - |
| *Pf* | + | + | - | |

*Desiccation resistance at 20°C*

At 20°C, the unadjusted maximum tolerable mass losses were closely correlated with body size (see Table 7). *Circellium bacchus* was the highest ranked species, and *P. gariepinus* and *S. rubripennis* formed the low rank group. *Pachylomerus femoralis* was intermediate (Table 9a and Diagram 5a). In the unadjusted rates of mass loss *P. femoralis* was the highest ranked species, *P. gariepinus* and *S. rubripennis* were ranked lowest and *C. bacchus* was intermediate (Table 9b and Diagram 5b).

When the effects of size were removed, there was no differences in the maximum tolerable water loss between the four species (Table 9c and Diagram 5c). *Pachysoma gariepinus* was the lowest ranked species, *P. femoralis* and *C. bacchus* formed the high rank group, and *S. rubripennis* was intermediate in the adjusted rate of mass loss analysis (Table 9d and Diagram 5d). There was no difference in survival time of the four species at 20°C (Table 9e and Diagram 5e).

**Table 9a.** Kruskal-wallis non-parametric one way analysis by ranks of unadjusted maximum tolerable mass loss at 20°C. The average ranks are sorted in descending order. Test statistic H = 25.1878 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 20 | 10 | 25.9000 |
| ***IR*** | ⇕*P. femoralis* | 20 | 10 | 22.7000 |
| | ▼*P. gariepinus* | 20 | 7 | 11.5714 |
| ***LR*** | ▼*S. rubripennis* | 20 | 7 | 4.0000 |

**Table 9b.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted rate of mass loss at 20°C. The average ranks are sorted in descending order. Test statistic H = 25.7375 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 20 | 10 | 24.7000 |
| ***IR*** | ⇕*C. bacchus* | 20 | 10 | 24.3000 |
| | ▼*P. gariepinus* | 20 | 7 | 11.0000 |
| ***LR*** | ▼*S. rubripennis* | 20 | 7 | 4.0000 |

**Diagram 5a.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted maximum tolerable mass loss at 20°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Cb* | *Pf* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Cb* | | - | + | + |
| *Pf* | - | | - | - |
| *Pg* | + | - | | - |
| *Sr* | + | - | - | |

**Diagram 5b.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted rate of mass loss at 20°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Cb* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Pf* | | - | + | + |
| *Cb* | - | | - | - |
| *Pg* | + | - | | - |
| *Sr* | + | - | - | |

**Table 9c.** Kruskal-Wallis non-parametric one way analysis by ranks of adjusted maximum tolerable mass loss at 20°C. The average ranks are sorted in descending order. Test statistic H = 0.3238 Significance level $\alpha$ = 0.9555 $Chi^2$ approximation = 20.9667.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| | *S. rubripennis* | 20 | 7 | 18.7143 |
| | *C. bacchus* | 20 | 10 | 18.0000 |
| | *P. femoralis* | 20 | 10 | 17.3000 |
| | *P. gariepinus* | 20 | 7 | 15.8571 |

**Table 9d.** Kruskal-Wallis non-parametric one way analysis by ranks of adjusted rate of mass loss at 20°C. The average ranks are sorted in descending order. Test statistic H = 16.4087 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ↕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 20 | 10 | 22.1000 |
| | ▲*C. bacchus* | 20 | 10 | 20.6000 |
| ***IR*** | ↕*S. rubripennis* | 20 | 7 | 20.0000 |
| ***LR*** | ▼*P. gariepinus* | 20 | 7 | 4.0000 |

**Table 9e.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted survival time at 20°C. The average ranks are sorted in descending order. Test statistic H = 17.4483 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| | *P. gariepinus* | 20 | 7 | 31.0000 |
| | *S. rubripennis* | 20 | 7 | 17.4286 |
| | *C. bacchus* | 20 | 10 | 13.5000 |
| | *P. femoralis* | 20 | 10 | 12.1000 |

**Diagram 5c.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted maximum tolerable mass loss at 20°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Sr* | *Cb* | *Pf* | *Pg* |
|---|---|---|---|---|
| *Sr* | | - | - | - |
| *Cb* | - | | - | - |
| *Pf* | - | - | | - |
| *Pg* | - | - | - | |

**Diagram 5d.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted rate of mass loss at 20°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Cb* | *Sr* | *Pg* |
|---|---|---|---|---|
| *Pf* | | - | - | + |
| *Cb* | - | | - | + |
| *Sr* | - | - | | - |
| *Pg* | + | + | - | |

**Diagram 5e.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted survival time at 20°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pg* | *Sr* | *Cb* | *Pf* |
|---|---|---|---|---|
| *Pg* | | - | - | - |
| *Sr* | - | | - | - |
| *Cb* | - | - | | - |
| *Pf* | - | - | - | |

*Desiccation resistance at 27°C*

At 27°C, *C. bacchus* and *P. femoralis* formed the high ranked group, and *P. gariepinus* and *S. rubripennis* formed the low rank group in the unadjusted maximum tolerable mass loss analysis (Table 10a and Diagram 6a). The unadjusted rates of mass loss showed *P. femoralis* and *C. bacchus* as the high rank group, and *P. gariepinus* and *S. rubripennis* as the low rank group (Table 10b and Diagram 6b).

When the data were adjusted for size *C. bacchus* and *S. rubripennis* formed the high rank group in the adjusted maximum tolerable mass loss analysis. *Pachylomerus femoralis* was the lowest ranked species and *P. gariepinus* was intermediate (Table 10c and Diagram 6c). *Pachysoma gariepinus* was the lowest ranked species in the adjusted rate of mass loss at 27°C, *P. femoralis* and *S. rubripennis* formed the high rank group, and *C. bacchus* was intermediate (Table 10d and Diagram 6d).

In the unadjusted survival time analysis at 27°C the two apterous species, *P. gariepinus* and *C. bacchus,* had the longest survival time (Table 10e and Diagram 6e). *Scarabaeus rubripennis* and *P. femoralis* showed similarly short survival times.

**Table 10a.** Kruskal-wallis non-parametric one way analysis by ranks of unadjusted maximum tolerable mass loss at 27°C. The average ranks are sorted in descending order. Test statistic H = 61.9850 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 27 | 14 | 63.5000 |
| | ▲*P. femoralis* | 27 | 16 | 46.5625 |
| | ▼*P. gariepinus* | 27 | 20 | 32.0500 |
| ***LR*** | ▼*S. rubripennis* | 27 | 20 | 10.5000 |

**Table 10b.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted rate of mass loss at 27°C. The average ranks are sorted in descending order. Test statistic H = 60.1752 Significance level $\alpha$ = <0.0001 Critical value $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 27 | 16 | 55.7500 |
| | ▲*C. bacchus* | 27 | 14 | 55.2143 |
| | ▼*P. gariepinus* | 27 | 20 | 30.4000 |
| ***LR*** | ▼*S. rubripennis* | 27 | 20 | 10.6000 |

**Diagram 6a.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted maximum tolerable mass loss at 27°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Cb* | *Pf* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Cb* | | - | + | + |
| *Pf* | - | | - | + |
| *Pg* | + | - | | - |
| *Sr* | + | + | - | |

**Diagram 6b.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted rate of mass loss at 27°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Cb* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Pf* | | - | + | + |
| *Cb* | - | | - | + |
| *Pg* | + | - | | - |
| *Sr* | + | + | - | |

**Table 10c.** Kruskal-Wallis non-parametric one way analysis by ranks of adjusted maximum tolerable mass loss at 27°C. The average ranks are sorted in descending order. Test statistic H = 25.7254 Significance level $\alpha$ = <0.0001 Chi$^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 27 | 14 | 56.9286 |
| | ▲*S. rubripennis* | 27 | 20 | 37.8500 |
| ***IR*** | ⇕*P. gariepinus* | 27 | 20 | 30.0000 |
| ***LR*** | ▼*P. femoralis* | 27 | 16 | 20.6875 |

**Table 10d.** Kruskal-Wallis non-parametric one way analysis by ranks of adjusted rate of mass loss at 27°C. The average ranks are sorted in descending order. Test statistic H = 33.3961 Significance level $\alpha$ = <0.0001 Chi$^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 27 | 16 | 53.0625 |
| | ▲*S. rubripennis* | 27 | 20 | 39.5000 |
| ***IR*** | ⇕*C. bacchus* | 27 | 14 | 39.0000 |
| ***LR*** | ▼*P. gariepinus* | 27 | 20 | 15.0000 |

**Table 10e.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted survival time at 27°C. The average ranks are sorted in descending order. Test statistic H = 26.9769 Significance level $\alpha$ = <0.0001 Chi$^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. gariepinus* | 27 | 20 | 49.5250 |
| | ▲*C. bacchus* | 27 | 14 | 46.4286 |
| | ▼*S. rubripennis* | 27 | 20 | 26.1750 |
| ***LR*** | ▼*P. femoralis* | 27 | 16 | 20.0625 |

**Diagram 6c.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted maximum tolerable mass loss at 27°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Cb* | *Sr* | *Pg* | *Pf* |
|---|---|---|---|---|
| *Cb* | | - | - | + |
| *Sr* | - | | - | + |
| *Pg* | - | - | | - |
| *Pf* | + | + | - | |

**Diagram 6d.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted rate of mass loss at 27°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Sr* | *Cb* | *Pg* |
|---|---|---|---|---|
| *Pf* | | - | - | + |
| *Sr* | - | | - | + |
| *Cb* | - | - | | - |
| *Pg* | + | + | - | |

**Diagram 6e.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted survival time at 27°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pg* | *Cb* | *Sr* | *Pf* |
|---|---|---|---|---|
| *Pg* | | - | + | + |
| *Cb* | - | | - | + |
| *Sr* | + | - | | - |
| *Pf* | + | + | - | |

*Desiccation resistance at 35°C*

In the unadjusted maximum tolerable mass loss analysis at 35°C, *C. bacchus* could tolerate the greatest water loss, *P. gariepinus* and *S. rubripennis* had the lowest tolerance to water loss, and *P. femoralis* was intermediate (Table 11a and Diagram 7a). In the unadjusted rates of mass loss *P. femoralis* had the highest rate of water loss, *P. gariepinus* and *S. rubripennis* had the lowest rates, and *C. bacchus* was intermediate (Table 11b and Diagram 7b).

When the data were adjusted for size *S. rubripennis* and *P. femoralis* had the highest tolerance to water loss in the adjusted maximum tolerable mass loss analysis at 35°C. *Pachysoma gariepinus* was the lowest ranked species and *C. bacchus* was intermediate (Table 11c and Diagram 7c). *Pachysoma gariepinus* had the lowest rate in the adjusted rate of mass loss and differed from the other three species (Table 11d and Diagram 7d).

In the unadjusted survival time at 35°C the small desert species, *S. rubripennis* had the shortest survival time (Table 11e and Diagram 7e) and differed from the other species.

**Table 11a.** Kruskal-wallis non-parametric one way analysis by ranks of unadjusted maximum tolerable mass loss at 35°C. The average ranks are sorted in descending order. Test statistic H = 27.3106 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 35 | 10 | 27.3000 |
| ***IR*** | ⇕*P. femoralis* | 35 | 10 | 21.7000 |
| | ▼*P. gariepinus* | 35 | 7 | 11.0000 |
| ***LR*** | ▼*S. rubripennis* | 35 | 7 | 4.0000 |

**Table 11b.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted rate of mass loss at 35°C. The average ranks are sorted in descending order. Test statistic H = 25.9311 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 35 | 10 | 25.5000 |
| ***IR*** | ⇕*C. bacchus* | 35 | 10 | 23.5000 |
| | ▼*P. gariepinus* | 35 | 7 | 11.0000 |
| ***LR*** | ▼*S. rubripennis* | 35 | 7 | 4.0000 |

**Diagram 7a.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted maximum tolerable mass loss at 35°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Cb* | *Pf* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Cb* | | - | + | + |
| *Pf* | - | | - | - |
| *Pg* | + | - | | - |
| *Sr* | + | - | - | |

**Diagram 7b.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted rate of mass loss at 35°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Cb* | *Pg* | *Sr* |
|---|---|---|---|---|
| *Pf* | | - | + | + |
| *Cb* | - | | - | - |
| *Pg* | + | - | | - |
| *Sr* | + | - | - | |

**Table 11c.** Kruskal-Wallis non-parametric one way analysis by ranks of adjusted maximum tolerable mass loss at 35°C. The average ranks are sorted in descending order. Test statistic H = 10.9667 Significance level $\alpha$ = 0.0119 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*S. rubripennis* | 35 | 10 | 21.8571 |
| | ▲*P. femoralis* | 35 | 10 | 20.6000 |
| ***IR*** | ⇕*C. bacchus* | 35 | 7 | 19.0000 |
| ***LR*** | ▼*P. gariepinus* | 35 | 7 | 6.5714 |

**Table 11d.** Kruskal-Wallis non-parametric one way analysis by ranks of adjusted rate of mass loss at 35°C. The average ranks are sorted in descending order. Test statistic H = 20.3105 Significance level $\alpha$ = <0.0001 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*P. femoralis* | 35 | 10 | 26.9000 |
| ***IR*** | ⇕*S. rubripennis* | 35 | 7 | 20.5714 |
| | ⇕*C. bacchus* | 35 | 10 | 14.1000 |
| ***LR*** | ▼*P. gariepinus* | 35 | 7 | 5.8571 |

**Table 11e.** Kruskal-Wallis non-parametric one way analysis by ranks of unadjusted survival time at 35°C. The average ranks are sorted in descending order. Test statistic H = 13.9555 Significance level $\alpha$ = 0.0030 $Chi^2$ approximation = 20.9667. ***HR*** ▲ = Low rank group, ***IR*** ⇕ = Intermediate rank group, ***LR*** ▼ =Low rank group.

| | Species | °C | n | Average ranks |
|---|---|---|---|---|
| ***HR*** | ▲*C. bacchus* | 35 | 10 | 25.4000 |
| ***IR*** | ⇕*P. gariepinus* | 35 | 7 | 19.8571 |
| | ⇕*P. femoralis* | 35 | 10 | 14.6000 |
| ***LR*** | ▼*S. rubripennis* | 35 | 7 | 8.0000 |

**Diagram 7c.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted maximum tolerable mass loss at 35°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Sr* | *Pf* | *Cb* | *Pg* |
|---|---|---|---|---|
| *Sr* | | - | - | + |
| *Pf* | - | | - | + |
| *Cb* | - | - | | - |
| *Pg* | + | + | - | |

**Diagram 7d.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the adjusted rate of mass loss at 35°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Pf* | *Sr* | *Cb* | *Pg* |
|---|---|---|---|---|
| *Pf* | | - | - | + |
| *Sr* | - | | - | - |
| *Cb* | - | - | | - |
| *Pg* | + | - | - | |

**Diagram 7e.** Pairwise non-parametric multiple comparison test by Kruskal-Wallis average ranks of the unadjusted survival time at 35°C. + = Species are different, - = Species are similar. Significance level $\alpha = 0.05$.
Mnemonics for the species: *Cb = Circellium bacchus, Pf = Pachylomerus femoralis, Pg = Pachysoma gariepinus, Sr = Scarabaeus rubripennis.*

| | *Cb* | *Pg* | *Pf* | *Sr* |
|---|---|---|---|---|
| *Cb* | | - | - | + |
| *Pg* | - | | - | - |
| *Pf* | - | - | | - |
| *Sr* | + | - | - | |

*Activation energies*

The small, winged desert dung beetle, *S. rubripennis,* had an $E_a$ of almost 27 kJ.mol$^{-1}$ higher than the larger, sympatric, apterous *P. gariepinus*. *Pachylomerus femoralis,* from the mesic savanna, had the lowest activation energy for the rate of water loss (Table 12).

**Table 12.** The activation energies of the rates of water loss of the four species at 15, 20, 27 and 35°C

| Species | Slope | $r^2$ | n | P | Activation energy |
|---|---|---|---|---|---|
| *C. bacchus* | -5.7077 | 57.11% | 44 | <0.0001 | 47,3742 kJ.mol$^{-1}$ |
| *P. femoralis* | -5.3192 | 49.05% | 46 | <0.0001 | 44.1492 kJ.mol$^{-1}$ |
| *P. gariepinus* | -5.9033 | 23.76% | 41 | 0.0012 | 48.9976 kJ.mol$^{-1}$ |
| *S. rubripennis* | -9.0622 | 84.40% | 41 | <0.0001 | 75.2165 kJ.mol$^{-1}$ |

## *WATER BALANCE AND OSMOREGULATION*

*Water balance*

Dehydration at 27°C resulted in relatively slow rates of water losses followed by rapid rates of increase in mass as the species were given access to water (Fig. 1a-e). Summary statistics for unadjusted mass lost and adjusted mass lost during every time interval and after rehydration are given in Table 13a-b. *Scarabaeus rubripennis* and *P. gariepinus* did not actively drink after the dehydration periods. They burrowed into moist sand where they remained for several hours during which their masses stabilised. None of the species gained mass when provided with high atmospheric humidities. A Kruskal-Wallis one way analysis of the unadjusted data indicated that the species lost water according to their sizes, i.e. larger species lost more water. However, the one way analysis of unadjusted water gain indicated that the two larger species gained similar amounts of water, but *S. rubripennis*, despite it being smaller than *P. gariepinus*, gained a similar amount of water to *P. gariepinus,* in the time it took for their masses to stabilise (Table 14). Adjusted data of water loss indicated that four species lost similar amounts of water. The adjusted water gain indicated that *S. rubripennis, C. bacchus* and *P. femoralis* gained similar amounts of water after rehydration, whereas *P. gariepinus* did not seem to be able to recover lost water rapidly (Table 14).

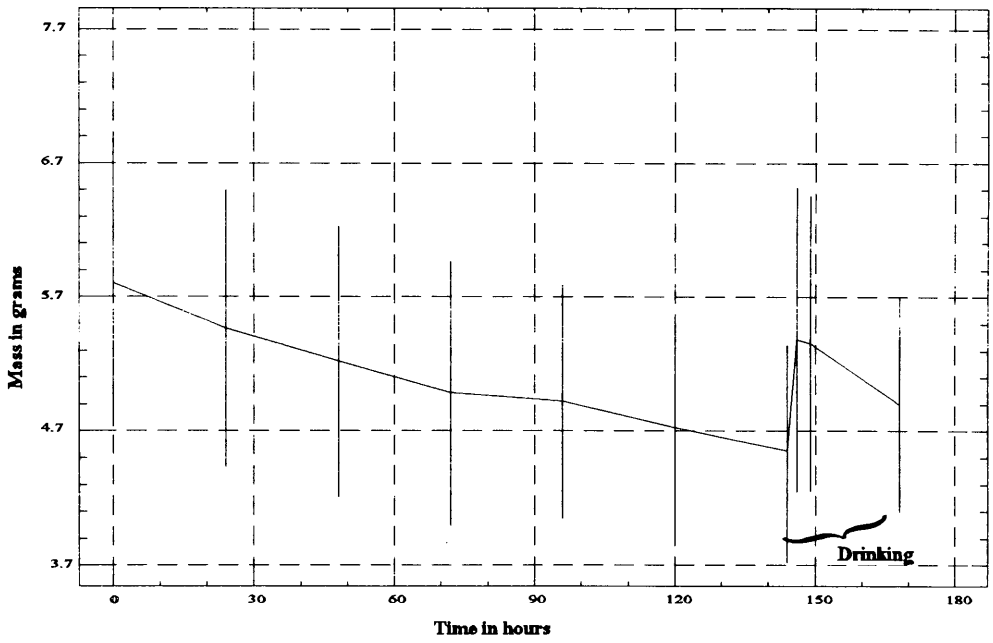


**Figure 1.** The mean (±SE) masses during the dehydration and rehydration periods for *C. bacchus*.

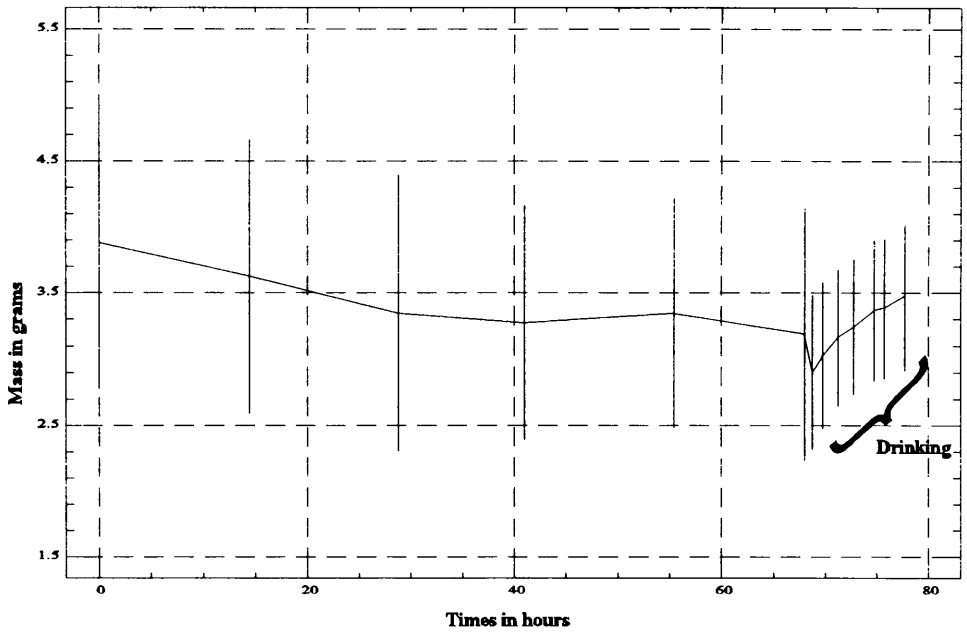


**Figure 2.** The mean (±SE) masses during the dehydration and rehydration periods for *P. femoralis*.

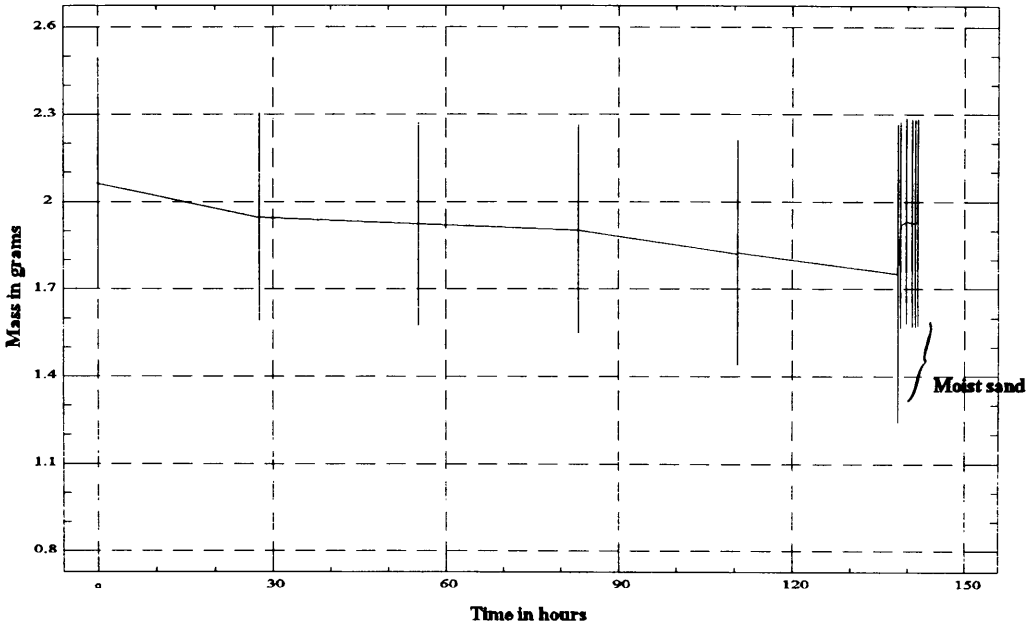


**Figure 3.** The mean (±SE) masses during the dehydration and rehydration periods for *P. gariepinus*.

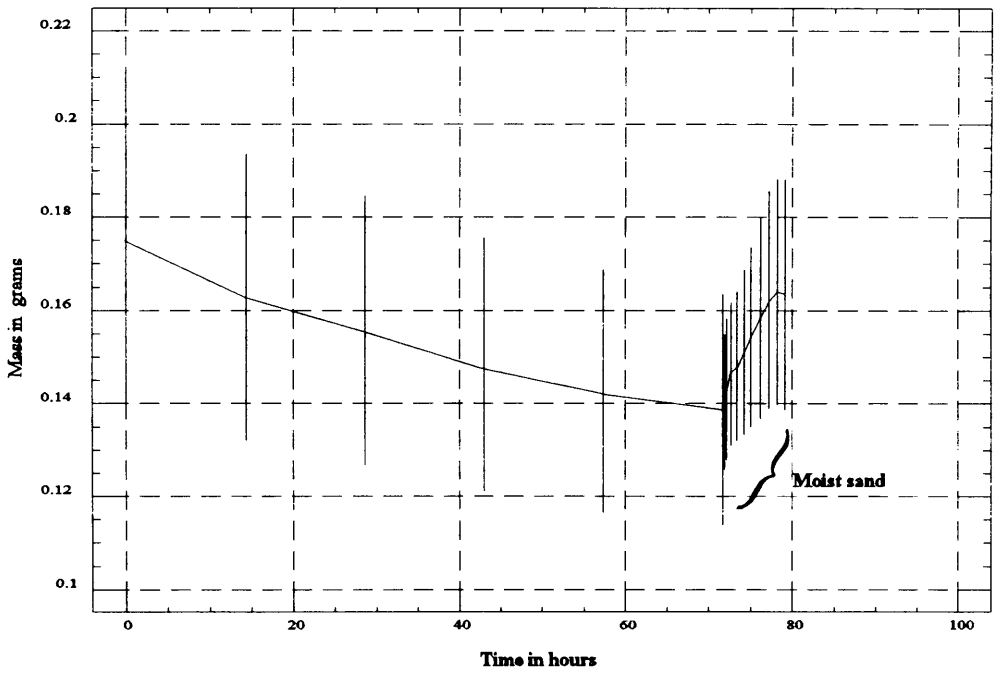


**Figure 4.** The mean (±SE) masses during the dehydration and rehydration periods for *S. rubripennis*.

**Table 13a.** Means, ±SD, ranges and sample sizes of the unadjusted mass lost of the four species during each time interval (hours) in the osmoregulation experiments.

| Species | *C. bacchus* | *P. femoralis* | *P. gariepinus* | *S. rubripennis* |
|---|---|---|---|---|
| **Initial mass** | 5.8022 | 3.8840 | 2.0640 | 0.1740 |
| **SD** | 1.0865 | 1.1225 | 0.3658 | 0.0350 |
| **Range** | 3.8360-8.0289 | 1.2478-6.0590 | 1.3811-2.8371 | 0.1017-0.2471 |
| **n** | 35 | 46 | 46 | 45 |
| **Mass loss** | | | | |
| **Time 1** | ** | 14 | 27.6 | 14.3 |
| **Mean** | ** | 0.2172 | 0.1009 | 0.0125 |
| **SD** | ** | 0.0511 | 0.0369 | 0.0038 |
| **Range** | ** | 0.1650-0.2851 | 0.0540-0.1521 | 0.0095-0.0189 |
| **n** | ** | 6 | 5 | 5 |
| **Time 2** | ** | 28 | 55.3 | 28.6 |
| **Mean** | ** | 0.4980 | 0.1782 | 0.0206 |
| **SD** | ** | 0.2127 | 0.0282 | 0.0049 |
| **Range** | ** | 0.1649-0.8522 | 0.1534-0.2256 | 0.0160-0.0274 |
| **n** | ** | 8 | 5 | 4 |
| **Time 3** | 72 | 42 | 83.0 | 43.0 |
| **Mean** | 0.9882 | 0.6464 | 0.2754 | 0.0344 |
| **SD** | 0.1064 | 0.1737 | 0.0257 | 0.0064 |
| **Range** | 0.8470-1.1320 | 0.4336-1.0200 | 0.2441-0.3009 | 0.0275-0.0427 |
| **n** | 6 | 9 | 5 | 5 |
| **Time 4** | ** | 55 | 110.6 | 57.3 |
| **Mean** | ** | 0.8095 | 0.3319 | 0.0125 |
| **SD** | ** | 0.2151 | 0.1483 | 0.0053 |
| **Range** | ** | 0.5607-1.1489 | 0.2125-0.5762 | 0.0388-0.0519 |
| **n** | ** | 5 | 5 | 5 |
| **Time 5** | 144 | 68 | 138.3 | 71.6 |
| **Mean** | 1.7492 | 0.8836 | 0.3549 | 0.0522 |
| **SD** | 0.4739 | 0.3399 | 0.0976 | 0.0108 |
| **Range** | 1.3000-2.6560 | 0.7012-1.2486 | 0.2683-0.4833 | 0.0447-0.0710 |
| **n** | 6 | 13 | 5 | 5 |
| **Dehydrated mass** | | | | |
| **Mean** | 4.6400 | 2.9597 | 1.8210 | 0.1364 |
| **SD** | 0.9071 | 0.6351 | 0.4247 | 0.0155 |
| **Range** | 3.2050-6.2660 | 2.0950-3.7274 | 1.2386-2.4395 | 0.1176-0.1597 |
| **n** | 22 | 6 | 8 | 8 |
| **Hydration time** | 5 | 9.75 | 3.5 | 7.5 |
| **Water gain** | | | | |
| **Mean** | 0.8572 | 0.5151 | 0.0260 | 0.0263 |
| **SD** | 0.3725 | 0.4451 | 0.0121 | 0.0411 |
| **Range** | 0.0520-1.5140 | -0.1367-0.9813 | 0.0132-0.0447 | -0.0309-0.0756 |
| **n** | 22 | 6 | 7 | 7 |
| **Rehydrated mass** | | | | |
| **Mean** | 5.4972 | 3.4748 | 1.8438 | 0.1595 |
| **SD** | 1.1718 | 0.6146 | 0.4330 | 0.0299 |
| **Range** | 3.7390-7.307 | 2.7475-4.2102 | 1.2386-2.4585 | 0.1171-0.1932 |
| **n** | 22 | 6 | 8 | 8 |

**Table 13b.** Means, ±SD, ranges and sample sizes of the adjusted mass loss of the four species during each time interval (hours) in the osmoregulation experiments.

| Species | *C. bacchus* | *P. femoralis* | *P. gariepinus* | *S. rubripennis* |
|---|---|---|---|---|
| **Adjusted mass loss** | | | | |
| **Time 1** | ** | 14 | 27.6 | 14.3 |
| **Mean** | ** | -0.0841 | 0.3287 | 0.5605 |
| **SD** | ** | 0.1246 | 0.0385 | 0.0067 |
| **Range** | ** | -0.2643-0.1103 | 0.2784-0.3865 | 0.5517-0.5672 |
| **n** | ** | 6 | 5 | 5 |
| **Time 2** | ** | 28 | 55.3 | 28.6 |
| **Mean** | ** | 0.3788 | 0.3786 | 0.5690 |
| **SD** | ** | 0.2769 | 0.0192 | 0.0050 |
| **Range** | ** | 0.1605-0.8122 | 0.3634-0.4106 | 0.5620-0.5740 |
| **n** | ** | 8 | 5 | 4 |
| **Time 3** | 72 | 42 | 83.0 | 43.0 |
| **Mean** | 0.4765 | 0.5096 | 0.3783 | 0.5794 |
| **SD** | 0.2698 | 0.1424 | 0.0225 | 0.0078 |
| **Range** | 0.1348-0.9226 | 0.2656-0.7293 | 0.3539-0.4031 | 0.5700-0.5866 |
| **n** | 6 | 9 | 5 | 5 |
| **Time 4** | ** | 55 | 110.6 | 57.3 |
| **Mean** | ** | 0.5284 | 0.5069 | 0.5877 |
| **SD** | ** | 0.1014 | 0.2068 | 0.0081 |
| **Range** | ** | 0.4263-0.6643 | 0.3782-0.8713 | 0.5764-0.5989 |
| **n** | ** | 5 | 5 | 5 |
| **Time 5** | 144 | 68 | 138.3 | 71.6 |
| **Mean** | 1.1009 | 0.6251 | 0.4718 | 0.5920 |
| **SD** | 0.3684 | 0.2392 | 0.0588 | 0.0098 |
| **Range** | 0.7914-1.7886 | 0.0996-0.8704 | 0.4131-0.5465 | 0.5855-0.6091 |
| **n** | 6 | 13 | 5 | 5 |
| **Adjusted dehydrated mass** | | | | |
| **Mean** | 1.2003 | 1.2297 | 1.2624 | 1.1430 |
| **SD** | 0.0881 | 0.1505 | 0.0450 | 0.0693 |
| **Range** | 0.9070-1.3055 | 1.1338-1.5264 | 1.1952-1.3145 | 1.0482-1.2395 |
| **n** | 22 | 6 | 8 | 8 |
| **Hydration time** | 5 | 9.75 | 3.5 | 7.5 |
| **Adjusted water gain** | | | | |
| **Mean** | 0.3594 | 0.3727 | 0.1097 | 0.4525 |
| **SD** | 0.2772 | 0.4678 | 0.0625 | 0.0433 |
| **Range** | 0.3534-0.8489 | 0.2364-0.7859 | 0.0157-0.2090 | 0.3940-0.5037 |
| **n** | 22 | 6 | 7 | 7 |
| **Adjusted rehydrated mass** | | | | |
| **Mean** | 1.3987 | 1.4395 | 1.2732 | 1.3853 |
| **SD** | 0.1011 | 0.1318 | 0.0425 | 0.3488 |
| **Range** | 1.0451-1.5292 | 1.1823-1.5614 | 1.2186-1.3220 | 0.9579-1.9205 |
| **n** | 22 | 6 | 8 | 8 |

**Table 14.** Kruskal-wallis non-parametric one way analysis by ranks of unadjusted and adjusted water losses of *C. bacchus, P. femoralis, P. gariepinus* and *S. rubripennis* after desiccation at 27°C for times equal to half their $LT_{50}$'s and their unadjusted and adjusted water gains at the times their masses stabilised. The average ranks are sorted in descending order.

| | Species | n | Average ranks | Time |
|---|---|---|---|---|
| **Unadjusted** | *C. bacchus* | 22 | 32.1818 | 144.00 |
| **Water loss** | *P. femoralis* | 6 | 21.6667 | 68.00 |
| | *P. gariepinus* | 8 | 13.5000 | 138.30 |
| | *S. rubripennis* | 8 | 5.5000 | 71.60 |

Test statistic = 30.4630, Significance level $\alpha$ = <0.00001, $Chi^2$ approximation = 20.9667.

| | | | | |
|---|---|---|---|---|
| **Unadjusted** | *C. bacchus* | 22 | 29.4545 | 5.00 |
| **Water gain** | *P. femoralis* | 6 | 22.1667 | 9.75 |
| | *S. rubripennis* | 7 | 9.1429 | 7.50 |
| | *P. gariepinus* | 7 | 8.2857 | 3.50 |

Test statistic = 24.4912, Significance level $\alpha$ = <0.00001, $Chi^2$ approximation = 20.9667.

| | | | | |
|---|---|---|---|---|
| **Adjusted** | *S. rubripennis* | 8 | 27.5000 | 71.60 |
| **Water loss** | *P. femoralis* | 6 | 27.5000 | 68.00 |
| | *C. bacchus* | 22 | 21.0909 | 144.00 |
| | *P. gariepinus* | 8 | 17.6250 | 138.30 |

Test statistic = 3.5382, Significance level $\alpha$ = 0.3158, $Chi^2$ approximation = 20.9667.

| | | | | |
|---|---|---|---|---|
| **Adjusted** | *S. rubripennis* | 7 | 26.5714 | 7.50 |
| **Water gain** | *P. femoralis* | 6 | 25.5000 | 9.75 |
| | *C. bacchus* | 22 | 22.9091 | 5.00 |
| | *P. gariepinus* | 7 | 8.5714 | 3.50 |

Test statistic = 9.8987, Significance level $\alpha$ = 0.01945, $Chi^2$ approximation = 20.9667.

*Lipid metabolism*

Summary statistics for unadjusted lipid contents and adjusted lipid contents during every time interval are given in Table 15a-b. The results of the two methods indicated that the two apterous species had lower lipid metabolism capabilities compared with the two macropterous species (Table 16).

The osmoregulation experiment for *P. femoralis* was done previously. The data for lipid metabolism of the first experiment, the previous season (1992), were kindly provided by F.J. Joubert. This indicated that no lipid metabolism took place to provide metabolic water. The second experiment, done in this study, used beetles from the following season (1993). This time a strong capacity for lipid metabolism was indicated.

**Table 15a.** Means, ±SD, ranges and sample sizes of the unadjusted lipid contents of the four species during each time interval (hours) in the osmoregulation experiments.

| Species | *C. bacchus* | *P. femoralis* | *P. gariepinus* | *S. rubripennis* |
|---|---|---|---|---|
| **Initial lipid content** | | | | |
| **Mean** | ** | 0.2543 | 0.1414 | 0.0281 |
| **SD** | ** | 0.1555 | 0.0242 | 0.0089 |
| **Range** | ** | 0.0963-0.5140 | 0.1128-0.1754 | 0.0201-0.0402 |
| **n** | ** | 5 | 5 | 5 |
| **Lipid content** | | | | |
| **Time 1** | ** | 14 | 27.6 | 14.3 |
| **Mean** | ** | 0.2582 | 0.1341 | 0.0216 |
| **SD** | ** | 0.0905 | 0.0087 | 0.0074 |
| **Range** | ** | 0.1555-0.4081 | 0.1252-0.1470 | 0.0156-0.0344 |
| **n** | ** | 6 | 5 | 5 |
| **Time 2** | ** | 28 | 55.3 | 28.6 |
| **Mean** | ** | 0.1475 | 0.1170 | 0.0199 |
| **SD** | ** | 0.1060 | 0.0265 | 0.0057 |
| **Range** | ** | 0.0189-0.3716 | 0.0883-0.1509 | 0.0148-0.0258 |
| **n** | ** | 8 | 5 | 4 |
| **Time 3** | 72 | 42 | 83.0 | 43.0 |
| **Mean** | 0.3822 | 0.1300 | 0.1847 | 0.0207 |
| **SD** | 0.0836 | 0.0426 | 0.0550 | 0.0054 |
| **Range** | 0.2887-0.4917 | 0.0662-0.1794 | 0.1229-0.2588 | 0.0158-0.0269 |
| **n** | 5 | 8 | 5 | 5 |
| **Time 4** | ** | 55 | 110.6 | 57.3 |
| **Mean** | ** | 0.2051 | 0.1247 | 0.0175 |
| **SD** | ** | 0.0669 | 0.0626 | 0.0044 |
| **Range** | ** | 0.1311-0.3052 | 0.0254-0.1841 | 0.0123-0.0234 |
| **n** | ** | 5 | 5 | 5 |
| **Time 5** | 144 | 68 | 138.3 | 71.6 |
| **Mean** | 0.4296 | 0.1411 | 0.1677 | 0.0212 |
| **SD** | 0.1390 | 0.0567 | 0.0485 | 0.0065 |
| **Range** | 0.2715-0.6238 | 0.0633-0.2299 | 0.1185-0.2291 | 0.0145-0.0309 |
| **n** | 5 | 11 | 5 | 5 |

**Table 15b.** Means, ±SD, ranges and sample sizes of the adjusted lipid contents of the four species during each time interval (hours) in the osmoregulation experiments.

| Species | *C. bacchus* | *P. femoralis* | *P. gariepinus* | *S. rubripennis* |
|---|---|---|---|---|
| **Adjusted initial lipid content** | | | | |
| **Mean** | ** | 0.1172 | 0.1171 | 0.1569 |
| **SD** | ** | 0.0510 | 0.0128 | 0.0124 |
| **Range** | ** | 0.0686-0.1967 | 0.0999-0.1341 | 0.1452-0.1759 |
| **n** | ** | 5 | 5 | 5 |
| **Adjusted lipid content** | | | | |
| **Time 1** | ** | 14 | 27.6 | 14.3 |
| **Mean** | ** | 0.1170 | 0.1244 | 0.1296 |
| **SD** | ** | 0.0316 | 0.0101 | 0.0433 |
| **Range** | ** | 0.0739-0.1685 | 0.1118-0.1377 | 0.0840-0.1915 |
| **n** | ** | 6 | 5 | 5 |
| **Time 2** | ** | 28 | 55.3 | 28.6 |
| **Mean** | ** | 0.0737 | 0.1018 | 0.1181 |
| **SD** | ** | 0.0343 | 0.0193 | 0.0194 |
| **Range** | ** | 0.0222-0.1406 | 0.0814-0.1274 | 0.0905-0.1348 |
| **n** | ** | 8 | 5 | 4 |
| **Time 3** | 72 | 42 | 83.0 | 43.0 |
| **Mean** | 0.1428 | 0.0677 | 0.1346 | 0.1138 |
| **SD** | 0.0218 | 0.0150 | 0.0365 | 0.0245 |
| **Range** | 0.1049-0.1578 | 0.0479-0.0867 | 0.0899-0.1784 | 0.0884-0.1477 |
| **n** | 5 | 9 | 5 | 5 |
| **Time 4** | ** | 55 | 110.6 | 57.3 |
| **Mean** | ** | 0.0984 | 0.0988 | 0.0945 |
| **SD** | ** | 0.0421 | 0.0414 | 0.0189 |
| **Range** | ** | 0.0659-0.1687 | 0.0276-0.1324 | 0.0799-0.1236 |
| **n** | ** | 5 | 5 | 5 |
| **Time 5** | 144 | 68 | 138.3 | 71.6 |
| **Mean** | 0.1554 | 0.0676 | 0.1240 | 0.1034 |
| **SD** | 0.0437 | 0.0276 | 0.0186 | 0.0251 |
| **Range** | 0.1070-0.2170 | 0.0388-0.1321 | 0.1093-0.1444 | 0.0831-0.1441 |
| **n** | 5 | 13 | 5 | 5 |

**Table 16.** The $r^2$ and P values for the regression of lipid content on waterloss. Results of both methods are given as well as both experiments of *P. femoralis*. The regressions are in the form Y = a + bX.

| Species | Method | $r^2$ | n | P | Results |
|---|---|---|---|---|---|
| *C. bacchus* | 1 | 52.12% | 19 | 0.0005 | Lipids are metabolised |
| | 2 | 51.24 | | 0.0006 | Lipids are metabolised |
| *P. femoralis* | | | | | |
| Experiment 1 | 1 | 2.50% | 37 | 0.3951 | No lipid metabolism |
| | 2 | 2.42% | | 0.4037 | No lipid metabolism |
| Experiment 2 | 1 | 64.46% | 31 | <0.0001 | Lipids are metabolised |
| | 2 | 66.74% | | <0.0001 | Lipids are metabolised |
| Combined | 1 | 21.04% | 68 | 0.0001 | Very weak metabolism |
| | 2 | 23.93% | | <0.0001 | Very weak metabolism |
| *P. gariepinus* | 1 | 18.10% | 28 | 0.0269 | Very weak metabolism |
| | 2 | 25.46% | | 0.0062 | Very weak metabolism |
| *S. rubripennis* | 1 | 68.41% | 27 | <0.0001 | Lipids are metabolised |
| | 2 | 68.54% | | <0.0001 | Lipids are metabolised |

*Haemolymph osmoregulation*

Summary statistics for haemolymph osmolalities, during every time interval, are given in Table 17. Because of *S. rubripennis*' small size, sufficient quantities of haemolymph could not be obtained for this analysis. The slopes of the regressions of water content on haemolymph osmolality of the three species (Table 18a & b) were compared with each other, and with a slope of zero, using a T-test method (Sokal & Rholf 1980). *Circellium bacchus*' and *P. gariepinus*' slopes did not differ significantly from zero, or from each other. *Pachylomerus femoralis*' slope differed from zero, and from the slopes of *C. bacchus* and *P. gariepinus*. This means that *C. bacchus*' and *P. gariepinus*' haemolymph osmolalities were regulated effectively enough not to differ much, despite vast differences in water content. *Pachylomerus femoralis,* on the other hand, had widely differing haemolymph osmolalities over slight changes in water content. This indicated that the apterous dung beetle species' ability to regulate their haemolymph osmolality during desiccation is far superior to that of *P. femoralis*.

**Table 17.** Means, ±SD, ranges and sample sizes of the haemolymph osmolalities of the four species during each time interval (hours) in the osmoregulation experiments.

| Species | *C. bacchus* | *P. femoralis* | *P. gariepinus* | *S. rubripennis* |
|---|---|---|---|---|
| **Initial osmolalities** | | | | |
| **Mean** | 415.688 | 411.550 | 688.150 | ** |
| **SD** | 18.702 | 35.810 | 54.315 | ** |
| **Range** | 392.500-451.500 | 352.500-449.500 | 619.750-739.500 | ** |
| **n** | 8 | 5 | 5 | ** |
| **Osmolalities** | | | | |
| **Time 1** | ** | 14 | 27.6 | |
| **Mean** | ** | 484.533 | 642.700 | ** |
| **SD** | ** | 14.480 | 56.804 | ** |
| **Range** | ** | 475.667-510.000 | 559.000-691.000 | ** |
| **n** | ** | 5 | 5 | ** |
| **Time 2** | ** | 28 | 55.3 | ** |
| **Mean** | ** | 537.300 | 648.450 | ** |
| **SD** | ** | 44.8520 | 20.3681 | ** |
| **Range** | ** | 4760000-581.000 | 615.250-668.333 | ** |
| **n** | ** | 5 | 5 | ** |
| **Time 3** | 72 | 42 | 83.0 | ** |
| **Mean** | 536.422 | 614.900 | 641.467 | ** |
| **SD** | 34.646 | 70.1056 | 21.263 | ** |
| **Range** | 502.333-571.600 | 549.500-712.000 | 619.000-674.000 | ** |
| **n** | 3 | 5 | 5 | ** |
| **Time 4** | ** | 55 | 110.6 | ** |
| **Mean** | ** | 631.667 | 641.500 | ** |
| **SD** | ** | 29.750 | 18.836 | ** |
| **Range** | ** | 602.000-661.500 | 617.500-662.250 | ** |
| **n** | ** | 3 | 5 | ** |
| **Time 5** | ** | 68 | 138.3 | ** |
| **Mean** | ** | 661.500 | 701.600 | ** |
| **SD** | ** | ** | 72.7862 | ** |
| **Range** | ** | ** | 616.250-796.750 | ** |
| **n** | ** | 1 | 5 | ** |
| **Osmolalities after rehydration** | | | | |
| **Mean** | 430.264 | ** | 692.625 | ** |
| **SD** | 34.499 | ** | 82.180 | ** |
| **Range** | 308.750-464.333 | ** | 578.500-832.250 | ** |
| **n** | 18 | ** | 6 | ** |

**Table 18a.** The regression data of water content on haemolymph osmolality during desiccation. t-Test comparing the slope with zero. The regressions are in the form logY = b logX + a.

| Species | Intercept ± SE | Slope ± SE | $t_s$ | $r^2$ | Differs from zero |
|---|---|---|---|---|---|
| *C. bacchus* | 521.386 ± 115.899 | -53.898 ± 66.494 | 0.81056 | 6.80% | No |
| *P. femoralis* | 780.298 ± 63.395 | -172.895 ± 42.234 | 4.32944 | 48.38% | Yes |
| *P. gariepinus* | 670.968 ± 76.544 | -7.041 ± 55.583 | 0.12719 | 0.06% | No |
| *S. rubripennis* | ** | ** | ** | ** | ** |

**Table 18b.** The regression data of water content on haemolymph osmolality during desiccation. The slopes are compared with each other with a t-Test. The regressions are in the form logY = b logX + a.

| Species | Intercept | Slope | $t_s$ | $r^2$ | Difference |
|---|---|---|---|---|---|
| *C. bacchus* | 521.386 | -53.898 | | 6.80% | |
| *x P. femoralis* | | | 4.4383 | | Yes |
| *x P. gariepinus* | | | -0.7047 | | No |
| *P. femoralis* | 780.298 | -172.895 | | 48.38% | |
| *x P. gariepinus* | | | -4.2421 | | Yes |
| *S. rubripennis* | ** | ** | ** | ** | ** |

# DISCUSSION

*For many animals, behavioral discretion is often the better part of regulatory valor.*

Albert F. Bennet 1987.

The percentage data obtained from the 17 species are, in general, similar to other such studies. The dung beetles from mesic habitats tolerated 22 - 33% mass loss before they died. In comparison, other insects species from mesic habitats also tolerate only 23 - 36% of body water loss. Curculionids from mesic habitats on Marion Island, (*Ectemnorhinus marioni* and *E. similis*), could tolerate 31 and 36% mass loss respectively (Chown 1993); populations of the perimylopid species, *Hydromedion sparsutum* and *Perimylops antarcticus*, from mesic areas on South Georgia Island, tolerated 23 and 26% mass loss respectively (Ring *et al.* 1990); and a mesic grasshopper, *Anacridium spp.,* tolerated 26% mass loss before death (Edney 1977). In this study dung beetle species from xeric habitas tolerated 33 - 43% mass loss before they died. Other xeric insects such as *Bothrometopus randi,* a curculionid from Marion Island, tolerated 36% mass loss (Chown 1993), the populations of perimylopid species, *H. sparsutum* and *P. antarcticus,* from xeric areas on South Georgia Island, tolerated 32 and 39% mass loss respectively (Ring *et al.* 1990) and a xeric grasshopper, *Poecilocerus sp.,* tolerated 35% mass loss before death (Abushama 1970).

The rates at which the dung beetles from the various habitats lost water were also similar to that found in other insects. Edney (1977) found that insect species from xeric habitats combined decreased rates of water loss with increased tolerances to high levels of water loss before death. The percentage data of the rates of mass loss of the dung beetles varied from 0.17% mass lost/hour for a very tolerant xeric species, *P. striatum,* to 2.4% mass lost/hour for the least tolerant mesic species, *G. nitens*. Chown (1993), Ring *et al.* (1990) and Abushama (1970) found that the rates of water loss of xeric species were also five to ten times lower than those of mesic species.

The larger dung beetles had longer survival times compared to the smaller ones. Zachariassen *et al.* (1987) studied carabid beetles in the arid areas of East Africa found that, in combination with increased tolerances to high levels of water loss and decreased rates of

water loss, larger beetles tended to have a higher resistance to desiccation than smaller species.

The results of this study and of previous studies (Abushama 1970, Zachariassen *et al.* 1987, Ring *et al.* 1990 and Chown 1993) confirm Edney's (1977) argument that improved desiccation resistance is a combined outcome of both a reduced rate of water loss and an increase in the capacity to tolerate reduced body water levels.

## *MULTIPLE COMPARISONS OF DESICCATION RESISTANCE*

*The seventeen species*

Analyses of the unadjusted data indicated that body size influences both maximum tolerable mass loss and the rates of mass loss (see also Edney 1977). The high rank group in the unadjusted mass loss analysis included all the large telecoprids (Fg I) and *C. tricornutus*, the largest of the fast burrowing paracoprids (Fg III). The low rank group included the rest of the species which are either small or medium-sized beetles. In general, the unadjusted maximum tolerable mass loss analysis demonstrated that larger species could tolerate greater absolute amounts of water loss due to the large pool of water available, a consequence of their larger sizes (see also Table 2).

Comparisons of the unadjusted rates of mass loss did not reveal as close a relationship between size and the variable in question as did unadjusted maximum tolerable mass losses (see Table 2). These weaker relations with body size indicate definite physiological adaptations to decrease the rate of water loss in order to improve desiccation resistance. However, the high rank group still contained mostly large telecoprids (Fg I), but also contained a medium-sized mesic species, *G. nitens*, and a medium-sized nocturnal species, *O. caffer*. The low rank group also contained mostly small and medium-sized beetles, because smaller beetles lose less mass per unit time than larger ones. However, the two large apterous desert telecoprids, *P. gariepinus* and *P. striatum,* were also included among the low rate of water loss species. The intermediate species, *P. adrea*, is small but active during very humid periods.

If the patterns in the diagrams are viewed from an ecological perspective a clear picture of the importance of the physiological adaptations to desiccation resistance in the context of the strategies of the species emerges. For example, most of the nocturnal species,

except for *C. amyntor,* showed similarities to each other with regard to their rates of mass loss, and their average rankings are in the high rank group (Table 3b and Diagram 1b). This shows that both size and physiology contribute to the desiccation resistance of each species. Differences between two species of different size may thus either be due to their difference in size alone, to definite and large differences in their physiological adaptations to desiccation resistance, or as a consequence of both, eg. *S. zambesianus* vs. *O. sapphirinus*, *P. femoralis* vs *P. gariepinus*, *A. convexus* vs *S. rubripennis* and *K. subaeneus* vs *L. militaris*. Similarities between two species of different size are easier to explain. This usually entails differences in physiological adaptation to desiccation resistance, eg. *C. bacchus* vs. *G. nitens*, *K. subaeneus* vs. *O. sapphirinus*, *K. cupreus* vs. *L. militaris* and *P. gariepinus* vs. *S. impressipennis*. Differences between species of similar size are also due to different physiological adaptations to desiccation resistance, eg. *C. amyntor* vs. *O. caffer*, *P. gariepinus* vs *C. tricornutus* and *S. zambesianus* vs. *P. striatum*. Similarities between species of similar size imply similar physiological adaptations, eg. *A. convexus* vs. *C. tricornutus*, *O. sapphirinus* vs. *L. militaris*. and *G. nitens* vs *O. caffer*.

The results obtained from this investigation of rate of water loss, imply that rate of water loss is more important than tolerance to water loss in promoting desiccation resistance, particularly because rate of water loss is not as closely related to the sizes of the species as is maximum tolerable water loss.

From the analysis of unadjusted survival times (Table 3c) it is clear that the apterous species, *P. striatum, C. bacchus* and *P. gariepinus* have the greatest resistance to desiccation, followed closely by the desert-adapted species *S. rubripennis*. These four species also illustrate that large body size and restriction of the rate of water loss are the most important factors contributing to desiccation resistance in these beetles and that maximum tolerable water loss is less important (see also Edney 1977). In fact, the species which have a high resistance to desiccation are, with the exception of *S. rubripennis* and *C. amyntor*, also the larger species in the group of seventeen species. This is direct evidence for the fact that body size has an important effect on desiccation resistance. However, these differences in body size also cloud the results of the analyses to a certain extent, prohibiting significant conclusions on the strict physiological mechanisms of desiccation resistance to be drawn. The data which were adjusted for differences in body mass circumvent this problem to a large extent.

The analysis of the adjusted maximum tolerable mass losses of the seventeen species

showed that those species with extended physiological adaptations for tolerating water loss. *Scarabaeus rubripennis*, *C. amyntor*, *C. bacchus* and *P. striatum*, all inhabit relatively dry to xeric habitats. The low rank species, on the other hand, do not require high tolerances to the maximum amount of water loss. These species either occupy mesic habitats, (*P. ardea, G. nitens* and *S. impressipennis),* are active during less desiccating periods, (*C. tricornutus, A. convexus* and *S. zambesianus*), have a behavioural ecology that exposes them minimally to desiccating conditions, (*O. sapphirinus, C. tricornutus* and *P. ardea*) and/or they rely more on a reduction in the rate of water loss to resist desiccation, (*O. sapphirinus, A. convexus, S. impressipennis* and *P. femoralis*).

In the analysis of adjusted rate of mass loss most species fell within the low rank group (i.e. species with comparably low rates of mass loss). All the species, except *C. bacchus*, that had high mass loss tolerances were also included in this group with the addition of two telecoprids and a diurnal paracoprid. The high rank group representing high rates of mass loss consisted mostly of species that either occupy mesic habitats, (*P. adrea* and *G. nitens),* are active during less desiccating periods, (*O. caffer, C. tricornutus* and *S. zambesianus),* and/or have a behavioural ecology that exposes them minimally to desiccating conditions, (*P. adrea, O. caffer, C.tricornutus* and *L. militaris).*

Finally, in the adjusted survival time analysis the combined effects of the non-size related tolerances to the maximum water loss and the non-size related rates of mass loss are apparent. The species with a high, non-size related resistance to desiccation were the three desert telecoprids, a grassland paracoprid, (*C. amyntor*), and a diurnal savanna paracoprid, (*O. sapphirinus).* All these species occur in xeric habitats. Aptery appears to be the most important character influencing desiccation resistance of the two *Pachysoma* species via reduction in water loss. The other three species rely on reduced rates of water loss and a large tolerance to water loss to counteract their small body size and hence the small pool of available water. The species in the low rank group again either occupy mesic habitats, (*P. ardea* and *G. nitens),* are active during less desiccating periods, (*C. tricornutus, O. caffer* and *S. zambesianus),* and/or have a behavioural ecology that exposes them minimally to desiccating conditions, (*C. tricornutus, O. caffer* and *P. ardea).* However, species such as *P. femoralis* and *K. subaeneus* rely more on their large sizes to resist desiccation because they resort in the high rank group in the unadjusted analysis of survival time.

The results obtained from this study not only show that large body size and low rates of water loss are the factors that contribute most to desiccation resistance in dung beetles,

but also that the species show specific adaptations to their habitats. *Scarabaeus rubripennis*, *P. striatum* and *P. gariepinus* are desert-living beetles and this obviously requires a high tolerance to desiccation. However, the mechanisms they employ are different. Although *P. gariepinus* and *P. striatum* have relatively high tolerances to the amount of body water lost, it appears that a low rate of water loss is a more important adaptation. This is accomplished by thick cuticles, water extraction from the faeces (personal observation) and closed sub-elytral chambers. Restriction of their activity periods to the early morning and the later afternoon and the utilisation of the moist layer of sand 10 - 25cm beneath the dune surface may also promote resistance to very dry conditions via avoidance (see also Mostert 1984, Scholtz 1989, C.H. Scholtz & E. Holm pers. comm., personal observations). *S. rubripennis* is a smaller, flying scarab which is sympatric with *P. gariepinus*. Its flying mode of foraging is consequently exposes it to very dry conditions and therefore this species requires an extremely high tolerance to the maximum amounts of body water lost. To further curb these losses, this species also has a greatly reduced rate of water loss. These two mechanisms are so effective that the beetle's small size does not affect it adversely in its xeric habitat and it can remain active for extended periods during the day. The object of its mode of foraging is, in contrast with *P. gariepinus*, high quality fresh dung or carrion. These food sources are high in nutrient contents and also have a high moisture content. Although not as abundant as dried gemsbok pellets, this food source is enough to sustain *S. rubripennis*. Through this mode of foraging, competition with the apterous species is avoided as arrival at the resources and processing of resources is usually accomplished long before the arrival of the slow, pedestrian *P. gariepinus*.

*Circellium bacchus*, a large flightless scarab, occurs in the xeric scrub dominated valley bushveld of the Addo Elephant National Park. It also has a bimodal activity period, foraging on foot for fresh rhino, elephant and buffalo dung (Coles 1994). Patches of these dung types are abundant in these areas, but the distances between the dung patches and the speed at which *C. bacchus* is able to reach them warrant the level of desiccation resistance brought about mainly by their high tolerance of the amount of body water lost. An increased body size allows *C. bacchus* to store more water per volume/surface area ratio. Its relatively low rate of water loss is brought about by the closed sub-elytral chamber. The abundant and stable dung resources in its habitat (Roff 1990, Chown *et al.* in press), its avoidance of competitors, and its desiccation resistance have ensured *C. bacchus*' survival (Coles 1994).

*Copris amyntor* occurs in the grassland biome of the Orange Free State during late

March to early May. It is a diurnal fast burrowing paracoprid (Fg III) and travels frequently as it does not remain for long periods at a particular dung pad. These characteristics, and the low abundance of resources explain its physiologically high tolerance to desiccation. *Copris amyntor*'s high non-size related resistance to the high amounts of body water lost and the low rates of these losses make it physiologically superior to most of the other species, but its relatively small size decreases the time of survival or the actual desiccation resistance (the opposite of *C. bacchus*).

*Onthophagus sapphirinus*, a small diurnal, slow burrowing paracoprid (Fg V), occurs in the savanna regions. In comparison with the other larger savanna telecoprids, *O. sapphirinus* shows a relatively superior non-size related resistance to desiccation, especially with respect to rate of water loss. However, when its small size is taken into account, it becomes clear that these physiological adaptations give rise to a desiccation resistance comparable to that of the telecoprids.

*Pachylomerus femoralis*, *K. cupreus*, and *K. subaeneus* are large diurnal savanna telecoprids (Fg I). Their non-size related physiological adaptations to desiccation resistance are intermediate. When their body sizes are taken into account, and when the desert species and *C. bacchus* are excluded, they number among the most desiccation resistant species. This was predicted from their ecological strategies (see Introduction). Being telecoprids in the savanna, they daily have to travel large distances between resources and, after arrival, they face fierce competition in allocating some of the resources for themselves (Heinrich & Bartholomew 1979). The act of cutting, constructing and rolling a dung ball to a secluded place further exposes them to dry conditions. Their large size definitely assists them, not only to overcome competitors but also to increase their resistance to desiccation (Edney 1977, Chown *et al.* in press, Mostert 1984, Doube 1991).

*Anachalcos convexus* and *S. zambesianus* are two nocturnal and/or crepuscular large, savanna telecoprids (Fg I). *Anachalcos convexus* is a carrion specialist but it will utilise dung, whereas *S. zambesianus* prefers dung (Tribe 1976, Mostert 1984). Both species do not have as high a non-size related physiological resistance to desiccation as do the other large telecoprids. Both have a very low tolerance to the maximum amount of body water lost. *A. convexus* has an intermediate rate of mass loss, but *S. zambesianus* has a very high rate. This does not facilitate desiccation resistance and even if their relatively large sizes are taken into account, they still show only slightly better resistances to desiccation. When their activity periods are considered, however, it becomes clear that these two species do not need very

igh physiological resistances to desiccation as the desiccating conditions are much reduced during nocturnal and crepuscular periods. Again this confirms the ecologically-based predictions of tolerance discussed in the Introduction.

*Garetta nitens* and *S. impressipennis* are small, diurnal savanna telecoprids (Fg II). *Garetta nitens* has, during my field excursions, only been observed in hot and very humid periods with frequent rains. During these times they are active during the morning and later afternoon or directly after rain. *Sisyphus impressipennis* is also active during humid periods after rains (C.H. Scholtz, pers. comm.). *Garetta nitens* doesn't have a very high non size-related resistance to desiccation with neither a high tolerance to the maximum amount of body water lost nor a very low rate of water loss. Its body size does not influence its desiccation resistance to a large extent. *Sisyphus impressipennis*, however, has better non size-related resistance with an intermediate tolerance to the maximum amount of water lost and rate of water loss. These factors compensate in a large way for its small body size, in such a way that its non size-related resistance to desiccation is much higher than that of the larger *G. nitens*.

*Catharsius tricornutus*, a nocturnal large fast burrowing paracoprid (Fg III) from savanna areas, has an intermediate non size-related tolerance to the maximum amount of body water lost, but also a very high rate of water loss. This makes it the dung beetle with the lowest non size-related tolerance to desiccation and only its relatively large body size improves its resistance to the extent that it is similar to the two nocturnal telecoprids, *A. convexus* and *S. zambesianus*. *Catharsius tricornutus* is subjected to similar, rather mesic circumstances as are *A. convexus* and *S. zambesianus*, but with the further advantage that it burrows directly under or beside its resource and is consequently not as exposed as *A. convexus* and *S. zambesianus* (Tribe 1976, Doube & Moola 1988).

*Onitis caffer* is a nocturnal large slow burrowing paracoprid (Fg IV) from the grassland biome of the Orange Free State. It occurs in the latter half of the summer season until mid-autumn. It has a high non size-related tolerance to the maximum amount of body water lost but it also has the highest rate of water loss. This gives it a very low tolerance to desiccation which is not improved when its body size is taken into account. The reason for this low desiccation resistance may be that it remains under dung pads for extended periods (slow burrowing paracoprid) and is rarely exposed to possible desiccating conditions. This is in stark contrast with the highly desiccation resistant *C. amyntor* which occurs sympatrically and at the same time as *O. caffer*. (*C. amyntor* is a fast burrower - see above).

*Phalops ardea*, a diurnal large slow burrowing paracoprid (FgIV), occurs sympatrically with *G. nitens* and also during the same humid conditions. It has the lowest non size-related tolerance to the maximum amount of water lost and its rate of water loss is also relatively high. This gives this species a low resistance to desiccation and when its small size is taken into account, it has the lowest actual resistance to desiccation. This explains its short, but very active period during the wet season. In addition, because it is a paracoprid, its needs for high desiccation resistance are minimal.

*Liatongus militaris* is a small, diurnally-active endocoprid from savanna areas. Its non size-related resistance to desiccation is intermediate but, because of its small size, it has a very low actual desiccation resistance. *Liatongus militaris*' habit is to colonize one week old dung pads (mostly undisturbed pads with a crust already formed), in which they dwell until most of the dung is utilized. This behaviour isolates them from most desiccating conditions and as a result high desiccation resistance is not necessary.

In this analysis of the seventeen species, it is clear that the three brachypterous species had the highest actual desiccation resistance. Their physiological adaptations to desiccation resistance in combination with being apterous make them extremely well adapted to dry conditions. Aptery is thus a key factor promoting desiccation resistance. However, these species' extreme values also statistically clouded the analysis of desiccation resistance in the macropterous species. Therefore, to gain a clearer understanding of the other factors that influence desiccation tolerances in macropterous and apterous species, these groups were separated and the statistical tests were repeated.

*The macropterous species*

The results of the analyses of macropterous species are very similar to the group of seventeen species. However, elimination of the strong confounding effects of the results of the three apterous species that influenced the placing of species in the low or high rank groups lead to clearer view of the physiological adaptations among the macropterous species. Several species showed higher resistances to desiccation than that found in the major seventeen species analyses.

Body size remains as a major influence on both maximum tolerable mass loss and the rates of mass loss (Edney 1977). The high rank group in the unadjusted mass loss analysis consisted of all the large macropterous telecoprids (Fg I) and *C. tricornutus*, the largest species of Fg III, and *O. caffer,* Fg IV. *Onitis caffer* moved up from an intermediate species to the high rank group of macropterous species. The low rank group consisted of the rest of

the species which are either small or medium-sized.

As with the seventeen species analysis, the weaker relationship of unadjusted rates of water loss to body size of the macropterous dung beetles points to specific physiological adaptations to decrease the rate of mass loss in order to improve desiccation resistance. In this analysis *P. adrea*, a small diurnal savanna paracoprid, moved from a previously intermediate position to the low rank group, consisting of small and medium-sized macropterous beetles with comparably low rates of water loss. The high rank group still contained mostly large telecoprids (Fg I) but also contained a medium-sized mesic species, *G. nitens*, and a medium sized nocturnal species, *O. caffer*.

The results of the analysis of the unadjusted survival time of the macropterous species showed that species in the high rank group, which have a high resistance to desiccation, are mostly the larger macropterous species. The exceptions are *S. rubripennis* and *C. amyntor,* and also the small *O. sapphirinus* which moved up from the intermediate group in the seventeen species analysis of survival time.

The analysis of the adjusted maximum tolerable mass losses of the macropterous species focused sharply on the high rank group. Of all the macropterous species *S. rubripennis* and *C. amyntor* have the highest non-size related maximum tolerable mass losses. Both species are active in very dry environments. The low rank group's species on the other hand do not require high tolerances to the maximum amount of water loss because they either occupy mesic habitats, (*S. impressipennis, P. ardea* and *G. nitens*), are active during less desiccating periods, (*S. zambesianus, A. convexus* and *C. tricornutus),* have a behavioural ecology that exposes them minimally to dry conditions, (*P. ardea* and *C. tricornutus),* and/or they rely more on decreased rates of water loss, (*S. impressipennis* and *A. convexus*).

The adjusted rate of mass loss analysis showed a much larger group of species in the low rank group (i.e. species with comparably low rates of mass loss) compared to the analysis of seventeen species. The species with high maximum mass loss tolerances were included in the low rank group of rate of mass loss together with the nocturnal telecoprid *A. convexus*. The high rank group consists of species that either occupy mesic habitats, (*P. ardea* and *G. nitens),* are active during less desiccating periods, (*O. caffer, C. tricornutus* and *S. zambesianus),* and/or have a behavioural ecology that exposes them minimally to desiccating conditions, *(O. caffer, C. tricornutus, P. adrea* and *L. militaris).*

In the analysis of the adjusted survival times the most important ecological factor influencing desiccation resistance appears to be ecological strategy and time of activity. the

most desiccation resistant species were diurnal ball rollers. Only *C. amyntor* is nocturnal, but it is a small species active in dry areas. The species in the low rank group occur in mesic habitats, (*P. ardea* and *G. nitens),* are active during less desiccating periods, (*O. caffer, C. tricornutus* and *S. zambesianus),* and/or have a behavioural ecology that exposes them minimally to desiccating conditions, *(O. caffer, C. tricornutus* and *P. adrea*). *Pachylomerus femoralis* and *K. subaeneus* rely on their large sizes to survive dry conditions, as they resort in the high rank group in the unadjusted analysis of survival time.

In this analysis of macropterous species, the species with the highest desiccation resistances in both the size and non-size related analyses are, with two exceptions, all diurnal. The exceptions, *C. amyntor* and *A. convexus*, however are resistant because of their strategies which expose them for long periods to their environment. Another important factor determining desiccation resistance is the strategies of the species, with telecoprids being more resistant than the other species. The exceptions in this case are again *C. amyntor,* and also *O. sapphirinus* and *L. militaris* which are, respectively, a small diurnally active paracoprid and a small diurnal endocoprid which both need high resistances to desiccation to survive the dry conditions of diurnal activity in the savanna. Therefore, the hypotheses of desiccation resistance, made in the Introduction on the grounds of ecological strategies, are strongly supported.

*The apterous species*

> ***It is quite reasonable to suppose that flightlessness will most likely evolve in circumstances where movement on a large scale is not required, i.e., in a spatially homogenous and temporally stable environment.***
>
> **Derek A. Roff, 1990.**

The unadjusted survival times of the three species did not differ statistically but *C. bacchus* did have the lowest survival time. This suggests that the two genera use different strategies to achieve similar results. The combination of the non-size related physiological adaptations, determined from adjusted analyses, indicated that the *Pachysoma spp.* are physiologically more desiccation resistant than *C. bacchus*. *Circellium bacchus*' relatively

large body size, therefore, improves its resistance to desiccation. Nevertheless, these three species remain some of the most desiccation resistant dung beetles. This appears to be a direct consequence of their aptery.

Aptery is a common characteristic of beetle species living in arid environments. The primary benefit of this structural adaptation is that it greatly reduces transpiratory and respiratory water loss (Slobodchikoff & Wismann 1981, Scholtz & Caveney 1988, Zachariassen 1991). The fused elytra usually become more curved and form an enlarged chamber enclosing the dorsal part of the abdomen. The abdominal spiracles also open inside this chamber. Relative humidity inside this chamber is very high because of transpiration from the permeable tergal surface and the water vapour produced by respiratory activity. This produces an enclosed boundary layer reducing both transpiratory and respiratory water loss.

A second benefit of the sub-elytral chamber of apterous beetles is that the boundary layer it creates, isolates the beetle from excessive radiative heat during daily foraging periods (Slobodchikoff & Wismann 1981). This facilitates thermoregulation and keeps the body temperature low, reducing the rate of transcuticular water loss.

Aptery evolves in environments where conditions are stable although they may be adverse (Roff 1990). In the Namib desert, and in the Addo Elephant National Park region, dung is relatively abundant and always available. The persistence of these resources in these adverse habitats allowed the evolution of aptery in these beetles which migrate constantly over short distances to new sources of dung. Since energy is not spent on maintaining flight activity, the *Pachysoma spp.* could switch to lower quality but highly abundant dung deposits. The added benefit of aptery for desiccation resistance has further precluded the necessity for high quality, moist food resources. In contrast, a flying scarab like *S. rubripennis* has to sustain flight and a large array of physiological adaptations to resist desiccation. Therefore, it specialises on high quality resources like fresh dung and carrion, which also have high water contents.

Chown *et al.* (in press) suggested that *C. bacchus'* ancestors probably evolved aptery in coastal forests, which are also highly stable but not particularly adverse habitats. The contribution of aptery to desiccation resistance allowed *C. bacchus* to migrate into more arid savanna areas of southern Africa, where it was once widespread. It was closely associated with the black rhinoceros, but extensive poaching greatly reduced the numbers and distribution of the black rhinoceros. Chown *et al.* (in press) argued that this caused range contraction in *C. bacchus* because the stable resources of rhino dung, deposited in middens,

were absent. Therefore as an ectotherm (Nicolson 1987), *C. bacchus* could no longer compete with the more aggressive large, endothermic telecoprids occurring in the same localities (Heinrich & Bartholomew 1979). Because of stable quantities of elephant dung, and the benefits of aptery to desiccation resistance, *C. bacchus* was able to survive in the xeric Addo Elephant National park (Chown *et al.* in press).

## *THE EFFECT OF TEMPERATURE ON DESICCATION RESISTANCE*

*Multiple comparisons of desiccation resistance at four temperatures.*

Animal activity is determined to a large extent by temperature which sets critical upper and lower limits. If the animals transgress these ecological or behavioural temperature tolerance limits the effects are often lethal (Mitchell *et al.* 1993). *Circellium bacchus* becomes active at ambient temperatures of 13 - 15°C (Coles 1994). Foraging activities of *C. bacchus,* such as walking and ball rolling occur at about 22 - 28°C. Being strict endotherms their $T_{th}$ never exceeded 1°C above $T_a$ (Nicolson 1987, Chown *et al.* in press). When the environmental temperatures rise to about 33°C, activity declines sharply, but is resumed later in the afternoon when temperatures drop, giving rise to a biphasic activity pattern. At high temperatures *C. bacchus* shelters either in dung or in nearby vegetation, and during the low temperatures overnight they shelter in burrows or in vegetation (Coles 1994, Chown *et al.* in press).

The relationships of $T_{th}$ to $T_a$ of *P. femoralis*, during feeding and preflight walking activity, are similar to that of the ectothermic *C. bacchus*. Activity in this species is initiated at 22°C, and at 25°C, after initial walking activity, they elevate their $T_{th}$'s to 40°C which they maintain during and shortly after flight. Their temperature excesses during these activities preceding flight, during flight, and during activities after flight vary between 10 and 17°C. By the time $T_a$ reaches 29°C most beetles have already allocated a dung source and are in the process of constructing or rolling dung balls or burrowing. The beetles which have not found a dung source, or which were unable to allocate dung, cease activity until the following day.

During a field excursion to Hohenfels in the southern Namib desert it was found that *P. gariepinus* becomes active in the mornings from about 08h00 when the $T_a$ at 2cm above the dune surface is 19°C and the dune surface is at 23°C. During activity *P. gariepinus* has

temperature excesses of 5 to 10°C above the 2cm $T_a$. This is probably brought about by solar radiation and conduction from the dune surface. The foraging activity of the beetles continues until $T_a$ and $T_{surface}$ reached 34°C and 45°C, respectively. When these temperatures drop in the afternoon, activity is resumed for a short period, giving rise to a biphasic activity pattern. However, during cooler and overcast days there is no break in activity. Critical minimum and maximum temperatures for *P. gariepinus* are 15.68±1.92°C (n = 10) and 48.51±1.07°C (n = 10) respectively. The preferred temperature is 23.82±3.93°C (n = 60) (Scholtz, Chown and Klok, unpublished data and personal observations). During the same periods the small *S. rubripennis* was observed to become active early in the morning when air temperatures were about 22.5°C. Their body temperatures were to a large extent regulated behaviourally by basking and movement into shade. As temperature reached 30°C activity ceased and the beetles buried into the dune. Activity was also prolonged during cooler overcast days.

This information on the thermal biology of the four species indicates that they would not be active at 15°C, but remain in burrows where temperature is constant and humidity is equivalent to 100% (Campbell 1977). Therefore, desiccation would not pose a problem, despite their high tolerance to it at this temperature. During the 15°C trial, starvation seemed to be more of a problem, because water losses were not correlated with the sizes of the four species as was found in the other temperature trials. However, at 20 and 27°C, temperatures at which these species would be active, the benefit of aptery is clearly illustrated. Although there was no difference in the survival times of the four species, the decreased rates of water loss of the two apterous, species, specifically that of *P. gariepinus*, were clearly illustrated. The increased tolerance to water loss in *S. rubripennis,* and the large body size of *P. femoralis* were the two factors that contributed to the similar survival times of the macropterous species compared to that of the apterous species at 20°C. In the unadjusted analysis at 27°C, however, the two desert species had the lowest rates of water loss, whereas *C. bacchus* and *P. femoralis* had the highest tolerance to water loss, and in the adjusted analyses *P. gariepinus* had the lowest rate of water loss, and *C. bacchus* was intermediate although it had the highest tolerance to water loss. These factors show that the two apterous species are the most desiccation resistant species at 27°C, as they had they longest survival times. Low rates of water loss observed in the apterous species, also illustrated in the previous, seventeen species trial, is the more important factor in resisting desiccation (Edney 1977), but the increased tolerance to water loss of *C. bacchus* at 27°C and of *S. rubripennis* at 20°C are notable, and influenced their survival.

Observations on the thermal biology of the four species indicated that $T_a$'s of 35°C are usually avoided, although their body temperatures may rise to these levels. However, the apterous species were still more resistant to desiccation at this temperature. This is brought about by *P. gariepinus'* very low rate of water loss, and *C. bacchus'* intermediate rate of water loss combined with a high tolerance to water loss. *Scarabaeus rubripennis,* despite its high tolerance of water loss, had a high non size-related rate of water loss which made it very sensitive to desiccation at this temperature. *Pachylomerus femoralis* was less sensitive to desiccation at 35°C because it has to maintain a $T_{th}$ of about 40°C for flight. However, this experiment kept the beetles fairly inactive and they thus reacted to temperature in a way similar to ectothermic species (Chown *et al.* in press).

Finally, the lack of a significant relationship between body mass and survival time in this trial, contrary to the former seventeen species trial, may have been a consequence of the species chosen.

*Activation energies*

High activation energies coincide with low frequencies of collisions between water molecules. This means more water occurs in the gaseous phase and its escape from the animal into the environment will increase as temperature increases (Yoder and Denlinger 1991). The three larger species have very similar activation energies, whereas *S. rubripennis'* activation energy is almost twice as large. This means that *S. rubripennis*, is very sensitive to higher temperatures, and to compensate for its size, it has developed an increased tolerance to water loss to counteract the high rates of water loss it experiences under high temperatures. *Circellium bacchus* and *P. gariepinus* are both apterous which restricts their rates of water loss adequately. The volume of air in the sub-elytral cavity formed by their fused elytra might also function as a buffer to shield the body from excessive temperature rises, as was observed in Tenebrionidae beetles by Slobodchikof and Wismann (1981). *Pachylomerus femoralis* is a fast moving telecoprid and it occurs in mesic savanna areas, it will therefore locate high quality resources rapidly and retreat into a burrow where desiccation will be further reduced. Furthermore, being an endotherm (Chown *et al.* in press), *P. femoralis* operates at body temperatures higher than 35°C, which means that a low sensitivity to temperature is necessary to avoid desiccation although it is active for brief periods.

## WATER BALANCE AND OSMOREGULATION

*Water balance*

Only *P. gariepinus* lost an amount of water similar to that found in several Namib tenebrionid species studied by various authors (as cited in Naidu and Hattingh (1988)). These species lost 5.6 to 12.9% of their body water in five to six days and *P. gariepinus* lost 11.78% after six days. The other three species studied here lost twice as much water as *P. gariepinus*. *Circellium bacchus* lost 20.03%, *P. femoralis* lost 23.8% and *S. rubripennis* lost 21.78% of their body water. After a ten day period of dehydration the tenebrionid, *Physadesmia globosa* recovered the 12% of water it lost within an hour, after which its body mass remained stable (Naidu and Hattingh 1988). *Circellium bacchus* and *P. femoralis* regained water at much slower rates. This may be due to the high availability of moist dung in their habitats which would allow them to rehydrate regularly. The results also suggest that they do not normally dehydrate to the levels shown in the laboratory. Therefore, the capability to rapidly rehydrate may not be routinely required. The two desert species replaced lost water much more rapidly, at rates similar to the desert tenebrionid, *Physadesmia globosa* (Naidu and Hattingh 1988). However, *P. gariepinus* ingested less water than the smaller *S. rubripennis*. Extensive rehydration may not be necessary for this species, it can burrow directly into the moist layer of sand beneath the dune surface when necessary. *Scarabaeus rubripennis* on the other hand has a highly desiccating, flying mode of foraging in xeric habitats, and it is also very sensitive to higher temperatures. Therefore it has to be very effective in recovering lost water rapidly, and in large quantities.

*Lipid metabolism*

The oxidation of stored nutrients, particularly lipids, is an obligatory mechanism of restoring lost water when access to environmental water is minimal (Edney 1977). During flight, body temperature and metabolism are elevated leading to increased water loss rates which are aggravated by the absence of water during the periods of flight. Therefore most flying insects, such as *Locusta migratoria* (Orthoptera, Acrididae) and *Aphis fabae* (Hemiptera, Aphididae), make extensive use of metabolic water to maintain water balance (Weis-Fogh 1967, Edney 1977). In this study, the two flying dung beetles also relied to a large extent on lipid metabolism to replace lost water. They lose water at high rates because of flight, but their resources, however, are of a very high quality in terms of utilisable

energy. *Circellium bacchus* could also metabolise lipids, although not to the same extent as the macropterous species. It also has high quality resources to provide it with free water and nutrients, but, being apterous, it loses water at a lower rate than the previous two species and, therefore, it is not necessary for *C. bacchus* to have a similarly effective means of producing metabolic water.

*Pachysoma gariepinus* gave similar results to *P. globosa* (Naidu and Hattingh 1988) Both species did not produce water by metabolising lipids. Although it feeds every day, and can thus maintain large lipid reserves, desiccation in this species is reduced to such a low rate that, during its activity period, its body water levels would not drop to levels so low that metabolic water production is necessitated. *Pachysoma gariepinus* also has a very large pool of water stored in the haemolymph as relatively large volumes of haemolymph were still present, even after an extended period of desiccation. In addition, environmental water is readily available 10 to 25cm beneath the dune surface in moist sand.

The discrepancies between the two *P. femoralis* experiments can possibly be explained by rainfall differences in the seasons. The first group was collected during the 1992 summer rainfall season, which was not very favourable. Only about 200 beetles were collected during one morning. The second group was collected during the much more favourable summer rainfall season of 1993. During this period more than 500 beetles were collected in less than 30 minutes. Thus, it seems that the beetles from the first experiment were already desiccated at the time they were collected, and their lipid reserves were utilised extensively in order to keep body water levels constant. The beetles from the second season did not experience such harsh conditions, and, therefore, did not use their lipid reserves to the extent observed in beetles from the previous season.

*Haemolymph osmoregulation*

*Pachylomerus femoralis* gave very similar results in comparison with the beetle species examined by Riddle (1986). Riddle examined a chrysomelid, *Chrysochus auratus*, a cerambycid, *Tertraopes tetrophthalmus*, and a tenebrionid, *Tenebrio molitor*, and got slopes of -190.30, -145.92 and -164.58 respectively. In their natural environments these beetles have access to high quality nutrients. Riddle also compared his data with that of Fielding and Nicolson (1980). Fielding and Nicolson found that the cetoniid, *Trichostetha fascicularis*, a nectar feeder, had a very weak haemolymph osmoregulatory ability, and the desert tenebrionid, *Onymacris plana*, a detritivore, had an excellent haemolymph osmoregulatory ability. *Circellium bacchus*' and *P. gariepinus*' superior osmoregulatory abilities can be

explained by the fact that, during extended periods of foraging in the field, they have to maintain water balance between haemolymph and tissues at very high levels. Free water is not available during these periods and only becomes available at the end of foraging when *C. bacchus* locates a dung source and when *P. gariepinus* burrows into moist sand layer in the dunes.

These abilities seem to be in contrast with the apterous species' abilities to replenish lost water by metabolising lipids. Lipid metabolism taps a beetles' energy reserves more severely than regulating haemolymph osmolality during desiccation. Thus, if dung beetles are living in habitats where the energy gain from available resources are liable to be rapid, regular, and relatively high, (*P. femoralis*), they will rather regulate internal water levels by metabolising lipids.

> *From a functional standpoint, then, the adaptations of Scarabaeinae can be viewed as responses to the problems posed by the exigencies of life in open habitats and to those inherent to the use of excrement.*
>
> Gonzalo Halffter and W.D. Edmonds, 1982.

# CONCLUDING REMARKS

*My head is now spinning, and it is high time to bring this topic to a close.*

Richard Dawkins, The Selfish Gene, 1989.

Firstly, the conclusions reached in this study confirmed the *a priori* predictions made in the Introduction. The physiology of the various species is intimately associated with their morphology and behaviour in particular habitats.

The apterous species were far more resistant to desiccation than the winged species, confirming previous speculations (Cloudsley Thompson 1964, Slobodchikoff and Wismann 1981, Scholtz and Caveney 1988, Roff 1990, Zachariassen 1991) that this morphological modification is conducive to desiccation resistance. Large body size of many of the species also facilitated desiccation resistance by having a larger pool of water available and by a reduced surface area to volume ratio reducing the route of trans-cuticular water loss (Edney 1977, Schmidt-Nielsen 1984).

The Scarabaeinae are a taxonomic group with a very uniform behavioural ecology among its species. Close study has, however, revealed more specific ecological/behavioural adaptations of the scarabs (Bornemissza 1969, Davis 1977, Doube 1991). It is among these ecological/behavioural adaptations of the scarab species, that the interactions between behaviour and physiology within particular habitats are manifested. Diurnal dung beetles were more desiccation resistant because is is generally drier during the day than during nocturnal or crepuscular periods. Among the species active at various times of the day the telecoprids are the most desiccation resistant. The telecoprid behaviour exposes beetles to the "external" environment from the start of foraging, during dung allocation and removal from the source until the burrow is constructed. Rate of water loss, therefore, needs to be minimised and tolerances to reduced body water content enhanced. The para- and endocoprid behaviours only expose beetles to dry conditions during the foraging period which mostly occurs at night, when temperatures are lower and humidities are higher than during the day. Therefore, risk of desiccation is minimal.

Secondly, this study also forms a basis for further research in scarab ecology. One specific area of research is the effect of habitat change on beetle assemblages. Important

factors of habitat change, concerning dung beetles, are the removal of closely associated species, habitat destruction and the changes in global climate. In the case of *C. bacchus*, the effects of the removal of a key species, the black rhino, has already been reported (Coles 1994, Chown *et al.* in press). The whole genus *Pachysoma*, comprising fourteen species, is threatened by open cast mining on the south-western coast of Africa where they occur. No ecological impact study of the effects of mining in these habitats on the various *Pachysoma* species has yet been done. The third factor, however, concerns all Scarabaeinae species, and also every other species on the planet. Current studies on the effects of global climatic changes illustrated that species with very definite ecophysiological adaptations will be severely affected by the continuing changes in atmospheric temperatures, and the consequences thereof, particularly on rainfall patterns (*American Zoologist*. vol. 32, 1992, Gates 1993, Holt 1994). Ranges of physiological tolerances, as illustrated in this study, will provide researchers with valuable information on what to expect in the future in terms of assemblage compositions in more severely affected habitats.

# ABSTRACT

The desiccation resistance of seventeen species of southern African dung-feeding Scarabaeinae is investigated. The species occur in a wide range of habitats including the Namib desert, savanna, grassland and valley bushfeld. It was found that the three apterous species, two from the Namib desert and one from Addo, have the highest resistance to desiccation. The principal mechanism promoting desiccation resistance is a reduced rate of water loss. Other factors that influence desiccation resistance are large body size, diel activity and the behavioural ecology of the species; telecoprids are more resistant to desiccation than the para- and endocoprids. The analyses were repeated excluding the apterous species. This indicated that habitat has an important influence on desiccation resistance. Of the macropterous species, two small species, one from the Namib desert and the other from the Orange Free State grassland, are the most resistant to desiccation. The principal mechanism promoting desiccation resistance is an increased tolerance to low body water levels. The resistances of the remaining species are influenced by their size, activity periods and ecological strategies.

Experiments to investigate osmoregulatory ability and the influence of temperature on water balance were done on four selected species - an apterous and a macropterous species from the desert biome and a similar pair from the savanna biome. Based on the thermal biology of the species it was found that their resistances to desiccation are optimal at the temperatures at which they are active in the field, and that the apterous species from both biomes are the most resistant to desiccation. The savanna species recover water faster than the desert species, but the desert species have a stable source of water in the moist layer beneath the dune surface. The macropterous species are able to produce water by metabolising lipids, but they have very poor haemolymph osmoregulatory capabilities. The apterous species in contrast are less able to produce water by metabolising lipids but they have excellent haemolymph osmoregulatory capabilities. These adaptations are closely related to the pedestrian and flying modes of foraging employed by the beetles.

# SAMEVATTING

Die droogte weerstand van sewentien miskruier spesies (Scarabaeinae) van Suidelike Afrika is ondersoek. Die spesies kom in 'n wye reeks habitatte voor wat die Namib woestyn, savanne, grasveld en die vallei bosveld insluit. Dis bevind dat die drie ongevleuelde spesies, twee van die Namib en een van Addo, die grootste weerstand teen droogte toestande het. Die hoof meganisme wat die weerstand teen droogte toestande beïnvloed is 'n verlaagde tempo van water verlies. Ander faktore wat droogte weerstand beïnvloed is liggaamsgrootte, diel aktiwiteit en die gedrags-ekologie van die spesies; telekoprides het 'n groter droogte weerstand as die para- en endokoprides. Die analises is herhaal sonder die ongevleuelde spesies. Dit het daarop gedui dat die habitat 'n belangrike invloed het op droogte weerstand. Van die gevleuelde spesies het twee klein spesies, een van die Namib en een van die Vrystaat grasveld die grootste weerstand teen droogte. Die hoof meganisme wat droogte weerstand beïnvloed is 'n verhoogde toleransie vir 'n lae liggaamswater inhoud. Die weerstande van die oorblywende spesies word beïnvloed deur hul grootte, aktiwiteits periodes en ekologiese strategieë.

Eksperimente is gedoen om die osmoregulatoriese vermoëns en die invloed van temperatuur op die water balans van vier geselekteerde spesies te ondersoek. 'n Ongevleuelde en 'n gevleuelde spesie van die woestyn bioom en 'n soorgelyke paar van die savanne bioom is gekies. Bevindinge gebaseer op die termale biologie van die spesies dui daarop dat droogte weerstand optimaal is by die temperature waarby die spesies aktief is in die veld. Die ongevleuelde spesies van beide biome het die grootste droogte weerstand. Die savanne spesies herwin water vinniger as die woestyn spesies, maar die woestyn spesies het 'n stabiele bron van water in die vogtige laag onder die duin oppervlaktes. Die gevleuelde spesies was daartoe instaat om water te produseer deur lipiede te metaboliseer, maar hulle het 'n baie swak hemolimf osmoregulatoriese vermoë. Die ongevleuelde spesies in teenstelling produseer min water deur lipied metabolisme maar het uitstekende hemolimf osmoregulatoriese vermoëns. Hierdie aanpassings skakel nou ineen met die voetganger of vlieënde voedsel opsporings strategieë wat deur die spesies aangewend word.

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Charles Darwin in a letter to William Darwin Fox on writing The Origin of Species, 27 March 1855.

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