The seasonality, diversity and ecology of cavernicolous guano dependent arthropod ecosystems in southern Australia.

Timothy A. Moulds

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy.

Environmental Biology
School of Earth and Environmental Sciences
The University of Adelaide, Adelaide, Australia

January 2006

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Timothy Moulds

Table of Contents

Index of Figures

Index of Tables

Acknowledgements

This work was only possible due to the financial support of the Australian Research Council through an Industry Linkage Grant (LP0229165); Department for Environment and Heritage, South Australia; the University of Adelaide; The Nature Conservation Society of South Australia; The Wildlife Conservation Fund of South Australia; and the Linnean Society of New South Wales.

Firstly I would like to thank my supervisors Andy Austin and John Jennings who provided ongoing support, editorial comments, advice and good humour. Their advice and comments have proved invaluable especially in the final stages of this project. Thankyou for helping me produce the best work I am capable of.

The staff of Naracoorte caves provided invaluable assistance throughout the project, especially Steve Bourne. Many thanks to all the field assistants who helped collected samples and provide humour in difficult conditions.

The following people are thanked for arthropod identifications: Mike Gray for so many identifications of so many spiders and access to his extensive speleological reprint collection; Dan Bickel for fly identification, encouragement to look beyond my own four walls for a project and finding the right scientific path to follow; Shane McEvey for encouraging me to find the right project; Mark Harvey for his numerous prompt pseudoscorpion identifications and general assistance; Alan Anderson for ant identications and discussions about ants in caves and for being a nice guy; Penny Greenslade for identifying collembola from Starlight and Bat Caves over several years; Owen Seeman for his friendly nature and selfless identication of numerous mites from guano caves all over southern Australia; Kerrie Davies kindly identified nematodes and search diligently for new species from guano samples provided. Michael Wall is thanked for reduviid identifications. David McAlpine is thanked for identifying flies and pointing out my taxonomic inadequacies ;o) . Many thanks to Gerry Cassis for imparting his taxonomic skills and giving me the initial opportunity to explore entomology as a career.

The small but highly dedicated Australian scientific caving community including Stefan Eberhard, Susan White, Nick White, Andy Spate, Elery Hamilton-Smith, Mark Harvey, Bill Humphreys and Arthur Clarke are all thanked for their assistance, encouragement, and field samples. I couldn’t have done it without you all.

Terry Reardon has gone above and beyond the help expected of anyone on this project. A person to continually chew the fat with, talk about caves, bats and their habits, discuss the vaugeries of life, drive expertly through the field, drink a coldie and chase snakes. What a (Bat)Man!

The lab group of the Insect Ecology and Evolution group have provided continued support through all aspects of this project, predominately through the numerous trips to the bar on Friday nights, but also Thursdays, and sometimes Wednesdays and the occasional Tuesday… Nick Murphy has corrupted my liver, helped in the molecular lab, and the subsequent analysis of data (possibly in that order). Kate Muirhead was always fun in the lab and shared the shear desperation for alcohol on a Friday afternoon and at conferences. Michelle Guzik was always a friendly face, snappy dresser and happy to provide advice and listening to my crap. Michelle Guzik, Nick Murphy, Marta Kasper and Sylvia Clarke are thanked for editorial comments. A big thankyou to all the labgroup both past and present, including Dannielle Carey, Sylvia Clarke, Travis Gotch, Steve Griffiths, Michelle Guzik, Elise Head, Mohammed Iqbal, Marta Kasper, Brenda Kranz, Kate Muirhead, Cate Paull, Claire Stephens, and Nick Stevens.

Chris Grant kindly accompanied my fieldwork in Starlight Cave, Warrnambool, and provided cave location information. Chris' immense hospitatiliy throughout this project made life much easier with great meals, conversation and plenty of home brew. Long live the purple van. Also a big thanks to Margy for her very welcome hot meals after a cold winters night caving.

All the landholders who allowed access to caves on their properties and permission to collect insects (despite thinking me a little peculiar). This project would not have been possible without access to the Nepabunna Aboriginal lands in the Flinders Ranges.

I would like to thank the Cave Exploration Group, South Australia for cave locality data, field assistance and knowledge of local bat populations. I would specifically like to thank Eddie Rubessa for his enthusiastic and generous knowledge of the caves of the Flinders Ranges. Graham Pilkington is thanked for assistance in finding caves and insects on the Nullarbor Plain. Marie Choi is especially thanked for her craziness and ability to encourage others to follow me into piles of bat guano. Wolfgang Glowacki is thanked for his field assistance, photos and pub attendance.

Adam Branford has been a continuing friend since our first meeting and not only arranged fieldtrips to caves of the south-east, but also immense hospitality and an unending supply of 'Jackass' DVD's and dirty humour. In the same capacity Bridget Larkin has provided an excellent cynical commentary on everything I do while always being more than ready to help out, despite thinking I am weird. Her art continues to inspire me to go caving and seek out the intrinsic beauty of the subterranean world.

Matilda Thomas has helped throughout this project, and prior in her enthusiasm for caving and the outdoors, helping with fieldwork, moral support and advice.

Finally this project would never have been as successful as it has been without the continual support of my fiancé Alice Shields, who has encouraged me throughout, helped in exstensive fieldwork, forgon holidays to tropical locals to be dragged into caves in the middle of dairy paddocks, and generally put up with the peculiarities and eccentricities of the wider caving fraternity. Her support has been unwavering throughout the extended and trying times of writing up which have caused much stress and greying of hair – for this I thankyou with all my heart.

Abstract

Guano deposits in caves form a rich food resource supporting diverse arthropod communities. Guano piles consist of distinct micro-habitats, fresh, moist, highly basic guano and older, dry, slightly acidic guano. Micro-habitat variation is strongly controlled by seasonal guano deposition that, in turn, effects the structure of arthropod communities.

The maternity chamber of Bat Cave, Naracoorte, South Australia, contains extensive guano deposits supporting 38 species from three classes and 12 orders. This community was studied to determine spatial and temporal variation of arthropod communities, and biogeographic relationships between different regions in Australia. Species richness forms a positive linear relationship with pH, *in situ* moisture content and guano deposition. Many species show strong associations with fresh guano and hence are strongly seasonal, although some species are present throughout the year. Arthropod community structure in winter was found to be more closely related to prior summer arthropod structure than to subsequent seasons.

Starlight Cave near Warrnambool, western Victoria, the only other maternity site for *Miniopterus schreibersii bassanii*, contained 43 species from 39 families and 14 orders. Seven species are common to both caves. The community structure of Starlight Cave was found to be more homogeneous than Bat Cave with samples clustering by season rather than sample year as was the case at Bat Cave. Different cave morphology was found to significantly alter the micro-habitat conditions and, hence, community structure in Starlight Cave compared with Bat Cave.

Migration of guano associated arthropods at local, regional and continental scales was assessed using mtDNA and allozyme electrophoresis the pseudoscorpion genus *Protochelifer* as a model organism. Phylogenetic tree reconstruction revealed a wide geographic distribution of cavernicolous species across southern Australia. Cave colonisation is believed to have occurred only once, followed by dispersal to the Nullarbor Plain and other caves in south-eastern Australia. Dispersal was possibly phoretic on cave bats or occurred prior to aridification of surface environments that currently restricts migration.

The distribution of guano-associated arthropods from arid, semi-arid and monsoonal karst areas in Australia are compared with temperate south-eastern

Australia. Different climatic areas show large biogeographical differences in community structure, although similar families (Urodinychidae, Reduviidae, Anobiidae, Carabidae and Tineidae) are present in many Australian guano communities. Several potential mechanisms of dispersal are discussed including phoresy, colonisation from soil, terrestrial migration and interstitial cavities. Endemism to specific caves cannot be definitely assigned to any species, although 13 species show restricted distribution.

Chapter 1: Cave ecology and guano ecosystems

1.1 Introduction to cave ecology

Caves form a very stable and generally homogenous environment in which to conduct various ecological and evolutionary experiments, such as on competition between species, resource partitioning, and the processes of speciation (Poulson and White 1969). The total absence of light severely alters or completely removes many circadian cycles affecting ecosystem function (Lamprecht and Weber 1992, Langecker 2000). Temperatures are usually constant, varying only slightly between seasons. Humidity is commonly high, providing an ideal habitat for many invertebrate species susceptible to desiccation (Norris 1996). The lack of photosynthetic plants changes the trophic structure of cave ecosystems, with energy sources usually being transported from the surface (Poulson and Lavoie 2000, Poulson 2005). Caves are defined as human-sized subterranean voids, although cave adapted animals are known to occur in the smaller spaces between large voids called micro- and mesocaverns (Howarth 2003).

Caves are divided into several distinct biological zones to aid interpretation (Figure 1.1). These correspond to the amount of available light and varying environmental conditions (Humphreys 2000a). The *Entrance Zone* is the area directly around the cave entrance; it is generally well lit, often supports photosynthetic plants, and undergoes daily temperature and humidity fluctuations. The *Twilight Zone* is just beyond the entrance zone and is often dominated by lichen and algae that require low light conditions. The temperature and humidity are still variable but fluctuations are dampened compared with epigean variation.

Deeper into a cave, light is reduced to zero and the *Dark Zone* is entered, which is subdivided into three zones, the transition, deep cave and stale air zones. The *Transition Zone* is perpetually dark, but still fluctuates in temperature and humidity determined by epigean conditions. The *Deep Cave Zone* is almost constant in temperature and humidity conditions. The *Stale Air Zone* is only found in certain caves and is an area of the deep zone that is constricted, and commonly contains elevated levels of CO_2 and lower levels of O_2 (Howarth and Stone 1990).

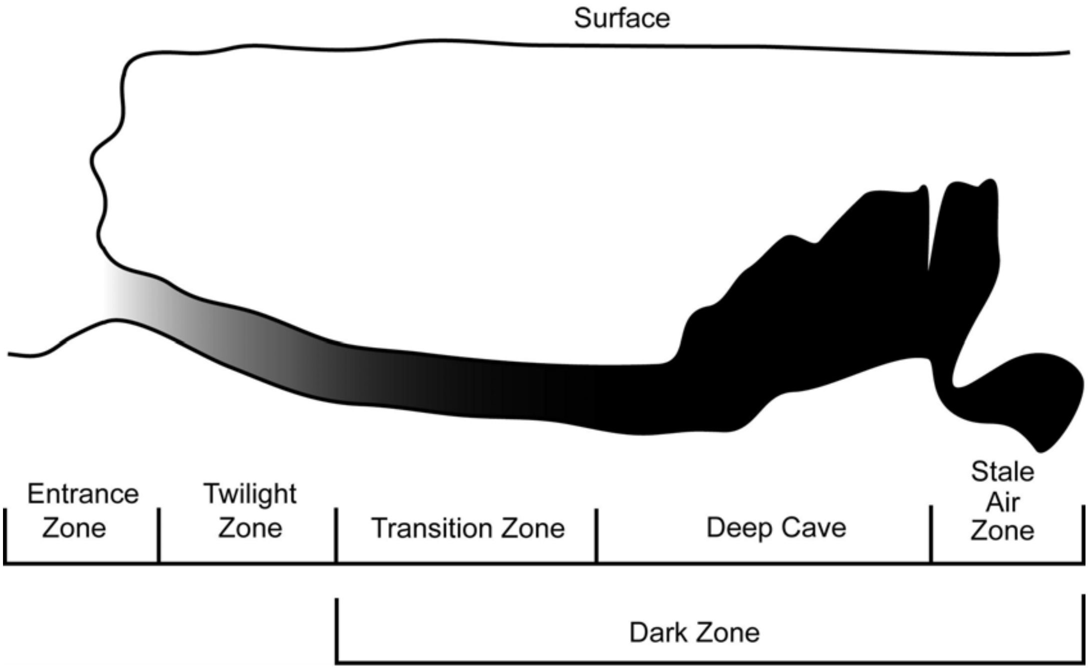

Figure 1.1. The environmental zones of a cave shown in cross section.

1.1.1 Classifications of cave dependence

Cave invertebrates are generally classified according to their degree of cave dependence using the Schiner - Racovitza system (Schiner 1854, Racovitza 1907), despite numerous other systems and variations being proposed and adopted by various authors (see references in Boutin 2004).

The Schiner - Racovitza system classifies organisms according to their ecological association with subterranean environments, and relies upon detailed ecological knowledge of animals that is commonly lacking for most species. In order to circumvent this lack of knowledge the concept of troglomorphy (Christiansen 1962), specific morphological adaptations to the subterranean environment, is used to define obligate subterranean species. The term troglomorphy, initially confined to morphology has since been used to describe both morphological or behavioural adaptations (Howarth 1973). This combination provides a practical system, easily applied in the field and with minimum of detailed ecological study required.

Troglobites are obligate animals that possess specific adaptations (troglomorphies) such as loss or reduction of pigmentation and/or eyes, flightlessness, elongate appendages and specific sensory adaptations (Barr 1968, Poulson and White 1969). These species rely solely on the cave environment for food and reproduction. They are generally restricted to the deep cave zone where conditions are the most stable and are rarely found closer to entrances in the twilight zone. *Troglophiles* are animals that can complete their entire lifecycle within a cave but possess no specific adaptations to the cave environment. These species are capable of living outside caves in suitably dark and moist epigean habitats. Troglophiles are further divided by Hamilton-Smith (1971) into *1st order Troglophiles* (occur only in subterranean habitats) and *2nd order Troglophiles* (occur in both subterranean and suitable epigean habitats). *Trogloxenes* are animals that regularly use caves for part of their lifecycle or for shelter, but must leave the cave to feed. *Accidentals* are animals that do not use caves on a regular basis and cannot survive in hypogean environments.

Aquatic hypogean animals are classified using a similar system to terrestrial hypogean animals except the prefix ‘stygo’ is used instead of ‘troglo’ (Humphreys 2000a).

1.1.2 The trophic basis of cave ecosystems

Cavernicolous populations are dependant for their survival upon energy inputs into cave systems. These inputs can vary widely, with availability of food usually being the primary limiting factor (Peck 1976). Many cave ecosystems revolve around periodic flooding (Hawes 1939, Humphreys 1991, Culver *et al.* 1995) that carries organic material and accidental epigean animals into cave systems. Tree roots penetrating the roofs and walls are another energy source found commonly in tropical caves and lava tubes (Hoch 1988, Hoch and Howarth 1999). Guano from bats, birds and Orthoptera is an important energy source (Park and Barr 1961, Harris 1970, Poulson 1972, Snow 1975, Martin 1977, Decu 1986, Blyth *et al.* 2002) with large, varied and unique ecosystems existing around such deposits. Dead animals can be a source of food for scavengers near cave entrances (Richards 1971). Accidentals wandering in from cave entrances also provide a food source, although this is generally periodic in nature and inconsistent in quantity.

1.2 The evolution of troglobites

The origin of troglobites has fascinated biologists from their first discovery in the mid 16th century in European caves. Early research on obligate cave dwelling animals was centred in Europe and North America. The geologically recent and extensive glaciation of these areas led biologists to believe that troglobites were climatic refugees, only occurring in previously glaciated regions where their surface relatives had become extinct. Initial expeditions to tropical regions during the early 20th century failed to identify troglobites for several reasons, including limited collecting and failure to recognise troglobitic species, further supporting the climatic refugia model (Howarth 2003). Modern investigations into the evolution of troglobites has revealed a much more complex origin with several recent theories being postulated for different regions.

Natural selection - Natural selection has been used to explain the evolution of troglobites and troglomorphies since the theory was first proposed by Charles Darwin in the 19th century. Reduction of characters, especially eyes, has been central in the evolutionary debate in biospeleology. This is primarily due to energy efficiency in an energy poor environment, such as caves lacking primary producers. Energy demanding structures such as eyes, both in their formation and use, are considered to place animals at an energy disadvantage to those with reduced or completely absent eyes (e.g. Kane and Richardson 2005). Compensatory changes have been recorded in other sensory structures such as increased antennal length and an increase in the olfactory brain lobe, suggesting areas of the brain previously used for sight have been adapted to provide troglobites with selective advantages (Culver *et al.* 1995). Energy efficiency is also used to explain behavioural and physiological changes in some species. Natural selection does not obviously explain the presence of troglobites in tropical caves where there is often large amounts of energy available throughout the year.

Neutral mutation theory - Neutral mutations are most likely to reduce complexity, or completely remove the expression of complex genes such as those responsible for eyes or pigmentation (Culver and Wilkens 2000). These mutations are stabilised in surface populations by the strong requirement for such structures but in hypogean species these mutations are likely to increase in frequency (Culver 1982). The rate of change by genetic drift and neutral mutation is considered by some (e.g. Barr 1968) to be too slow to account for the extreme physical changes observed in some troglobitic populations. This does not take into account that these attributes are polygenic (multiple genes for a single structure), and when this is considered neutral mutations can proceed at rates necessary to explain, for example, observed degrees of eye reduction (Culver and Wilkens 2000).

Adaptive shift hypothesis - This hypothesis was first proposed to explain the presence of troglobites in Hawaiian lava tubes with close epigean relatives (Howarth 1987). The widely accepted climatic refugia model predicts a lack of closely related surface relatives. The adaptive shift hypothesis requires the active colonisation of subterranean habitats by surface species that are common accidental visitors to the cave environment. In resource-rich caves, commonly occurring in the tropics, such accidentals may find sufficient food and other resources to enable them to make an adaptive shift and establish a self-sustaining population within the cave (Eberhard and Humphreys 2003). This hypothesis is well suited to explaining the troglobitic (Soulier-Perkins 2005) and stygobitic populations (Watts and Humphreys 1999, Watts and Humphreys 2000, Cooper *et al.* 2002) in northern Australia where closely related surface populations are present.

1.2.1 The evolution of guano dependant animals and ecosystems

For the most part cave environments are generally depauperate in food and consequently are sparsely populated by cavernicolous animals. However, caves containing guano deposits differ fundamentally because there is a virtually unlimited food supply, commonly resulting in large populations of guano dependant arthropods (guanobites, see section 1.4.3). Guanobites possess no specific behavioural or morphological adaptations, presumably because of the lack of selection pressure to minimise energy expenditure that dominates the evolution of troglobites. The colonisation and establishment of guano dependent communities in caves is poorly understood. Mechanisms for the dispersal of guano dependent arthropods are potentially numerous, but most are poorly investigated at best (see Section 5.5).

1.3 Cave ecology in Australia

While the majority of Australian caves and karst areas have been surveyed to some degree for hypogean biodiversity, detailed information is available for very few systems. This is especially true when considering purely ecological studies of cave fauna. The ecological approach to cave biology in Australia was Richards' (1971) study on the various invertebrate ecosystems of the Nullarbor Plain caves. This study identified four different ecosystems; the twilight and entrance zones, guano, dark zone and water systems. Richards also constructed a food web incorporating the 64 species of cave-associated arthropods collected.

The earliest publications concerning Australian biospeleology consist of taxonomic descriptions of isolated new cavernicolous species, commonly forming part of larger works. Higgins and Petterd (1883) was the first work on Australian cavernicolous fauna, describing the spider *Hickmania troglodytes* Higgins and Petterd (Austrochilidae) with notes on its behaviour. Rainbow (1904, 1905, 1907) was first to publish a series of papers concerned with troglobitic and troglophilic spider and collembolan species in Australia. Lea (1910) described the first troglobitic beetle species from Australia, *Idacarabus troglodytes* (Carabidae) and provided a foundation for future studies on the cavernicolous beetle fauna of Tasmania. These early researchers noted the importance of cave fauna for evolutionary studies but Australia was considered to be depauperate in troglobitic species as the continent experienced glaciation only during the Pleistocene (Eberhard and Humphreys 2003).

In recent decades this perception has been dramatically altered as communities of troglobites and other significant hypogean faunal communities have been discovered across the continent. The realisation that factors apart from glaciation, can lead to the establishment of hypogean communities provided stimulus for the biological exploration of tropical caves. The discovery of significant tropical troglobitic faunas (Howarth 1988, Hoch 1990, Howarth and Stone 1990, Hoch 1993, Hunt 1993, Humphreys 2000b) across northern Australia has negated the belief that troglobites only occur in temperate climates.

As well, the calcrete aquifers within the cratons of Western Australia contain some of the most diverse stygofaunal communities in the world (Watts and Humphreys 1999, Watts and Humphreys 2000, Humphreys 2005). These communities have been found in all aquifers from the Pilbara and Yilgarn cratons examined thus far, with almost every aquifer possessing a unique, although related, fauna. These communities are dominated by dytiscid diving beetles, but also contain crangonyctoid and niphargiid amphipods (Bradbury and Williams 1997, Bradbury 2000, Humphreys 2001, Humphreys 2005).

1.4 Review of the ecology of guano ecosystems and guanophilic invertebrates

Australian cave guano ecosystems are poorly known with very few communities studied in any detail (e.g. Richards 1971, Harris 1973, Bellati *et al.* 2003). Previous work concerned with the terrestrial cavernicolous fauna of Australia have mentioned species associated with guano, but have provided little information on the ecology and diversity of specialised guano species and communities. When present, guano from bats, birds and Orthoptera (crickets and grasshoppers) generally forms the major energy source (Park and Barr 1961, Poulson 1972, Martin 1977). Guano deposits are also extremely variable, unlike other cave habitats, and consist of numerous micro-habitats differentiated by fluctuating temperature, moisture and pH.

1.4.1 Sources and diversity of cave guano

Cave guano deposits from specific sources can each possess a unique assemblage of taxa (Horst 1972, Poulson 1972). Throughout the world's biogeographic provinces different taxa are responsible for being the most important guano producers.

The most widespread and common guano is that produced by bats and these deposits are generally the largest in volume. The spatial and temporal deposition of bat guano differs from tropical to temperate caves. Cave-dwelling bats in temperate regions show an annual cycle of occupancy over summer months when pups are born, before colonies disperse to cooler, wintering caves where they enter torpor. This annual cycle results in large amounts of guano deposited over summer months and then a cessation of guano input for at least half the year. In contrast, tropical caves generally show constant bat occupancy rather than an annual cycle, and less aggregation of individuals due to warmer ambient temperatures (Trajano 1996, Gnaspini and Trajano 2000). Gnaspini and Trajano (2000) note that many bat populations in tropical Brazil are, however, commonly nomadic, resulting in roaming colonies varying their location in an irregular and non-seasonal fashion. This results in non-continuous guano deposition in a single locality over several years. The diet of bats (either haematophagous, insectivorous, frugivorous, or nectarivorous) also influences the composition of guano piles and, hence, the associated guanophilic communities (Gnaspini 1992, Ferreira and Martins 1998, Ferreira and Martins 1999). Large populations of the common vampire bat (*Desmodus rotundus* Geoffroy) predominate in Brazilian karst near inhabited areas, due to large numbers of domestic livestock, resulting in haematophagous guano deposits. Guano from non-haematophagous bats is absent, or greatly reduced as vampire bats exclude other bat species, thus altering the species composition of the guanophilic communities present.

Birds are common guano producers in the northern parts of South America, the Caribbean and tropical caves of south-east Asia. Cave-dwelling birds nest in the dark zone, providing an important energy resource for many cavernicolous animals. Cave-dwelling birds in South American and Caribbean caves include guácharos (*Steatornis caripensis* Humboldt) (Snow 1975, Gnaspini and Trajano 2000). This bird discards palm seeds, sometimes with flesh still attached, and deposit droppings in caves, thus providing a wide range of organic matter for cavernicolous arthropods. Because of the presence of discarded seeds, some taxa associated with seeds and detritus, such as lygaeid bugs, are found only in guano of this type. Swiftlets (*Aerodramus* spp.) nest in the entrance and dark zones of tropical caves in south-east Asia, northern Australia and the Pacific, and are insectivorous (Medway 1962, Humphreys and Eberhard 2001, Koon and Cranbrook 2002). The volumes of bird guano deposited are comparable to similar sized bat populations. Richards (1971) also reported that droppings from several species of birds nesting in the entrance zone of Nullarbor Plain caves support a wide variety of cavernicolous arthropods.

Rhaphidophorid crickets are often important producers of guano in temperate caves such as those of the Nullarbor Plain (Richards 1971) and Mammoth Cave, Kentucky (Poulson 1992). Cricket guano has a low calorific value as they eat predominately decomposing organic material and have a high assimilation rate (Studier *et al.* 1986). Rhaphidophorid crickets in sections of Mammoth Cave form populations of up to 5000 individuals and can accumulate sizeable guano deposits with tens to thousands of 0.01 g faecal pellets deposited per day beneath colonies (Poulson 1992). This large and ubiquitous species within entrance zones of the Mammoth Cave system provide the largest energy input supporting the majority of the terrestrial animals found there (Poulson 1992). On the Nullarbor Plain these deposits are important as few other food sources exist because the low mean rainfall limits organic flood debris and bat populations are generally small.

Small mammals are often significant guano producers in temperate caves of North America. The guano of porcupines (*Erethizon dorsatum* L.) is reported by Calder (1965) to support a community of collembolans and mites active throughout the year in Frenchman's Cave (Hants County, Nova Scotia). Cave rats (*Neotoma* spp.) also produce guano deposits in the Mammoth Cave system. Rats commonly deposit a few to tens of faecal pellets per individual per day, depending on the season, approximately 0.1 g in size (Poulson 1992). These high energy faecal deposits are exploited by specialised consumers e.g. Mycetophyilidae sp. (Diptera) and predatory species e.g. *Quedius* sp. (Staphylinidae), before being utilised by generalist consumers (Poulson 1992).

1.4.2 Micro-habitat variation in bat guano

Guano is extremely variable, comprising numerous micro-habitats when compared with the majority of subterranean habitats (Harris 1970). Bat guano deposits have been found to exhibit variable temperature of both the ambient air above deposits and within deposits (Harris 1970). In addition, the relative humidity, CO_2 concentration, and ammonia concentration also change when bats occupy a cave due to respiration and urine output (Decu 1986). Variations in pH can be extreme, resulting in strong differentiation between fresh and old guano deposits. The annual cycle of bat roosting adds a temporal component to many guano deposits and also serves to alter air temperature especially in maternity chambers (Harris 1970).

Large numbers of bats can raise the air temperature in a chamber by up to 10ºC. This effect is most prevalent in high-domed chambers where heated air is trapped. Harris (1970) also noted small increases in air temperature close to guano piles of up to 1.4ºC due to heat released from guano decomposition. Increased air temperature of up to 12ºC has also been noted in Cuban caves where large numbers of the leaf-nosed bat, *Phyllonycteris poeyi* Gundlach, roost (Decu 1986). This temperature increase can act as a barrier for colonisation by generalist cavernicolous invertebrates, but allows guanophilic and guanobitic populations to reach large numbers.

Temperature within single guano piles can increase significantly with depth. For example temperatures 5 cm below the surface of guano piles in Carrai Bat Cave, New South Wales, are 1.7ºC higher compared with surface temperatures, while 15 cm below the surface temperatures are 3.0ºC higher

(Harris 1970). Surface guano temperatures have also been reported to increase by 9.3ºC, and these increases in both surface and subsurface temperatures were attributed to the increase in the metabolic rate of the organisms inhabiting the guano pile (1970).

Varying water content of guano, due to desiccation with increasing age, results in noticeable micro-habitat differentiation. The surface of guano deposits commonly exhibit a patchwork appearance of dark moist areas and light grey drier areas. Guano moisture content increases with the birth of pups as their faecal matter prior to being weened is predominately liquid (approximately 6-8 weeks after birth for the large bent-wing bat *Miniopterus schreibersii bassanii* Cardinal and Christidis) (Moulds 2004). Different invertebrate species within guano ecosystems prefer different micro-habitats. For example, Richards (1971) noted the majority of guanophilic arthropods in Nullarbor Plain caves were only found in completely or partially dry guano.

Guano shows a marked difference in pH between fresh and old deposits. Fresh guano is commonly basic, with the pH varying according to the volume of urine deposited with faeces. Fresh guano commonly has a pH of 8.5-9.0 that rapidly becomes acidic (5.0-5.5) with age and depth, although the centre of guano piles has a stable pH of around 4 (Harris 1971). In bat maternity caves the pH of piles will gradually decrease over winter as no fresh guano is deposited. The ever changing pH of guano piles due to age and urine content creates marked micro-habitats used by differing species.

Micro-habitat variation in bat chambers is further complicated by the movement of bat roosts in a chamber within a breeding season. These movements are apparently a response to avoiding unfavourable conditions caused by ammonia concentrations and high local temperatures (Poulson 1972).

1.4.3 Guano invertebrate classification

The ecological classification of guano invertebrates is usually considered separately to an animal's degree of cave dependence. This is because guano is considered a substrate within the cave environment that attracts a range of cavernicolous and epigean species due to its high food value. Thus animals are categorised not only according to their degree of cave dependence (troglobite, troglophile trogloxene) but also according to their degree of guano dependence. This was first proposed by Decu (1986) but has since been refined by Gnaspini (1992) to enable the parallel use of cave and guano dependence classification systems. This enables both an animal’s degree of cave and guano dependence to be categorised, however, in practise detailed study of an animal is required to accurately determine its degree of guano dependence. This limits the effectiveness of this classification system and, without prior knowledge, most communities found in guano can only be referred to as ‘guano associated’ rather than guanobitic or guanophilic.

Guanobites are animals that require the presence of guano for survival. They will only feed on guano or its associated microflora and will not use other food sources within caves. Although guanobitic species are occasionally found on other substrates in caves as they move between discontinuous guano deposits, they do not feed or reproduce on these substrates (Gnaspini and Trajano 2000). When guano deposition is seasonal (e.g. bat maternity caves), guanobites will commonly become quiescent until bats return and restore fresh guano input. Other guanobite populations crash when guano input ceases and then quickly reproduce when guano input recommences.

Guanophiles use guano resources opportunistically and are able to complete their entire life cycle using the guano substrate. Guanophiles will however utilise other cave food resources when available and do not have to rely upon guano to feed or reproduce. Abundance of guanophilic animals will decrease if fresh guano is not available, simply due to food limitation, but individuals will attempt to exploit other food resources to survive until fresh guano is available. Troglobites and troglophiles that have a generalist role in hypogean ecosystems are classified as guanophiles if they utilise guano when available, even though they are capable of surviving subterranean habitats without this resource (Gnaspini and Trajano 2000).

Guanoxenes will exploit a guano resource for feeding or reproduction but require other substrates within a cave to complete their life cycle (Gnaspini and

Trajano 2000). Guanoxenes can be either troglobites, troglophiles or trogloxenes (Gnaspini and Trajano 2000).

1.4.4 Guano ecosystems and food webs

The cyclical nature of many guano deposits resulting from the annual breeding cycle of bats generally leads to a similar cycle in arthropod abundances. Low population numbers of many species reflect changes in micro-habitat conditions resulting from the cessation of fresh guano deposition and lower air and guano temperatures. Guano communities decrease in numbers as many species stop breeding until the food supply (i.e. fresh guano) is restored. This has been observed for the mite *Uroobovella coprophila* Womersley, that is quiescent during winter months in Carrai Bat Cave, New South Wales (Harris 1971).

Arthropods in guano communities feed either directly on guano or, more commonly, upon fungus growing on guano deposits. These guanivores and mycetophages in turn support a number of predators scavengers and omnivores (Gillieson 1997). Guano, as the trophic basis for this ecosystem, requires fungi and bacteria for its partial breakdown before it can be used by the majority of arthropod consumers. This is especially true during moulting season of mammals when faecal pellets contain a substantial amount of hair that is especially difficult for many animals to digest, but more easily consumed by fungi and bacteria (Poulson and Lavoie 2000). The relative size and moisture content of faecal pellets is important in determining the succession of fungi that is able to grow. Low humidity results in rapid desiccation of fresh guano, severely reducing fungal growth as many of the opportunistic phycomycetes found on fresh guano are susceptible to drying out (Poulson 1992, Poulson and Lavoie 2000). The substrate on which faeces are deposited is also important, as the amount of leaching is determined by the substrate’s porosity. Highly porous substrates such as sand remove nutrients, allowing fungi to dominate deposits, while on non-porous surfaces nutrients will concentrate at the interface in low oxygen conditions encouraging bacteria, nematodes and specialist mites (Poulson and Lavoie 2000).

Guano food webs are based upon a guano source and associated fungi and other micro-organisms directly supporting guanivores and fungivores, including Phoridae (Diptera), Anobiidae (Coleoptera), Tineidae (Lepidoptera), Collembola and mesostigmatid mites (Acarina). Predators that prey upon these consumers include spiders, pseudoscorpions, beetles and opiliones. Specialised parasites and parasitoids are also active in many guano ecosystems. Braconid wasps (Hymenoptera) are found in several eastern Australian guano caves (Moulds 2004) and parasitise the larvae of *Monopis* spp. (Lepidoptera: Tineidae) (Austin and Dangerfield 1992). The minute eggs of the guanobite *Derolathrus* sp. (Coleoptera: Jacobsoniidae) hidden in fresh guano are possibly parasitised by small myrmarid wasps (Hymenoptera), specialists in concealed eggs (Naumann 1991). Parasitic relationships in guano ecosystems are generally poorly understood and further research will undoubtedly reveal many more examples. Some of the most numerous taxa associated with guano deposits are mites (Acarina), particularly from the families Gamasidae, Actinedidae, Oribatidae and Armadillidae (Womersley 1963a, Womersley 1963b, Gnaspini and Trajano 2000). Extremely high numbers (>33 million/m^2) have been recorded on fresh guano (Harris 1973, Bellati 2001). Guanivores and fungivores from all biogeographic regions are taxonomically similar, usually belonging to the same families. However, differences exist among the predators of guanivore communities and are often represented by taxa from different families depending on the biogeographical region (Gnaspini and Trajano 2000). For example, in the New World, scorpions, amblypygids and opiliones are common predators on cave guano deposits but are absent in Australia.

1.5 The unique guano dependent community within the Naracoorte Caves World Heritage Area, South Australia.

The Naracoorte Cave World Heritage Area was designated in 1994 primarily for its immense Pleistocene vertebrate fossil record (Brown and Wells 2000). The world heritage listing also takes into account the other natural features of the park and hence the large breeding site for the southern bent-wing bat

(*Miniopterus schreibersii bassanii* Cardinal and Christidis) was also protected with an understanding for future management. The guano dependent arthropods located within Bat Cave were identified during the 1950’s and early 1960’s (Womersley and Domrow 1959, Womersley 1960, Womersley 1963a, Womersley 1963b). Qualitative surveys of Bat Cave arthropods were conducted by Hamilton-Smith during this period. Following world heritage listing in 1998 this cave was reassessed as part of a new management plan and it was postulated to have undergone a catastrophic collapse in diversity and abundance (Hamilton-Smith 2000). This qualitative survey provided impetus for a more detailed quantitative diversity study of the arthropod community resulting in several additional species being recorded for the cave, and a better understanding of the taxonomy of the species present (Bellati *et al.* 2003). This increased knowledge was a useful first step in the knowledge base of this unique community, but there was still little or no information regarding the ecology and seasonality of the majority of the species present in the cave.

Accordingly a collaborative project was initiated, and funded through the Australian Research Council Industry Linkage Scheme, the Department of Environment and Heritage South Australia, and The University of Adelaide.

1.6 Project aims

The primary aims of this project were to:

1) Document the diversity and biology of guanophilic invertebrates and the precise environmental conditions associated with such communities within the Naracoorte Caves World Heritage Area, and in particular for Bat Cave;

2) Determine their seasonal pattern of abundance and whether this varies significantly between years;

3) Assess the level of gene flow for a specific examplar species between distant populations in separate cave systems;

4) Document the diversity and biology of guanophilic invertebrates in Starlight Cave, near Warrnambool western Victoria, the only other breeding site for *M. s. bassanii* and compare it with that occurring in the maternity chamber of Bat Cave;

5) Assess and compare the invertebrate community in Bat Cave with other biogeographical regions within Australia; and

6) Determine any real or potential threats to the invertebrate community in Bat Cave and, using the outcomes of this research, make recommendations for the future conservation and management of this unique community.

This thesis is written as a series of stand alone chapters in a format suitable for submission as a journal article, and thus some overlap between individual chapters exists. Sections of Chapters 1 and 5 have been published as (Moulds 2004) and (Moulds 2005) respectively.

Chapter 2: Seasonality, micro-habitat preference and ecology of guano dependent arthropods

2.1 Introduction

Compared with epigean environments, the availability of food resources in caves is usually the primary limiting factor for the development of complex hypogean food webs (Camassa 2004). Bat caves with large guano deposits contain a virtually unlimited food supply and therefore support a radically different ecosystem compared with other cave environments.

Bat Cave (Naracoorte, South Australia), is the largest of only two maternity sites of the large bent-wing bat (*Miniopterus schreibersii bassanii* Cardinal and Christidis). Approximately 30,000 bats occupy the maternity chamber of Bat Cave from October until April every year to give birth and raise young. The large quantities of guano deposited during summer months in the maternity chamber supports an extremely rich and diverse arthropod community (Bellati *et al.* 2003). The maternity chamber is located approximately 150 m from the cave entrance and is a 15 m high domed chamber containing numerous ‘bell holes’ in the roof used by the bats for roosting (Figure 2.1). Bell holes are vertical blind roof holes that act as heat traps and are preferentially used as bat roosts (Decu 1986, Humphreys 2000). Guano piles up to 3 m high form beneath bell holes in Bat Cave. Temperature and humidity at ground level within the chamber remain nearly constant year round, ranging from 19°-21°C with >95% relative humidity, although the vertical temperature profile varies by up to 10ºC during bat occupancy (Baudinette *et al.* 1994, Sanderson and Bourne 2002).

Guano forms a heterogenous substrate composed of numerous micro-habitats with varying moisture and pH conditions (Harris 1970). Previous studies have shown that fresh highly basic guano (pH >9.5) becomes increasingly acidic (pH ~4.5) with exposure to air over several months (Poulson 1972, Harris 1973). Guano also becomes desiccated with age unless subject to direct contact with bat urine or water, either from subterranean sources or water drips from cave roofs. The result of these continuously changing conditions is a mosaic of micro-habitats.

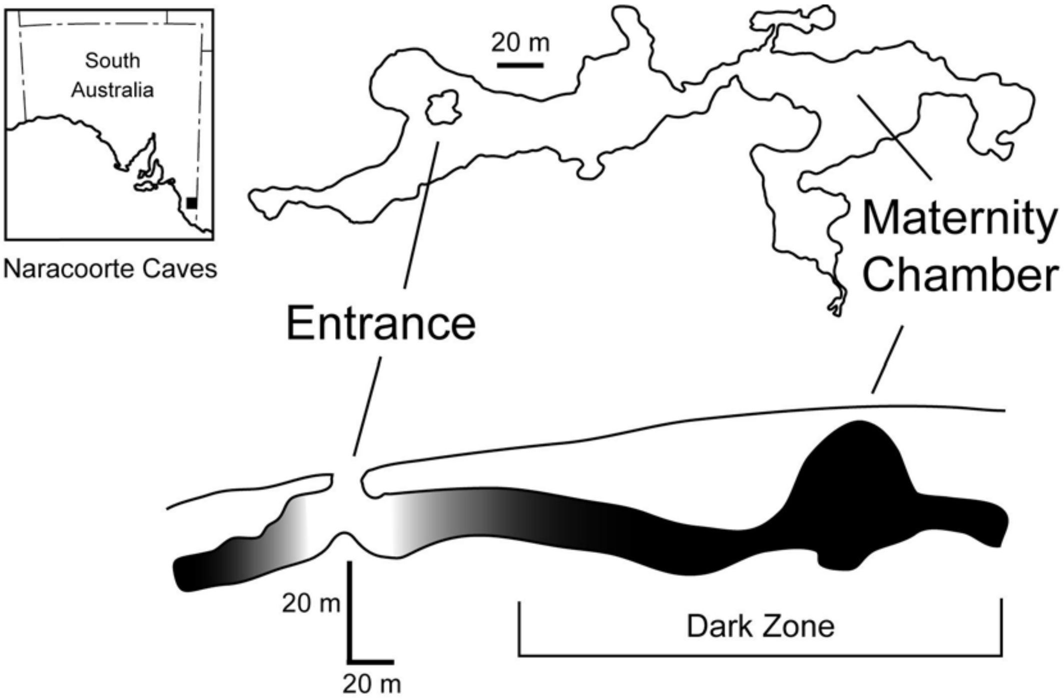

Figure 2.1. Plan and cross-section of Bat Cave, Naracoorte.

Guano micro-habitat and microclimate vary significantly between seasons, resulting in changes to the arthropod community. The seasonal bat occupancy of the maternity chamber between mid October and mid April is the most direct influence on guano micro-habitat. The departure of bats results in a virtual absence of fresh guano and urine in the maternity chamber for six months of the year. The strongly basic and moist conditions associated with bat occupancy therefore alter during winter months to slightly acidic and much drier conditions (Harris 1970, Harris 1973, Moulds 2004).

Previous studies in Bat Cave have provided lists of species, or descriptions of new taxa (Womersley and Domrow 1959, Womersley 1960, Womersley 1963, Hamilton-Smith 1967, Beier 1968, Bellati *et al.* 2003, Moulds 2004), with little or no information regarding their biology or interactions. The life history of the ubiquitous guano mite, *Uroobovella coprophila* Womersley (Urodinychidae), was studied in detail by Harris (1973) albeit in Carrai Bat Cave, northern New South Wales. Only Sanderson (2001) has provided any insight into the ecology of the unique fauna in Bat Cave, and then only at a superficial level. This project aims to rectify this disparity by providing an in-depth study of the seasonality, micro-habitat preferences and environmental conditions that control the arthropod community within the maternity chamber. These aims were achieved using systematic pitfall sampling combined with direct observation. Specifically this study aims to: **1)** identify environmental variation in guano micro-habitats by analysis of pH, moisture content and amount of deposition; **2)** describe the biology of the dominant species from the maternity chamber using direct observation and previously available information to develop a food web summarising interactions among key species within the maternity chamber; and **3)** document and explain the differences in community structure at a spatial, temporal and seasonal level.

A comprehensive diversity study, completed by Belati *et al.* (2003), reported several sampling techniques (Tullgren funnels, sticky traps and hand collecting) that collected species such as Collembola spp., Diplura sp., and Theridiidae spp. in low abundances. Therefore, the present study used only pitfall traps, as this technique collected the highest and most even diversity and abundance of arthropods compared to other collecting techniques. It is for this reason that several species included in the full species list for the maternity chamber were not recorded in this study, although many were observed to be present in the maternity chamber during the study period.

2.2 Methods

2.2.1 Arthropod sampling

The study commenced in July 2002, and included two years' fieldwork in Bat Cave incorporating two consecutive seasons, 2002/2003 and 2003/2004. Bimonthly sampling was conducted in the maternity chamber from October 2002 until August 2004, and consisted of 36 pitfall traps, 55 mm in diameter and 70 mm deep, positioned in a systematic pattern throughout the maternity chamber (Figure 2.2). The pitfall traps were placed in pairs at the 'Tops' and 'Bottoms' of 18 separate guano piles. The separation between pairs of traps depended on the size of the guano pile and ranged from 0.5 m – 2 m horizontally and 0.5 m – 1.5 m vertically. The piles were selected for both their position within the chamber as well as showing signs of guano deposition within the past two years. Pitfall traps were equally divided among three sample areas, 'Front', 'Central' and 'Rear' to enable comparison among different areas of the chamber, that are possibly subject to different environmental conditions and bat activity. Environmental variables and species richness/abundance data were averaged in nested groups to enable more accurate analysis and to remove the affect of possible outliers (Figure 2.3). Data were nested in two ways. Firstly, the 18 traps located at the Tops of guano piles for each bimonthly sample period were combined to produce a single average value for each species and environmental variable. The same procedure was used for the 18 traps located at the Bottoms of guano piles. Secondly, to enable a more detailed analysis of spatial variables throughout the chamber, data were averaged for each guano pile from each of the three sample areas within the maternity chamber (‘Front, ‘Central’ and ‘Rear’). This produced average values for each species and environmental variable measured, from both the combined Top and Bottom of each guano pile in the three discrete areas within the maternity chamber.

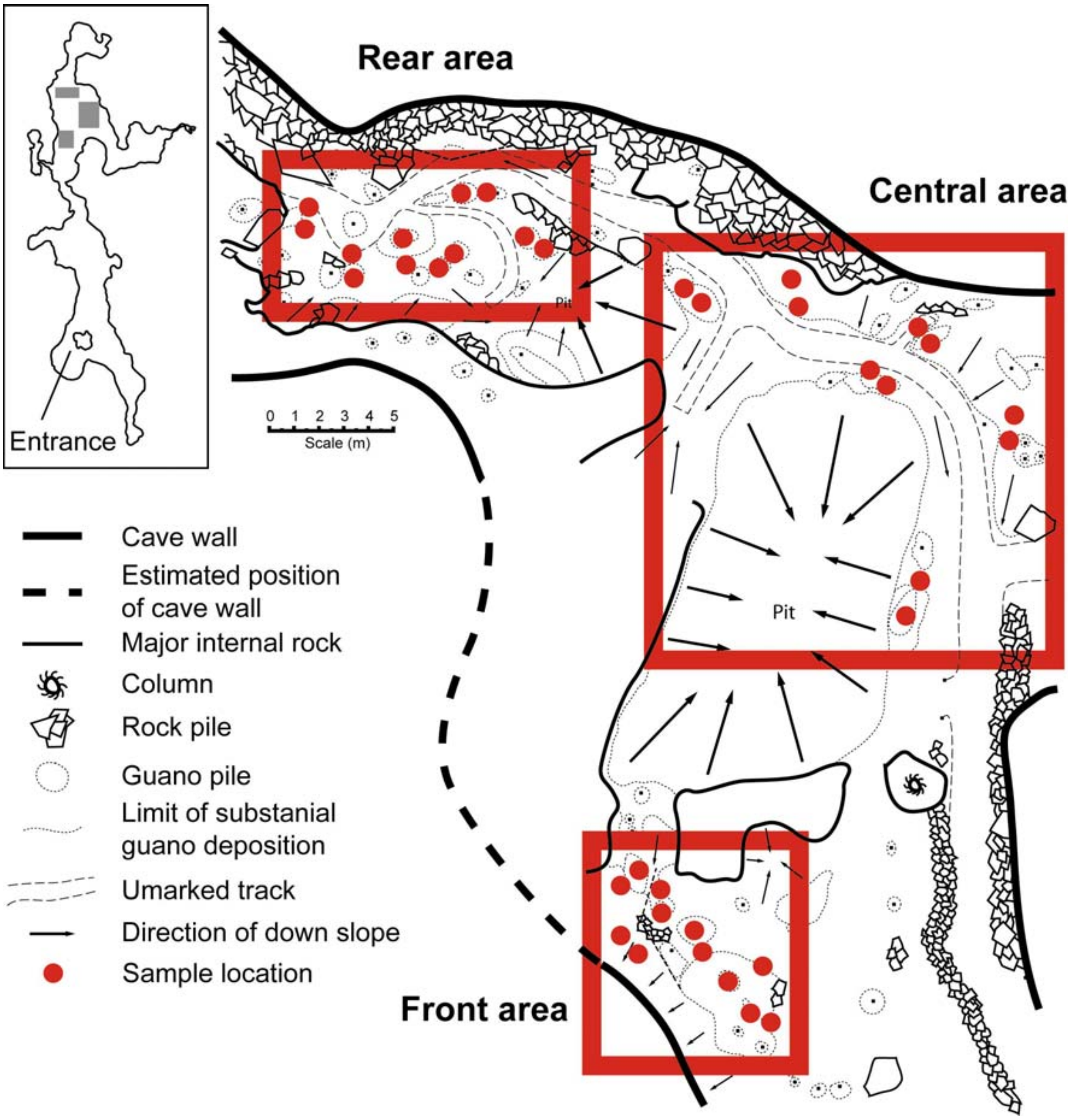

Figure 2.2. Pitfall trap locations and sample areas in the maternity chamber of Bat Cave.

During sampling periods pitfall traps were held within sections of plastic pipe permanently positioned in the guano to a depth of approximately 10 cm and which remained *in situ* for the duration of the study. This ensured pitfall traps remained in the same location throughout the study and mimimised disturbance compared to if traps were removed between sample periods. Between sampling periods the pipes were capped. Displaced guano from pitfall sites was placed in the immediate vicinity to ensure arthropod populations remained in their respective micro-habitats. Pitfall traps, containing salt water and a small amount of detergent, were opened for approximately 48 h each sampling period and were set and retrieved at night, coinciding with minimum bat numbers in the cave to keep disturbance of the maternity chamber to a minimum.

During sampling periods observations of species' biology was undertaken opportunistically. This involved close proximity observation of species in natural conditions, noting predatory behaviour and species' interactions.

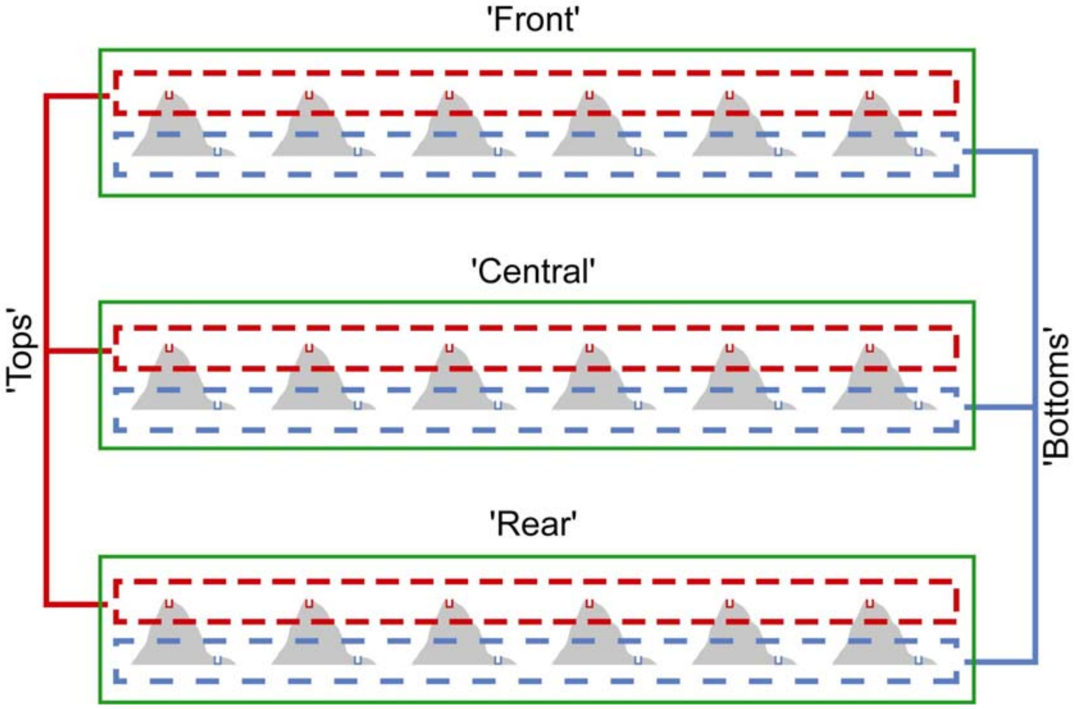

Figure 2.3. Schematic diagram of sampling design, showing groupings for nested analysis. Red dashed lines show all 18 sample Tops while blue dashed lines show sample Bottoms. The unbroken green lines show the grouping of six Tops and six Bottoms each for the three areas of the maternity chamber, 'Front', 'Central' and 'Rear'.

Each pitfall sample was sorted to species and their abundance recorded. Samples containing greater than approximately 1000 individuals of any one species had their abundance estimated to avoid excessive sorting time. Such samples were placed on a 10 x 5 cm grid with 5 mm squares, and 10 randomly selected squares were counted and averaged to provide an estimate of total numbers.

Voucher material of all arthropod samples have been deposited in the invertebrate collections of the South Australian Museum, Adelaide. Acarina vouchers have additionaly been deposited in the Queensland Museum, Brisbane. Additional Collembola vouchers have also been deposited within the Australian National Insect Collection, Canberra.

2.2.2 Guano sampling

Relative rates of guano deposition were calculated for all 36 pitfall trap sites. During sampling periods, fresh guano was collected in large high-sided containers (approximately 0.8 m^2) above pitfall sites (Figure 2.4). These samples were subsequently weighed, providing an accurate measure of guano deposition rates throughout the maternity chamber, enabling relative bat activity rates to be determined. The highest guano deposition rates recorded from the Tops of piles during summer correspond to the peak bat population of approximately 35,000 individuals occupying the maternity chamber (T. Reardon pers. Comm. 2004). Guano was not collected between sampling periods so that guano habitat for guanobitic or guanophilic arthropods was not unduly affected.

The moisture content and pH of guano surrounding pitfall trap sites was also measured by random sampling within 20 cm of sites. A ‘Manutec’ soil test kit was used to measure the pH of samples to an accuracy of 0.5. Moisture content of guano piles was determined by weighing samples and then drying them for approximately 96 h under two 100 watt light globes in Tullgren funnels. The dried samples were then reweighed allowing for moisture content to be calculated by weight.

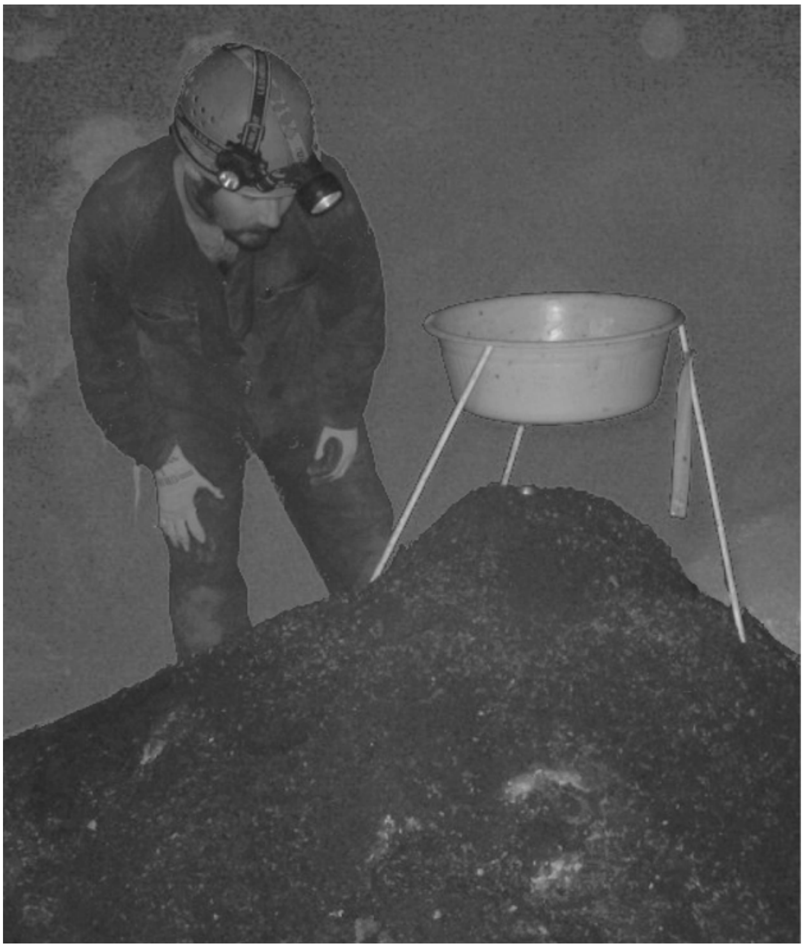

Figure 2.4. Guano collecting tray at top of guano pile in the maternity chamber, Bat Cave. Photo A. Branford.

2.2.3 Species richness and diversity indices

Species richness in this study is defined as the number of discrete species in a pre-defined sampling area (Magurran 1988). **Species abundance** is defined as either the raw number of individuals collected using pitfall trap sampling, or the percentage of the total number of individuals collected. A rank abundance plot using $\log_{10}$ transformed species abundances, fitted with a two site binding hyperbola non-linear regression, was used to determine a model of species abundance (Magurran 1988).

A diversity index was employed to represent the combined species richness and individual species abundances. The two most widely applied indices for diversity studies are the Shannon-Weiner and Simpson indices (Magurran 1988). Both combine species richness and abundance into a single value in slightly different ways to enable comparison of sites and communities. Simpson's index is most sensitive to abundances of the most common species while reducing the effect of rare species (Whittaker 1965, Hill 1973). The Shannon-Weiner index, while taking account of rarer species, relies on samples containing all species present in the community (Peet 1974). When this is not the case substantial errors can arise. Because the majority of samples do not contain all known species from the community, it was most appropriate in the study to use the Simpson index. The index was calculated as:

$$D = \Sigma \, p_i^{\,2}$$

where 'D' is the diversity value and 'p_i' the relative abundance of species 'i'. Values for 'D' are inversely proportional to diversity so are expressed as 1/D for the purposes of analysis. Data were analysed and graphed using GraphPad Prism Version 3.03 (GraphPad 2002). Two-tailed P-values were calculated using Pearson's correlation coefficient.

2.2.4 Quantile regression

Quantile regression was used to estimate multiple rates of change from minimum to maximum response, enabling a more in-depth analysis of the likely variables affecting relationships (Koenker and Bassett 1978). Variation in the relationship between environmental variables and Simpson's diversity index was assessed using quantile regression as it enables analysis of the upper or lower limits of a variable rather than the mean or median (Scharf *et al.* 1998). The rates of change of quantiles near the maximum response show relationships not limited by ecological restraints, thus providing a more powerful tool for identifying functional ecological relationships (Cade and Noon 2003). Due to the sometimes limited data available, 75th and 50th upper quantiles bands were selected to ensure reliable estimates of variance (Scharf *et al.* 1998).

2.2.5 Non-metric Multidimensional Scaling (NMS) Ordination

Non-metric Multidimensional Scaling (NMS) ordinations implemented in (PC-ORD version 4.10) was used to describe patterns of environmental gradients and species composition in the maternity chamber (McCune and Mefford 1999). NMS was run using the default options of Sorensen (Bray-Curtis) distance measure and the 'Auto-Pilot: slow and thorough' option to locate optimal solutions. The most dominant environmental variables for each axis were determined using Pearson's correlation coefficient. NMS ordination using raw species and environmental data did not produce an acceptable ordination due to high stress levels (>30) associated with high degrees of variation both within the sample areas and between bimonthly sample periods. When averages (refer section 2.3.1) were analysed acceptable stress levels (<15) were obtained, enabling reasonable confidence to be placed in the results (McCune and Grace 2002). All average values were $\log_{10}+1$ transformed prior to ordination to reduce the effect of outliers.

2.2.6 Cluster analysis

Cluster analysis was performed using PC-ORD (version 4.10) to describe groupings of community similarity between samples (McCune and Mefford 1999). Default options within PC-ORD were used to create a neighbour joining dendrogram. Data were averaged according to Section 2.2.1 and $\log_{10}+1$ transformed prior to analysis to reduce the affect of outliers.

2.2.7 Indicator species analysis

Indicator species analysis as defined by Dufrene and Legendre (1997) was used in PC-ORD to determine the species that best indicated specific micro-habitat conditions and seasons. The method combines the concentration of species and their abundance in particular habitats, to identify indicator taxa that are found exclusively in a single habitat or season. Indicator species' values are scored between 0 (no indication of the habitat) and 1.0 (a perfect indicator species found exclusively in the habitat). Indicator values obtained were tested for statistical significance ($p < 0.05$) in PC-ORD using Monte Carlo random permutations. Data used for this analysis were averaged as described in Section 2.2.1.

2.3.1 Results - guano micro-habitat

The pH within the maternity chamber of Bat Cave was found to increase dramatically during summer months when guano deposition was highest (Figure 2.5). This increase was also seen most strongly at the tops of guano piles where the highest amount of guano was deposited and within the central area of the chamber (Fig 2.2) situated under the main bat roost. pH at the bottom of guano piles showed little variation between seasons and was relatively stable at slightly below pH 6 (Figure 2.5).

The moisture content of guano surrounding trap sites is significantly higher ($p > 0.05$) at the top of guano piles than at the base (Figure 2.6). The base of guano piles show very little variation between seasons apart from distinctly higher values during October in both 2002 and 2003. A similar peak occurred at pile tops in October 2002, but not in October 2003. A slight increase in moisture content during summer months occurred in 2002 and especially during 2003. The early return of bats into the maternity chamber in August 2004 (instead of October) corresponded with this early increase in moisture content at the top but did not affect the bottom of guano piles.

The amount of guano deposited during each 48 h sample period indicated the relative level of bat activity throughout the study, with the total volume of guano being estimated by the area under the curve (Figure 2.7). Fresh guano was deposited significantly more during summer months and always at the Tops of guano piles, corresponding to peak bat occupancy of the maternal chamber. When each of the three areas was examined separately it was found that more guano was deposited in the Central area of the maternity chamber over summer months than in either the Front or Rear areas (Figure 2.8). However, the Central area had the highest total volume but not the most sustained. All areas showed significant variation in the amount of guano deposited during summer indicating the bat population moves between these areas throughout the birthing period. During November (2002) and February (2003) bats moved from the Rear area to the Front area and then back again between February and April 2003 (Figure 2.8). When the bats returned to the maternity chamber from over-wintering sites in October 2003 they occupied the Rear and Central areas preferentially, but then moved from the Rear to the Front area in November 2003. Guano deposition from April 2004 shows that most bats remaining in the chamber at this time were situated in the Central area with few bats in the Front or Rear areas. The final sample period in August 2004 shows a return of the bats to all three areas but predominately to the Central area.

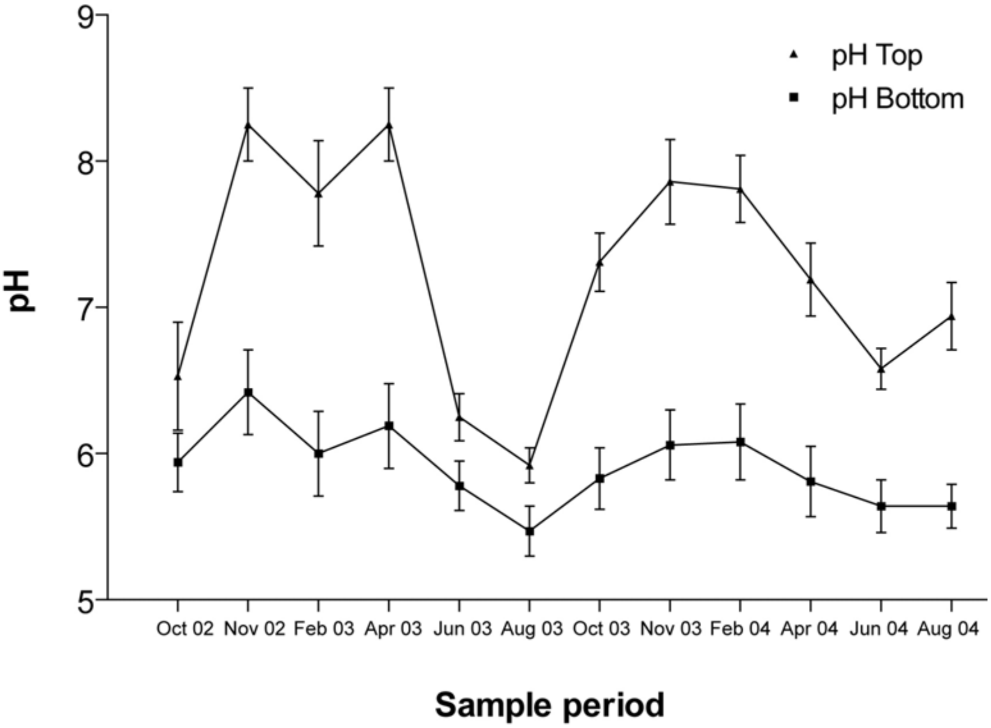

Figure 2.5. pH of *in situ* guano at Tops and Bottoms of guano piles in the maternity chamber of Bat Cave.

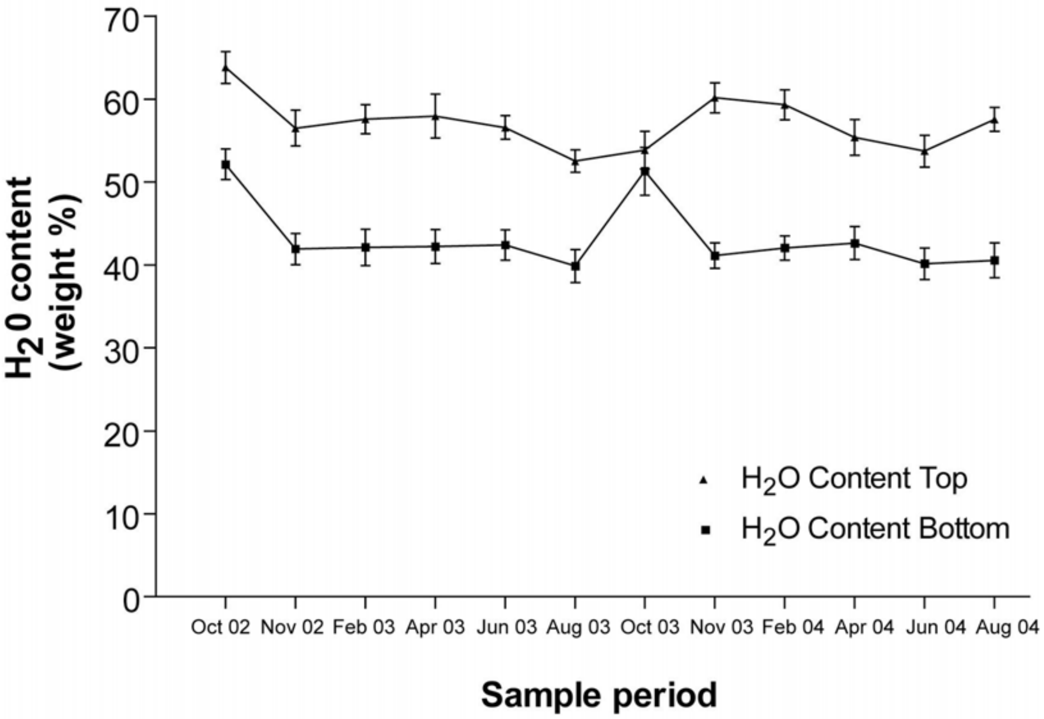

Figure 2.6. Moisture content of *in situ* guano at Tops and Bottoms of guano piles in the maternity chamber of Bat Cave.

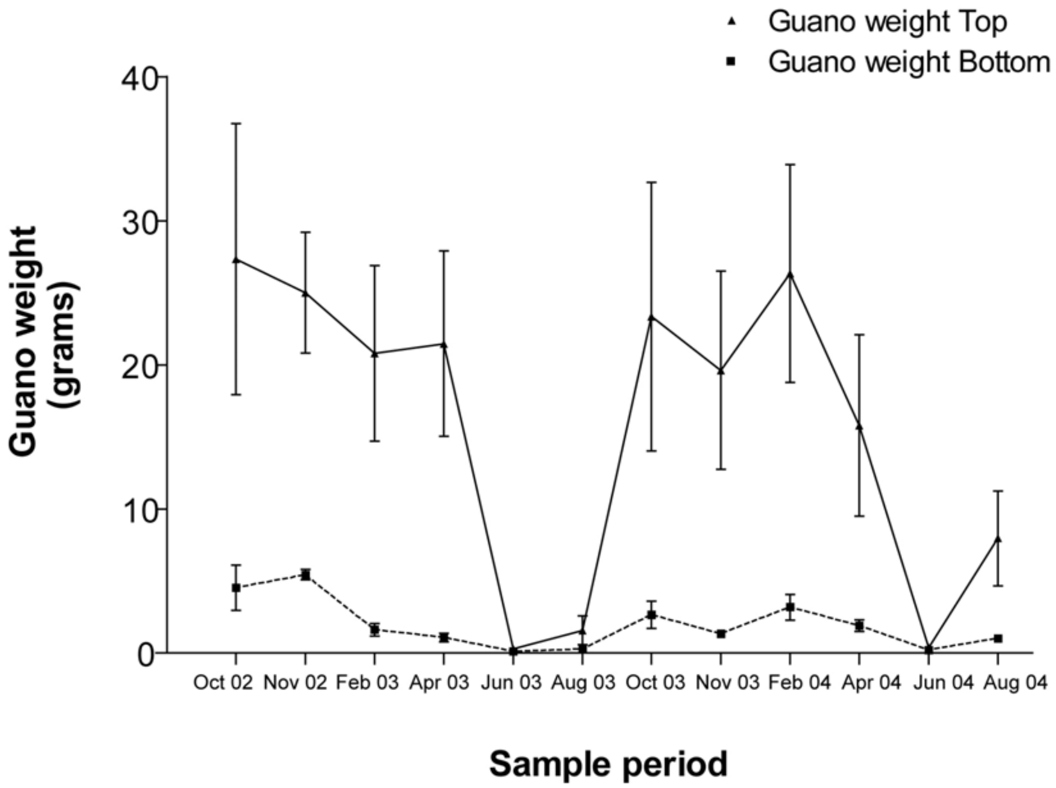

Figure 2.7. Fresh guano deposition on the Tops and Bottoms of guano piles in the maternity chamber of Bat Cave.

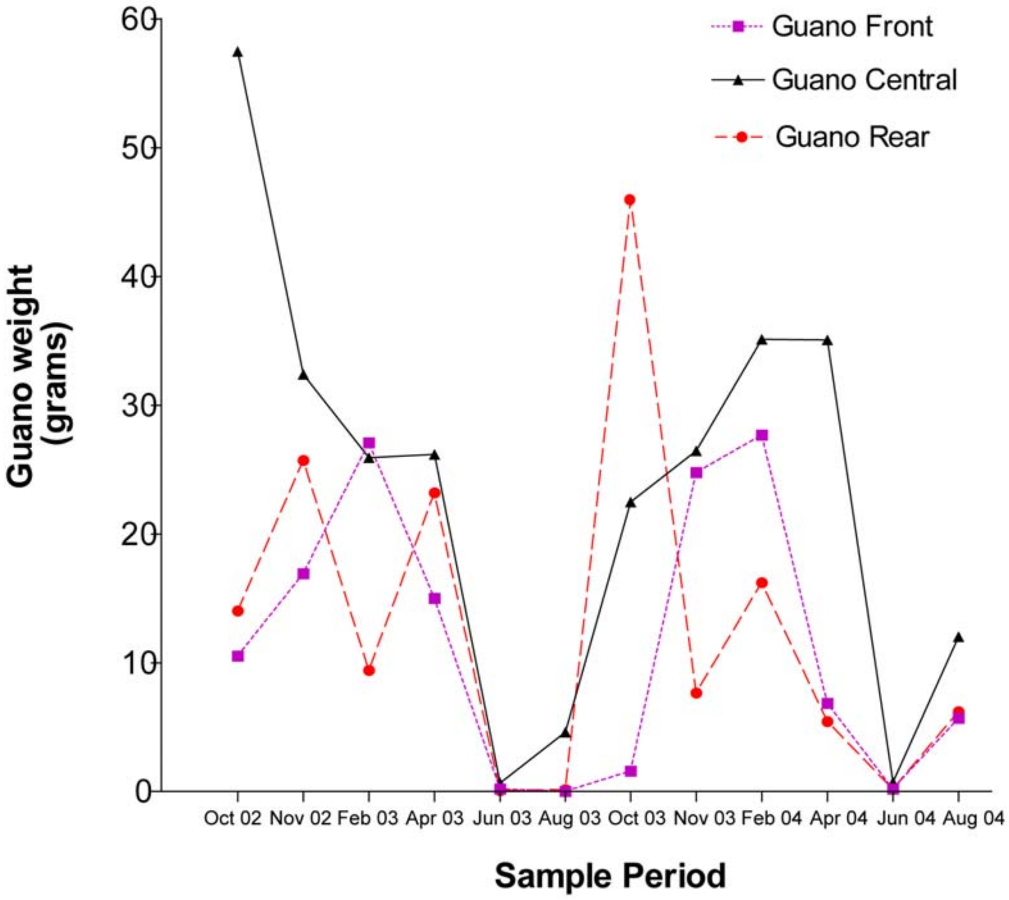

Figure 2.8. Fresh guano deposition from Front, Central and Rear areas of the maternity chamber of Bat Cave.

Increasing deposition of fresh guano showed a significant ($p < 0.0001$) positive correlation with pH ($r^2 = 0.74$) (Figure 2.9). Fresh guano deposition also formed a positive correlation with increased *in situ* moisture content ($r^2 = 0.57$) (Figure 2.10).

A two-dimensional NMS ordination described 95% of the environmental variance for the averaged data for all Top and Bottom traps for each sample period (Figure 2.11). Axis 1 describes 84.2% and Axis 2 describes 10.8% of the variation, demonstrating Tops of guano piles during summer months are distinctly different to all other micro-habitats. As expected they are characterised by high amounts of fresh guano deposition, high *in situ* moisture contents and high pH. The sites group strongly into Tops and Bottoms of guano piles and also between summer and winter with few exceptions. The site from 'August 2004 Top' groups with the summer area, probably due to the exceptional early return of substantial numbers of bats into the maternity chamber during this period. The October samples from both seasons also fall outside these groupings due to the unpredictable bat occupancy of the chamber during this time.

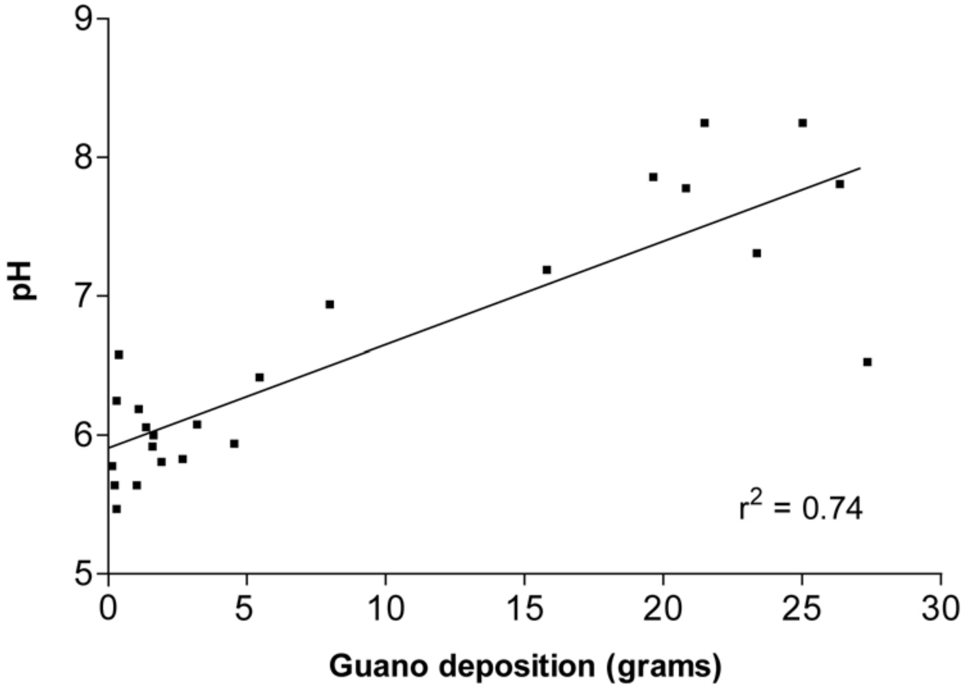

Figure 2.9. Linear regression between increasing fresh guano deposition and increasing pH ($y = 0.07x + 5.9$) .

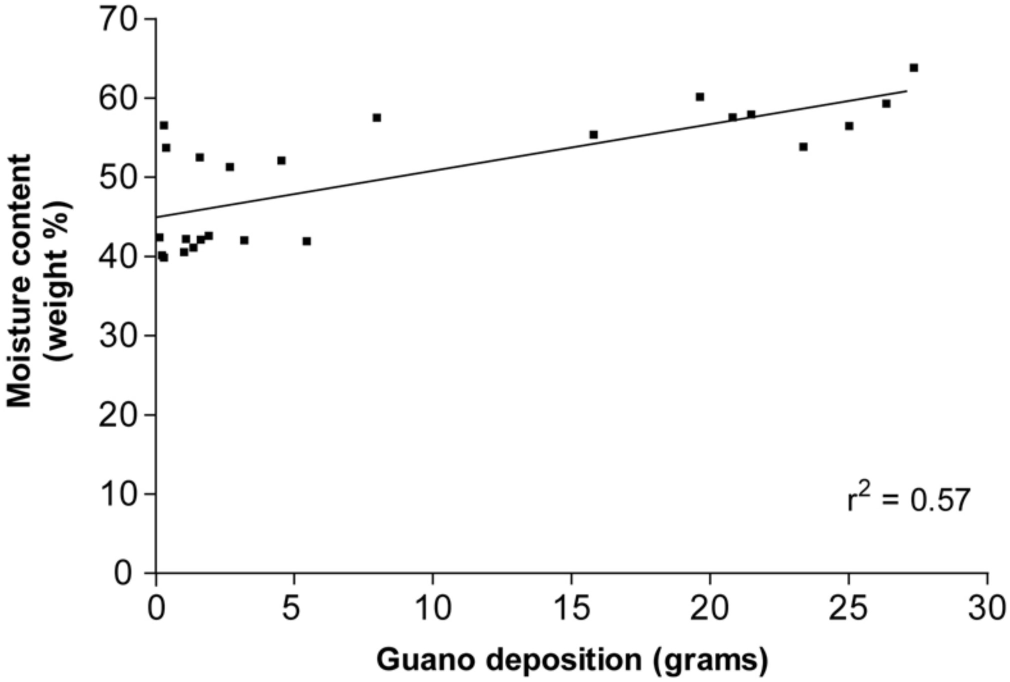

Figure 2.10. Linear regression between increasing guano deposition and increasing moisture content ($y = 0.59x + 44.9$).

A two-dimensional NMS ordination described 94.4% of the environmental variance for the averaged data for the three areas of the maternity chamber, Front, Central and Rear (Figure 2.12). Axis 1 describes 80% and Axis 2 describes 14.4% demonstrating that guano piles in the Central area group together most strongly for the three environmental gradients measured, when compared with the Front and Rear areas. The samples from the Front and Rear are more scattered in environmental variation for pH, moisture content and guano deposition than those in the Central area where environmental conditions are more homogeneous between the Tops and Bottoms of guano piles.

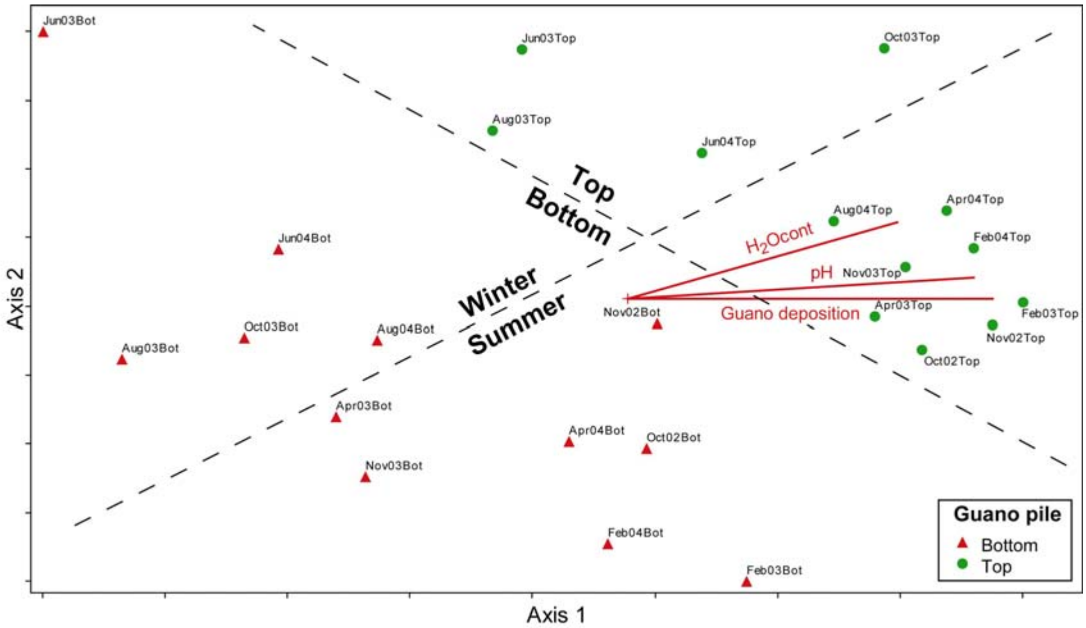

Figure 2.11. A two-dimensional NMS ordination on environmental variables measured in the maternity chamber. This ordination yielded a stress value of 8.72%, a final instability of 0.00001 and an r^2 value of 0.95 (indicating 95% of the variance in the data is explained by the model). Varimax rotation was invoked to align the maximal explained variance with Axis 1. The r^2 vectors are produced by overlaying the original data on itself. The length of the vector indicates the variance explained by the named variable, and the orientation shows the direction of increase. The vectors in this plot are constrained to $r^2 >= 0.25$.

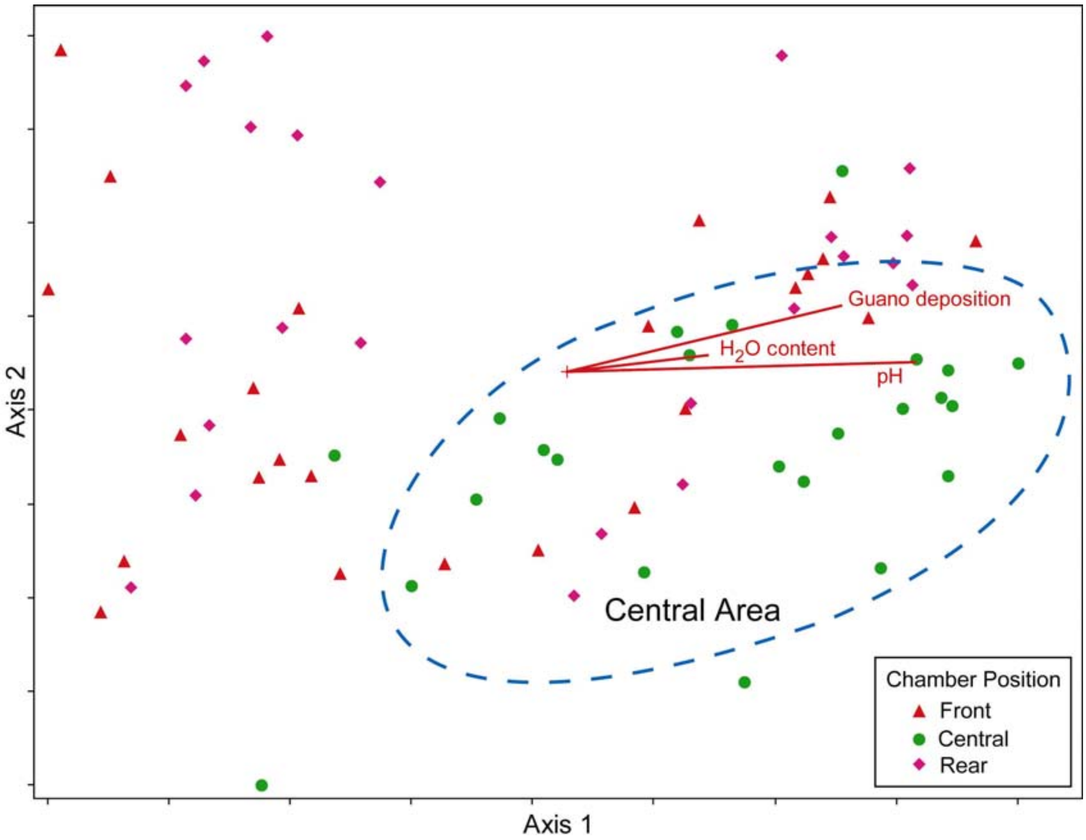

Figure 2.12. A two-dimensional NMS ordination on environmental variables measured in the maternity chamber. This ordination yielded a stress value of 10.67%, a final instability of 0.00009 and an r^2 value of 0.944 (indicating 94.4% of the variance in the data is explained by the model). Varimax rotation was invoked to align the maximal explained variance with Axis 1. The r^2 vectors are produced by overlaying the original data on itself. The length of the vector indicates the variance explained by the named variable, and the orientation shows the direction of increase. The vectors in this plot are constrained to r^2 >=0.25.

2.3.2 Results - species richness, abundance and biology

2.3.21 Species richness and abundance of guanophilic arthropods

Thirty-eight species of arthropods from three classes and 12 orders were recorded from the maternity chamber of Bat Cave (Table 2.1). Acarina were the most diverse with 10 species followed by Coleoptera with seven species, Diptera with six species and Collembola with four species.

Table 2.1. Arthropod species diversity of the maternity chamber, Bat Cave. The first reference to provide the most complete identification of the taxon listed is provided in The Previously Recorded Column. Species richness is shown by the Present Study Column. Note, this study did not encompass all available trapping techniques used in previous studies as its aim was to determine the ecology and small-scale spatial and seasonal variation in the arthropod community. [1]The two species of Nycteribiidae from the maternity chamber were not identified until the conclusion of the study. [2]Juvenile cockroach specimens believed to be *N. australis* were sighted during the study although none were collected.

Class and Order	Family	Genus species	Previously recorded	Present study
Crustacea: Isopoda	Porcellionidae	*Porcellio scaber*	Bellati *et al.* 2003	yes
Arachnida: Araneae	Theridiidae	*Theridon* sp.	Bellati *et al.* 2003	no
		Steatoda sp.	Bellati *et al.* 2003	no
Acarina	Ameroseiidae	*Ameroseius plumosus*	Bellati *et al.* 2003	no
	Histiostomatidae	*Histiostoma* sp.	Bellati *et al.* 2003	no
	Hypochthonioidea	sp.	Bellati *et al.* 2003	no
	Ixodidae	*Ixodes* simplex simplex	new record	yes
	Laelapidae	*Hypoaspis* sp.1	Bellati *et al.* 2003	no
		Hypoaspis sp.2	Bellati *et al.* 2003	no
	Spinturnicidae	*Spinturnix loricata*	new record	yes
	Trombiculidae	*Trombicula* or *Myotrombicula* sp.	new record	yes
	Urodinychidae	*Uroobovella coprophila*	Womersley 1960	yes
	Uropodidae	sp.	new record	yes
Pseudoscorpionida	Cheliferidae	*Protochelifer naracoortensis*	Beier 1968	yes
Collembola	Brachystomellidae	sp.	new record	yes
	Entomobryidae	*Lepidocyrtus* sp.	Bellati *et al.* 2003	no
		Lepidosira australica	Bellati *et al.* 2003	no
	Hypogastruridae	*Hypogastrura* sp.	Bellati *et al.* 2003	yes
Diplura		sp.	Bellati *et al.* 2003	no
Insecta: Blattodea	Blattellidae	*Neotemnopteryx australis*	Hamilton-Smith 1967	no[2]
Psocoptera	Psyllipsocidae	*?Psyllipsocus ramburi*	Hamilton-Smith 1967	no
	Trogiidae	*?Lepinotus reticulatus*	Hamilton-Smith 1967	no
Coleoptera	Anobiidae	*Ptinus exulans*	Hamilton-Smith 1967	yes
	Carabidae	*Speotarus lucifugus*	Hamilton-Smith 1967	yes
	Cryptophagidae	*Anchicera* sp.	Bellati *et al.* 2003	yes
	Dermestidae	sp.	Bellati *et al.* 2003	no
	Histeridae	*Tomogenius ?ripicola*	Bellati *et al.* 2003	yes
	Jacobsoniidae	*Derolathrus* sp.	Bellati *et al.* 2003	yes
	Leiodidae	*Nargomorphus miniscusus*	Hamilton-Smith 1967	yes
Diptera	Nycteribiidae	*Nyteribia parilis vicaria*	new record	yes[1]
		Penicillidia tectisentis	new record	yes[1]
	Phoridae	sp.	Hamilton-Smith 1967	yes
	Psychodidae	sp.	Hamilton-Smith 1967	no
	Sciaridae	sp.	Hamilton-Smith 1967	no
	Sphaeroceridae	sp.	Hamilton-Smith 1967	no
Lepidoptera	Tineidae	*Monopis crocicapitella*	Bellati *et al.* 2003	yes
Hymenoptera	Braconidae	*Apanteles ?carpatus*	Bellati *et al.* 2003	yes
	Myrmaridae	sp.	Bellati *et al.* 2003	no

In total 378,354 individuals were collected (Table 2.2). A rank abundance plot shows that species follow a log series model of abundance with extreme abundances at either end of the species rank, and that the majority of species show similar relative abundances when represented on a logarithmic scale

(Figure 2.13). Numerically the chamber is dominated by the guano mite, *Uroobovella coprophila* (Table 2.2), that reached enormous numbers during summer months, often completely covering the Tops of guano piles in the Central area of the maternity chamber. Over 360,000 individuals of this mite were collected during the study accounting for 95.2% of total arthropod abundance. Excluding *U. coprophila*, over 18,000 other arthropod specimens were collected and their proportions are shown in Table 2.2. The arthropod assemblage is otherwise numerically dominated by the mycetophageous scavenging anobiid beetle *Ptinus exulans* and two predatory species, the histerid beetle *Tomogenius ?ripicola* and the pseudoscorpion *Protochelifer naracoortensis*. Together these three species comprise 89% of arthropods (excluding *U. coprophila*) found in the maternity chamber.

Table 2.2. Arthropod abundance and percent composition of the 13 most abundant species recorded in the in the maternity chamber, Bat Cave. All other species recorded from the maternity chamber were in abundances <10 individuals comprising <0.1% of total abundance excluding Urodinychidae.

Species	Total abundance	% of Total abundance	% of Total abundance excluding Urodinychidae
Uroobovella coprophilla (Urodinychidae)	360 264	95.2%	
Ptinus exulans (Anobiidae)	6 668	1.8%	36.9%
Protochelifer naracoortensis (Pseudoscorpionida)	5 413	1.4%	29.9%
Tomogenius ?ripicola (Histeridae)	4 020	1.0%	22.2%
Speotarus lucifugus (Carabidae)	536	0.1%	3.0%
Derolathrus sp. (Jacobsoniidae)	325	0.1%	1.8%
Monopis crocicapitella (Tineidae)	313	0.1%	1.7%
Apanteles ?carpartus (Braconidae)	290	0.1%	1.6%
Phoridae sp.	183	0.1%	1.0%
Nycteribiidae sp.	158	<0.1%	0.9%
Anchicera sp. (Cryptophagidae)	78	<0.1%	0.4%
Porcellio scaber (Isopoda: Porcellionidae)	61	<0.1%	0.3%
Ixodes simplex simplex (Ixodidae)	45	<0.1%	0.3%
Total abundance	378 354	100.0%	100.0%

The Tops of guano piles are more species rich than the Bottoms ($p < 0.0001$) (Figure 2.14). Also the Tops during the first year's sampling (2002/03) show an increase in species richness over summer, not found during the second year's sampling (2003/04). The pattern of species richness at the Bottoms of guano piles is less clear, but shows peaks in October and November possibly associated with increasing in guano deposition after winter. Not surprisingly, species richness is positively correlated (r^2=0.68) with both moisture content (Figure 2.15) and pH (Figure 2.16), given that the Tops of guano piles have already been shown to have higher moisture content and pH.

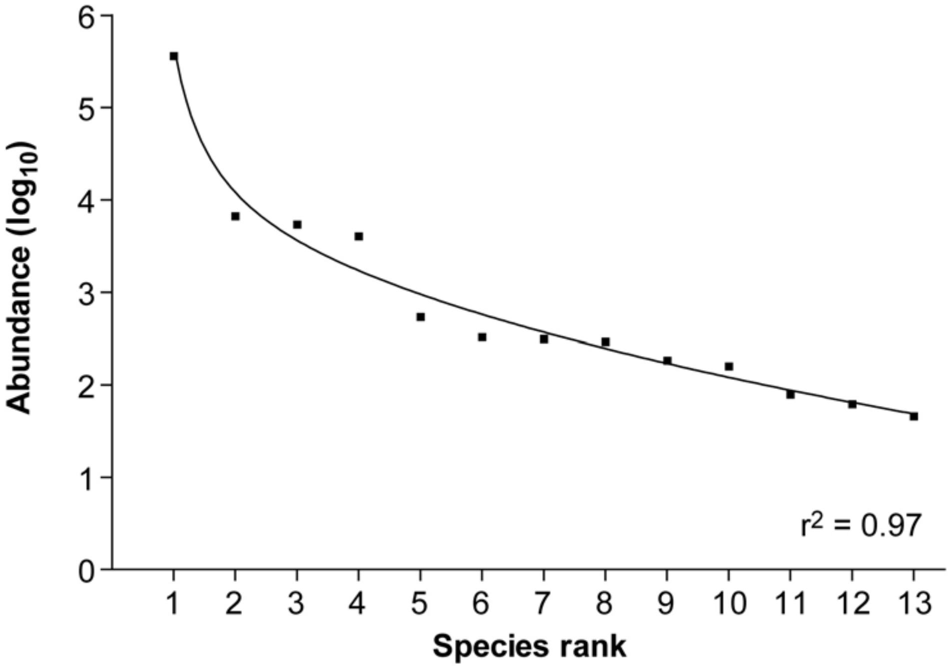

Figure 2.13. Rank abundance graph of 13 species collected in the maternity chamber, Bat Cave. A two binding hyperbola was fitted to the data. Species in ascending order are *Uroobovella coprophila* (Urodinychidae), *Ptinus exulans* (Anobiidae), *Protochelifer naracoortensis* (Pseudoscorpionida), *Tomogenius ?ripicola* (Histeridae), *Speotarus lucifugus* (Carabidae), *Derolathrus* sp. (Jacobsoniidae), *Monopis crocicapitella* (Tineidae), *Apanteles ?carpartus* (Braconidae), Phoridae sp., Nycteribiidae sp., *Anchicera* sp. (Cryptophagidae), *Porcellio scaber* (Porcellionidae) and *Ixodes simplex simplex* (Ixodidae). Abundances were $\log_{10}$ transformed prior to analysis.

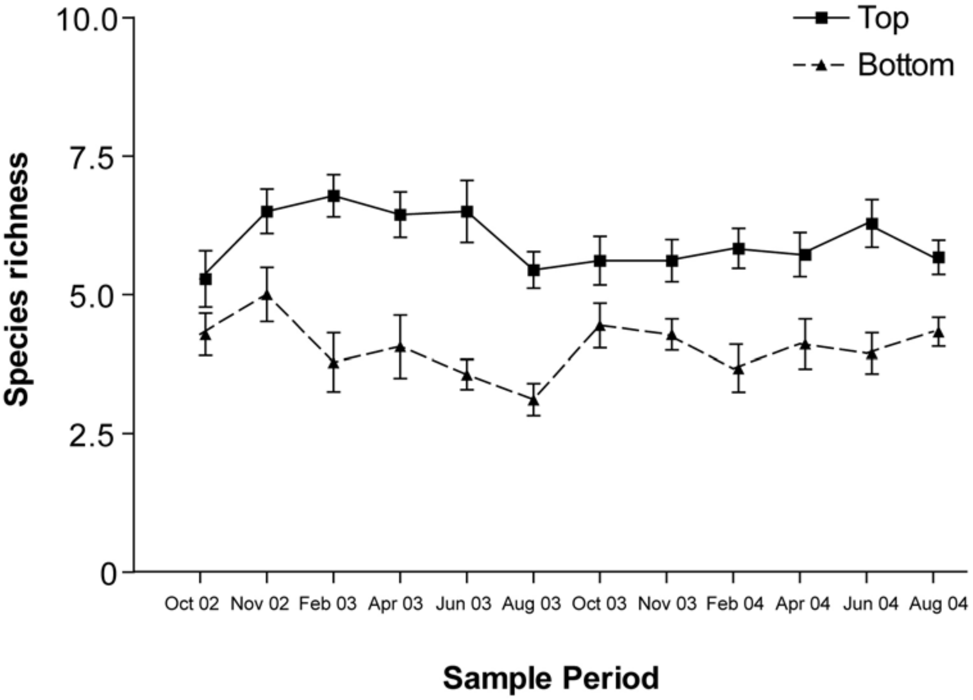

Figure 2.14. Average species richness from 12 sample periods in the maternity chamber, Bat Cave. Error bars are standard errors.

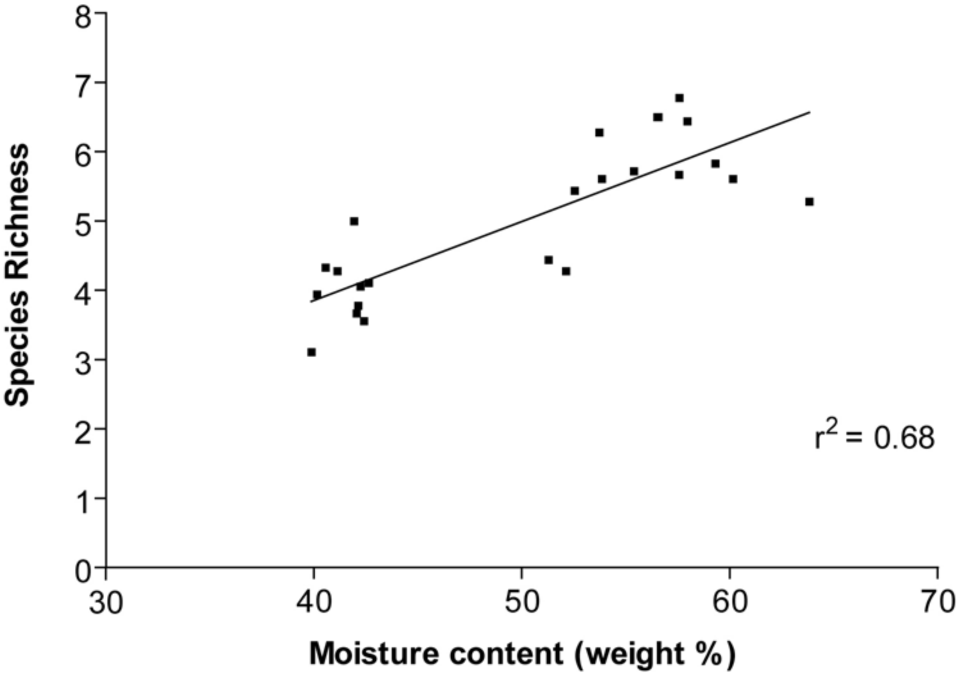

Figure 2.15. Linear regression of moisture content plotted against species richness from Tops and Bottoms of guano piles in the maternity chamber of Bat Cave (y = 0.11x-0.7).

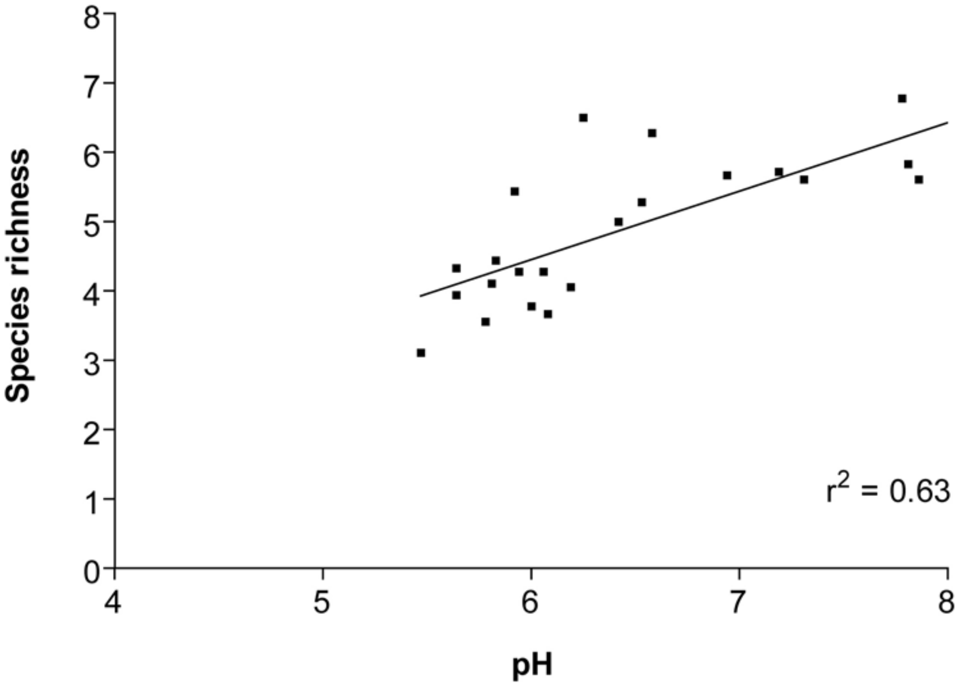

Figure 2.16. Linear regression of pH plotted against species richness for all pitfall traps regardless of position within the maternity chamber of Bat Cave (y = 0.99x-1.46).

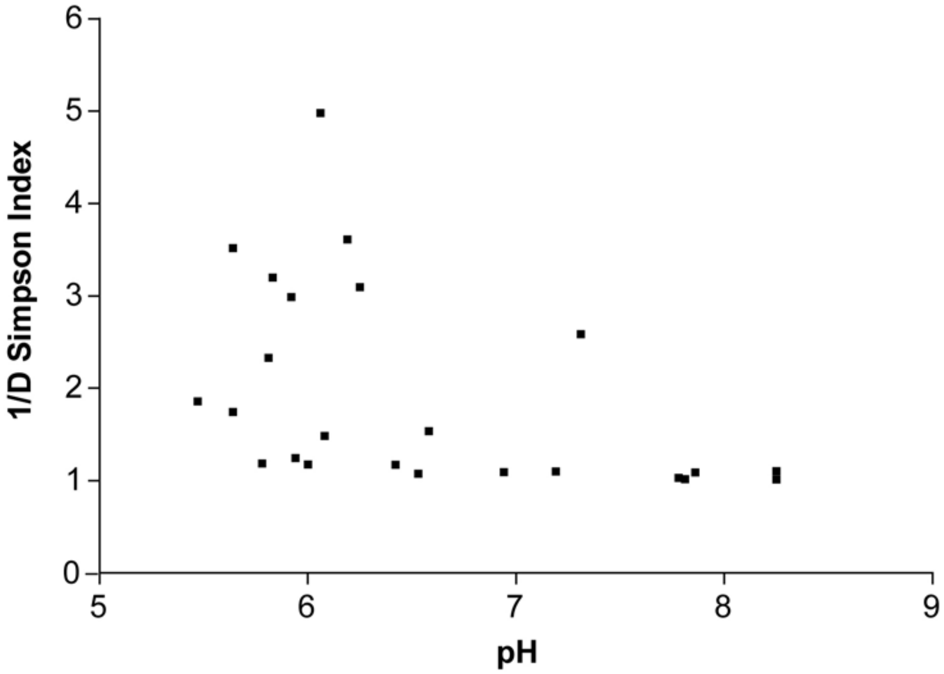

Figure 2.17. Simpson diversity index values averaged for all pitfall traps regardless of position within the maternity chamber of Bat Cave plotted against pH. The data show little relationship and linear and non-linear regression both show r^2 values less than 0.3.

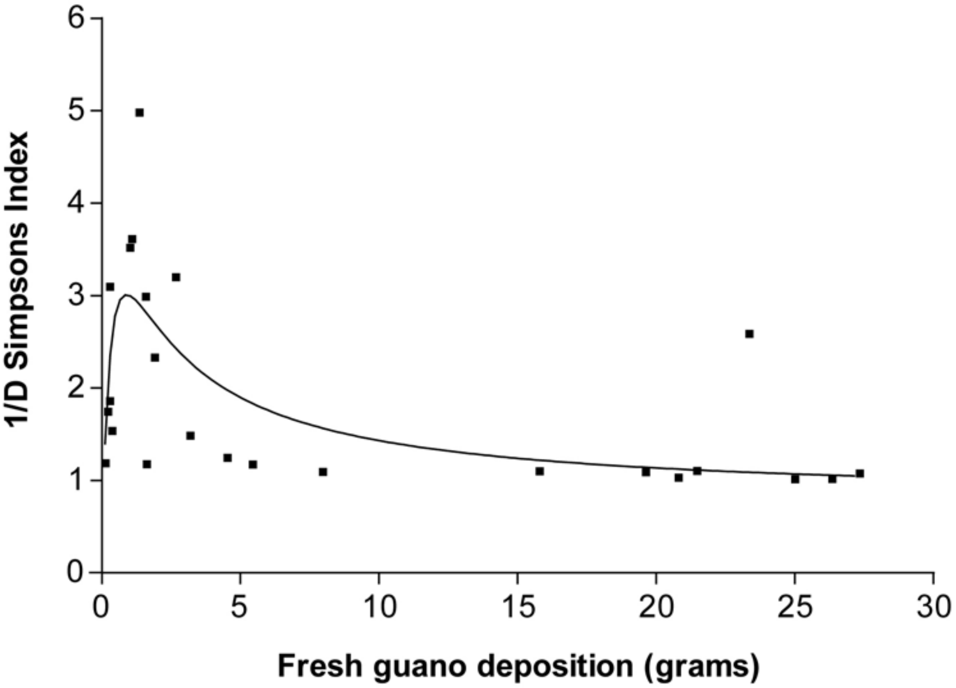

Figure 2.18. Simpson diversity index values averaged for all pitfall traps regardless of position within the maternity chamber of Bat Cave with fresh guano deposition. Data are fitted with a two site binding hyperbola with an $r^2 = 0.48$, however, when the outlier of 23 g guano deposition is removed this fit improves to $r^2 = 0.57$.

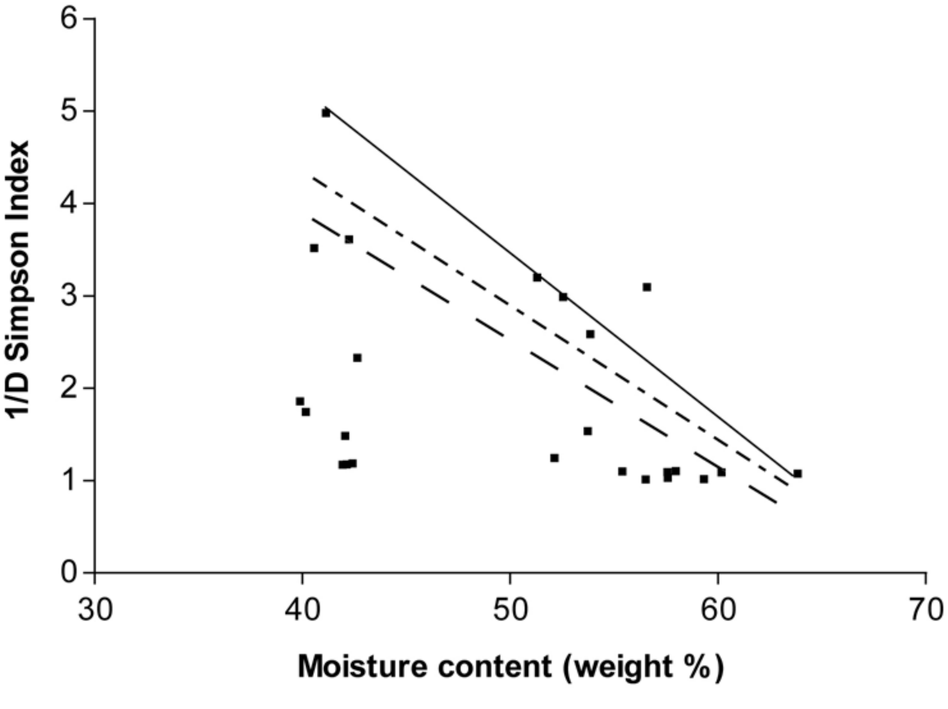

Figure 2.19. Simpson diversity index values averaged for all pitfall traps regardless of position within the maternity chamber of Bat Cave plotted against moisture content. Quantile regression (Koenker and Bassett 1978) estimates for upper 25th ($y = -0.18x+12.32$), 50th ($y = -0.15x+10.13$) and 75th ($y = -0.14x+9.39$) percentile bands in descending order.

Unlike species richness values that increase with moisture and pH, Simpson's diversity index values show the most diverse micro-habitats in the maternity chamber are those with slightly acidic pH (Figure 2.17) and lower amounts of guano deposition (Figure 2.18), although substantial variation among the data exists particularly for low pH values. Moisture content and Simpson's diversity index show a strong negative linear relationship when using quantile regression to remove unmeasured limiting factors from the data (Figure 2.19). The upper 25% of data points show a significant ($p = 0.0034$) negative linear relationship ($r^2 = 0.91$) between moisture content and Simpson's diversity index whose fit lowers, although still being significant, with the upper 50% ($r^2 = 0.75$) and upper 75% ($r^2 = 0.62$), as limiting factors reduce potential diversity.

2.3.22 Biology of key species

Protochelifer naracoortensis (Pseudoscorpionida: Cheliferidae) was observed feeding on *Monopis crocicapitella* adults (Tineidae) in the maternity chamber and *Ptinus exulans* larvae (Anobiidae) in nearby Blanche Cave. Pseudoscorpions are generalist predators (Weygoldt 1969) and can be assumed to predate all small arthropods within the maternity chamber including Acarina, Lepidoptera, beetle larvae, Collembola, Psocoptera and dipteran larvae. Individuals occur throughout the year (Figure 2.20a) but peak in late winter/early spring. They roam freely within the maternity chamber but are not as active in the flyway and entrance zone of Bat Cave.

Uroobovella coprophila (Acarina: Urodinychidae) is found in every maternity cave of the large bent-wing bat (*M. schreibersii*) in south-eastern Australia (Moulds 2004). It was observed in large numbers on a freshly dead bat in October 2003 in the maternity chamber indicating it may feed upon carrion or perhaps the fungi and bacteria on such cadavers. A detailed life history and dietary study in Carrai Bat Cave northern New South Wales by Harris (1971, 1973) demonstrated that this species feeds on bacteria, yeasts and fungi growing on fresh guano deposits. In the maternity chamber *U. coprophila* is almost exclusively found at the tops of guano piles, with abundance being strongly biased to summer (Figure 2.20b) where it is almost ubiquitous in fresh guano.

Ixodes simplex simplex (Acarina: Ixodidae) is a bat ectoparasite. Individuals were not directly observed during the study but were collected in pitfall traps predominately during summer (2003/04) (Figure 2.20c) corresponding to when most bats are present in the chamber.

Porcellio scaber (Isopoda: Porcellionidae) is an introduced species and a general detritivore (Zimmer and Topp 1998). It is common in the front area of the maternity chamber and generally at the Tops of piles throughout the year (Figure 2.20d). Large numbers of individuals can be found in caves near Bat Cave (e.g. Cathedral Cave), under rocks and organic debris.

Nyteribia parilis vicaria and *Penicillidia tectisentis* (Diptera: Nycteribiidae) are both bat ectoparasites (Maa 1971). They have been observed moving upward in an attempt to locate a wall to climb back onto the roof to find further hosts, but commonly they move to the Tops of guano piles where numerous dead individuals have been observed. These species are commonly found during summer after detaching from bats (Figure 2.20e) with abundances increasing with the bat population.

Phoridae sp. (Diptera) within the maternity chamber are associated with fresh guano. Adult and larva phorids are known to scavenge in carrion and decomposing matter including guano (Colless and McAlpine 1991, Gnaspini and Trajano 2000), and were found in fresh guano at the tops of recently active guano piles. Population levels are highly variable although they are usually highest during summer months but tended to be restricted to only a few piles (Figure 2.20f).

Monopis crocicapitella (Lepidoptera: Tineidae) is commonly recorded in caves containing guano deposits. Larvae are known to feed on bat hair, and chitin of insects from guano and fungi growing within the guano (Robinson and Nielsen 1993). Larvae and adults were ubiquitous throughout the year in the maternity chamber with population peaks in June and November suggesting the species is multi-voltine (Figure 2.21a).

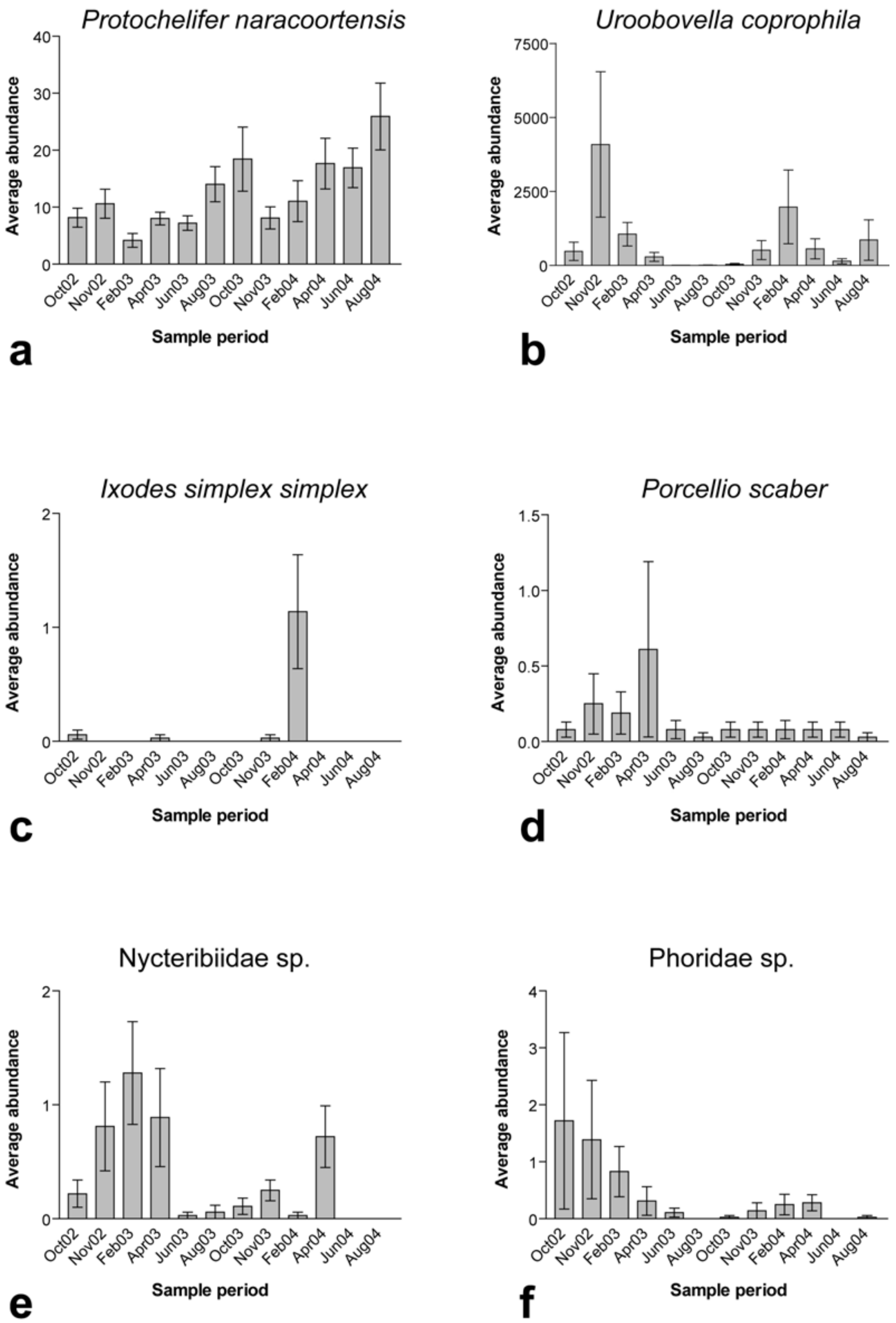

Figure 2.20. a-f. Average species abundances and standard errors for six key species in the maternity chamber.

Apanteles ?carpatus (Hymenoptera: Braconidae) is highly likely to be a larva parasitoid of the lepidopteran *M. crocicapitella* (Austin and Dangerfield 1992). Population levels closely follow those of their *Monopis* host (Figure 2.21a).

Adults were commonly observed walking over the surface of the guano searching for larvae to parasitise. The presence of the parasitoid is interesting in a subterranean environment as parasitic Hymenoptera are generally absent from major subterranean guano ecosystems (Gnaspini 2005). However, wasp parasitiods may be more common than presently believed as this species was not recorded from Bat Cave until a thorough diversity survey was conducted by Bellati *et al.* (2003).

Ptinus exulans (Coleoptera: Anobiidae), a cosmopolitan species, is a scavenger and detritivore, commonly of dry arthropod remains but also of other dried plant and animal material (Lawrence and Britton 1991). It has also been recorded feeding on fungi and insect remains, both in guano deposits and spider webs (Richards 1971, Hickman 1974). Within the maternity chamber it is most likely eating chitin contained in the guano and also fungi. The lower moisture content of guano during winter means more dry chitin is available and probably enables this species to increase in abundance during these conditions (Figure 2.21b).

Speotarus lucifugus (Coleoptera: Carabidae) adults and larvae are generalist predators not associated with any particular micro-habitat. This species is undoubtedly the highest in the food chain due to its large size (~10 mm). It was more common in summer (Figure 2.21c) when arthropod abundance is highest, suggesting that increased prey abundance is a factor influencing its population size.

Anchicera sp. (Coleoptera: Cryptophagidae) is believed to be mycetophageous within the maternity chamber although little is known about its biology. Cryptophagids generally feed on spores or hyphae of moulds and other fungi (Lawrence and Britton 1991), which is consistent with population peaks occurring during winter months (Figure 2.21d) when fungal growth is maximal in the maternity chamber.

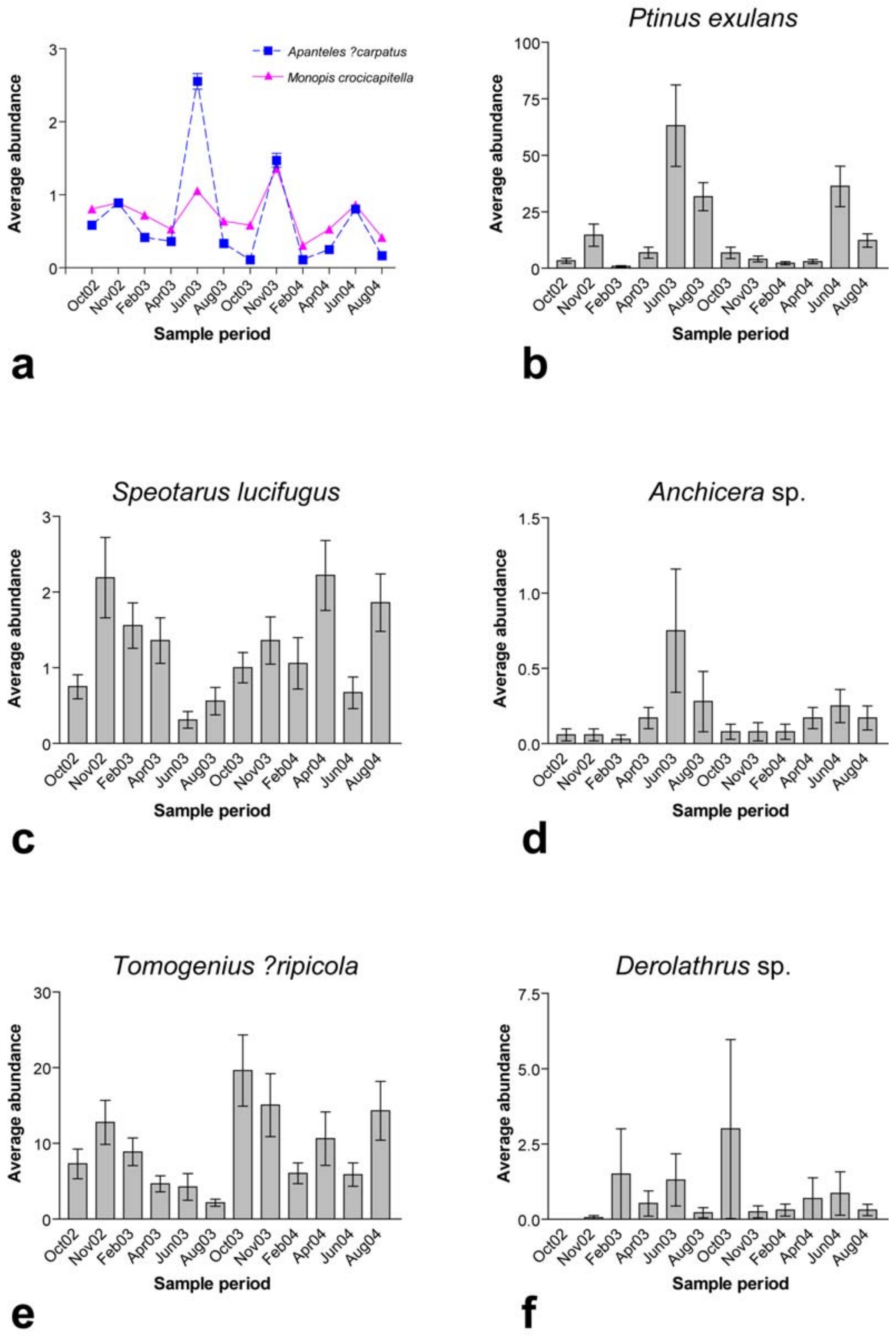

Figure 2.21. a. Average abundances of braconid parasitoids and *Monopis* moths demonstrating very similar population levels. Error bars are standard errors. **b-f.** Average abundances for five key species in the maternity chamber.

Tomogenius ?ripicola (Coleoptera: Histeridae) adults and larvae are predatory (Lawrence and Britton 1991). They were mostly associated with tops of guano piles in the centre of the chamber. During summer months this micro-habitat was dominated by *U. coprophila* suggesting they form a significant part of the beetle's diet. However, *T. ?ripicola* are present throughout the year (Figure 2.21e) and the virtual absence of *U. coprophila* during winter suggests the species consumes other small arthropods.

Derolathrus sp. (Coleoptera: Jacobsoniidae) is exclusively associated with fresh guano at the Tops of active piles. This family contains numerous fungal feeders (Lawrence and Britton 1991) and this species is therefore believed to feed on fungi due to its favoured habitat within fresh guano. Its abundance was variable, with sometimes very large numbers occurring at the tops of piles (Figure 2.21f). The continual presence of this species in the maternity chamber suggests it may use a variety of food sources, as fresh guano and the microflora it contains is present only during summer.

2.3.23 Maternity chamber food web

A simplified food web for the maternity chamber of Bat Cave is shown in Figure 2.22. This was constructed using direct field observations for many taxa (refer to section 2.3.2) combined with previously documented feeding biology for specific species or for the family generally.

Guanophages consist of mycetophages and animals that directly consume guano (Gnaspini and Trajano 2000). This is the most diverse and abundant assemblage of arthropods in the maternity chamber and is further divided in Figure 2.22 into mycetophages that eat micro-organisms (*U. coprophila*, *Derolathrus* sp., *Anchicera* sp. and Psocoptera), and those that consume chitin, either directly from guano or within fungi (*Ptinus exulans*, *Porcellio scabe*r, *M. crocicapitella* and Phoridae sp.).

The three main predatory species present within the maternity chamber are the histerid beetle *T. ?ripicola*, the pseudoscorpion *P. naracoortensis* and the carabid beetle *S. lucifugus*.

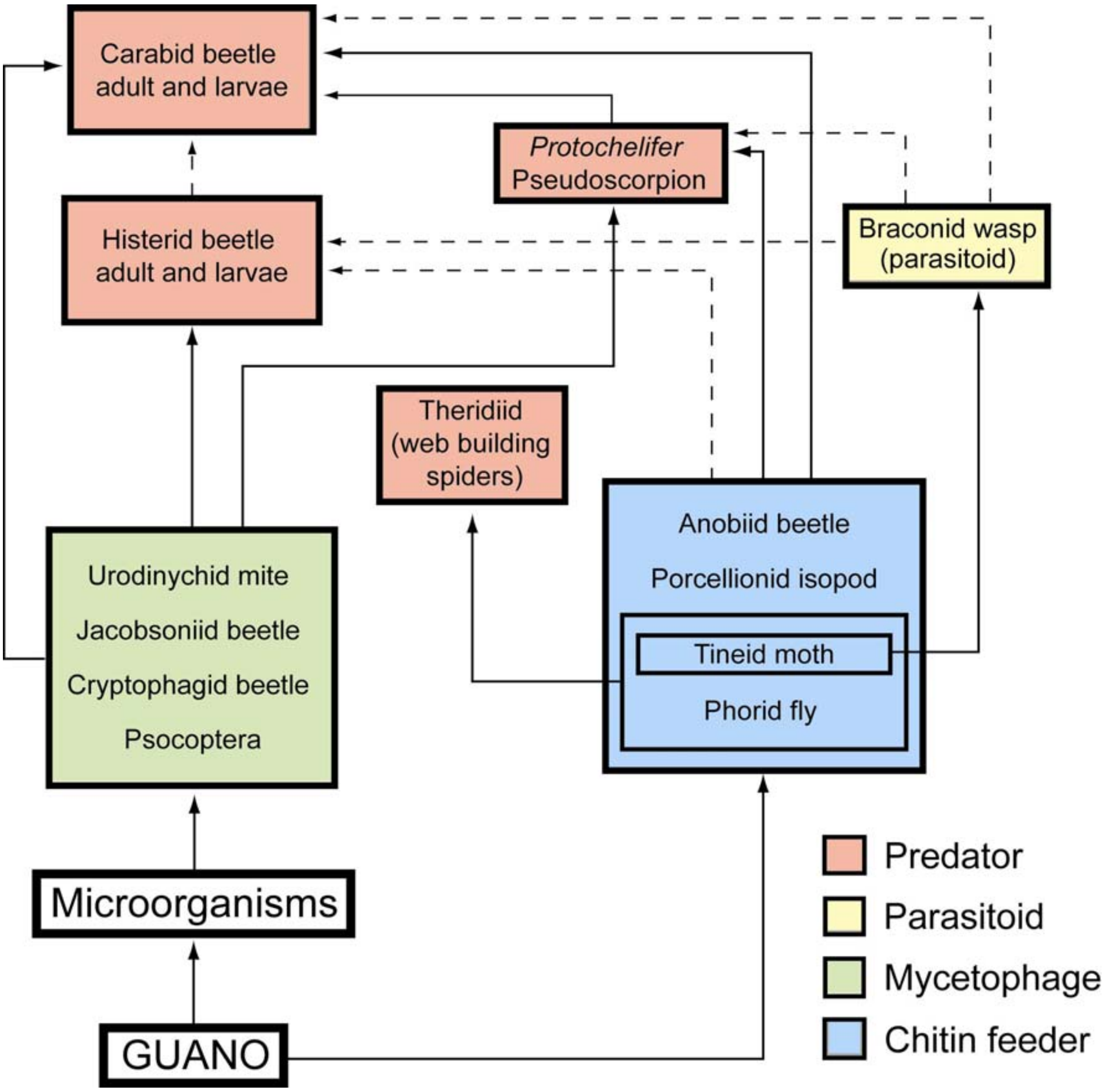

Figure 2.22. Simplified food web for arthropods in the maternity chamber, Bat Cave, Naracoorte. Arrows indicate direction of energy flow. Broken lines indicate possible interactions between taxa while continuous lines represent observed or previously published interactions. Bat parasites, including Nycteribiidae spp. and *Ixodes simplex simplex*, have been excluded from the diagram as they only contribute a minor amount of energy to the system due to their low abundances and lack of interaction with most other arthropods present.

2.3.3 Results - community structure

A two-dimensional NMS ordination of the arthropod community described 95.0% of the variance in the data for all Top and Bottom traps averaged from each sample period. Axis 1 describes 83.5% and Axis 2 describes 11.5%, clearly demonstrating that Tops of guano piles during summer months contained a distinct arthropod assemblage compared with other micro-habitats and seasons (Figure 2.23). The long species' vectors for the mite *U. coprophila* and histerid *T. ?ripicola* shows these two species dominate Tops of guano piles during summer. The assemblage during winter is different and is represented by *P. exulans* at the bottoms of piles and *Anchicera* sp. at the tops of guano piles. The exact date of the bat occupation of the maternity chamber is governed by external factors, including temperature and food availability, thus sampling on the cusp of this activity at the beginning of October can represent depositional or non-depositional arthropod assemblages. This affects the positioning of the summer/winter divide, suggesting *P. naracoortensis* and *Derolathrus* sp. are only associated with the Tops of guano piles and are not related to a particular season. The 'August 2004 Top' trap falls into the summer quadrant due to the uncharacteristic early return of the bat population that resulted in early guano deposition during this sampling period (Figure 2.7). The summer Bottom quadrant does not contain any strongly associated arthropod assemblage.

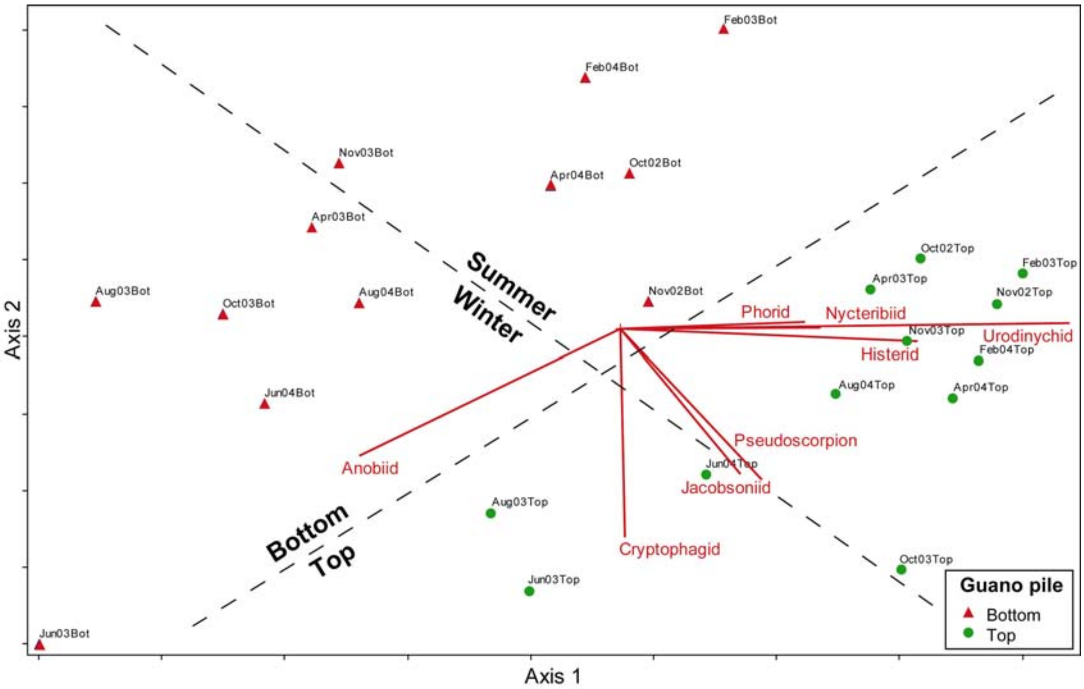

Figure 2.23. A two-dimensional NMS ordination of arthropod community data measured in the maternity chamber. This ordination yielded a stress value of 8.72%, a final instability of 0.00003 and an r^2 value of 0.95 (indicating 95.0% of the variance in the data is explained by the model). Varimax rotation was invoked to align the maximal explained variance with Axis 1. The r^2 vectors are produced by overlaying the original data on itself. The length of the vector indicates the variance explained by the named variable, and the orientation shows the direction of increase. The vectors in this plot are constrained to r^2 >=0.35.

A two-dimensional NMS ordination of the arthropod community for 'Chamber Position' combining Tops and Bottoms from the three chamber positions (Front, Central and Rear) described 94.4% of the variance in the data (Figure 2.24). Axis 1 described 78.9% of the variance and Axis 2 described

15.5% of the variance, showing a strong association of *U. coprophila* and *T. ?ripicola* populations with the Central area. *Ptinus exulans* shows little association with any of the three areas. The traps from the Central area cluster more strongly than the Front or Rear areas, suggesting more homogeneous environmental conditions and species assemblages are present. *Ptinus exulans* is the only species to show a negative relationship with all the environmental variables measured. This species was mostly found in drier areas, with less guano deposition and lower pH conditions.

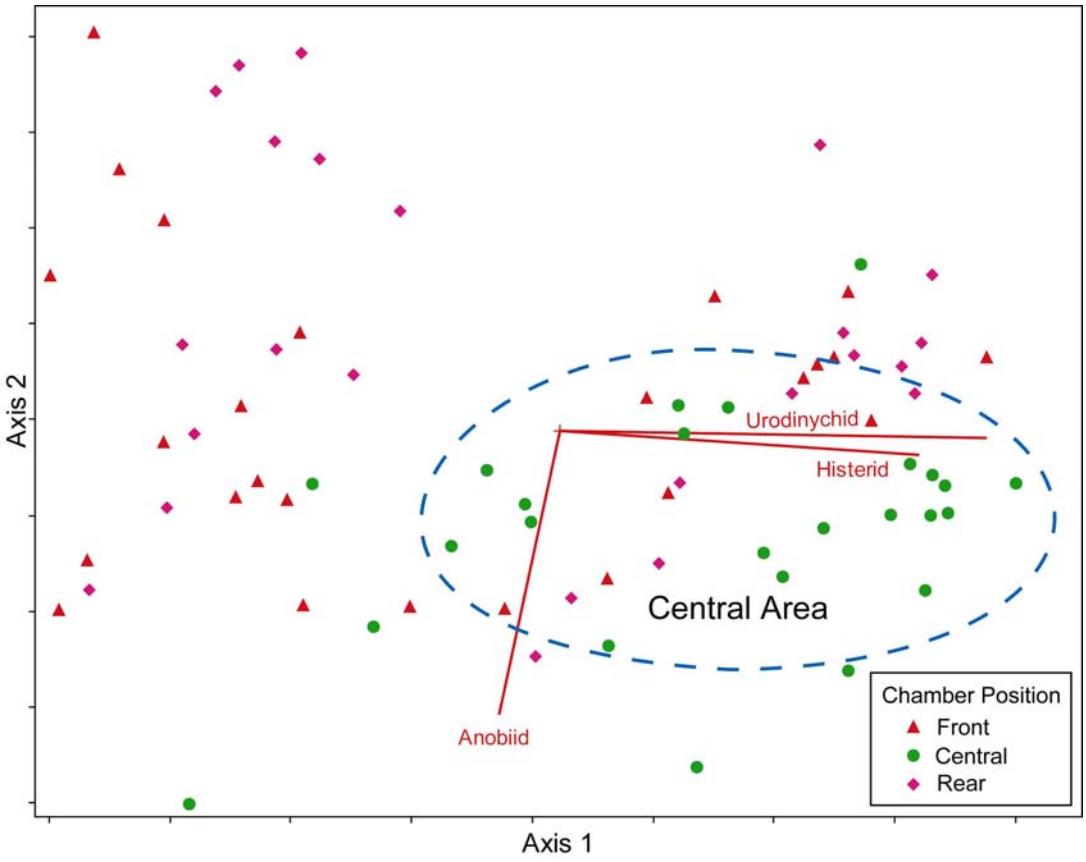

Figure 2.24. A two-dimensional NMS ordination of arthropod community data measured in the maternity chamber. This ordination yielded a stress value of 10.67%, a final instability of 0.00005 and an r^2 value of 0.944 (indicating 94.4% of the variance in the data is explained by the model). Varimax rotation was invoked to align the maximal explained variance with Axis 1. The r^2 vectors are produced by overlaying the original data on itself. The length of the vector indicates the variance explained by the named variable, and the orientation shows the direction of increase. The vectors in this plot are constrained to r^2 >=0.35.

Cluster analysis revealed annual similarity is most important in the composition of the maternity chamber arthropod assemblage (Figure 2.25). The summer 2002/03 and winter 2003 samples group more closely than the winter sample from both years. This suggests that the winter species assemblage is more influenced by the previous summer’s assemblage and environmental conditions than the conditions and community that prevail during the previous winter. Within each season the Tops and Bottoms group together. The October samples are distinctly different from either summer or winter arthropod assemblages, further supporting the premise that they represent a transition assemblage influenced by the time when bats return to the maternity chamber (Figure 2.7). The samples from the first year are more dissimilar between summer and winter than those of the second years sampling, but still group together as indicated above.

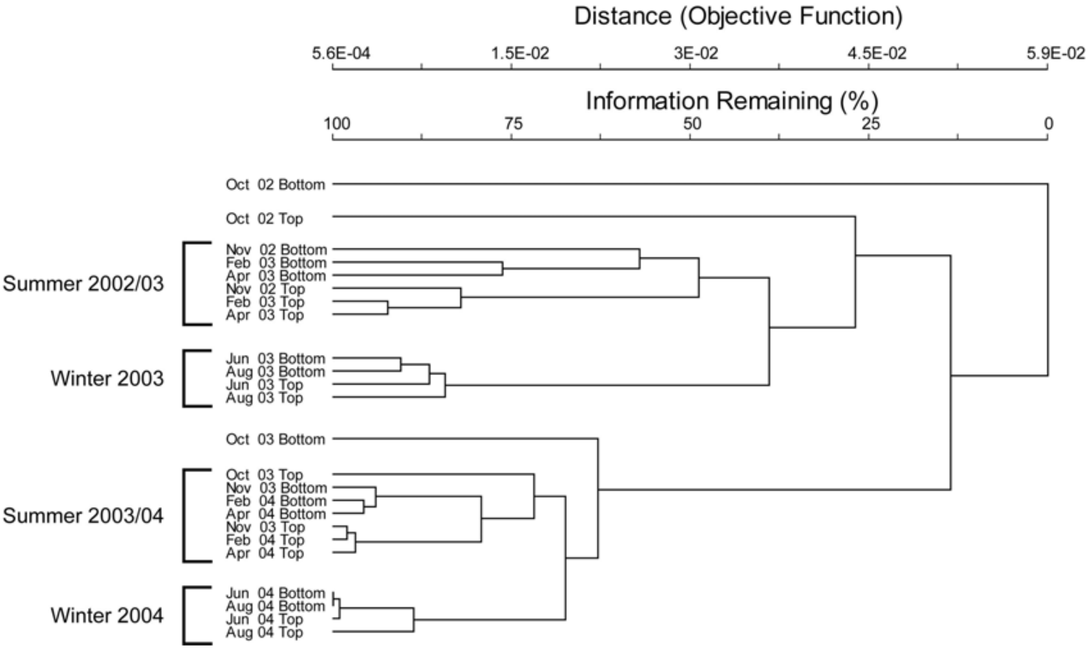

Figure 2.25. Relativised Sorensen cluster dendrogram of community assemblage based on seasonal species diversity and abundance data.

2.3.31 Indicator species analysis

Indicator species analysis shows 12 of the 13 most abundant species collected during the study (Table 2.2) are contributing to the community patterns observed. The position, either Top or Bottom on guano piles, is indicated by eight species (Table 2.3) with all significant results being found at the Tops of guano piles. The arthropod assemblage at the Tops of piles is best indicated by *U. coprophila* (80.1% indication), *T. ?ripicola* (68.8% indication) and *P. naracoortensis* (61.6% indication). The anobiid *P. exulans* is not significant (p = 0.064) in contributing to the assemblage found at the Bottoms of guano piles.

Table 2.3. Significant indicator species for position on guano piles (Top or Bottom) in the maternity chamber of Bat Cave calculated using the method of Dufrene and Legendre (1997) and Monte Carlo significance observed maximum indicator value for each species (1000 permutations). * Anobiidae was included in this table despite the P value > 0.05 as the result was deemed biologically important.

Taxa	Pile Position	% Indication	P
Tomogenius ?ripicola (Histeridae)	Top	68.8	0.001
Anchicera sp. (Cryptophagidae)	Top	57.7	0.001
Derolathrus sp. (Jacobsoniidae)	Top	49.2	0.001
Protochelifer naracoortensis (Pseudoscorpion)	Top	61.6	0.001
Uroobovella coprophila (Urodinychidae)	Top	80.1	0.001
Phoridae sp.	Top	45.8	0.001
Nycteribiidae sp.	Top	56.6	0.001
Porcellio scaber (Porcellionidae)	Top	46.1	0.001
Ptinus exulans (Anobiidae)*	Bottom	57.4	0.064

Table 2.4. Significant indicator species for position within the maternity chamber of Bat Cave (Front, Central and Rear) calculated using the method of Dufrene and Legendre (1997) and Monte Carlo significance observed maximum indicator value for each species (1000 permutations).

Taxa	Chamber Position	% Indication	P
Ptinus exulans (Anobiidae)	Central	41.6	0.039
Apanteles ?carpatus (Braconidae)	Central	64.4	0.001
Tomogenius ?ripicola (Histeridae)	Central	48.2	0.001
Porcellio scaber (Porcellionidae)	Front	24.8	0.033
Derolathrus sp. (Jacobsoniidae)	Central	32.2	0.006
Monopis crocicapitella (Tineidae)	Rear	44.4	0.005
Uroobovella coprophila (Urodinychidae)	Central	44.4	0.014

Seven species are indicators of chamber position (Front, Central and Rear) with five of these contributing to the Central area assemblage (Table 2.4). *Apanteles ?carpatus* and *T. ?ripicola* are the best indicators of the Central area with indicator values of 64.4% and 48.2%, respectively. The only species to indicate the Front area is the isopod *P. scaber*, although the indication value is quite low at 24.8%. The moth *M. crocicapitella* is the sole indicator species for the Rear area of the chamber.

Only five species are significant indicators of seasonal arthropod assemblages within the maternity chamber (Table 2.5). The most significant of these is *P. exulans* with a 55.5% indication value for winter (p = 0.001). *Anchicera* sp. is only a weak indicator of winter arthropod assemblages (34.0% p =0.047), possibly due to the extremely low abundance of this species (Table 2.2). *Speotarus lucifugus*, Nycteribiidae spp. and *U. coprophila* are all significant indicators of summer arthropod assemblages. No species was found to be an indicator of the cusp of guano deposition, (generally during the month of October).

Table 2.5. Significant indicator species for seasonal presence within the maternity chamber of Bat Cave (Summer, Winter and October) calculated using the method of Dufrene and Legendre (1997) and Monte Carlo significance observed maximum indicator value for each species (1000 permutations).

Taxa	Season	% Indication	P
Ptinus exulans (Anobiidae)	Winter	55.5	0.001
Speotarus lucifugus (Carabidae)	Summer	44.3	0.004
Anchicera sp. (Cryptophagidae)	Winter	34.0	0.047
Nycteribiidae sp.	Summer	33.6	0.024
Uroobovella coprophila (Urodinychidae)	Summer	46.0	0.020

The most useful indicator species in the maternity chamber were those found in distinct micro-habitats and seasons. This includes *U. coprophila* found in association with pile Tops and the Central area during summer, and *P. exulans* associated with pile Bottoms and the Central area during winter. *Tomogenius ?ripicola* and *Derolathrus* sp. were both indicators of pile Tops in the Central area.

2.4 Discussion

The arthropod community within the maternity chamber varied in diversity and abundance at several different spatial and temporal scales. Species' distribution and abundance varied spatially within the maternity chamber as different species show preferences for different areas, either Front, Central or Rear.

These areas are differentiated by different amounts of fresh guano deposition during summer. Species also exhibit a preference for particular micro-habitats associated with either the Tops or Bottoms of guano piles resulting in significant differences between arthropod communities found there. Strong seasonal patterns of diversity and abundance were directly associated with fresh guano. Because epigean seasonal effects within the chamber are minimal the variation seen in the arthropod community is undoubtedly a flow on effect of the bat's seasonal rhythm. This is clearly demonstrated by the effect of guano deposition on pH, moisture, and consequently on the resident arthropod community. Micro-habitats associated with guano can be separated at fine spatial scales by often large changes in pH, moisture content and amount of guano deposition. These environmental factors appear to directly influence the arthropod community both spatially and temporally within the maternity chamber. Patches of fresh and old guano form a continuous mosaic of micro-habitats ranging from guano that has been immediately deposited to guano at the edges of depositional areas that may be years or even centuries old. Arthropods and micro-organisms form a succession of communities on guano deposits as micro-habitats alter with time (Gnaspini and Trajano 2000, Poulson and Lavoie 2000).

The composition and calorific value of bat guano are variable according to the diet of the bat species concerned (Hutchinson 1950, Studier *et al.* 1994). The energy contained within insectivorous bat guano is difficult to access for most arthropods as much of the calorific content is held in complex and difficult to breakdown compounds such as chitin. The majority of this energy is made available to higher trophic levels by bacteria, fungi and yeasts that consume and breakdown much of the chitin (Fletcher 1975). This in turn provides food for mycetophageous arthropods such as *U. coprophila*, *Derolathrus* sp., *Anchicera* sp., and Psocoptera (Figure 2.22).

The positive linear relationship between increasing pH and moisture content and species richness show that increasing guano deposition is associated with higher species richness (Figures 2.15 and 2.16). However, Simpson's index shows an inverse relationship with increasing moisture content and, to a lesser extent, guano deposition, indicating that the relationship is more complex than shown by species richness alone. This indicates that areas subject to the largest amount of fresh guano deposition and, hence, higher pH and moisture content, are numerically dominated by a handful of species (Table 2.2), despite consistently containing the highest species richness. The strong linear relationship between the upper 25% quantile of Simpson's diversity index and moisture content show that while increased moisture can lead to dominance by a small number of species, other factors are influencing diversity at lower levels. The same can be observed with guano deposition, where maximal diversity values are achieved from low, but not entirely absent, deposition rates. The strong correlation between pH, moisture content and amount of guano deposited in any location obscures the precise relationships of these variables with species richness.

The apparent absence of the guanophilic cockroach *Neotemnopteryx australis* Saussure in this study may indicate a real decline in the abundance of this species within Bat Cave. Bellati *et al.* (2003) recorded only a few juvenile specimens during their study. This is in stark contrast to previous visually assessed abundances by Hamilton-Smith and Clarke (Bellati *et al.* 2003). This may linked to the established populations of invasive species such as the isopod *Porcellio scaber* into the maternity chamber.

2.4.1 Spatial variation in arthropod communities

The Central area of the maternity chamber, situated under the main bat roost, receives the largest quantity of fresh guano during each birthing season and shows higher overall abundances of virtually all species. Due to the large amount of fresh guano the largest abundance of *U. coprophila* was found in this area, while *T. ?ripicola,* a predator of this mite, is also present in high numbers. Five different arthropod species, occupying differing micro-habitats within the Central area, have been identified as significant indicators for this area (Table 2.4). The parasitoid *A. ?carpatus* was the best indicator species for the central area despite its host species, the moth *M. crocicapitella,* being an indicator species for the rear of the chamber (Table 2.4) and occurring there in higher abundance throughout the study. The lack of season or micro-habitat preference for *A. ?carpatus* is most likely because it moves freely over guano piles in search of lepidopteran larvae to parasitise.

The Front and Rear areas of the maternity chamber have much lower species richness and consequently fewer indicator taxa. The amount of guano deposited in both these areas varies substantially compared with the Central area and their micro-habitats are more similar to each other than to the Central area. The less predictable amount of guano deposition results in a more variable arthropod assemblage as *U. coprophila* and *T. ?ripicola* are unable to dominate the guano resource, as occurs in the Central area during summer. The isopod *P. scaber* is a significant indicator of the Front area probably due to the close proximity to the cave entrance where this species is ubiquitous throughout the year. Individuals of *P. scaber* may move into the maternity chamber in search of food or higher temperatures and humidity, thus increasing the population of this species within the Front area of the chamber.

The direct correlation between increased fresh guano deposition and increased pH and moisture content results in the Tops of guano piles exhibiting very different micro-habitats to the Bottoms. Tops of piles contain the highest species richness with many species acting as significant indicators for this micro-habitat, such as *U. coprophila*, *T. ?ripicola* and *P. naracoortensis*. *Uroobovella coprophila* requires fresh guano as a food source, living on associated micro-organisms, while *T. ?ripicola* and *P. naracoortensis* must favour this environment as prey density is higher there. It is unknown whether the high moisture content or pH are also important in determining species richness at these sites.

The bottom of guano piles receive virtually no fresh guano deposition and, hence, have lower *in situ* moisture content. The bottoms of piles are generally inhabited by the beetle *P. exulans* that consumes chitin from the drier guano (see 2.3.22). Despite not being a significant indicator species for the bottom of piles (Table 2.3), this species is strongly associated with conditions found at these sites. This lack of statistical significance is possibly because, during winter months, this species also occupies the top of guano piles in large numbers, but migrates to the bottom as piles dry out and the pH drops as a result of the cessation of guano deposition. This drying effect means that the micro-habitat conditions at Tops of piles during winter months are very similar those at the Bottoms of guano piles during summer. This has a major impact on the arthropod assemblage found at the Tops of piles during winter, which becomes more similar to that commonly associated with the Bottoms of piles during summer, due to environmental conditions becoming more homogeneous.

2.4.2 Seasonal variation in arthropod communities

The summer arthropod assemblage in the maternity chamber is more diverse and has overall higher abundances than the winter assemblage. However, the vast majority of this abundance comprises *U. coprophila* with few other species represented by significant numbers aside from *T. ?ripicola*. *Uroobovella coprophila* is ubiquitous throughout the Central area, and also dominates the Tops of piles in the Front and Rear areas.

The arthropod assemblage in the maternity chamber as a whole during summer shows a remarkable diversity. Species such as the carabid *S. lucifugus*, a generalist predator, shows no preference for any area of the chamber or position on guano piles (Table 2.3 and 2.4), but is a significant indicator species for summer. The higher prey density during summer is believed to allow this general predator to increase in abundance during this period. The NMS ordination (Figure 2.23) shows the species vectors for *P. naracoortensis* and *Derolathrus* sp. are near the summer/winter boundary, indicating that the presence/absence of these taxa is associated with a change in the level of fresh guano, although they are not completely reliant on this change.

As guano deposition in the maternity chamber almost ceases in winter, the abundance of fungal and chitin feeding species such as *M. crocicapitella, P. exulans*, *N. minusculus* (Leiodidae), and *Anchicera* sp. (Cryptophagidae) increases. During winter, the top of guano piles dry out with the cessation of guano deposition, enabling *P. exulans,* and other chitin feeders that rely on it as a primary food source, to exploit these altered conditions and greatly increase their populations. *Ptinus exulans* is found throughout the year at the bottom of guano piles but can be found across the entire chamber when micro-habitat conditions become more homogeneous during winter. Individuals are absent only from Tops of consistently active piles in the Central area. The population of *A. ?carpatus* peaks during June, its emergence matching that of its lepidopteran host, indicating that its emergence occurs near the maturity of moth larvae.

The majority of strongly seasonal guanophilic and guanobitic species found in the maternity chamber were still present throughout the year, although in much reduced numbers outside their preferred seasons. It is unknown what strategies many of the fresh guano specialists use to survive the winter months in Bat Cave as only U. coprophilla has been the subject of a detailed ecological study (Harris 1973). Many cavernicolous guano species are believed to lay eggs at the end of summer allowing the next generation to hatch as guano deposition recommences in the following spring. For example, *U. coprophila* was extremely abundant during summer (<150,000) but only a few hundred were collected in winter. This species quiesces during winter when fresh guano is unavailable and becomes active again when guano deposition recommences (Harris 1973).

The dendrogram of arthropod assemblages (Figure 2.25) shows that seasonal assemblages cluster together. The samples from October collected at the cusp of the return of the bat population are distinct within these clusters and do not group strongly with any season. The first (2002/03) and second (2003/04) sample years cluster more closely than seasonal assemblages, suggesting that the summer assemblage largely affects the composition of the subsequent winter assemblage. This is not unexpected as the amount and spatial pattern of guano deposited during summer months provides the entire energy input for the following winter until the bat population returns around October. Assemblages associated with the Bottom and Top of piles for each season group together, indicating that micro-habitat conditions are more strongly influenced by the deposition of guano in the chamber than by the absolute location at the top and bottom of piles. The terminal branches of the dendrogram for 2003/04 are much shorter than those from 2002/03 indicating that conditions within the chamber during the second year were much more uniform between sampling periods.

2.4.3 Temperate guano arthropod communities compared with other regions

Guano dependent arthropod communities have been the subject of very few studies in contrast to other cave communities, especially in Australia (Moulds 2004). This study is the first to quantitatively describe the micro-habitat and seasonal variables affecting the structure of a guano dependent arthropod community. Arthropod assemblages were found to be more indicative of guano micro-habitat than particular seasons and alter when unseasonal bat occupation occurs during winter within the maternity chamber. The fauna of the maternity chamber of Bat Cave is extremely diverse when compared with the majority other cave communities in Australia and is one of the most diverse guano communities in Australia (Bellati *et al.* 2003, Moulds 2004). Due to the paucity of knowledge in this field only broad comparisons can be made with other guano dependent arthropod communities around the world. Several studies have been conducted in the tropical caves of Brazil and these describe guano communities supported by fruit, insect and vampire bats (Trajano and Gnaspini 1991, Ferreira and Martins 1999, Gnaspini and Trajano 2000). These studies recognised different arthropod communities in each guano type and indicate that differences between tropical and temperate guano communities are often related to different patterns of bat activity and seasonal versus non-seasonal cave occupancy. Temperate guano communities from North America (Horst 1972, Poulson 1972, Martin 1975, Martin 1977, Poulson 1992, Poulson and Lavoie 2000) reveal similar community structures to those found in Bat Cave although the diversity, especially at family level, is undoubtedly dictated by biogeographic patterns between continents and latitude. Poulson and Lavoie (2000) hypothesise that pulsed guano deposition, which generally occurs in temperate regions, leads to dominance by a few species, while low, steady rates of deposition allow for a more diverse community. This study supports their hypothesis as fresh guano that is highly moist and basic is dominated by three taxa, the mite *U. coprophila*, the pseudoscorpion *P. naracoortensis* and the beetle *T. ?ripicola*. Guano deposits in the maternity chamber during winter were also dominated by a single species, *P. exulans*, further supporting the hypothesis of Poulson and Lavoie (2000).

2.4.4 Conclusions

The structure of the guano dependent arthropod community in the maternity chamber of Bat Cave Naracoorte shows significant differences at several spatial and temporal scales. Highly seasonal guano deposition results in a strongly structured series of guano micro-habitats with associated arthropod communities. This occurs both within each guano pile (Tops vs Bottoms) and between different areas of the maternity chamber. The relationships between species richness, and associated diversity measures cannot be determined by this study alone. It is almost certain that several other (unknown) variables are affecting these relationships given the significant relationships determined using quantile regression techniques. Further experimental work is required to determine the extent of pH, moisture content and guano deposition in influencing species richness. In the future comparisons of guano associated arthropod communities in tropical regions, the northern hemisphere, and those in Australia could provide an intriguing and potentially informative method of studying community interactions (e.g. competition, niche partitioning) as these relatively simple communities reflect major biogeographical patterns.

Chapter 3: Arthropod diversity, seasonality and ecology of Starlight Cave, western Victoria

3.1 Introduction

The southern bent-wing bat, *M. s. bassanii* uses only two maternity sites: Bat Cave at Naracoorte, South Australia, and Starlight Cave, near Warrnambool, western Victoria (Cardinal and Christidis 2000). While the majority (~35,000) of the estimated 50,000 total population of bats use Bat Cave as a maternity site, some 15,000 individuals (Chris Grant pers. comm. 2004) use Starlight Cave as an annual maternity site, returning each summer to give birth and raise young.

The guano deposited by the population of southern bent-wing bat in Starlight Cave supports a diverse arthropod assemblage, although prior to this study few arthropods had been recorded from the cave (Hamilton-Smith and Adams 1966, Hamilton-Smith 1967, Moulds 2004). As Starlight Cave is the only other maternity cave for this bat it provides an ideal comparison with Bat Cave for examining factors that shape the structure of the arthropod community associated with bat guano. This study was undertaken to **1)** examine arthropod species richness and diversity and its association with different guano micro-habitats; **2)** document the physical environment of the cave; **3)** examine seasonal fluctuations in population abundances in Starlight Cave; and **4)** compare the results obtained to that documented for Bat Cave.

3.2 Methods

3.2.1 Physiography of Starlight Cave

Starlight Cave is situated approximately 10 km east of Warrnambool near Allansford, in Miocene marine limestone overlain with Pleistocene aeolianite (Gill 1948). The entrance is a large 30 m wide opening near the top of a near-vertical sea cliff with a large, generally level, outer cavern followed by a steeply dipping ramp down to several high open chambers (Figure 3.1). The Birthing Chamber, located at the base of the ramp, is a small circular chamber containing a single 1.2 m high guano pile at the centre. Moving deeper into the cave, the central corridor is dominated by a very high arched roof approximately

40-50 m high at the centre. A small daylight hole provides a diffuse blue light into the chamber. The floor here is covered in a thin veneer of mostly desiccated guano comprising several small piles (<50 cm high). This area grades into the sloping sides of the corridor. A large (10 m) rise separates the Central Corridor from the Terminal Chamber. This chamber is approximately 50 m high and 30 m in diameter, with two daylight holes in the roof. A soil cone slopes from the northern edge of the chamber and is covered with a thin veneer of mostly desiccated guano.

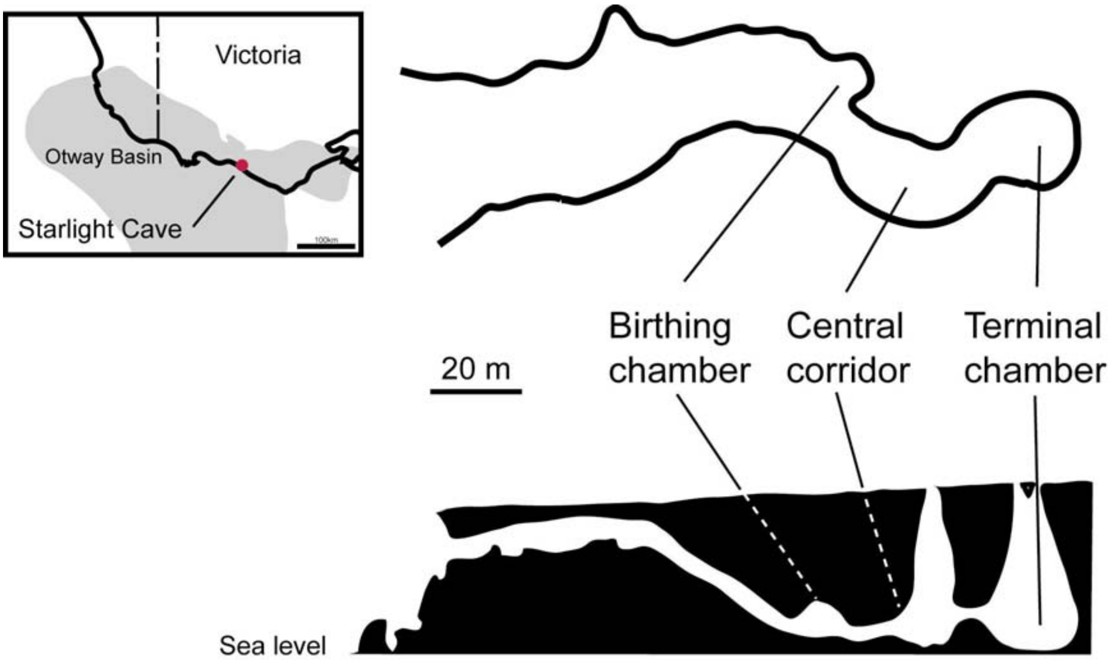

Figure 3.1. Plan and cross-section of Starlight Cave, Warrnambool western Victoria. Cross-section modified after Gill (1948). Plan view developed from a sketch made in the cave by the author.

3.2.2 Arthropod sampling

The study commenced in November 2002, and included two years of sampling over the 2002/2003 and 2003/2004 seasons. The cave was visited in late November and early August each year when arthropod and guano samples were collected. Sampling consisted of the same procedure used in Bat Cave (outlined in Section 2.2.1). The pitfall traps were placed in a systematic pattern, in pairs at the Tops and Bottoms of five guano piles (Figure 3.2). The distance between pairs of pitfall traps was 60 - 150 cm horizontally and 20 – 100 cm vertically. As in Chapter 2, the pitfall traps contained salt water and a small amount of detergent, and were opened for approximately 48 h each sampling period and were set and retrieved at night. All samples were sorted to species in the laboratory and there abundance recorded.

3.2.3 Guano sampling, species richness and diversity indices

Guano depositional rates and environmental variables were calculated using the methods described in section 2.3.2. Averages were calculated for all samples per season for the three areas of the cave; Birthing Chamber, Central Corridor and Terminal Chamber. Species richness and diversity indices were calculated using Simpsons index described in section 2.2.3.

3.2.4 Data Analysis

Data analysis was conducted using a variety of methods. These included Quantile regression as described in Section 2.2.4. Environmental and community structure variables were analysed using Nonmetric Multidimensional Scaling (NMS) ordinations in PC-ORD as described in section 2.2.5. Cluster analysis was completed as described in section 2.2.6. Indicator species analysis was conducted according to Dufrene and Legendre (1997) in PC-ORD as described in section 2.2.7.

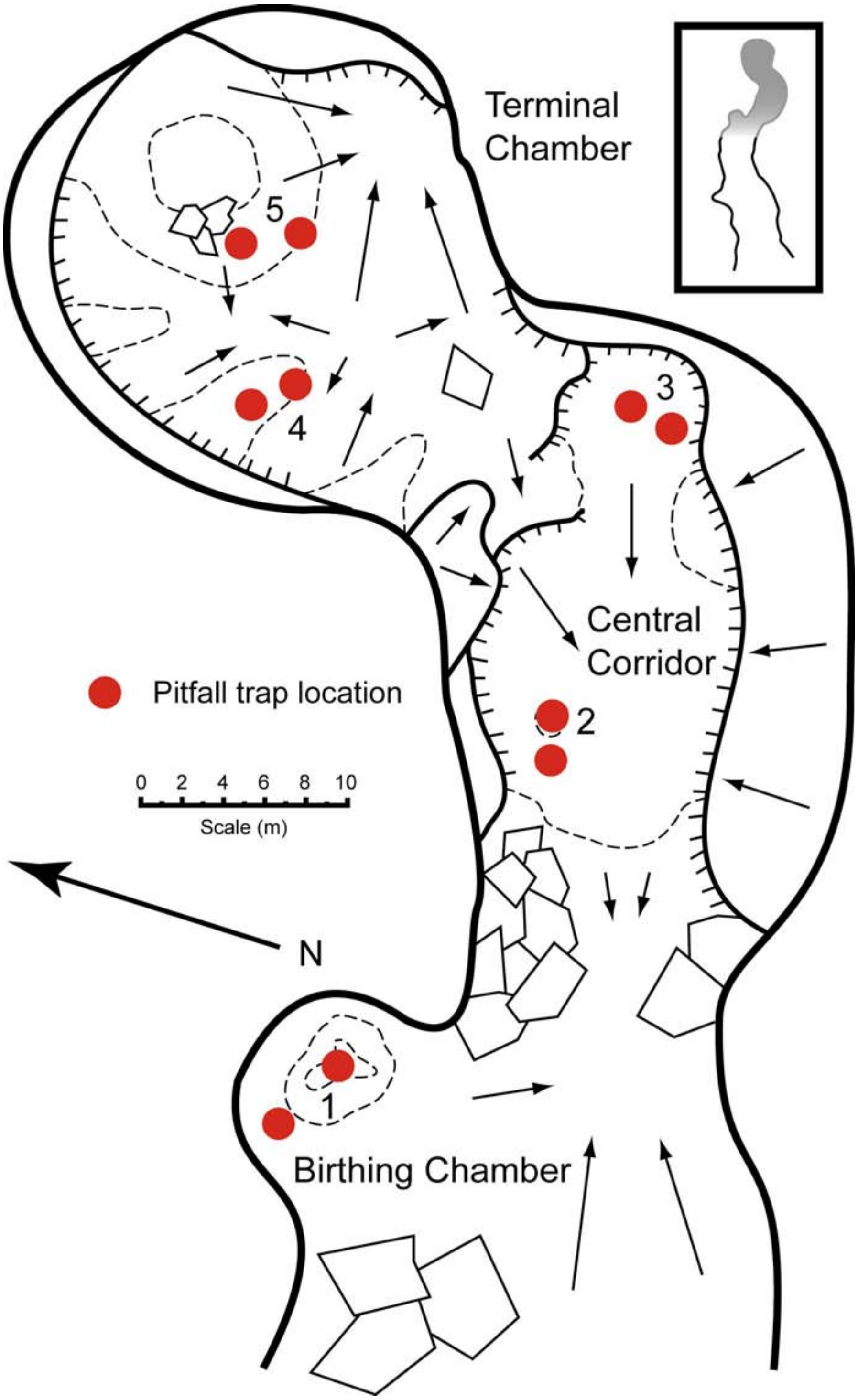

Figure 3.2. Plan view of Starlight Cave, Warrnambool western Victoria showing pitfall trap locations at five sites in the rear of the cave. Arrows indicate downward slope direction.

3.3.1 Results - guano micro-habitat conditions

The Tops of piles had consistantly higher pH than at the Bottoms of guano piles (Figure 3.3). The Tops of guano piles showed an increase in average pH during summer while the Bottoms showed a continuing decrease across all sample periods. The pH of *in situ* guano from Starlight Cave was more variable at the Tops of guano piles than at the Bottoms The average pH of the Birthing Chamber and Central Corridor were very similar (8.0 and 7.8 respectively) (Figure 3.4), but different from that of the Terminal Chamber which was significantly lower (6.2) and experienced less variation among replicates than the other sites. This indicates that deposition of fresh guano in the Terminal Chamber is less or the area dries out faster, causing the guano to become more acidic.

Moisture content of *in situ* guano was found to remain almost constant throughout the study with the Tops of guano piles containing approximately 33% water by weight and the Bottoms of guano piles containing approximately 27% water by weight (Figure 3.5). The maximum to minimum guano moisture content were 13% by weight at the Bottoms and 50% at the Tops of piles. There was little seasonal variation in moisture content suggesting that seasonal guano deposition associated with bat occupancy does not control the moisture content of the guano found within the cave. Average moisture content did vary among the three sample areas with the Terminal Chamber having the driest conditions (21.1%, Figure 3.6), Birthing Chamber the wettest conditions (43.2%), and the Central Corridor being intermediate (33.9%). This indicates that even during summer when bats are present in the cave and urinating onto the guano less moisture is retained in the more exposed areas of the cave i.e. Terminal Chamber and Central Corridor.

Fresh guano deposited during sampling periods was strongly concentrated, as expected, toward the Tops of guano piles (Figure 3.7). The amount of guano deposited at the Tops of piles was variable among piles presumably due to different roosting preferences for bats. Virtually no guano found its way to the Bottoms of guano piles during any sample period as indicated by the almost horizontal line for this location. When comparing the average amount of fresh guano deposited in each area, regardless of season or position on the pile, the most guano was deposited in the Birthing Chamber and Central Corridor (Figure 3.8). However, due to the large variation in deposition among the replicated piles, the apparent differences were not statistically significant among the three locations.

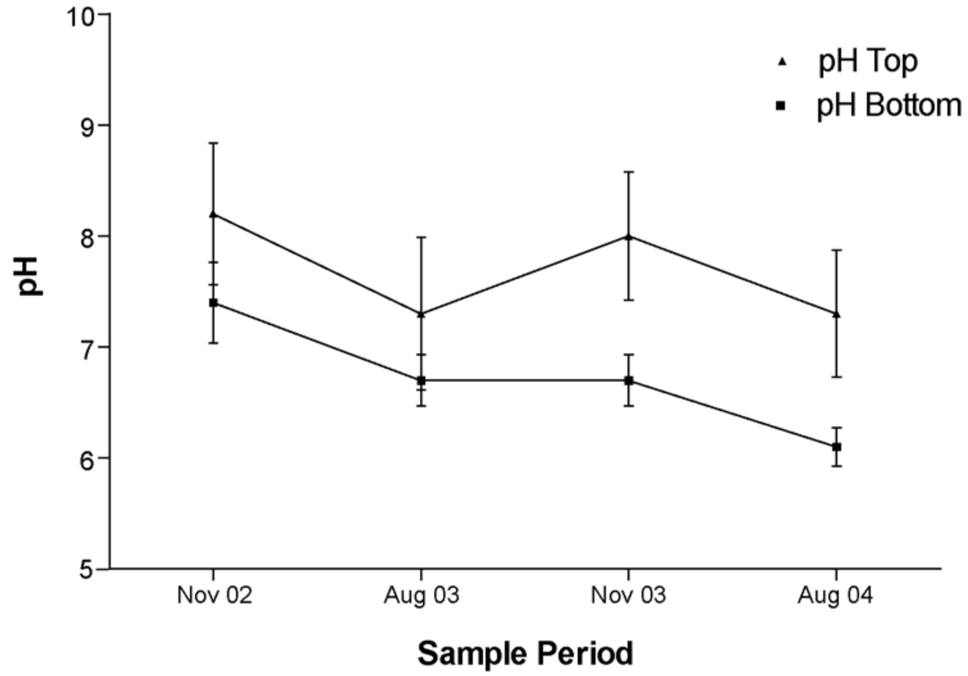

Figure 3.3. pH of *in situ* guano at the Tops and Bottoms of guano piles in Starlight Cave, Warrnambool, Victoria. Error bars are standard errors.

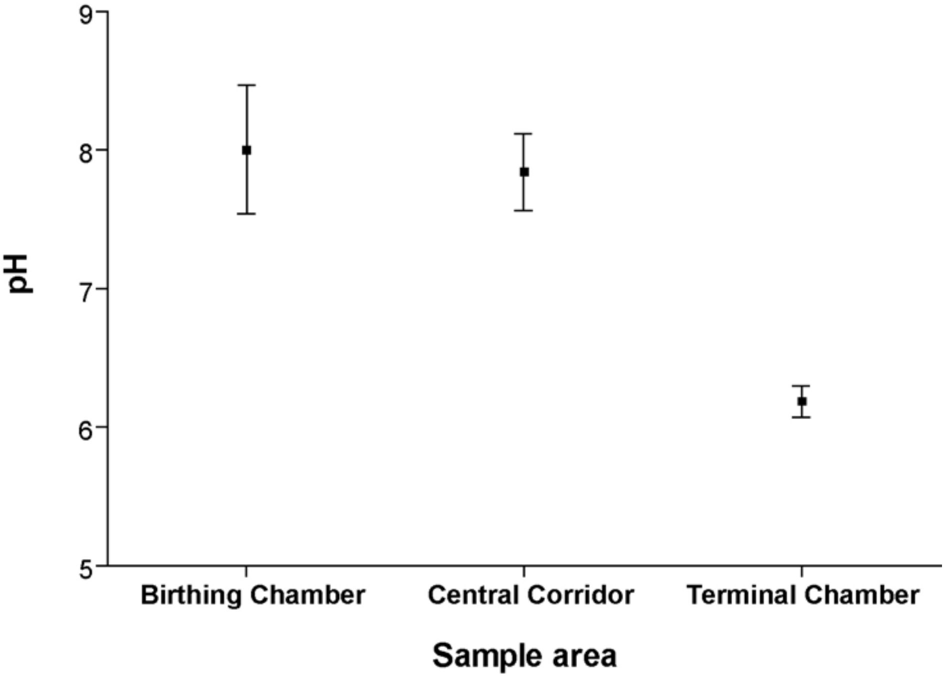

Figure 3.4. Average pH of guano for Tops and Bottoms, summer and winter combined in three areas of Starlight Cave, Warrnambool, western Victoria. Error bars are standard errors.

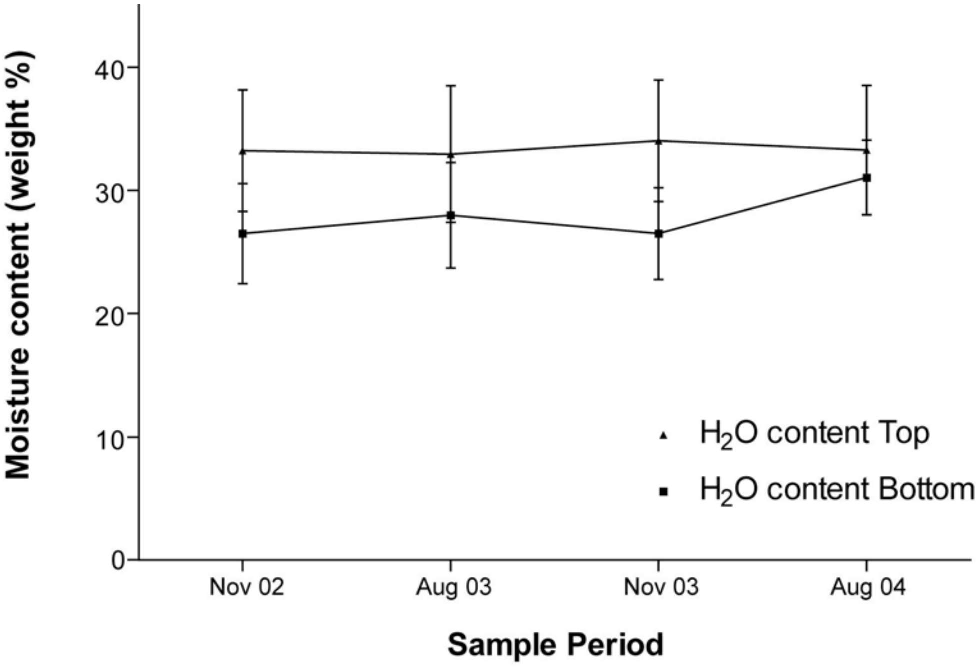

Figure 3.5. Moisture content of *in situ* guano at the Tops and Bottoms of guano piles in Starlight Cave, Warrnambool, Victoria. Error bars are standard errors.

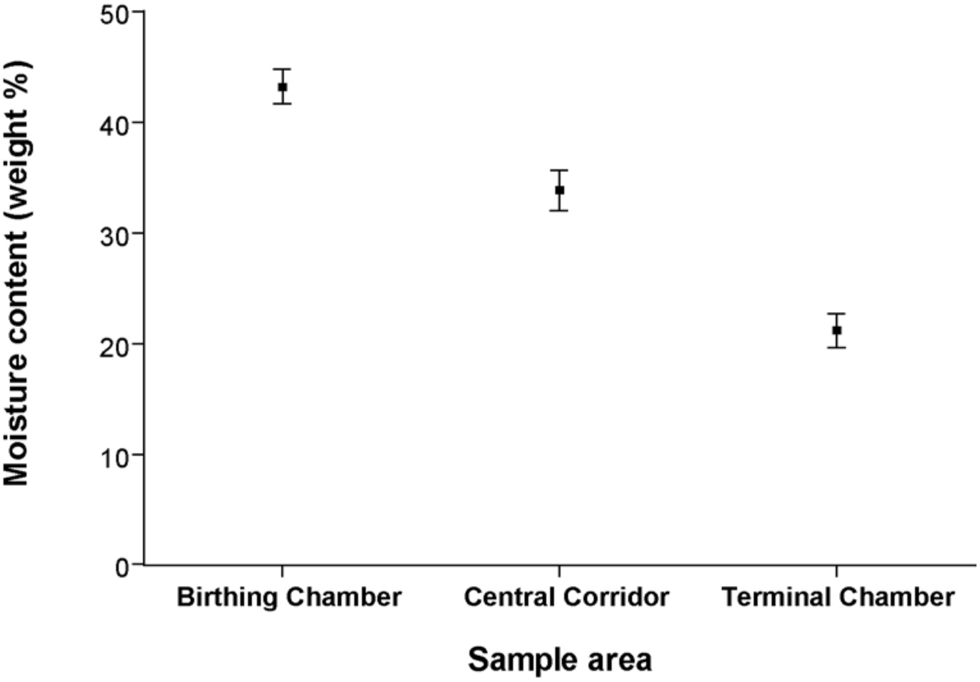

Figure 3.6. Average moisture content of *in situ* guano from Tops and Bottoms, summer and winter combined in three areas Starlight Cave, Warrnambool, Victoria. Error bars are standard errors.

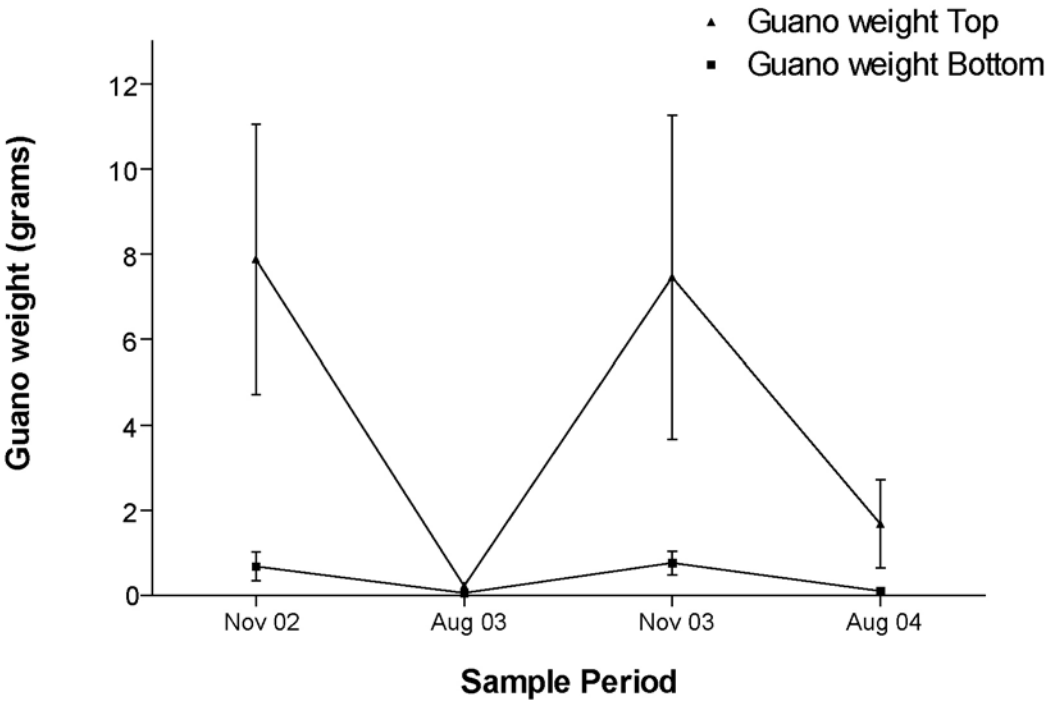

Figure 3.7. Fresh guano deposition at the Tops and Bottoms of guano piles in Starlight Cave, Warrnambool, Victoria. Error bars are standard errors.

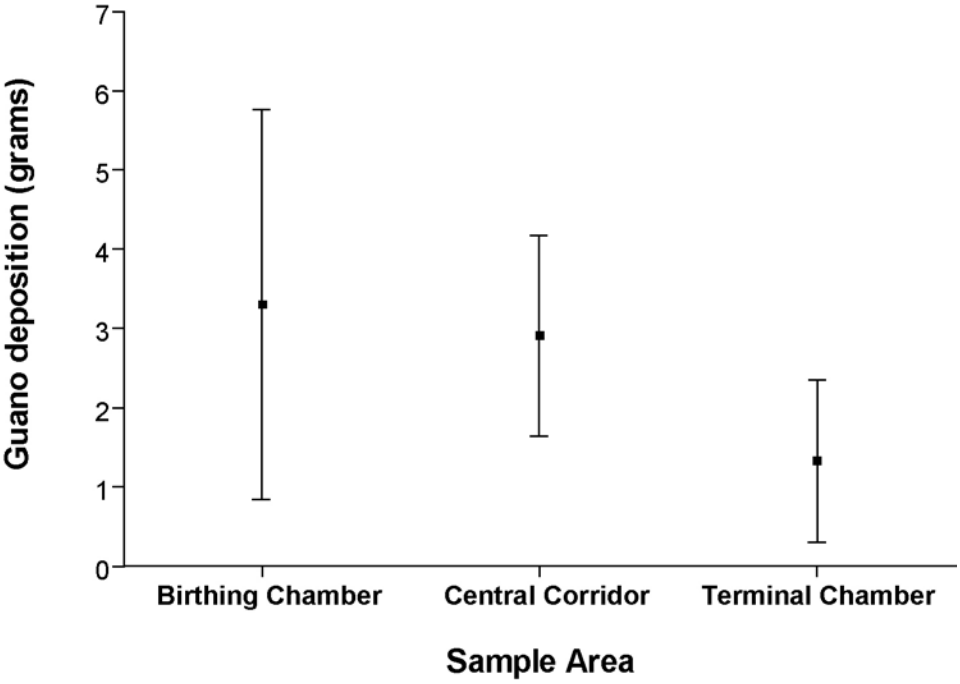

Figure 3.8. Average fresh guano deposition for Tops and Bottoms, summer and winter combined in three areas of Starlight Cave, Warrnambool, Victoria. Error bars are standard errors.

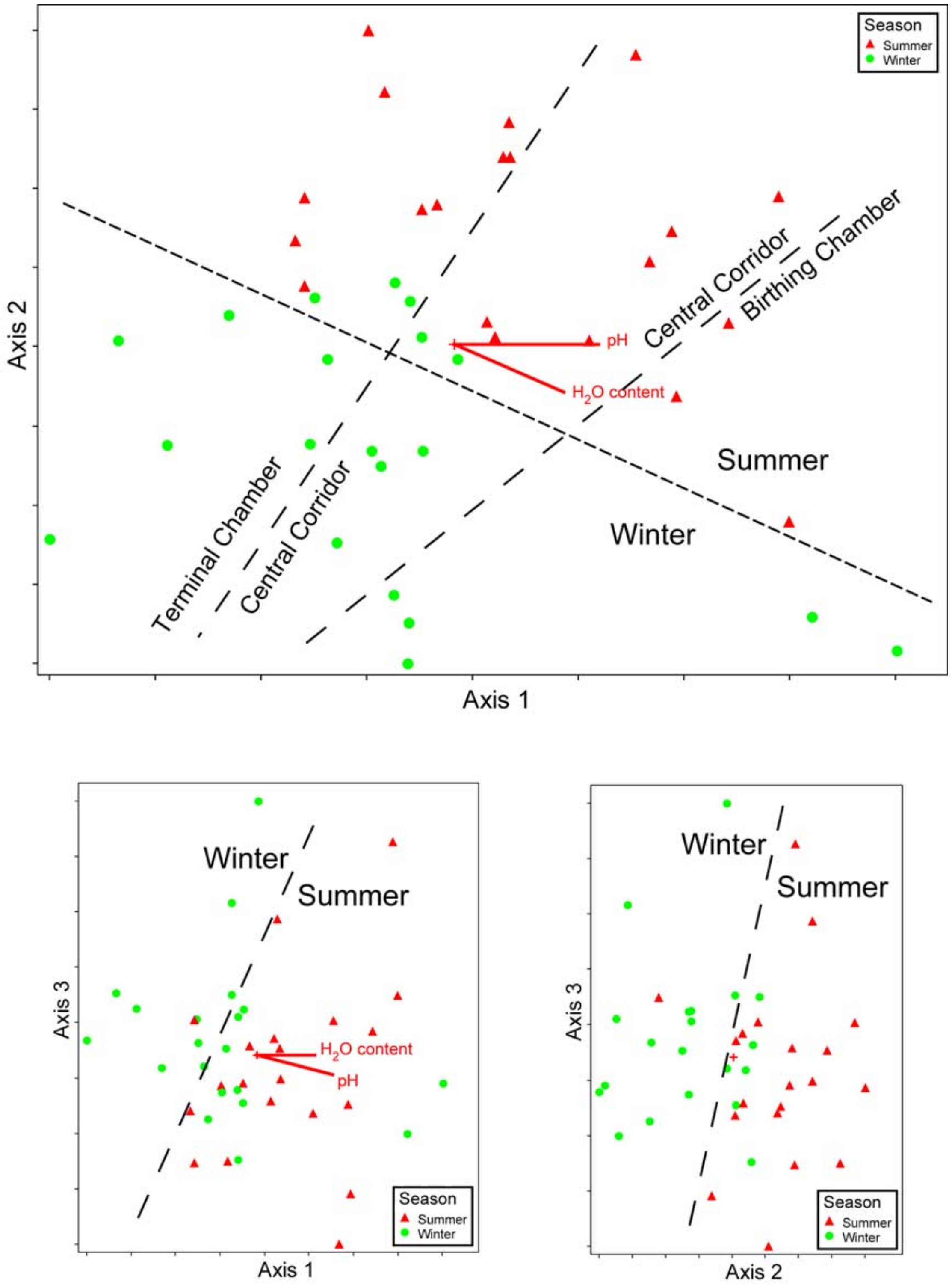

Figure 3.9. A three-dimensional NMS ordination of environmental variables measured in Starlight Cave. This ordination yielded a stress value of 15.14%, a final instability of 0.00001 and an r^2 value of 0.839 (indicating 83.9% of the variance in the data is explained by the model). Varimax rotation was invoked to align the maximal explained variance with Axis 2. The r^2 vectors are produced by overlaying the original data on itself. The length of the vector indicates the variance explained by the named variable, and the orientation shows the direction of increase. The vectors in this plot are constrained to $r^2 > 0.25$.

A three-dimensional NMS ordination described 83.9% of the variance among the environmental variables (pH, guano deposition and moisture content) for Starlight Cave from all sample periods (Figure 3.9). Axis 1 describes 23.7%, Axis 2 describes 39.8% and Axis 3 describes 20.4% of the variation, demonstrating the most important factor controlling the guano micro-habitat is season. The division between summer and winter can be clearly seen in all three aspects of the ordination with the remaining variation being divided by the position of guano piles within the cave. The ordination shows no division of samples according to Top or Bottom of guano piles indicating that the position within the cave and the season during which sampling occurred are the most influential factors in this system. The two significant environmental variables, pH and moisture content, are both associated with summer, and increase toward the birthing chamber where the largest individual guano pile is located.

3.3.2 Results - Species richness and abundance

A total of 44 arthropod species from 39 families and 14 orders were recorded from Starlight Cave (Table 3.1). These include species recorded in previous studies and the present research, with 35 (81%) of previously recorded species also being collected during this study. In addition, 17 species not previously known from Starlight Cave were recorded, representing approximately 40% of the known fauna. The most diverse groups collected were Coleoptera (12 species from 9 families), Diptera (8 species from 7 families) and Acarina (6 species from 6 families).

A total of 14,542 individuals were collected (Table 3.2). A rank abundance graph shows that species conform to a log series model of abundance (Figure 3.10) with *Ptinus exulans* (Anobiidae) showing extremely high abundances and many species having very low abundances.

Table 3.1. Arthropod and nematode species recorded from of Starlight Cave, Warrnambool, western Victoria. Forty-three arthropod and nematode species from 39 families and 14 orders were recorded from this and previous studies. * Unpublished data from Hamilton-Smith recorded in Moulds (2004).

Class and Order	Family	Genus and species	Previous Study	Present study
Nematoda	?Rhabditida	sp.		yes
Crustacea: Isopoda	Porcellionidae	*Porcellio* sp.		yes
	Oniscoidea	sp.	Hamilton-Smith unpublished data	no
Arachnida: Araneae	Thomisidae	*Sidymella* sp.		yes
Acarina	Ixodidae	*Ixodes simplex simplex*		yes
	Macrochelidae	*Macrocheles penicilliger*		yes
	Laelapidae	sp.		yes
	Parasitidae	sp.		yes
	Spinturnicidae	*Spinturnix loricata*		yes
	Urodinychidae	*Uroobovella coprophila*		yes
Pseudoscorpionida	Cheliferidae	*Protochelifer australis*		yes
Collembola	Entomobryidae	*Discocyrtus cinctus*		yes
	Hypogastruridae	*Hypogastrura vernalis*		yes
Insecta: Orthoptera	Rhaphidophoridae	sp.		yes
Psocoptera		sp.		yes
Hemiptera	Lygaeoidea	sp.		yes
Thysanoptera	Thripidae	*Thrips imaginis*		yes
Coleoptera	Anobiidae	*Ptinus exulans*	Hamilton-Smith 1967	yes
	Carabidae	*Mecyclothorax ambiguus*	H-S unpublished data*	no
		Speotarus princeps		yes
	Cryptophagidae	*Atomaria* sp.	Hamilton-Smith 1967	yes
	Dermestidae	sp.	H-S unpublished data*	no
	Histeridae	*Saprinus* sp.	H-S unpublished data*	no
		Tomogenius ?ripicola		yes
	Jacobsoniidae	*Derolathrus* sp.	Hamilton-Smith 1967	yes
	Leiodidae	*Pseudonemadus* sp.	Hamilton-Smith 1967	yes
	Silphidae	*Ptomaphila lachrymosa*	H-S unpublished data*	no
	Staphylinidae	*Myotyphlus jansoni*	Hamilton-Smith and Adams 1966	yes
		Philonthus parcus		yes
Diptera	Fannidae	*Fannia* sp.	H-S unpublished data*	no
	Nycteribiidae	sp.		yes
	Phoridae	sp.		yes
	Psychodidae	sp.		yes
	Sciaridae	sp.		yes
	Sphaeroceridae	*Leptocera* sp.	H-S unpublished data*	no
		Limosininae sp.		yes
	Tipulidae	sp.		yes
Lepidoptera	Tineidae	*Monopis crocicapitella*		yes
Hymenoptera	Braconidae	*Apanteles ?carpatus*		yes
	Ceraphronidae	sp.		yes
	Diapriidae	sp.		yes
	Formicidae	*Amblyopone australis*	H-S unpublished data*	no
	Ichneumonidae	Cryptinae sp.		yes

The species richness in Starlight Cave was higher during the second year's sampling than during the first, and greater at the Tops of guano piles compared with the Bottoms during the second year (Figure 3.11). Species richness at the bottom of guano piles remained almost constant at approximately six species per sample. The Birthing Chamber had the highest average species richness, compared with both the Central Corridor and Terminal Chamber (Figure 3.12). Species richness shows a positive correlation with moisture content and pH, although the fit (r^2 = 0.11 and 0.25 respectively) is poor (Figure 3.13 and 3.14).

Table 3.2. Arthropod abundance and percent composition in Starlight Cave. [1]Abundances for the two species of Staphylinidae, *Myotyphlus jasoni* and *Philonthus parcus*, and the Collembola, *Discocyrtus cinctus* and *Hypogastrura vernalis* were grouped as the species were not identified until after the study was complete.

Taxa	Total Abundance	% of Total Abundance
Ptinus exulans (Anobiidae)	12 271	84.4%
Tomogenius ?ripicola (Histeridae)	783	5.4%
Laelapidae sp.	350	2.4%
Phoridae sp.	338	2.3%
Monopis crocicapitella (Tineidae)	198	1.4%
Nycteribiidae sp.	123	0.9%
Atomaria sp. (Cryptophagidae)	86	0.6%
Cryptinae sp. (Ichnuemonidae)	68	0.5%
Protochelifer australis (Pseudoscorpionida)	64	0.4%
Staphylinidae spp.[1]	64	0.4%
Sciaridae sp.	52	0.4%
Limosininae sp. (Sphaeroceridae)	46	0.3%
Uroobovella coprophila (Urodinychidae)	31	0.2%
Macrocheles pencilliger (Macrochelidae)	18	0.1%
Collembola spp.[1]	17	<0.1%
Spinturnix loricata (Spinturnicidae)	10	<0.1%
Derolathrus sp. (Jacobsoniidae)	8	<0.1%
Lygaeoidea sp.	5	<0.1%
Sidymella sp. (Tnomisidae)	3	<0.1%
Curculionidae sp.	2	<0.1%
Speotarus princeps (Carabidae)	2	<0.1%
Porcellio sp. (Porcellionidae)	1	<0.1%
Pseudonemadus sp. (Leiodidae)	1	<0.1%
Rhaphidophoridae sp.	1	<0.1%
Total Abundance	14542	100%

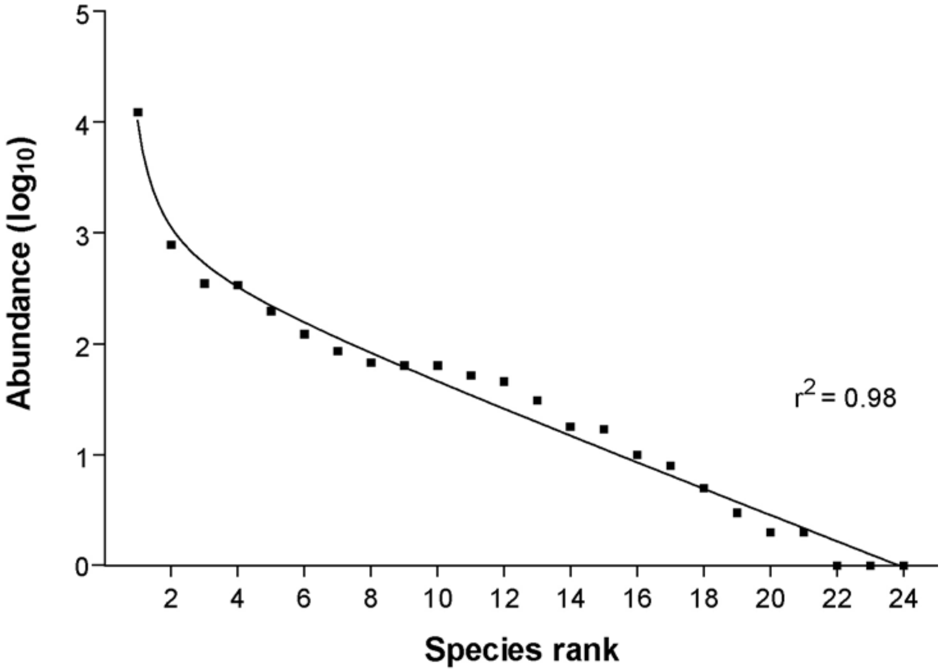

Figure 3.10. Rank abundance graph of 24 taxa collected from Starlight Cave presented as a two binding hyperbola fitted to the data. Taxa in ascending order are *Ptinus exulans* (Anobiidae), *Tomogenius ?ripicola* (Histeridae), Laelapidae sp., Phoridae sp., *Monopis crocicapitella* (Tineidae), Nycteribiidae sp., *Atomaria* sp. (Cryptophagidae), Cryptinae sp. (Ichneumonidae), Staphylinidae spp., *Protochelifer australis* (Pseudoscorpionida), Sciaridae sp., Sphaeroceridae sp., *Uroobovella coprophila* (Urodinychidae), *Macrocheles penicilliger* (Macrochelidae), Collembola spp., *Spinturnix loricata* (Spinturnicidae), *Derolathrus* sp. (Jacobsoniidae), Lygaeoidea sp., *Sidymella* sp. (Thomisidae), *Speotarus princeps* (Carabidae), Curculionidae sp., *Porcellio* (Porcellionidae), *Pseudonemadus* sp. (Leiodidae) and Rhaphidophoridae sp.. Abundances were $\log_{10}$ transformed prior to analysis.

Simpson's diversity index values show the most diverse arthropod assemblages are associated with micro-habitats with higher pH (Figure 3.15). Quantile regression of the upper 25th quantile showed a significant ($p < 0.0001$) positive linear relationship between pH and Simpson's diversity index (r^2 = 0.90). The relationship remains significant ($p < 0.0001$) when using the upper 50th quantile (r^2 = 0.62). Moisture content and amount of fresh guano show no significant relationship between with Simpson's diversity index (Figures 3.16 & 3.17).

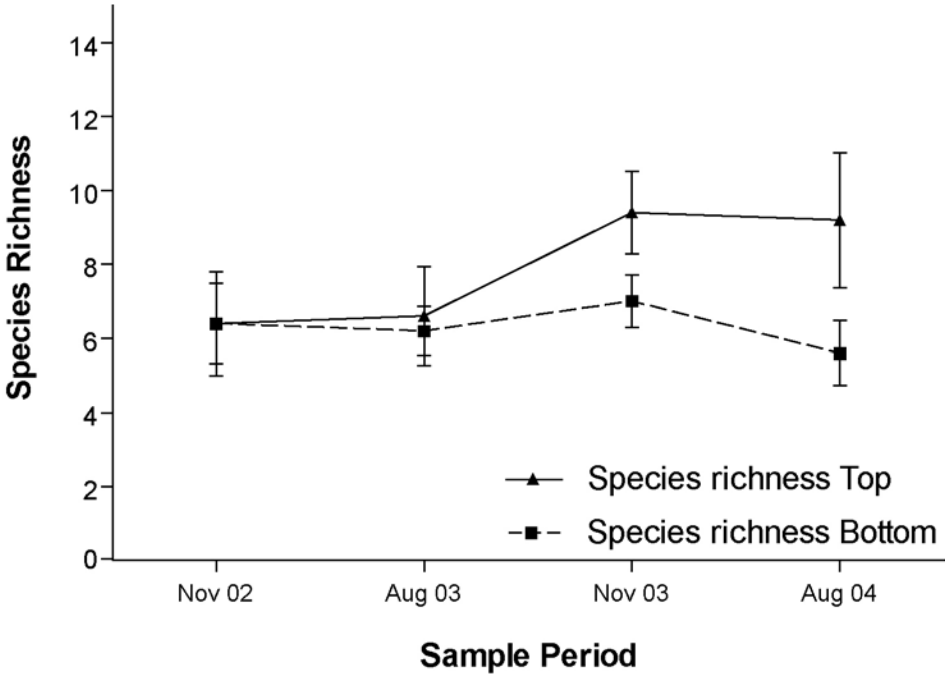

Figure 3.11. Average species richness from Tops and Bottoms of guano piles from 4 sample periods in Starlight Cave. Error bars are standard errors.

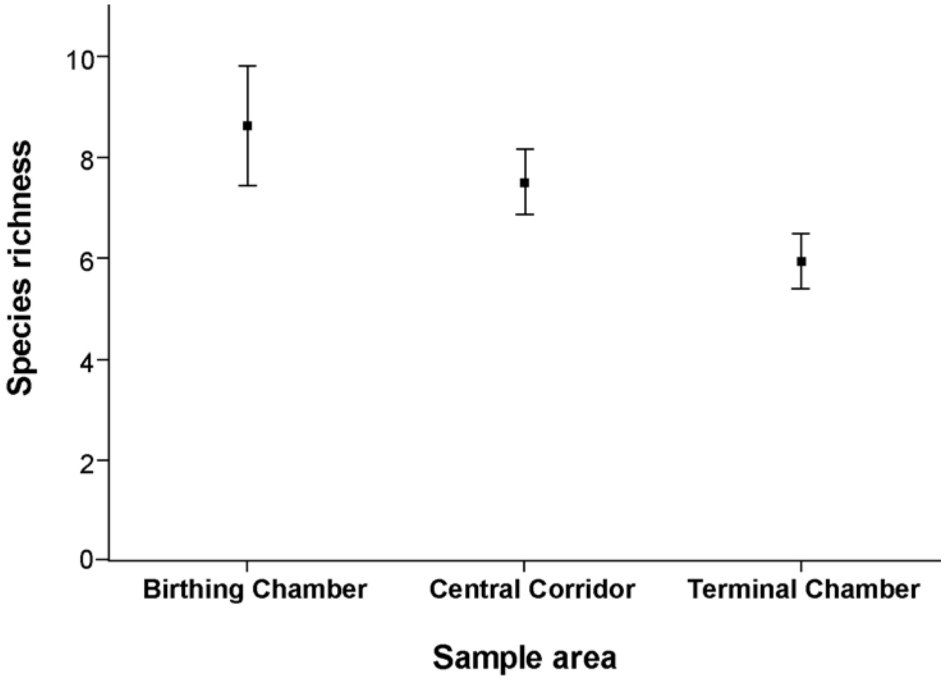

Figure 3.12. Average species richness for three areas of Starlight Cave, for Tops and Bottoms of all sample periods combined. Error bars are standard errors.

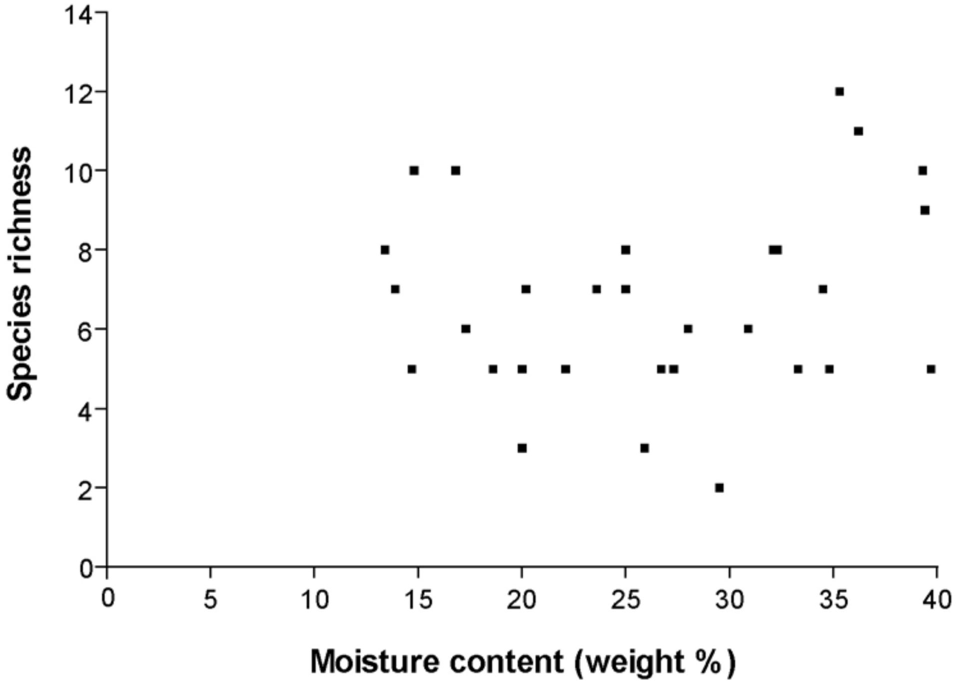

Figure 3.13. Moisture content of *in situ* guano plotted against species richness from 40 pitfall traps and four sample periods in Starlight Cave. The data show a significant correlation ($p<0.05$) although r^2 values for linear regression is 0.11.

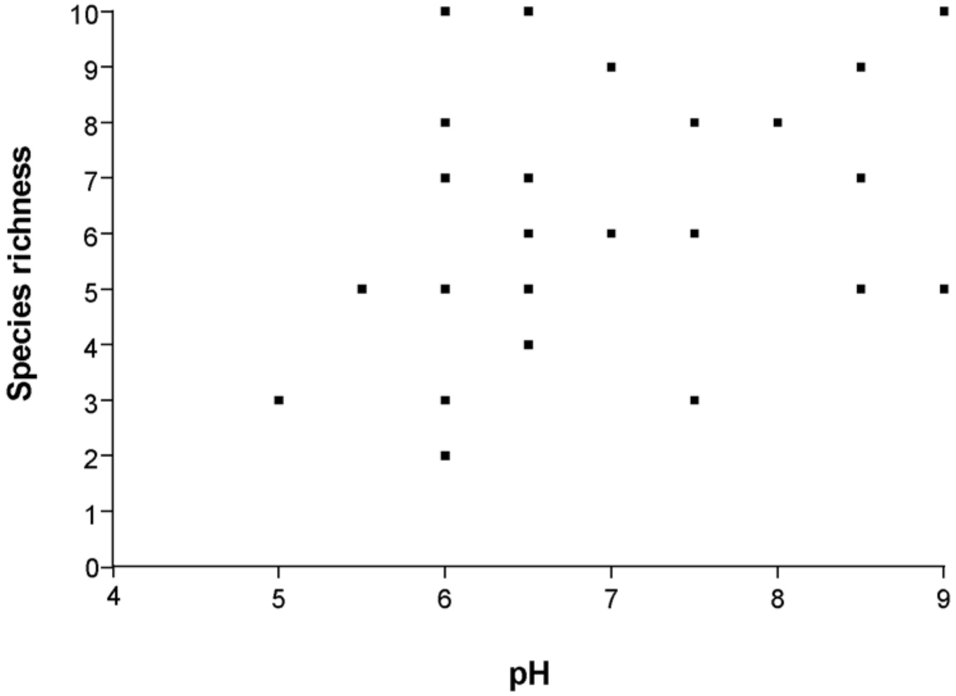

Figure 3.14. pH plotted against species richness from 40 pitfall traps and four sample periods in Starlight Cave. The data show a significant correlation ($p<0.001$) although r^2 values for linear regression is 0.25.

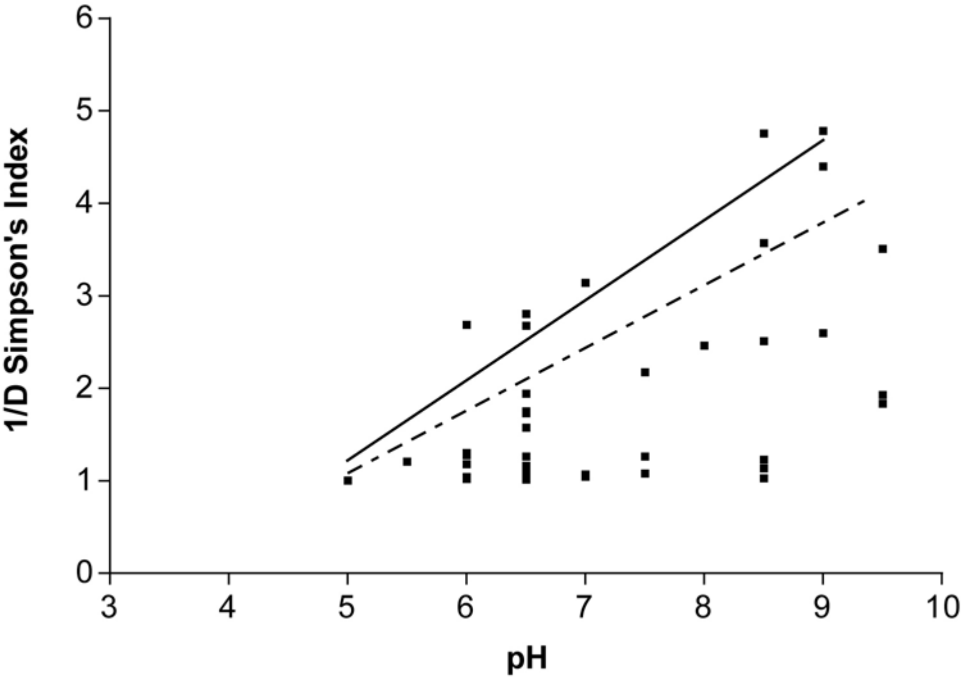

Figure 3.15. pH plotted against Simpson's diversity index from all pitfall traps from all four sample periods combined for Starlight Cave. Quantile regression estimates for upper 25th (y = 0.85x-2.95) and 50th (y = 0.66x-2.21) percentile bands in descending order.

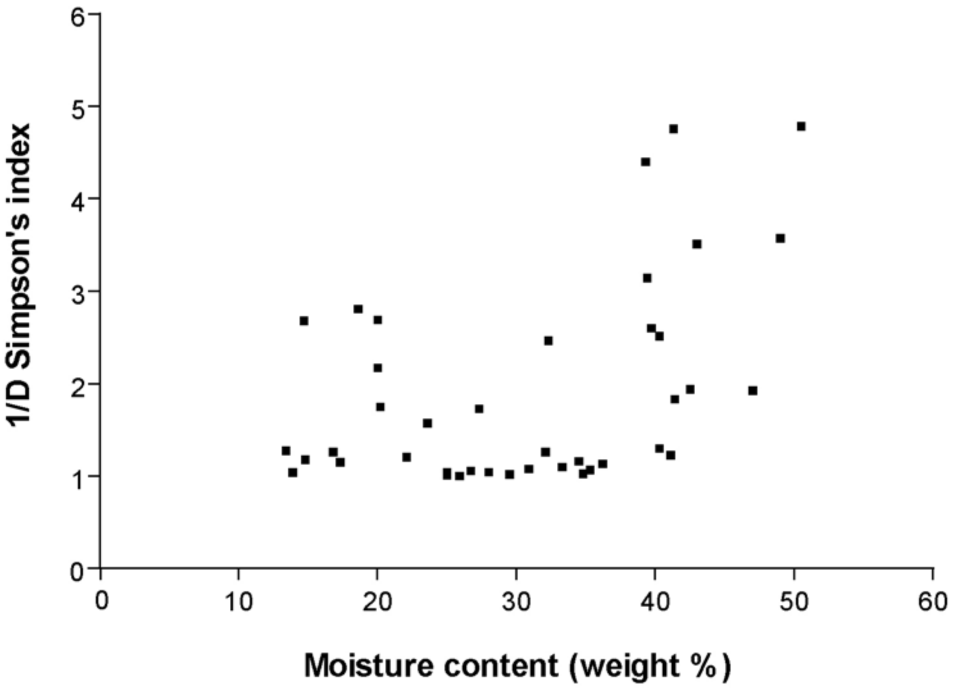

Figure 3.16. Moisture content of *in situ* guano plotted against Simpson's diversity index from 40 pitfall traps and four sample periods, combined for Starlight Cave. A five site binding hyperbola fitted the data with an r^2 value of 0.42 although the result was not significant.

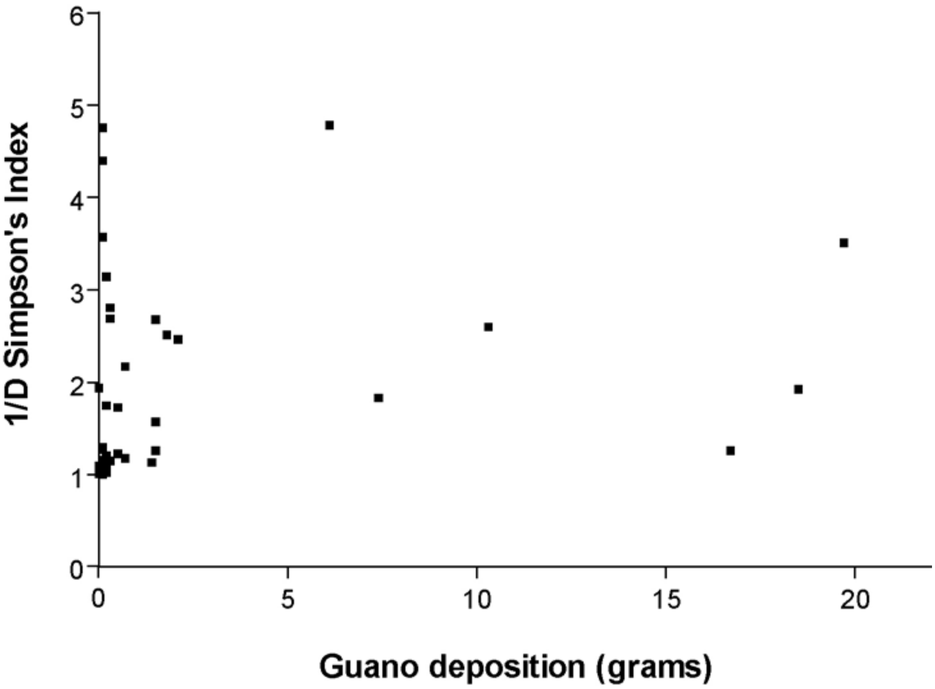

Figure 3.17. Fresh guano deposition plotted against Simpson's diversity index from 40 pitfall traps and four sample periods combined for Starlight Cave. The data show no significant linear correlation ($p=0.19$) with an r^2 value of 0.04.

3.3.3 Results - Community structure

The composition of the arthropod community within Starlight Cave varied with different guano micro-habitats. This variation was affected by several factors including the deposition of fresh guano by bats and, to a much lesser extent, by seasonal weather impacting through the daylight holes located in the rear of the cave. Distribution patterns throughout the cave and relative species abundances were further elucidated using multiple analyses.

A three-dimensional NMS ordination described 83.9% of the variance of the arthropod community for Starlight Cave from all sample periods (Figure 3.18). Axis 1 describes 17.5%, Axis 2 describes 32.0% and Axis 3 describes 34.3% of the variation, demonstrating that the most important factor controlling the guano micro-habitat was season. The division between summer and winter is clearly seen in all three aspects of the ordination while there is no separation between Tops and Bottoms of guano piles. Summer is dominated by *T. ?ripicola*, *M. crocicapitella*, the ichneumonid wasp and the nycteribiid fly ectoparasite. The winter arthropod assemblage is dominated by *P. exulans*, as well as many of the dipteran species including Phoridae sp., Sciaridae sp., Limosininae sp. and the beetle *Atomaria* sp.

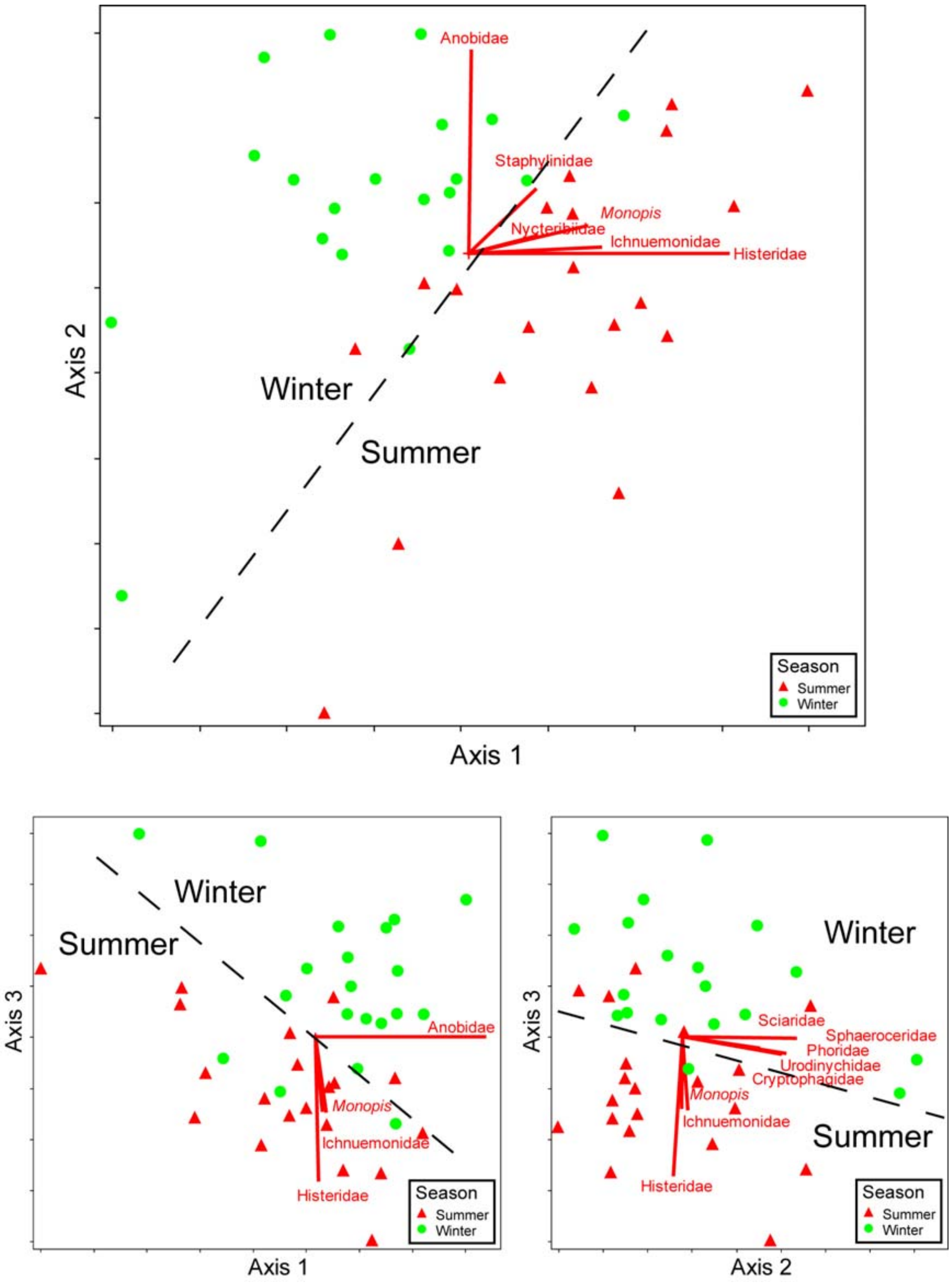

Figure 3.18. A three-dimensional NMS ordination of the arthropod assemblage in Starlight Cave. This ordination yielded a stress value of 15.14%, a final instability of 0.00001 and an r^2 value of 0.839 (indicating 83.9% of the variance in the data is explained by the model). Varimax rotation was invoked to align the maximal explained variance with Axis 3. The r^2 vectors are produced by overlaying the original data on itself. The length of the vector indicates the variance explained by the named variable, and the orientation shows the direction of increase. The vectors in this plot are constrained to $r^2 > 0.30$.

Cluster analysis performed on the average species abundance data for Tops and Bottoms of guano piles from four sample periods showed there was little similarity between sample period or season, as indicated by the very long terminal branch lengths in the dendrogram (Figure 3.19). The arthropod assemblage for Tops of guano piles during winter (August) cluster together and separate from all other samples indicating that their composition is markedly different from the rest. The only samples to group closely are the Bottoms of winter and summer piles from 2003. The summer samples from 2002 are distinctly different between Tops and Bottoms of piles suggesting that significant differences existed in micro-habitat conditions between these sample areas for this period. There is virtually no other sub-structuring in the dendrogram, indicating that the arthropod assemblages are somewhat stochastic rather than being influenced by the assemblage in the preceding period, as appeared to be the case for Bat Cave at Naracoorte (Chapter 2).

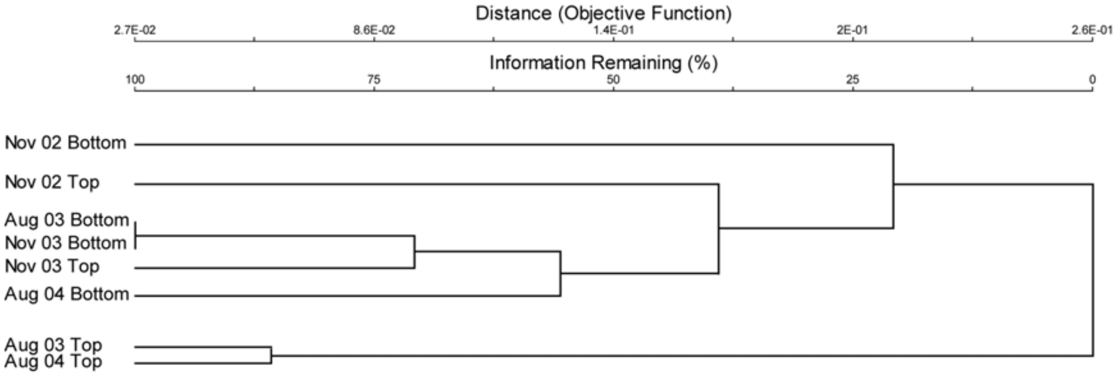

Figure 3.19. Relativised Sorensen cluster dendrogram of community assemblage based on seasonal species diversity and abundance data.

3.3.31 Indicator species analysis

Indicator species analysis shows that while many species are indicative of a particular area within Starlight Cave, there are few species that can be used to effectively predict micro-habitat. Three species are significant indicators of position within individual guano piles, although all are for the Bottoms of piles (Table 3.3). This suggests that there is little fidelity between taxa and micro-habitat within Starlight Cave or, alternatively, no marked difference in micro-habitat between Tops and Bottoms of guano piles. The mite *U. coprophila* is not considered to be genuinely associated with the bottom of guano piles, despite the marginally significant result (p =0.049), as this species was conclusively shown to inhabit fresh guano found at the Tops of guano piles (Chapter 2). Rather the extremely low number of individuals collected during this study (Table 3.2) has probably resulted in a statistical artefact that should be disregarded.

Table 3.3. Significant indicator species for position on guano piles (Top or Bottom) from Starlight Cave calculated using the method of Dufrene and Legendre (1997) and Monte Carlo significance observed maximum indicator value for each species (1000 permutations).

Taxa	Pile Position	% Indication	P
Crytinae sp. (Ichnuemonidae)	Bottom	47.2	0.030
Protochelifer australis (Pseudoscorpion)	Bottom	51.6	0.040
Uroobovella coprophila (Urodinychidae)	Bottom	29.4	0.049

Seven species are indicators of different areas within Starlight Cave (Table 3.4). The Birthing Chamber is most clearly represented with five of the seven indicator species for the whole cave. The lower roof height and greater concentration of guano deposition makes this area more similar to micro-habitats found in Bat Cave. The homogeneous conditions probably contribute to the higher degrees of species fidelity found in this area, especially amongst guanophilic Diptera such as Phoridae sp. (71.6% indicator value) and Sciaridae sp. (58.8% indicator value). *Uroobovella coprophila* is also an indicator of this area along with *Atomaria* sp. (Cryptophagidae). The only indicator species for the Terminal Chamber is *P. exulans*, but it has a low value (39.2%) presumably because this species is found at all sampled locations but in much greater abundance at sample sites four and five in the Terminal Chamber.

Table 3.4. Significant indicator species for the position of guano piles within Starlight Cave (Birthing Chamber, Central Corridor or Terminal Chamber) calculated using the method of Dufrene and Legendre (1997) and Monte Carlo significance observed maximum indicator value for each species (1000 permutations).

Taxa	Cave Position	% Indication	P
Ptinus exulans (Anobiidae)	Terminal	39.2	0.017
Atomaria sp. (Cryptophagidae)	Birthing	52.8	0.002
Laelapidae sp.	Central	47.8	0.027
Phoridae sp.	Birthing	71.6	0.001
Sciaridae sp.	Birthing	58.8	0.001
Limosininae sp. (Sphaeroceridae)	Birthing	31.0	0.046
Uroobovella coprophila (Urodinychidae)	Birthing	51.0	0.002

Only four species are significant indicators for season in Starlight Cave (Table 3.5). Summer has two species with highly significant indicator values, the beetle *T. ?ripicola* (72.5%) and the ichneumonid wasp (53.1%). The beetle *P. exulans* and Collembola are indicator taxa for winter although their lower values and significance levels suggest these taxa are not exclusively restricted to winter.

Indicator species analysis shows that several taxa exhibit significant associations with more than a single micro-habitat, cave area or season, although none are significant indicators for all three. *Ptinus exulans* is an indicator of the Terminal Chamber during winter. *Uroobovella coprophila* is an indicator of the Bottoms guano piles in the Birthing Chamber, and the ichneumonid wasp is an indicator of the Bottoms of guano piles during summer. The lower degree of micro-habitat specialisation and seasonal specificity in Starlight Cave compared with Bat Cave is interesting as it occurs among some of the few species common to both caves. This may be due to variation in micro-habitats between the caves rather than differences in behaviour between species.

Table 3.5. Significant indicator species for season (Summer or Winter) from Starlight Cave calculated using the method of Dufrene and Legendre (1997) and Monte Carlo significance observed maximum indicator value for each species (1000 permutations).

Taxa	Season	% Indication	P
Ptinus exulans (Anobiidae)	Winter	55.8	0.019
Collembola spp.	Winter	32.6	0.022
Tomogenius ?ripicola (Histeridae)	Summer	72.5	0.001
Cryptinae sp. (Ichneumonidae)	Summer	53.1	0.002

3.4 Discussion

The structure of the arthropod community in Starlight Cave appears to be influenced by the guano micro-habitat conditions, that vary spatially and seasonally. The morphology of Starlight Cave (Section 3.2.1) dictates the distribution of guano because the lack of roof bell holes, preferentially used for roosting sites in the maternity chamber of Bat Cave, results in more scattered guano and urine deposition. Only a single large ‘pile’ (1 m high) was present in the Birthing Chamber of Starlight Cave compared with approximately 100 individual guano piles (of the same size or larger) in the maternity chamber of

Bat Cave. Daylight holes also prevent the air from remaining still and forming a heat trap in avens (vertical blind roof holes). The presence of daylight holes in Starlight Cave allows substantial airflow significantly limiting humidity and thus preventing the thin homogenous guano layer from remaining moist, as in Bat Cave. The larger size of the Central Corridor and Terminal Chamber of Starlight Cave also prevents the temperature increasing much above ambient.

The moisture content of guano throughout the cave does not change significantly between seasons and is not significantly different between the Tops and Bottoms of guano piles (Figure 3.5). Guano moisture content does however vary significantly among the three cave areas, with guano becoming increasingly drier towards the Terminal Chamber because of increased airflow caused by roof holes (Figure 3.6). The Birthing Chamber, situated in an alcove, is protected from drying winds and has several significant water drips from the roof of the cave ensuring the guano is always moist, even when fresh guano deposition is negligible. During summer when guano deposition is at its greatest, the daylight hole in the Central corridor results in significantly drier *in situ* guano in the Central corridor compared with the Birthing Chamber.

The pH of guano in the Birthing Chamber and Central Corridor is also significantly higher than that in the Terminal Chamber, possibly due to more rapid desiccation and exposure to air in this area. The pH of guano, although higher at the Tops of piles compared with the Bottoms, was not significantly different between the micro-habitats. This is most likely because of the even pattern of guano deposition through most of the cave. The seasonal pattern of pH shows a continual downwards trend (Figure 3.3) that does not correspond to decreased numbers of bats (amount of guano deposition remains virtually constant, see Figure 3.7) and is probably an artefact of small sample sizes from the cave, that would be eliminated with increased sampling.

The annual change in species richness indicates a possible change in micro-habitat conditions between sampling years. The almost identical species richness of Tops and Bottoms in the first year suggests that there was little or no micro-habitat variation, supported by the uniform pH and moisture content values. In the second sampling year however, pH became more distinct between Tops and Bottoms of piles. This is further supported by the weak positive correlation between increasing pH and species richness (Figure 3.14). Micro-habitats with higher pH also have higher Simpson diversity values (Figure 3.15), indicating that these conditions reduce dominance by a single, or a few species, enabling a greater species richness with more even abundances across species.

3.4.1 Spatial variation in arthropod communities

Arthropod communities in Starlight Cave show little small-scale spatial variation due to the absence of large individual guano piles. The even veneer of guano substantially reduces variation in micro-habitat between moist, highly basic Tops of piles and the older, drier, sightly acidic guano at the Bottoms of piles. The only spatial variation observed within Starlight Cave occurs at a larger scale, i.e. between the Birthing Chamber, Central Corridor and Terminal Chamber.

The Birthing Chamber contains a distinctive arthropod fauna dominated by Diptera (Phoridae sp., Sciaridae sp., Sphearoceridae sp. and Nycteribiidae sp.), Coleoptera (*Atomaria* sp. and Staphylinidae spp.) and the mite *U. coprophila*, with many of these species being significant indicator species (Table 3.4). This area also has the highest average species richness (8.63 spp.) compared with other areas (Figure 3.12), due to the higher average moisture content of the guano irrespective of season.

The even veneer of guano and the virtual absence of discrete guano piles in the Central Corridor, despite being beneath the major bat roost, results in a significantly different arthropod community to that in the Birthing Chamber. The Central Corridor contains only a single significant indicator species, the laelapid mite, but is characterised by a distinct arthropod community including *Derolathrus* sp. (Jacobsoniidae), Collembola, and spinturnicid and macrochelid mites.

Minimal guano deposition combined with the significant airflow results in much drier guano with lower pH allowing a very different arthropod assemblage to dominate the Terminal Chamber, favouring those which prefer dry, and/or acidic guano. During winter all guano in the Terminal Chamber was continually dry with an average moisture content of 21% (Figure 3.6) and extremely high abundances of *P. exulans*, a chitin feeder (see 2.3.22), were collected from both Tops and Bottoms of guano piles. This suggests that moisture content of *in situ* guano is influencing their choice of micro-habitat, not the absolute position within a guano pile. *Protochelifer australis* (Pseudoscorpionida) in Starlight Cave have only been observed under rocks near site 5 in this chamber, although they have been collected from pitfall traps in all three areas (see Chapter 4). The other species collected primarily from this area are the moth *M. crocicapitella* and the ichneumonid wasp.

3.4.2 Seasonal variation in arthropod communities

Distinct seasonal differences occur between arthropod populations in Starlight Cave. These differences are found in both the distribution of species within the cave and more commonly in the abundance of individual species. The few discrete guano piles present show seasonal environmental variation as the result of summer bat occupation and hence guano deposition (Figure 3.7). Environmental conditions in each cave area are uniform throughout the year (as detailed above), with only a slight increase in the amount of fresh guano deposited during summer.

The summer arthropod assemblage is numerically dominated by *T. ?ripicola*, Laelapidae sp. and Phoridae sp. These species inhabit different areas of the cave during summer according to their micro-habitat preferences. Significant species vectors produced in the ordination (Figure 3.18) show *T. ?ripicola*, *M. crocicapitella*, the ichneumonid wasp and Nycteribiidae sp. are all associated with summer in Starlight Cave.

The winter arthropod assemblage was numerically dominated by *P. exulans*, with over two-thirds of individuals collected during winter (Table 3.2). The NMS ordination shows the species vector for *P. exulans* is very different in direction to all other species examined (Figure 3.18). This highlights their extremely different micro-habitat preference for dry, slightly acidic guano compared with the majority of guano dependent species that favour fresh, moist, basic guano (Figures 2.14 and 2.15). This is presumably due to *P. exulans'* diet of chitin either from dry guano or from fungi (Section 2.3.22). The remaining species associated with winter were *Atomaria* sp., *U. coprophila*, Sciaridae sp., Limosininae sp. and Phoridae sp., although all these species were primarily collected in the Birthing Chamber where micro-habitat conditions were more moist and basic than other areas of the cave (Figures 3.4 and 3.6).

3.4.3 Arthropod community differences between Starlight and Bat Caves

The major differences in cave morphology between Starlight and Bat Caves account for correspondingly large differences in environmental conditions, and the subsequent differences in arthropod dominance and distribution. The total amount of guano is considerably less in Starlight Cave because the bat population is approximately half or less that of Bat Cave. The arthropod communities in Starlight and Bat Caves were numerically dominated by different species, *P. exulans* and *U. coprophila* respectively, that undoubtedly affect overall community structure and diversity index values. Significant differences were present in the families and species comprising the respective communities.

Differing cave morphologies clearly affect the distribution of arthropod communities within each cave. The single main chamber in Bat Cave constrains the bat population resulting in more concentrated guano deposition. This produces many individual guano piles which are subject to concentrated urination resulting in highly moist, basic conditions in close proximity to drier acidic guano. This situation is different to conditions encountered in Starlight Cave where bat roosts were more dispersed, resulting in a more even spread of guano deposition. The lower concentration of fresh guano and urine produced a more homogeneous environment. The removal of substantial areas of highly moist and basic guano also limited the distribution of some species such as the mite *U. coprophila* which required this specific micro-habitat. The Starlight Cave arthropod community varies primarily at a larger spatial scale than Bat Cave, and also with season. These variables result in a mosaic of species' distributions within the cave, both spatially and temporally.

The relationship between summer and winter arthropod assemblages in Starlight Cave was also significantly different from that identified in Bat Cave. The cluster dendrogram for Starlight Cave shows little association between summer and subsequent winter samples (Figure 3.19). The terminal branch lengths are also long compared with those from the analysis of Bat Cave, indicating less homogeneity in arthropod assemblages among traps (*cf* 3.19 and 2.25). This is probably mainly due to the distinct separation of micro-habitat in Starlight Cave according to area rather than by season and associated presence or absence of the bat population.

The relatively low number of summer indicator species in Starlight Cave compared to that of Bat Cave is surprising. While the moisture content near the Bottoms of guano piles (Figure 3.5) is comparable to that of Bat Cave, the Tops of piles in Starlight are significantly drier than the often 70 - 80% moisture content often recorded from the Maternity Chamber in Bat Cave (Chapter 2 and Appendix 2). The lower moisture content and pH of most guano in Starlight Cave, eliminates a distinct guano micro-habitat linked to summer conditions common in Bat Cave.

A number of species were common to both caves, e.g. *P. exulans*, *T. ?ripicola*, *M. crocicapitella*, *Apanteles ?carpatus* (Braconidae), *U. coprophila*, *Ixodes simplex simplex* (Ixodidae), and *Spinturnix loricata* (Spinturnicidae). Taxa from several families, including Porcellionidae, Laelapidae, Hypogastruridae, Psocoptera, Jacobsoniidae, Nycteribiidae, Sciaridae, Phoridae, Psychodidae, and Sphaeroceridae require further identification to establish whether the species are common between the caves. Several other genera, including the pseudoscorpion genus *Protochelifer* have closely related species in each of the respective caves (see Chapter 4). Even with these taxonomic limitations Starlight Cave and Bat Cave share nearly 45% of species in common. This demonstrates their biogeographic similarities within the Otway Basin that straddles the South Australian and Victorian border. Both caves have probably experienced immigration from epigean populations as well as colonisation by troglophilic species. This will be discussed further in Chapters 4 and 5, which detail the phylogeography of *Protochelifer*, biogeographical patterns in Australian guano dependent faunas, and potential dispersal mechanisms.

3.4.4 Conclusions

The morphology of Starlight Cave has a significant effect on the spatial distribution of the guano-dependent arthropod community by influencing environmental variables. The seasonal deposition of guano, while essential for survival of the arthropod community, is subject to severe changes in moisture content and pH that subsequently controls the spatial distribution of many species within the cave. The community structure varies in composition and abundance of individual species to that of Bat Cave. This is probably due to a differing suite of initial colonising species and the absence of extreme environmental conditions associated with concentrated guano deposition allowing for the dominance of a few species in Bat Cave. Increased species richness was probably the result of a reduction in extreme environmental conditions for the duration of this two year study in Starlight Cave that was limited only by lower *in situ* moisture contents compared with Bat Cave.

Chapter 4: Phylogeography of the pseudoscorpion genus *Protochelifer* Beier (Cheliferidae) in Australia.

4.1 Introduction

Pseudoscorpions are a speciose order of predatory arachnids, 1 – 7 mm long, found in a broad variety of epigean and hypogean terrestrial habitats (Weygoldt, 1969). Worldwide the family Cheliferidae is currently represented by 59 genera and 274 species placed in two subfamilies, the Cheliferinae and Philomaoriinae (Harvey, 1991; Harvey, 1992). The latter is represented by the genus *Philomaoria* Chamberlin from New Zealand and Lord Howe Island, and has also been found in New Caledonia (Harvey, unpublished data).

Protochelifer Beier is the dominant cheliferid genus in Australia, with only two other genera recorded, *Australochelifer pygmaeus* Beier (Beier, 1975) from the Australian Alps, and *Nannochelifer paralius* Harvey (Harvey, 1984) from littoral habitats in the Coral Sea. Other populations of *Nannochelifer* are known from coastal Western Australia but their specific identity has not been determined (Harvey, unpublished data). Also, specimens attributable to the genera *Papuchelifer* Beier, *Lissochelifer* Chamberlin and *Lophochernes* Simon are represented on the continent but are as yet undescribed species (Harvey, unpublished data). *Protochelifer* (Cheliferidae) has a wide distribution across eastern and southern coastal Australia, and New Zealand (Beier, 1966; Beier, 1967; Beier, 1968; Harvey, 1991). Five species are currently recorded from Australia; *P. australis* (Tubb), *P. brevigiditatus* (Tubb), *P. cavernarum* Beier, *P. naracoortensis* Beier and *P. victorianus* Beier (Figure 4.1) (Harvey, 1991). Cavernicolous *Protochelifer* species commonly show an association with bat guano (Moulds, 2004).

Protochelifer naracoortensis is known only from Bat Cave, Naracoorte, in the northern extreme of the Otway Basin, South Australia (Figure 4.1) (Boult & Hibburt, 2002), and is currently the only, apparently endemic, species in this cave (Moulds, 2004). Bellati *et al.* (2003) identified *P. naracoortensis* in the flyway and entrance areas of Bat Cave and subsequent analysis showed these populations expressed slightly different morphometrics, possibly indicating the presence of cryptic species.

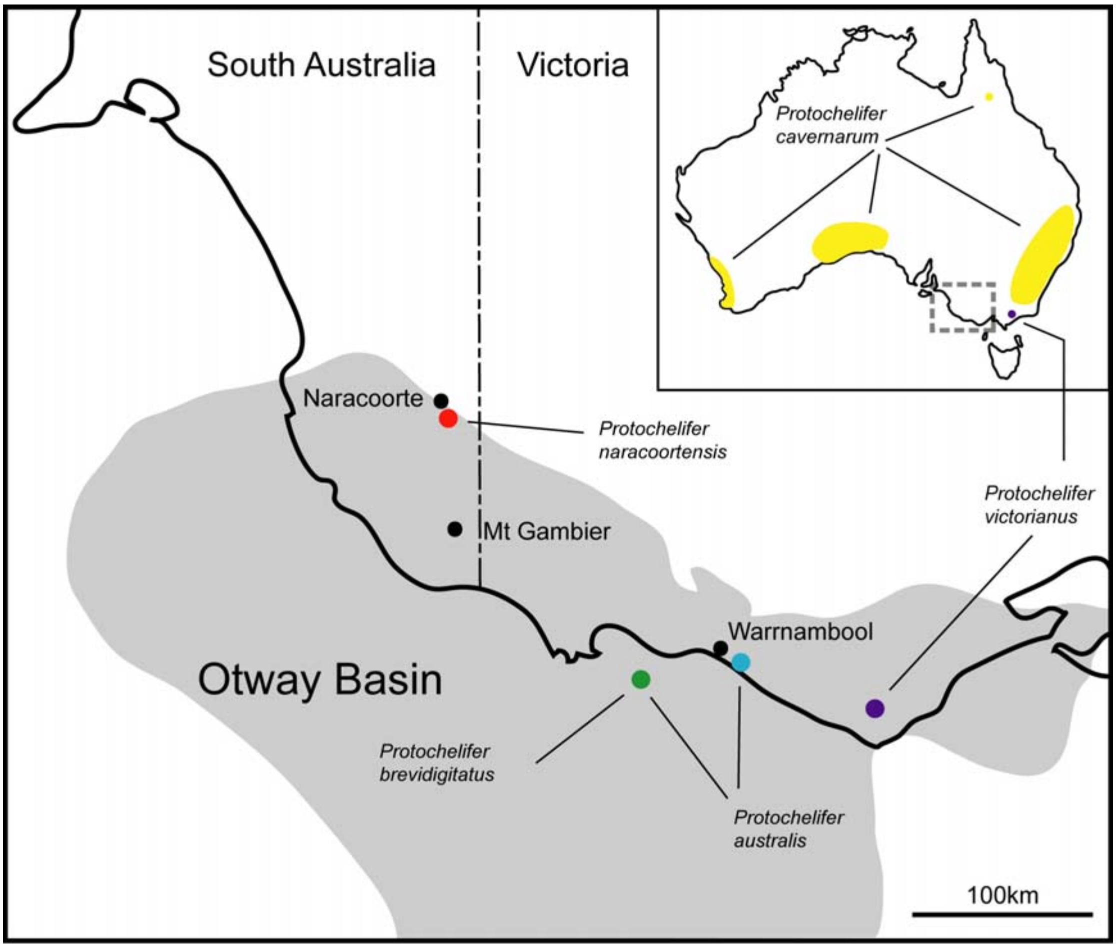

Figure 4.1. Distribution of the five described *Protochelifer* species in Australia using published records. The Otway Basin incorporates the southeast region of South Australia and western Victoria. The cavernicolous Miocene – Oligiocene Gambier Limestone Unit covers much of the onshore area of the Otway Basin from west of Naracoorte to east of Warrnambool. *Protochelifer australis* and *P. brevidigitatus* are recorded from Lady Julia Percy Island but only *P. australis* is recorded from Starlight Cave on the nearby mainland. *P. victorianus* is recorded from under bark in the Otway Ranges and Gippsland, Victoria.

The continuous cavernicolous nature of the Otway Basin limestone may allow for hypogean movement of species via micro and meso caverns (Howarth, 1983). Therefore using *Protochelifer* as a representative cavernicolous taxon, the migration of species at local (<10 km) and regional scales (10 - 300 km) was examined using allozyme electrophoresis and mitochondrial DNA sequencing. Local migration of *Protochelifer* species was examined within the Naracoorte Caves World Heritage Area to determine if *P. naracoortensis* is endemic to Bat Cave, or if specimens found inhabiting surrounding caves and surface habitats represent the same species. Regional scale migration was investigated using specimens from a selection of caves within the Otway Basin.

Protochelifer australis and *P. brevidigitatus* have been recorded from under rocks, in the vicinity of a guano cave on Lady Julia Percy Island, a small basaltic island approximately 50 km west of Warrnambool, Victoria (Tubb, 1937). *Protochelifer australis* has subsequently been recorded from Starlight Cave (Chapter 3), a coastal cliff cave approximately 10 km east of Warrnambool, but is not considered a cave dependent species. *Protochelifer australis* is the only other species in the genus besides *P. naracoortensis* recorded from the Otway Basin. This study aimed to determine the degree of endemism, and number of cave colonisation events of *Protochelifer* species in southern Australia, and also aimed to determine the distribution of *P. australis* within the Otway Basin.

Protochelifer cavernarum, originally described from Cliefden Caves in central western New South Wales and Timor Caves in north-eastern New South Wales (Beier, 1967), has subsequently been recorded from caves in Victoria, coastal Western Australia, the Nullarbor Plain, and northern Queensland (Beier, 1968; Howarth, 1988; Richards, 1971). The Nullarbor Plain population, from Abrakurrie Cave, Western Australia, was given subspecies status and named *P. cavernarum aitkeni* Beier (1968; 1969) but synonymised by Harvey (1981). The extremely widespread and disjunct distribution of *P. cavernarum* suggests this species may constitute a species complex, and recent morphological investigations have supported this assertion (M. Harvey and T. Moulds unpublished data). As a formal taxonomic division of *P. cavernarum* was not attempted herein and it was not possible to collect at the type locality. All *Protochelifer* specimens from caves previously identified as containing *P. cavernarum* are referred to by cave name only, and treated as potentially undescribed species for the purposes of this study.

4.2 Methods

4.2.1 Survey of caves for Protochelifer *specimens*

Specimens were collected in both 100% ethanol and liquid nitrogen to enable a combination of mtDNA sequencing and allozyme electrophoresis to be used. A list of all caves examined and specimens recorded is shown in Table 1. Specimens were collected using forceps, and located by visual searches of rocks and walls. An initial morphological identification was undertaken to determine if specimens could be assigned to any previously described species. Except for the Naracoorte region, populations from all caves and surface locations, were morphological and morphometrically distinguishable from one another, suggesting the existence of additional species in the genus.

Table 4.1. Caves in southern Australia sampled for pseudoscorpions and the respective species present. Further information regarding the location and morphology of caves in the Flinders Ranges can be found in (Moulds, 2005).

Region	Cave	Pseudoscorpion Family and genus present
Nullarbor Plain	Murra-El-Eleyvn Cave	Cheiridiidae, *Cryptocheiridium australicum*
	Murrawijinie No.3 Cave	Cheliferidae, *Protochelifer 'cavernarum'*
	Warbla Cave	Cheliferidae, *Protochelifer 'cavernarum'*
	Tommy Grahams Cave	Absent
	Koonalda Cave	Absent
	Weebubbie Cave	Absent
Flinders Ranges	McKinleys Daughters Cave	Absent
	Chambers Gorge cave 1	Absent
	Chambers Gorge cave 2	Absent
	Bunyeroo Gorge cave 1	Absent
	Bunyeroo Gorge cave 2	Absent
	Brachina Gorge river cave	Absent
	Brachina Gorge hillside cave	Absent
	Moro Bat Cave	Absent
	Oraparinna Bat Cave	Absent
	Eregunda Mine	Cheliferidae, *Protochelifer* sp.
	Weetootla Gorge mine 1	Absent
	Weetootla Gorge mine 2	Absent
Kangaroo Island	Kelly Hill Cave	Cheliferidae, *Protochelifer* sp.
Naracoorte	Bat Cave	Cheliferidae, *Protochelifer naracoortensis*
	Blanche Cave	Cheliferidae, *Protochelifer* sp.
	Fox Cave	Cheliferidae, *Protochelifer* sp.
	Robertson Cave	Cheliferidae, *Protochelifer* sp.
	Wet Cave	Absent
	Victoria Fossil Cave	Absent
	Alexandra Cave	Chthonidae, *Austrochthonius cavicola*
	Cathedral Cave	Chthonidae, *Austrochthonius cavicola*
SE Region South Australia	Cave Park Cave	Absent
	Monbulla Cave	Absent
	Glencoe West Cave	Absent
	Snake Hill Cave	Absent
	Wondillo Bat Cave	Absent
	Gran Gran Cave	Chernetidae sp.
	Quarry Cave	Absent
Western Victoria	Starlight Cave	Cheliferidae, *Protochelifer australis*

Specimens of *P. naracoortensis* were collected from the entrance, flyway and maternity chamber of Bat Cave, enabling genetic comparison of the three populations. Seven other caves within the Naracoorte Caves Park were also surveyed, with *Protochelifer* populations found in Blanche, Fox and Robertson Caves (Figure 4.2). These populations were genetically assessed to determine if they represented *P. naracoortensis* or another, perhaps undescribed, species. Surface areas within the Naracoorte Caves World Heritage Area were also sampled to determine if an epigean *Protochelifer* was present in close proximity to the population of *P. naracoortensis* in Bat Cave but no such population was found.

A selection of caves, used primarily as bat over-wintering sites, were surveyed in the south-east of South Australia. No pseudoscorpion populations were discovered apart from a small population of a Chernetidae sp. from the entrance area of Gran Gran Cave approximately 70 km north-east of Mount Gambier. A single immature *Protochelifer* specimen was collected from Eregunda Mine in the Flinders Ranges but was not included in this study as no other specimens could be obtained (Moulds, 2005). Six caves on the Nullarbor Plain were sampled, with *Protochelifer* populations found only in Warbla and Murrawijinie No.3 Caves on the eastern side of the plain. Voucher specimens of all species/populations have been lodged in the South Australian Museum collections.

A single outgroup was selected for the study, *Cryptocheiridium australicum* Beier (Cheiridiidae) from Murra-El-Eleyvn Cave, Nullarbor Plain (Harvey, 1992).

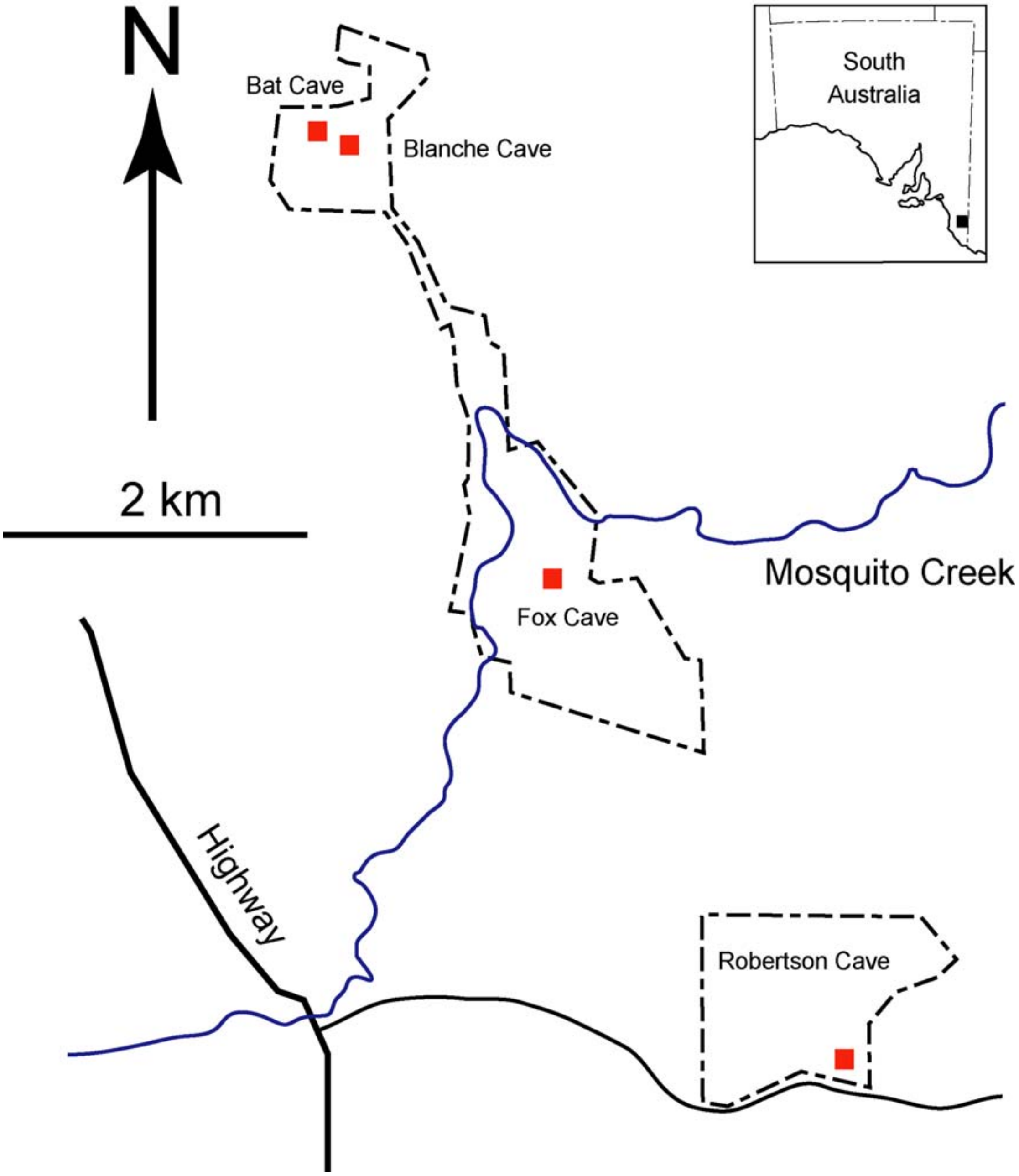

Figure 4.2. Naracoorte Cave World Heritage Area, showing caves containing *Protochelifer* populations.

4.2.2 Mitochondrial DNA extraction and sequencing

Genomic DNA was extracted from 22 *Protochelifer* individuals and two individuals of *Cryptocheiridium australicum*, using the Gentra Systems Puregene® DNA Purification Kit following the protocol for DNA purification from a single *Drosophila melanogaster* (GentraSystems, 2005). A 569 base pair (bp) fragment of *COI* mtDNA was amplified for each sample using Folmer's universal primers LC01490 (5’-GGTCAACAAATCATAAAGATATTGG-3’) and reverse primer HC02198 (5’-TAAACTTCAGGGTGACCAAAAAATCA-3’) (Folmer *et al.*, 1994). Each extraction was amplified using the polymerase chain reaction (PCR) in 25 μL reaction volumes that comprised 1 μL (5 μM) of each primer, 2.5 μL (25 μM) buffer, 2.5 μL (10 μM) dNTP, 2 μL MgCl, 0.1 μL (10 units/μL) AmpliTaq Gold® DNA Polymerase (Applied Biosystems Inc.) and 2 μL of genomic DNA. Polymerase chain reactions were conducted using an Eppendorf thermal sequencer adopting the following temperature profile; an initial 5 minute denaturation step at 95°C followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 50°C for 30 s, extension at 72°C for 30 s and the program terminated with a final 3 minute extension at 72°C. PCR products were purified using the Ultraclean™ PCR Clean-up™ Kit (MoBio Laboratories inc.) and sequenced using ABI Big Dye Terminator Chemistry. Fragments were resolved on an ABI 3700 sequencer.

4.2.21 Sequence alignment and analysis

Sequences obtained were manually aligned using BioEdit Sequence Alignment Editor version 7.0.1. (Hall, 1999). Samples with unclear chromatographs were resequenced with the reverse primer. A single representative of each of the 15 haplotypes found were then aligned with the sequences of *C. australicum* (Cheiridiidae). Gaps were not necessary to align haplotypes. Sequences determined here have been deposited in GenBank under Accession Nos. DQ184915-DQ184938. The sequences were translated into amino acid sequences in MEGA version 3.0 (Kumar *et al.*, 2004) to test for the presence of nuclear paralogues such as stop codons. The most appropriate evolutionary model was determined via hierarchical likelihood testing using Modeltest version 3.6 (Posada & Crandall, 1998). A transversional model with gamma distribution (TVM+G) was selected by Modeltest as most appropriate for this data set (Posada & Crandall, 1998). The following parameters were used; base frequencies A: 0.2895 C: 0.1547 G: 0.1389 T: 0.4169, estimated value of gamma shape parameter = 0.274, and rates of base substitution (A-C) = 1.3988, (A-G) = 6.9233, (A-T) = 1.3486, (C-G) = 1.0622, (C-T) = 6.9233, (G-T)

= 1.0000, for subsequent analysis using PAUP* version 4.0b10 (Swofford, 2000).

Two different methods of phylogenetic reconstruction were applied to the data, maximum parsimony (MP) and Bayesian inference. MP was analysed with PAUP* (Swofford, 2000), while MrBayes version 3.0b4 (Huelsenbeck & Ronquist, 2001) was used for a Bayesian Markov chain Monte Carlo approach. MP was performed using heuristic searches with 100 random stepwise additions. The robustness of trees was assessed using bootstrap procedures over 1000 replicates. The ability of Bayesian inference and maximum likelihood (ML) methods in phylogenetic reconstruction to eliminate the problem of multiple base substitutions at a site makes them attractive in such analyses. Bayesian analysis was selected for this study due to its reduced computational requirements compared with ML, thus allowing for more thorough analyses to be performed. Bayesian analysis was conducted using four Markov chains simultaneously, initially run for 200,000 generations, and sampled every 100 generations, to establish the number of generations for parameters to reach stationarity. Post run analysis of log likelihoods and model parameters revealed stationarity was reached well prior to 100,000 generations, so the first 100 trees were discarded as burn-in. A run of two million generations, sampling every 100 generations and applying a burn-in of 100,000 generations, produced the final result. Posterior probabilities for each branch bipartition were calculated using the proportion of sampled trees for a 50% majority rule consensus containing each branch. The hypotheses of a single cave invasion was phylogenetically tested using comparisons between optimal trees and those obtained using the SH test (Shimodaira & Hasegawa, 1999) for enforced topological constraints using the MP tree as a basis.

4.2.3 Allozyme electrophoresis

Material for electrophoretic analysis was collected fresh in the field and placed directly into liquid nitrogen and subsequently stored at -80°C until required. Allozyme electrophoresis was performed on cellulose acetate gels (Cellogel©) according to the principles and procedures of Richardson *et al.* (1986). Fifty-seven specimens were used in a single electrophoretic run, incorporating multiple specimens from each site. Specimens of the epigean Perth species, *P. victorianus* and from Kangaroo Island were not available for electrophoresis.

The following enzymes displayed sufficient electrophoretic activity and band resolution for allozymic interpretation to be undertaken:- aminoacylase (ACYC, EC 3.5.1.14), adenosine deaminase (ADA, EC 3.5.4.4), alcohol dehydrogenase (ADH, EC 1.1.1.1), arginine kinase (ARGK, EC 2.7.3.3), enolase (ENOL, EC 4.2.1.11), esterase (EST, EC 3.1.1.), fructose-bisphosphatase (FDP, EC 3.1.3.11), fumarate hydratase (FUM, EC 4.2.1.2), glyceraldehyde-3-phosphate dehydrogenase (GAPD, EC 1.2.1.12), aspartate aminotransferase (GOT, EC 2.6.1.1), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), alanine aminotransferase (GPT, EC 2.6.1.2), isocitrate dehydrogenase (IDH, EC 1.1.1.42), malate dehydrogenase (MDH, EC 1.1.1.37), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), purine-nucleoside phosphorylase (NP, EC 2.4.2.1), nucleoside-triphosphate-adenylate kinase (NTAK, EC 2.7.4.10), dipeptidase (PEPA, EC 3.4.13.), tripeptide aminopeptidase (PEPB, EC 3.4.11.), phosphoglycerate mutase (PGAM, EC 5.4.2.1), phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), phosphoglucomutase (PGM, EC 5.4.2.2), pyruvate kinase (PK, EC 2.7.1.40), and triose-phosphate isomerase (TPI, EC 5.3.1.1). The nomenclature used to designate multiple loci and allozymes follows Adams *et al*. (1987).

4.2.31 Analysis of allozyme data

The genetic relationships among populations and/or species were quantified by calculating Nei's genetic distance (Nei D, Nei, 1978) for each relevant pairwise comparison. These genetic relationships were then displayed visually in a Neighbour Joining (NJ) tree, based on the Nei Ds. This tree was constructed using the NEIGHBOR program contained within PHYLIP version 3.5c (Felsenstein, 1993) and drawn using TREEVIEW version 1.6.0 (Page, 1996). *Cryptocheiridium australicum* (Cheiridiidae) was used to root the NJ tree. A measure of the robustness of lineages was obtained by bootstrapping the allele frequencies and generating a series of 100 genetic distance matrices (using a BASIC program written by M. Adams). These matrices were then input directly into NEIGHBOR and the resultant 100 trees used to generate a consensus tree (which details the bootstrap support for the key nodes) using the CONSENSE program of PHYLIP 3.5c.

4.3 Results

4.3.1 Phylogenetic reconstruction of Protochelifer *populations using mtDNA* COI *gene*

In total, 569 characters were available for phylogenetic analysis, with 225 variable sites, of which 182 were informative. Saturation levels for the data were assessed by plotting the observed number of transitions and transversions against the uncorrected distance for all pairs of sequences (Figures 4.3 and 4.4). The results of both these analyses indicate that neither show any sign of saturation for the ingroup. Saturation is present between the ingroup and outgroup suggesting that a deeper level analysis would require different genes to be analysed.

The MP and Bayesian phylogenetic analyses produced almost identical trees showing seven major ingroup clades (I-VII) (Figure 4.5 and 4.6). These seven clades form a strongly supported group with some long terminal branch lengths, especially for clades (I, II and III). Each clade was well supported with high bootstrap values (>85, Figure 4.5) and posterior probabilities (>0.96, Figure 4.6) except for internal relationships amongst haplotypes from Naracoorte and the deeper relationship among *P. australis*, *P. victorianus* and the remainder of the ingroup.

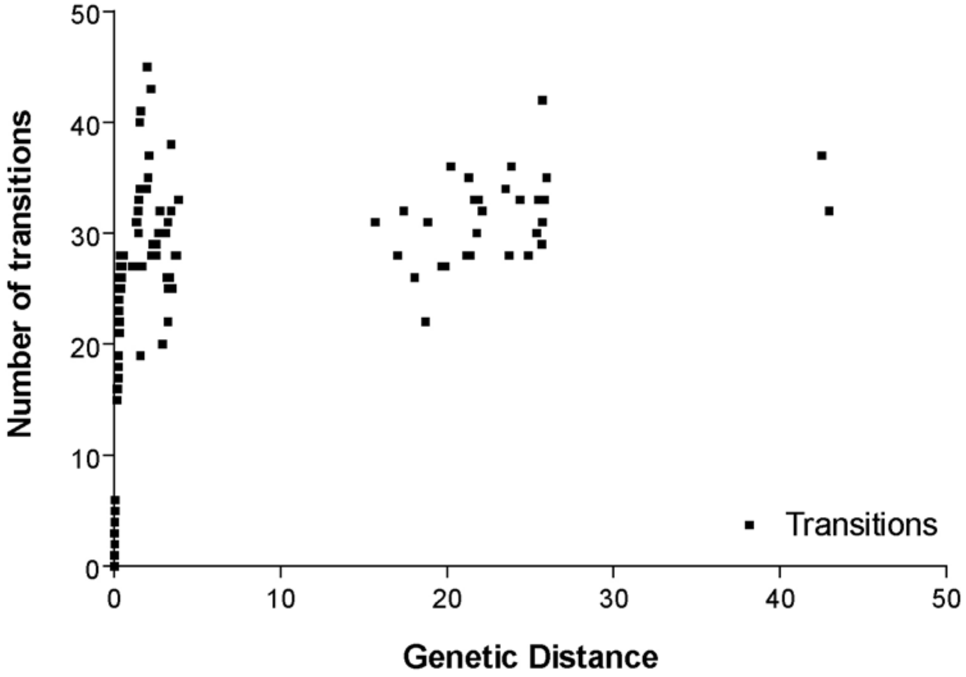

Figure 4.3. Uncorrected genetic distance and transitions.

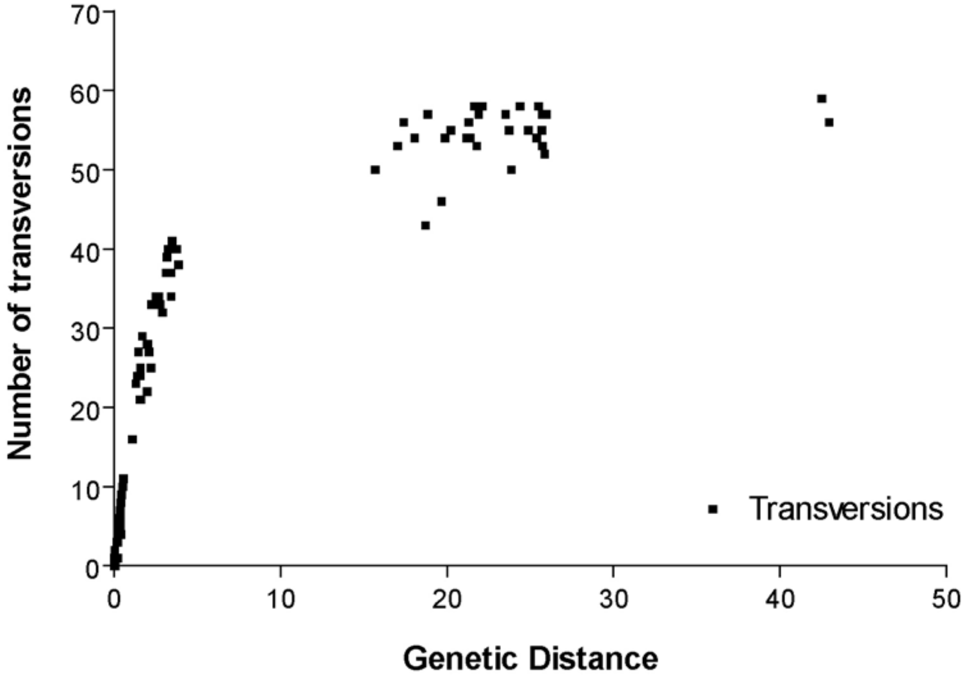

Figure 4.4. Uncorrected genetic distance and transversions.

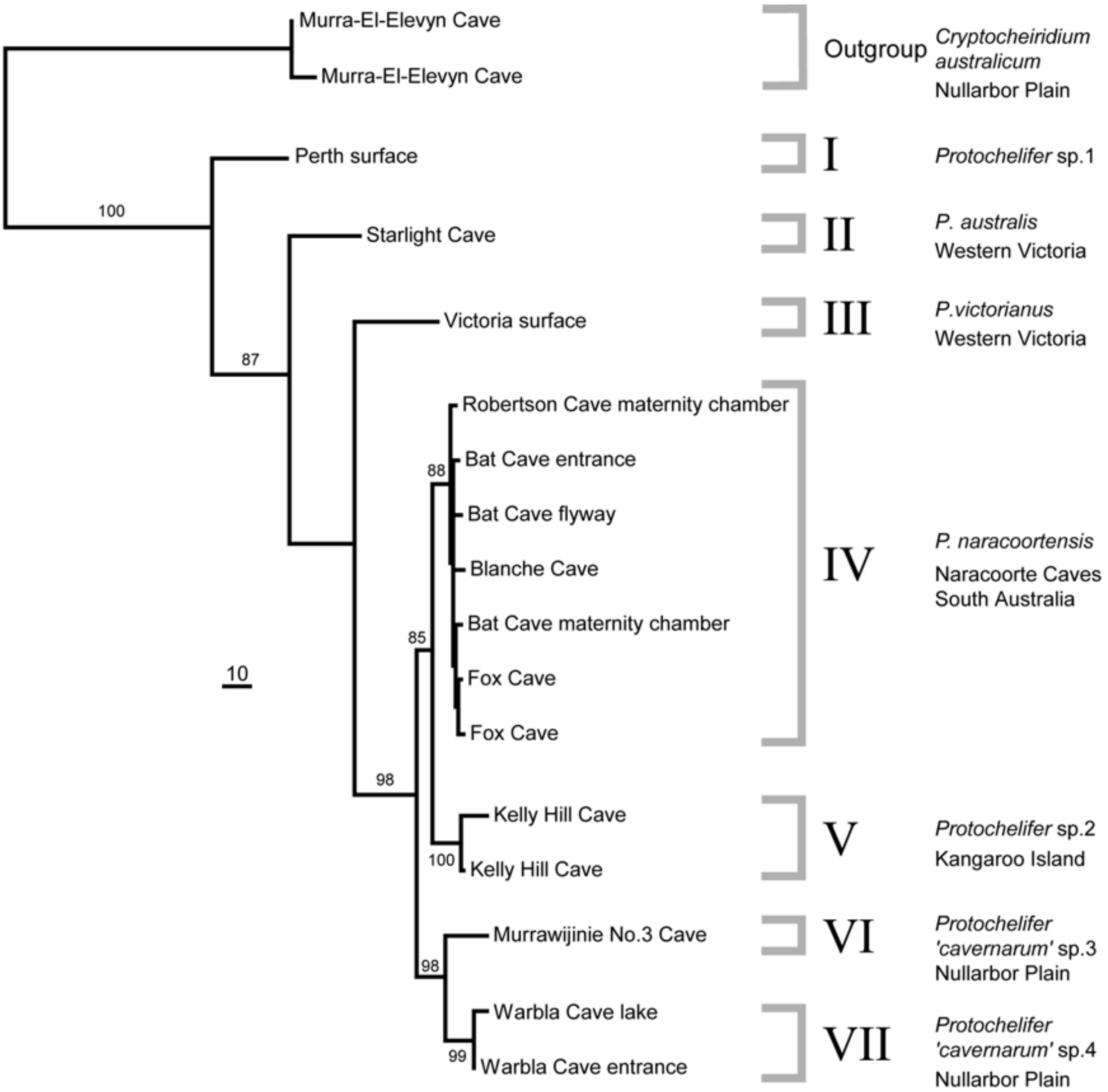

Figure 4.5. *Protochelifer* maximum parsimony phylogram. Bootstrap values based on 1000 replicates.

The cave-associated *Protochelifer* populations divide broadly into two clades, one from temperate South Australia, including Naracoorte and Kangaroo Island, the other from the semi-arid Nullarbor Plain. The Naracoorte clade (IV) shows a small amount of sub-structuring, however support for these terminal divisions is poor. The population from Fox Cave is the best supported group although absolute divergence is still minimal and a larger study would be required to provide evidence for any significant degree of genetic isolation. The Kangaroo Island clade (V) forms a genetically distinct and strongly supported sister clade with Naracoorte. The western clades (VI and VII) from the Nullarbor Plain show the two populations from Warbla and Murrawijinie No.3 caves forming genetically distinct groups. These clades show genetic divergence from the Naracoorte and Kangaroo Island clades that are strongly supported with high bootstrap and posterior probabilities.

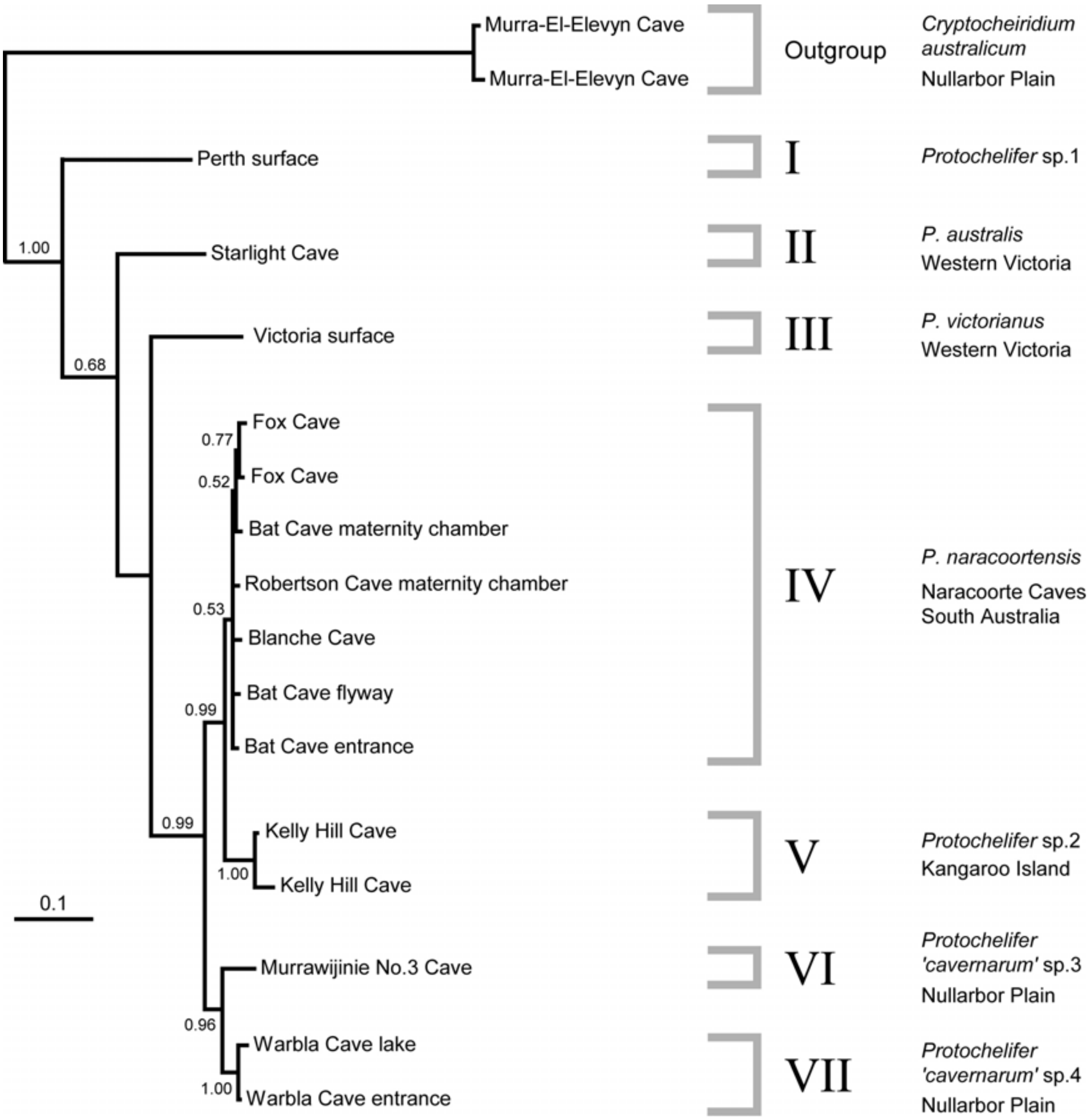

Figure 4.6. Bayesian phylogram, based on 2 million generations sampling every 100 generations with a burn in of 100 000 generations. Posterior probabilities calculated from percent of tree containing each bipartition from a 50% majority consensus rule.

Clades I, II and III show an interesting relationship as I and III represent surface species while clade II consists of *P. australis*, a possible cavernicolous species from Starlight Cave in western Victoria. However, trees obtained by enforcing the monophyly of *P. australis* with clades IV-VII were not significantly inferior (p>0.05) to the unconstrained analysis.

4.3.2 Results of allozyme analysis

A total of 30 putative loci were scored during the allozyme study, providing allozyme profiles for 57 individuals from 13 locations (Table 2). The NJ tree generated using the allozyme data revealed the presence of four major lineages (labelled II, IV, VI-VII and corresponding to the same clades in Figures 4.5 and 4.6) for *Protochelifer* (Figure 4.7). Lineage IV comprised a well-supported clade of genetically-similar populations from Naracoorte, consistent with the presence of a single species, *P. naracoortensis*, in all caves. Two further lineages were evident among Nullarbor Plain populations, with the three Warbla Cave populations forming a genetically-homogeneous clade (lineage VII) and the population from Murrawijinie No.3 Cave forming another (lineage VI) which was genetically distinct from both lineages IV and VII. The pattern and levels of genetic divergence encountered suggest the presence of three distinct and separate species (corresponding to lineages IV, VI, and VII), rather than the two species currently recognised (Figure 4.1). The monophyly of these three putative species was supported by bootstrap analysis. Further the remaining ingroup species *P. australis* from Starlight Cave in western Victoria occurred as a separate, and genetically very distinctive lineage (II).

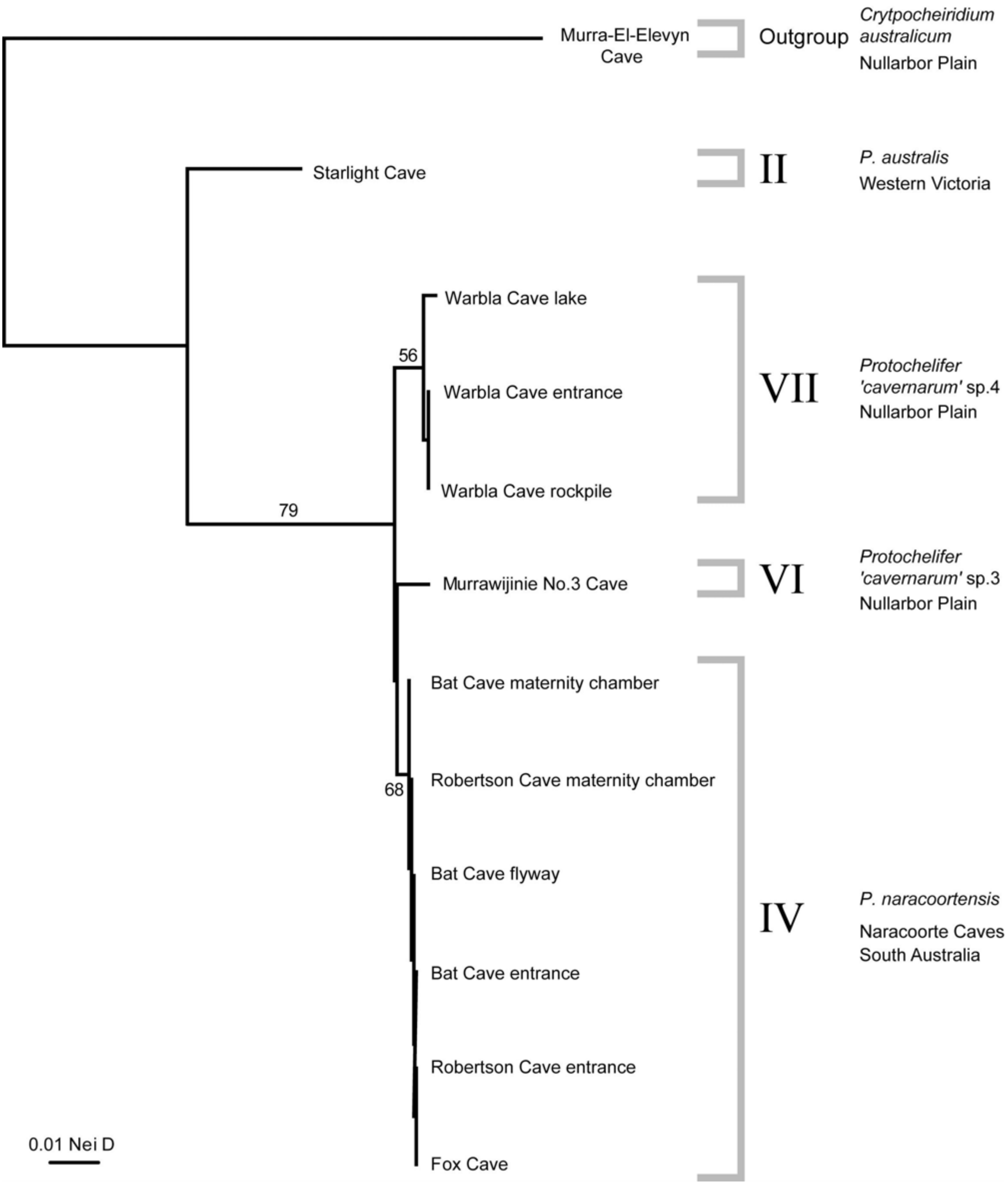

Figure 4.7. Neighbour-joining tree depicting genetic distances among cavernicolous *Protochelifer* populations in southern Australia as assessed by allozyme analysis of 30 loci. Bootstrap values are based on 100 pseudoreplicates.

4.6 Discussion

The almost identical topologies for phylogenetic reconstruction based on the COI gene and allozymes suggest that the data sets are robust at both the mitochondrial and nuclear levels, enabling a high degree of confidence to be placed in the results. The genetic divergence of *Protochelifer* populations is relatively high among the more basal clades, indicating these species have been genetically isolated for significant time periods.

The early splitting of the surface species from Perth, *Protochelifer* sp. 1, and the western Victorian species *P. victorianus* suggests a possible dispersal event occurred early in the evolution of *Protochelifer*. The exact nature of these relationships are, however, unable to be determined by this study. The epigean *Protochelifer* species (*Protochelifer* sp. 1 and *P. victorianus*) inhabit a different ecological niche, living under bark of *Eucalyptus* and *Nothofagus*, rather than beneath rocks where the remainder of *Protochelifer* species from this study are found. This adaptive shift in behaviour probably enabled the initial colonisation of caves and, hence, allowed exploitation of the nearly inexhaustible food resources associated with guano deposits (Howarth & Hoch, 2005).

There are two explanations for cave colonisation in *Protochelifer*, either a single event, followed by dispersal between caves and karst areas at local, regional and continental scales; or as a series of separate events across southern Australia. Due to the large geographic distances separating cavernicolous populations, a single colonisation event requires adequate dispersal mechanisms for cavernicolous species to migrate between caves in order to explain their currently disjunct distribution. Mechanisms such as migration via micro and mesocaverns at local scales, and phoresy, at regional and continental distances can reasonably explain these distributions. Multiple cave colonisations, as proposed for cixiid planthoppers in northern Australia (Soulier-Perkins, 2005), suggest the presence of related surface species with intermediate epigean distributions between caves. The apparent absence of these populations could be a result of inadequate surface collecting between cave areas or possibly recent extinction due to increasing aridity.

The genetic similarity of all Naracoorte *Protochelifer* populations shows *P. naracoortensis* is not endemic to Bat Cave as previously thought (Hamilton-

Smith, 2000; Moulds, 2004). This suggests a significant amount of migration between cave populations within this small geographic area. However, the lack of surface populations of *P. naracoortensis* and its generally restricted distribution suggest this species is incapable of regional or continental distance epigean dispersal as all populations occur within approximately 6 km of each other. Subterranean dispersal, via micro and meso caverns is most likely within the immediate Naracoorte area and explains the low genetic variation between Bat and Robertson caves, the two most widely separated *P. naracoortensis* populations. Phoretic transport between nearby caves is another scenario, possibly utilising the southern bent-wing bat (*Miniopterus schreibersii bassanii* Cardinal and Christidis), a rhaphidophorid cave cricket (*Novotettix naracoortensis* Richards), or the cave carabid beetle *Speotarus lucifugus* Moore*.* The latter is found in every cave within the immediate area, and, although not occurring on the surface, *S. lucifugus* is far more capable of epigean dispersal because it has wings and long legs. These beetles show no genetic structuring within the Naracoorte area suggesting they are relatively frequent migrants between caves (T. Moulds unpublished data). Interestingly, phoretic dispersal of pseudoscorpions via harlequin beetles in central America has been documented by Zeh *et al.* (2003).

The possibility of regional migration (10 - 300 km) between caves in the same karst area via micro and meso caverns is unlikely. The Otway Basin forms a continuous cavernicolous unit from Naracoorte in South Australia to mid-western Victoria, with many hundreds of known caves (Figure 4.1). Despite searching a representative sample of the largest of these caves between Naracoorte Caves, and Starlight Cave in western Victoria, no Cheliferidae were found apart from *P. australis* from Starlight Cave some 300 km from Naracoorte Caves. The genetically distinct populations on the Nullarbor Plain, despite being within a continuous cavernicolous unit of limestone also suggest that subterranean migration at distances larger than tens of kilometres is unlikely.

Cave-dwelling bats with a Bassian distribution (i.e. both eastern and western sides of southern Australia), such as the chocolate wattled bat (*Chalinolobus morio* Gray), may provide a regional or longer distance dispersal mechanism for pseudoscorpions as phoretic species have previously been recorded from bats, albeit from a different family to *Protochelifer* (Harvey & Parnaby, 1993). The substantial genetic divergence between cavernicolous *Protochelifer* populations on the Nullarbor Plain, however, suggests this would be a rare occurrence. Dispersal mechanisms differ with increasing distance. Local dispersal, as within the Naracoorte Caves area is most likely occurring via micro and meso caverns and/or phoresy on insects. However, regional and continental scale dispersal possibly relies on phoresy by cave-dwelling bats, capable of traversing distances greater than several hundred kilometres.

The possibility of unknown or presently extinct intermediate surface species between Kangaroo Island and the Nullarbor Plain is a possible alternate explanation for the disjunct distribution of *Protochelifer* species, indicating multiple cave colonisation events. The single juvenile specimen collected in the Flinders Ranges supports this explanation and further populations may occur in other intermediate karst areas such as the Davenport Ranges or the western Eyre Peninsula. However, several caves in these latter regions containing suitable habitat have been examined without specimens being found. The lack of species, both epigean and hypogean, in intermediate areas despite extensive collecting suggests that multiple cave colonisations is less likely than a single event followed by regional and continental dispersal. Intermediate surface *Protochelifer* populations may have become extinct with the onset of aridity during the Pliocene (Hopper & Gioia, 2004), producing isolated cavernicolous populations. Reduced opportunity for migration among cave species has led to the present situation of different *Protochelifer* species in separate cave systems across southern Australia. This explanation is still unlikely due to the absence of hypogean species in caves on the Eyre Peninsula situated between Kangaroo Island and the Nullarbor Plain. The strong support for the grouping of all cavernicolous *Protochelifer* populations, apart from *P. australis,* and absence of intermediate surface populations suggests these populations share a common cave colonisation event and have subsequently dispersed and radiated across southern Australia.

The genetic separation of *P. australis* from the cavernicolous species suggests it is not cave dependent but may be an opportunistic species exploiting the rich food supply found within extensive guano deposits. The presence of daylight holes in the terminal chambers of Starlight Cave (Figure 3.1) provide diffuse light to the majority of the guano deposits, which suggests this species may not be a true troglophile, but one requiring some light. Further study using a greater number of haplotypes will provide more confidence in the phylogenetic placement of this species. However, the similar placement of *P. australis* using allozymes and mtDNA suggests a significant genetic divergence between *P. australis* and the cavernicolous species.

The findings of this study indicate that the taxonomy of *P. cavernarum* requires further study. Two species are now recognised from caves on the Nullarbor Plain where previously all *Protochelifer* species were thought to be *P. cavernarum* (Beier, 1975; Richards, 1971). Indeed, it is highly likely that *P. cavernarum* is not as widely distributed as previously thought, and thus represents a number of cryptic species (M. Harvey unpublished data). A much broader morphological and molecular study is required to resolve this.

4.6.1 Conclusions

The distribution of cavernicolous *Protochelifer* species is shown to be much greater than previously recorded. Based on data from the Naracoorte Caves area subterranean migration of *Protochelifer* species utilising micro and meso caverns appears to be restricted to local scales (<10 km). Larger scale dispersal by subterranean migration is not supported by this study. Dispersal of cavernicolous species is believed to occur using a combination of subterranean migration and phoresy at local levels, and phoresy only at regional (10-300 km) and continental scales (>300 km). The restricted distribution of all the cavernicolous *Protochelifer* species in this study makes them short range endemics, similar to other Australian terrestrial groups such as cavernicolous schizomids and millipedes (Harvey, 2002). The ecological dependence of *P. australis* on the cave environment needs to be investigated further and a broader molecular study conducted to provide a confident phylogenetic position for this species. This research provides an initial phylogenetic framework for *Protochelifer* in Australia and an indication of the speciose nature of the genus. However, a broader study is required to determine the relationships of bark-dwelling versus rock-dwelling species. A single cave colonisation by

Protochelifer is the most well supported theory, although it remains to be conclusively proven by the current study.

Chapter 5: Distribution and dispersal of Australian guano associated arthropods

5.1 Introduction

Guano associated invertebrate communities are poorly known for the vast majority of Australian caves. Until recently, the only exception was a study by Richards (1971) who documented the diversity and ecology of several subterranean arthropod communities on the Nullarbor Plain, including those associated with guano. Caves containing guano are now known from every mainland state of Australia with over 120 families of guano associated arthropods being recorded (Appendix 1, Moulds 2004). However, despite recent work on guanophilic arthropods many regions remain unstudied or have been examined only fleetingly as part of larger works.

To begin to address this lack of knowledge, three karst areas from different climatic regions of Australia were examined to provide a comparison with Bat and Starlight Caves (Otway Basin, Figure 4.1) from temperate south-eastern Australia (described in Chapters 2 and 3). These karst areas were in the Flinders Ranges (South Australia), the eastern Nullarbor Plain (South Australia), and Broken River (Queensland), representing semi-arid, arid and monsoonal tropical regions of Australia respectively (Figure 5.1). Arthropod sampling was undertaken in several caves at each location to provide a representative sample of guano associated arthropod communities in order to compare the diversity, community structure and ecology among different climatic and biogeographical regions across the continent.

This study therefore seeks to synthesise information on guano dependent ecosystems and to examine the broad impacts of climate on guano communities. The climatic effects on guano micro-habitats and their subsequent influence on arthropod diversity and abundance in different areas is discussed. Potential dispersal mechanisms for guano dependent species are also examined and assessed for their effect on resulting biogeographic patterns.

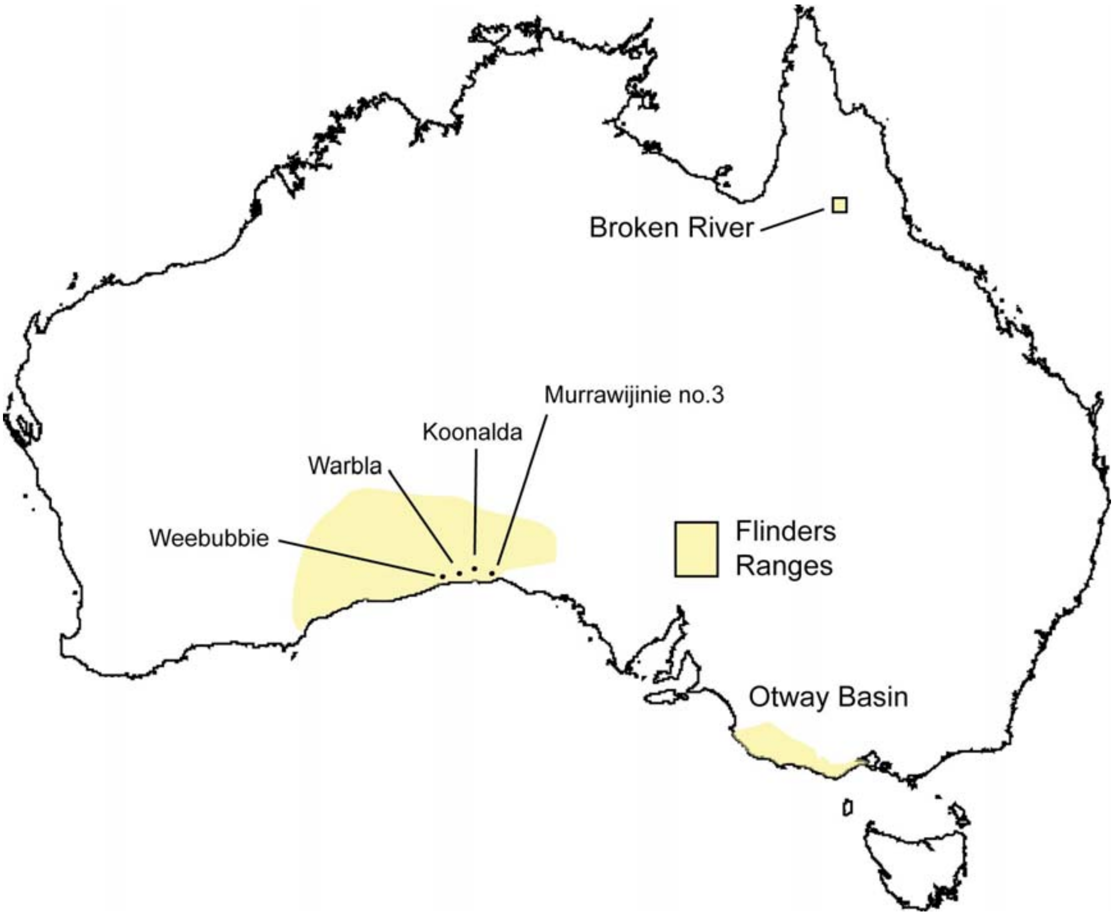

Figure 5.1. Four Australian karst areas sampled for guano arthropods and used to compare community structure from different climatic zones. The Otway basin in south-east South Australia and western Victoria is the most well sampled of the four areas followed by the Nullarbor Plain.

5.2 Methods

5.2.1 Sampling locations and site descriptions

The Flinders Ranges contain a number of widely scattered caves in horizontal or gently dipping Neoproterozoic crystalline limestone (Lewis 1976, Webb *et al.* 2003). The caves examined (Figure 5.2) do not include every guano bearing cave in the area, but rather represent a sample of active bat caves found throughout the region. Guano deposits in all caves were small, generally forming a thin veneer (further details can be found in Moulds 2005). A list of all caves in the Flinders Ranges caves known to contain guano can be found in Hamilton-Smith *et al.* (1997).

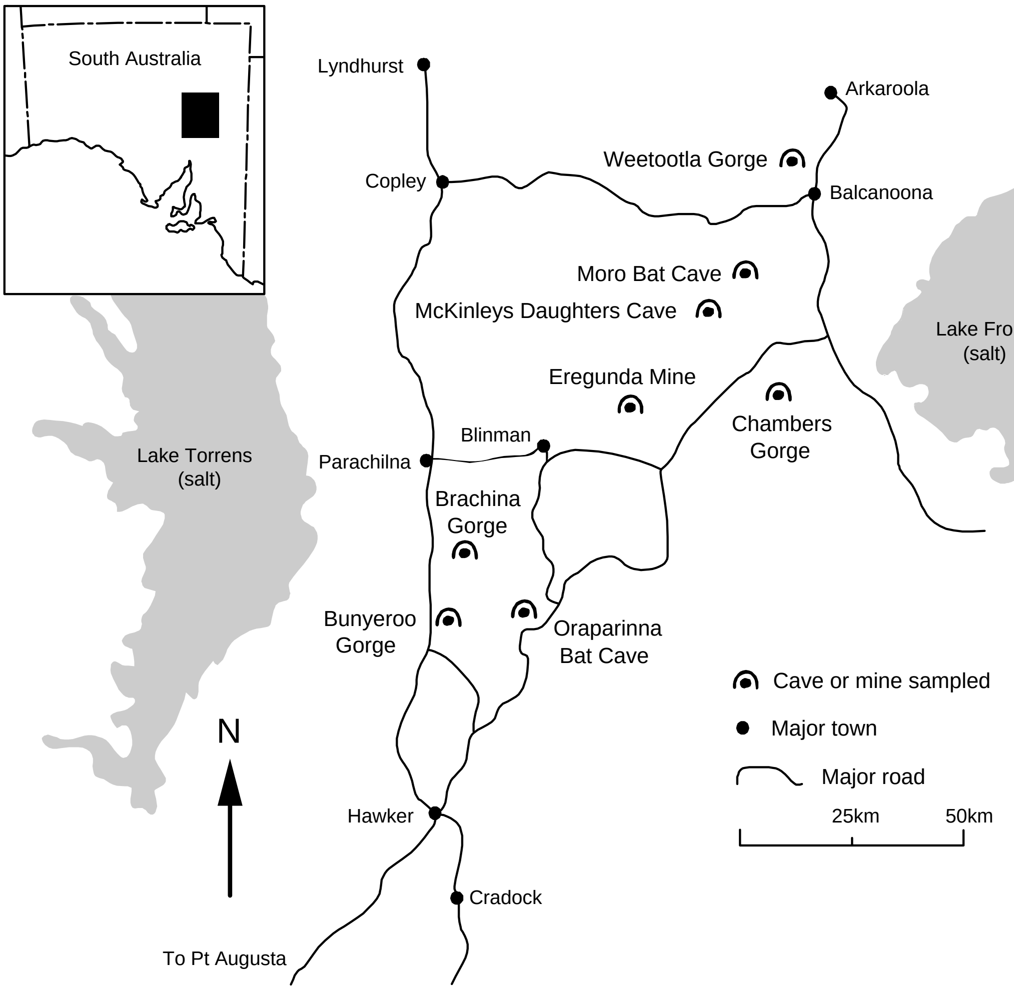

Figure 5.2. Localities of guano sites sampled in the Flinders Ranges. Brachina, Bunyeroo, Chambers, and Weetootla Gorges all contain two sites.

The Nullarbor Plain, located in central southern Australia, extends north from the Great Australian Bight to the Great Victorian Desert, forming one of the world's largest karst areas with over 200,000 km^2 of cavernous carbonate rock (Webb *et al.* 2003). Over 1,700 caves and karst features are known with many additional caves discovered each year. The four caves examined on the Nullarbor Plain (Figure 5.1) contain varying amounts of guano. The largest deposit is in the rear chamber of Weebubbie Cave. This approximately circular chamber, 20 m in diameter is almost completely filled with dry powdery guano formed into several piles. Recent guano deposition was evident in only relatively small areas at the Tops of several piles. Warbla Cave contains scattered guano throughout the large interior of the cave with small piles forming near the terminal lake. The guano deposition within Koonalda and Murrawijinie no. 3 Caves was minimal, with isolated guano pellets, sometimes in small clusters that were patchily distributed across the floor of the caves.

The Broken River Karst area (Figure 5.1), in tropical monsoonal Australia, is situated approximately 200 km west of Townsville in northern Queensland, and supports large colonies of both cave-dwelling bat and swiftlet bird populations. The area consists of numerous karst towers similar in form to those in the Chillagoe-Mungana area to the north. Populations of swiftlets are generally smaller than bat populations although their guano piles are still significant and support guano arthropod communities.

Two caves, Crazy Cracks Cave and Not Another Frig Tree Crave [sic] that were sampled for guano invertebrates are located on either side of Jacks Gorge, a 25 m deep limestone gorge created by Broken River. Arthropods were collected from guano of the Australian swiftlet (*Aerodramus terraereginae* Ramsay), little bent-wing bats (*Miniopterus australis* Tomes), and the common sheath tail bat (*Taphozous georgianus* Thomas). Crazy Cracks Cave is inhabited exclusively by the Australian swiftlet, and Not Another Frig Tree Crave is used as a maternity site for the little bent-wing bat (*M. australis*). Approximately 100 - 150 bats roost in a rift passage in Not Another Frig Tree Crave, with the majority of guano situated on an elevated shelf above the main passage.

Two swiftlet nesting sites were sampled for guano invertebrates. The first, located approximately 30 m from daylight, contained 25 nests situated between 1.5 - 2.5 m above the floor. The second nesting site, located deeper into the cave within a small chamber, contained nearly 40 nests. A 1 m high guano pile was situated in the centre of the chamber.

5.2.2 Arthropod and guano sampling

Sampling for guano arthropods occurred in May 2003 (Broken River), September 2003 (Flinders Ranges) and November 2003 (eastern Nullarbor Plain), and was conducted only once in each karst area due to the remoteness of the locations. Specimens were collected individually using hand-held forceps due to the extremely small and localised guano deposits at most sites. When sufficient quantities of guano were present, approximately 30 g samples from each site were collected and placed in Tullgren funnels to extract arthropods as described by Upton (1991). Specimens were identified to genus and, where possible, to species by appropriate taxonomic experts (see Acknowledgements).

Guano was collected from each cave when available in sufficient quantities and measured for pH, allowing micro-habitat conditions to be assessed. Humidity data was collected for sites within the Flinders Ranges using a handheld electronic temperature and humidity recorder. This recorder was unavailable for use in Broken River or the eastern Nullarbor Plain.

5.3 Results - Diversity patterns of Australian guano arthropods

5.3.1 Flinders Ranges subterranean guano arthropods

Twenty-two species from 12 orders and two classes were recorded from 12 caves and mines in the Flinders Ranges (Table 5.1). This represents a five-fold increase in species richness from previous records for this region (Mathews 1986, Moulds 2004). Speciose groups in the Flinders Ranges include the tenebrionid genus *Brises* and the emesine reduviid genus *Armstrongula* (Hemiptera) (1950). Eregunda Mine and Weetootla Gorge Mine 2 were the most diverse with five and six species recorded respectively. Weetootla Gorge Mines 1 and 2 had humidities less than 20% and the guano beneath an active bat roost in Weetootla Gorge Mine 2 had a pH of 5.5.

Brises acuticornis duboulayi Bates (Tenebrionidae) was found in Oraparinna Bat Cave and unidentified *Brises* larvae in Eregunda Mine. The emesine reduviid genus *Armstrongula* (Table 5.1) has a wide distribution in the Flinders Ranges, with three undescribed species recorded. The presence of an unidentified *Protochelifer* species (Pseudoscorpionida) in Eregunda Mine in the central Flinders Ranges is an important intermediate record for this widespread, and often cavernicolous genus, between the Nullarbor Plain and the south-east of South Australia (Chapter 4). The cosmopolitan beetle *Ptinus exulans* Erichson (Anobiidae), and an unidentified anobiid, were also recorded from

Oraparinna Bat Cave. The abundance of all species collected was less than 10 individuals from any site, and the majority of records are for single specimens.

Table 5.1. Arthropods collected from guano deposits in the caves and mines of the Flinders Ranges. Caves are listed alphabetically by the area in which they are found. Some specimens could only be identified to subfamily or genus.

Location	Cave	Order	Family	Genus and Species
Brachina Gorge	Unnamed river cave	Coleoptera	Anobiidae	sp. 1
		Neuroptera	Myrmeleontidae	*Aeropteryx* sp. 1
	Unnamed hillside cave	Neuroptera	Myrmeleontidae	*Aeropteryx* sp. 1
Bunyeroo Gorge	Unnamed cave no.1	Hemiptera	Reduviidae	*Armstrongula* sp. 1
	Unnamed cave no.2	Hemiptera	Reduviidae	*Armstrongula* sp. 2
Chambers Gorge	Unnamed cave no.1	Neuroptera	Myrmeleontidae	*Aeropteryx* sp. 1
		Zygentoma	Nicoletiidae	*Trinemura* sp. 1
	Unnamed bat cave	Araneae		sp. 1
		Neuroptera	Myrmeleontidae	*Aeropteryx* sp. 1
		Orthroptera	Gryllidae	sp. 1
Mount McKinley	McKinleys Daughters Cave (F175)	Diptera		sp. 1
		Hemiptera	Reduviidae	*Armstrongula* sp. 1
		Neuroptera	Myrmeleontidae	*Aeropteryx* sp. 1
Moro Gorge	Moro Bat Cave (F47)	Lepidoptera	Noctuidae	*Dasypodia selenophora*
		Lepidoptera	Pyralidae	sp. 1
		Neuroptera	Myrmeleontidae	*Aeropteryx* sp. 1
Oraparinna	Oraparinna Bat Cave (F8)	Coleoptera	Anobiidae	*Ptinus ?exulans*
		Coleoptera	Anobiidae	sp. 1
		Coleoptera	Tenebrionidae	*Brises acuticornis*
Point Well	Eregunda Mine	Araneae	Pholcidae	sp. 1
		Coleoptera	Tenebrionidae	*Brises* undetermined sp.
		Hymenoptera	Formicidae	*Iridomyrmex purpureus*
		Pseudoscorpionida	Cheliferidae	*Protochelifer* sp. 1
		Psocoptera		sp. 1
Weetootla Gorge	Mine 1	Araneae	Pholcidae	sp. 2
		Coleoptera	?Dermestidae	sp. 1
	Mine 2	Araneae	Pholcidae	sp. 3
		Blattodea		sp. 1
		Coleoptera	Tenebrionidae	*Brises caraboides*
		Hemiptera	Reduviidae	*Armstrongula* sp. 3
		Neuroptera	Myrmeleontidae	*Aeropteryx* sp. 1
		Orthroptera	Gryllidae	sp. 1

5.3.2 Eastern Nullarbor Plain cave guano arthropods

Twelve species from seven orders and two classes were collected from four deep, inland caves on the Nullarbor Plain (Table 5.2). Species of *Protochelifer* were collected at Warbla and Murrawijinie No. 3 caves, and these represent two previously undescribed species (see Chapter 4). The relative abundance of species varied between caves with *Protochelifer* spp. being relatively abundant, 50 individuals collected during a 1 h search in Warbla and Murrawijinie No.3 Caves. The populations of the carabid and tenebrionid beetles were also relatively large. However, abundance of species in Koonalda Cave was low with less than five individuals of any species collected.

Table 5.2. Guano associated cavernicolous arthropods collected from the eastern Nullarbor Plain during November 2004.

Cave	Class	Order	Family	Genus and species
Warbla (5N1)	Arachnida	Araneae	Desidae	*Forsterina alkirna*
	Arachnida	Pseudoscorpionida	Cheliferidae	*Protochelifer* sp. nov.
	Insecta	Psocoptera	Psyllipsocidae	*Psyllipscous ramburii*
	Insecta	Siphonaptera	Ischnopsyllidae	*Porribius* sp. 1
	Insecta	Coleoptera	Anobiidae	*Ptinus exulans?*
	Insecta	Coleoptera	Carabidae	*Speotarus lucifugus*
	Insecta	Coleoptera	Tenebrionidae	*Brises acuticornis*
Weebubbie (6N2)	Arachnida	Araneae	Desidae	*Forsterina alkirna*
	Arachnida	Acarina		sp. 1
	Insecta	Psocoptera	Psyllipsocidae	*Psyllipscous ramburii*
	Insecta	Coleoptera	Carabidae	*Speotarus lucifugus*
	Insecta	Coleoptera	Tenebrionidae	*Brises acuticornis*
	Insecta	Lepidoptera	Tineidae	*Monopis* sp. 1
Koonalda (5N4)	Arachnida	Araneae	Theridiidae	sp. 1
	Insecta	Psocoptera	Psyllipsocidae	*Psyllipscous ramburii*
	Insecta	Coleoptera	Carabidae	*Speotarus lucifugus*
Murrawijinie No. 3 (5N9)	Arachnida	Pseudoscorpionida	Cheliferidae	*Protochelifer* sp. nov.
	Arachnida	Acarina		sp. 1
	Insecta	Diptera	Tachinidae	sp. 1
	Insecta	Psocoptera	Psyllipsocidae	*Psyllipscous ramburii*
	Insecta	Coleoptera	Anobiidae	*Ptinus exulans?*
	Insecta	Coleoptera	Carabidae	?*Notospeophonus pallidus*
	Insecta	Coleoptera	Tenebrionidae	*Brises acuticornis*

5.3.3 Northern Queensland tropical cave guano arthropods

Seven species from seven orders and two classes were recorded from the Broken River karst area (Table 5.3). The largest guano deposits supported emesine reduviid bugs, Pscoptera, tineid larvae and adults (Lepidoptera), and isopods. The relative abundance of species collected was greater in the swiflet guano than in the bat guano. The abundance of *P. cunnamulla* (Reduviidae) was, however, significantly greater in the bat guano (10 individuals) than in the swiftlet guano (2 individuals). The remainder of species were present in low numbers, with less than 10 individuals collected of any species.

Table 5.3. Species diversity from two caves in the Broken River karst area, west of Townsville, Queensland. The caves were situated on either side of Jacks Gorge. Some species could only be identified to order or family.

Cave	Class	Order	Family	Genus and species
Crazy Cracks Cave	Crustacea	Isopoda	Undetermined	sp 1
	Insecta	Coleoptera	Cryptophagidae	sp 1
		Blattodea	Blattidae	sp 1
		Hemiptera	Reduviidae	*Ploiaria cunnamulla*
		Hymenoptera	Formicidae	*Oligomyrmex* sp 1
		Lepidoptera	Tineidae	*Monopis crocicapitella*
		Psocoptera	Undetermined	sp 1
Not Another Frig Tree Crave [sic]	Crustacea	Isopoda	Undetermined	sp 1
	Insecta	Hemiptera	Reduviidae	*Ploiaria cunnamulla*
		Lepidoptera	Tineidae	*Monopis crocicapitella*
		Psocoptera	Undetermined	sp 1

5.4 Discussion

The pattern of cave occupation by bat populations in arid and semi-arid Australia is different to that of temperate south-eastern Australia and monsoonal areas, primarily because bat occupation is stochastic rather than seasonal. The numerous small caves of the Flinders Ranges support small (< 50) transient populations of cave-dwelling bats that are dominated by the inland cave bat (*Vespadelus findlaysoni* Kitchener, Jones and Caputi), with the chocolate wattled bat (*Chalinolobus morio* Gray) being occasionally recorded (Hamilton-Smith *et al.* 1997, Moulds 2005). These species provide limited guano input to these caves, and hence species richness and abundance of arid guano communities is significantly lower than those occurring caves in temperate coastal Australia, such as Bat and Starlight Caves.

Monsoonal Australia has patterns of bat activity that are different to southern and eastern Australia (Churchill 1998), but are similar to that recorded in Brazil (Gnaspini and Trajano 2000), with bats active all year round. This provides constant guano deposition and hence a constant and reliable food source for guano dependent arthropods. This would suggest the presence of large guano associated communities, however, the sites investigated during this study contained orders of magnitude less bats than the maternity caves of south-eastern Australia (Chapters 2 and 3). The roosting preferences of different bat species dictates the relative deposition of guano in different cave areas with some species, such as the common sheath tail bat (*Taphozous georgianus*), preferring roosts near cave entrances (Churchill 1998).

Guano caves in arid Australia (e.g. Flinders Ranges and Nullarbor Plain) often have extremely low relative humidities and are commonly characterised by dry, acidic, pellet-like guano, even under active bat roosts (Harris 1970, Poulson and Lavoie 2000, Moulds 2005). Low humidity affects the water content of guano deposits which, in the Flinders Ranges, has been historically recorded from 3.3% (Arcoota Creek Cave) to 12.7% (Clara St. Dora Cave) (Winton 1922). This is comparable to the driest guano found in Bat Cave, Naracoorte (Appendix 2, Moulds 2003). Low humidity severely reduces fungal growth as many of the opportunistic *Phycomycete* fungi spp found on fresh guano are susceptible to rapid desiccation (Poulson 1992, Poulson and Lavoie 2000). Fungi are the primary food source of guanophilic communities and reduced growth results in lower arthropod abundance and diversity when compared with guanophilic communities in more humid coastal locations (Yen and Milledge 1990, Eberhard and Spate 1995, Bellati *et al.* 2003). Further, the paucity of moist substrate removes key refugia for moisture-dependant arthropods commonly found in guano. Consequently families such as Jacobsoniidae, Sciaridae and Sphaeroceridae are notably absent from guano in arid and semi-arid Australia, and have been replaced by more arid-adapted taxa such as tenebrionid beetles (Moulds 2005).

5.4.1 Distribution of Australian guano invertebrates

The often long distances between cave and karst areas provides significant barriers to the dispersal of guano associated arthropods and this is reflected in the few species with truly broad distributions. Further, the aridity of much of the Australian mainland exacerbates the isolation of karst areas by limiting the potential size of large bat colonies that would be capable of supporting large and diverse guano arthropod communities. Consequently, the largest differences in arthropod communities occur between arid/semi-arid Australia and those of the large maternity colonies in coastal south-eastern Australia (Table 5.4).

The first checklist for Australian guano-associated invertebrates (Appendix 1, Moulds 2004) provides a detailed compilation of species and their distributions. Many species have been shown to have unexpectedly broad or disjunct distributions, sometimes spanning several climatic regions, while others are apparently unique to individual caves or karst areas. However, there are several possible reasons to question these patterns. Firstly, taxonomic misidentification may sometimes lead to the lumping of several similar species into one. Similarly, inadequate species definitions from groups requiring systematic revision can also result in species being artificially lumped or split (e.g. Diptera: Phoridae David McAlpine, pers. comm. 2002). The presence of cryptic species may also explain these broad distributions, such as revealed for *Protochelifer* spp. (see Chapter 4). Finally, a lack of collections from most karst areas, both above and below ground, has resulted in large gaps in distributions and a poor knowledge of morphological variation within species. Indeed, the limited fieldwork undertaken during this study in the Flinders Ranges has dramatically increased species recorded for this region, and this is also the case for monsoonal Australia (Table 5.4).

However, given these taxonomical and distributional shortcomings, several well characterised species do show interesting distributional patterns. For example, several cosmopolitan epigean species such as *Monopis crocicapitella* (Tineidae) (Figure 5.3a) and *Ptinus exulans* (Anobiidae) (Figure 5.3b) that regularly exploit guano resources have broad distributions. These species are found in caves from mid-northern New South Wales across the Nullarbor Plain to the west coast of Western Australia. The single record of *M. crocicapitella* from Broken River indicates previously unidentified tineid moths recorded from several nearby Queensland karst areas, including Camooweal, Chillagoe, and Fanning River, are most likely this species, indicating that it is extremely widespread and inhabits cave gauno deposits across several climatic regions.

Table 5.4. Arthropod families found in cave guano deposits from four different regions of Australia. The Otway Basin and Nullarbor Plain have had the most collecting efforts.

Class & family	South-eastern Australia (Otway Basin)	Flinders Ranges	Nullarbor Plain	Broken River north Queensland
Isopoda: Armadillidae			+	
Porcellionidae	+			
Philosciidae			+	
Oniscoidea	+		+	
Arachnida: Araneae: Desidae			+	
Theridiidae	+		+	
Tnomisidae	+			
Pholcidae		+		
Acarina: Ameroseiidae	+			
Histiostomatidae	+		+	
Hypochthonioidea	+			
Ixodidae	+			
Laelapidae	+			
Macrochelidae	+			
Macronyssidae			+	
Neotrombidiidae			+	
Parasitidae	+		+	
Sejidae	+			
Spinturnicidae	+		+	
Rosensteiniidae	+		+	
Trombiculidae	+			
Urodinychidae	+			
Uropodidae	+			
Pseudoscorpionida: Cheliferidae	+	+	+	
Cheiridiidae			+	
Chernetidae	+		+	
Chthoniidae	+			
Collembola: Brachystomellidae	+			
Entomobryidae	+			
Hypogastruridae	+			
Insecta: Zygentoma: Nicoletiidae		+		
Blattodea: Blattellidae	+	+	+	
Blattidae			+	+
Orthoptera: Gryllidae		+		
Rhaphidophoridae	+		+	
Psocoptera: Psyllipsocidae	+		+	
Trogiidae	+			
Hemiptera: Lygaeoidea	+			
Reduviidae		+		+
Neuroptera: Myrmeleontidae		+		
Coleoptera: Anobiidae	+	+	+	
Carabidae	+	+	+	
Crytophagidae	+			+
Dermestidae	+	+		
Histeridae	+		+	
Jacobsoniidae	+			
Lathridiidae	+		+	
Leiodidae	+		+	
Scarabaeidae	+			
Staphylinidae	+		+	
Tenebrionidae		+	+	
Trogidae			+	
Siphonaptera: Ischnopsyllidae			+	
Diptera: Chironomidae	+			
Fanniidae	+			
Muscidae	+			
Nycteribiidae	+	+		
Phoridae	+		+	
Psychodidae	+			
Sciaridae	+		+	
Sphaeroceridae	+			
Tachinidae			+	
Trichoceridae	+			
Lepidoptera: Pyralidae		+		
Noctuidae	+	+		
Tineidae	+		+	+
Hymenoptera: Braconidae	+			
Ichneumonidae	+			
Ceraphronidae	+			
Diapriidae	+			
Formicidae	+	+		+
Myrmaridae	+			

Brises acuticornis (Tenebrionidae) is found throughout arid and semi-arid karst regions in Australia (Figure 5.3c), including the Nullarbor Plain (Hill 1966, Mathews 1986), and further east in the Flinders Ranges (Moulds 2005). This distribution indicates these karst areas share arid-adapted species and significant dispersal may have occurred between them in the past. The isolated record from Riverton in northern New South Wales is most likely spurious, (possibly a misidentification), considering the dramatic differences in climate compared with that across the remainder of its distribution.

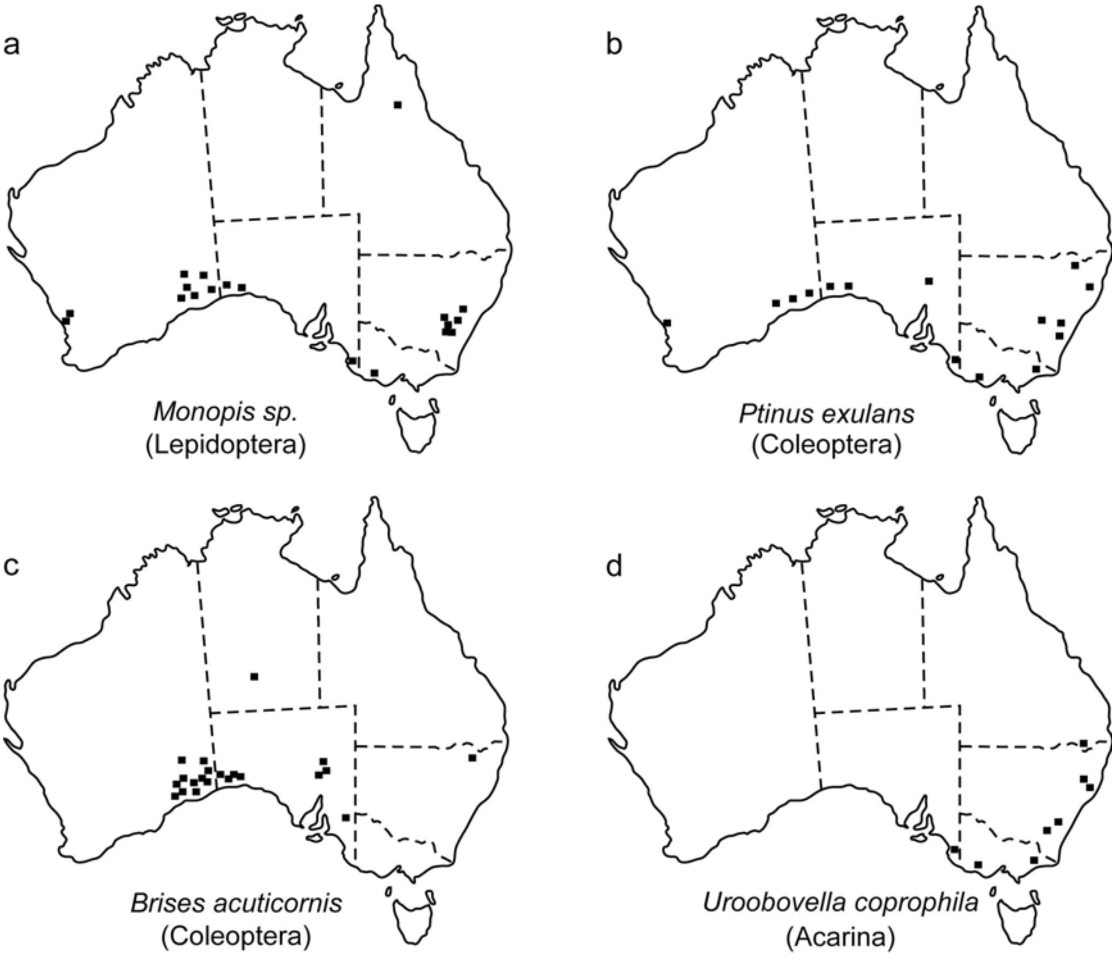

Figure 5.3. a - d. Distribution of four species of guano associated arthropods in Australia, showing disjunct patterns (e.g. *Monopis* sp.) and those associated with bat maternity colonies (*Uroobovella coprophila*).

The guano mite *Uroobovella coprophila* (Urodinychidae) (Figure 5.3d), ubiquitous in southern Australian bat caves, is notably absent from the Flinders Ranges and other arid localities (Moulds 2004, Moulds 2005). The distribution of this species appears to be directly linked to the distribution of maternity sites of the large bent-wing bat *M. schreibersii,* as adults mites rely on the presence of fresh moist guano for survival. As no records exist between southern and northern Queensland, despite large bat maternity caves around Rockhampton, the single record of this species from Undara (north Queensland) may be spurious, a misidentification, or an individual transported via phoresy.

The isolation of three species of *Armstrongula* within the Flinders Ranges suggests that increasing aridity surrounding the region may have prevented the movement of hydrophilic cavernicolous species between karst areas. The disjunct karst formations of the region are also likely to have restricted the dispersal of other species. The occurrence of emesine reduviid bugs in guano caves, including those of the Flinders Ranges, is presently poorly understood. No records are known for this subfamily from the wetter southern karst areas of Australia, with all previous records of *Armstrongula* being from under bark near the Bogan River, New South Wales (Wygodzinsky 1950).

The change in faunal composition moving south-east from the Nullarbor Plain and Flinders Ranges into the wetter costal areas of south-eastern Australia is marked, with several taxa such as the guano mite *U. coprophila*, histerid beetles and phorid flies becoming dominant on fresh guano. The guanophilic fauna of the Flinders Ranges is most similar in species diversity to that of the Nullarbor Plain and isolated karst areas to the north. The tenebrionid beetles *Brises acuticornis*, *B. caraboides* and the carabid *Thenarotes speluncarius* are found in both regions (Moore 1967, Richards 1971, Mathews 1986). The major extension to the known distribution of *B. caraboides* into the northern Flinders Ranges (previously recorded only from near Eucla on the Nullarbor Plain to the Gammon Ranges), is significant as it provides additional evidence for the similarity between these two regions. The second record of *B. caraboides*, from Weetootla Gorge Mine 2, greatly increases the distribution of this species, where it was previously known only from the type locality near Eucla. Similar distributions are exhibited by the beetles *Speotarus lucifugus* (Carabidae) and *Ptinus exulans* (Anobiidae), both previously recorded from guano caves in the Nullarbor Plain and at Naracoorte (Moulds 2004).

Tropical guano invertebrates are perhaps the least studied in Australia and, apart from records collated in the present study (Appendix 1), and compared with caves in southern Australia, field data for this region is minimal. Emesine reduviids may prove useful in future biogeographic analyses, as they have been recorded in many guano deposits from both northern Queensland, the Flinders Ranges and Nullarbor Plain, although detailed taxonomic study is yet to be conducted.

Clearly the biogeography of Australia’s guano associated arthropods is in its infancy. The diversity of Australian guano arthropods is currently skewed toward southern Australia where virtually all research has been conducted to date. Some distribution patterns, however, show species with worldwide distributions while others are restricted to particular climatic regions. Regional similarities exist in the composition of arthropod communities at both the family and generic level between the Flinders Ranges and the Nullarbor Plain, and within southern coastal Australia including Victoria and south-eastern South Australia. The paucity of records among some taxa also provides a focal point for future collecting priorities. The most significant effect of biogeographic separation identified thus far appears to be climatic variation and this should be investigated more fully in the future.

5.4.2 Potential dispersal mechanisms

The dispersal of guano associated arthropods is poorly understood despite the numerous species that apparently have wide geographical ranges. The ability of species to migrate between guano sites is potentially important as bat colonies can move between roosts because of changing conditions, such as disturbance, chamber collapse, and roost areas filling completely with guano. Several potential mechanisms may be involved in the transport of guano dependent invertebrates between roosts, such as phoresy on bats or insects, direct movement from the surface, terrestrial dispersal or via micro- and mesocaverns. These potential mechanisms are discussed and assessed below.

Phoresy – Phoretic dispersal allows potentially long distance and relatively rapid migration for species that are otherwise completely cave or guano dependent. Phoresy has been recorded for a pseudoscorpion found in the fur of a bat (Harvey and Parnaby 1993). It has also been recorded for other pseudoscorpion species on cerambycid beetles (Zeh and Zeh 1992) and aulacid wasps in central America and southern USA (Haack and Wilkinson 1987). Although these examples do not involve cavernicolous species they do demonstrate the potential for long distance phoretic migration of small sedentary arthropods. Another distinct advantage of phoresy for dispersal is that troglophilic and trogloxenic carriers will most likely rapidly locate another cave with minimal time spent in adverse epigean conditions.

The Australian guano mite *U. coprophila* shows a strong association with breeding colonies of the large bent-wing bat, *M. schreibersii* (Harris 1973, Moulds 2004). The similar distribution pattern of *U. coprophila* and *M. schreibersii* strongly suggests that this mite may be possibly phoretic on bats or very mobile guano associated invertebrates such as carabid beetles, although no observations have yet been reported. The transport of nematodes and dipteran eggs and larvae through bat faeces and urine is also possible (Decu 1986) as a rapid mode of colonisation into new guano deposits. Although the occurrence of phoretic dispersal has not been demonstrated for guano associated species there are few researchers in a position to recognise it. However, it is potentially an important colonisation mechanism in new guano deposits and if so, is likely to be responsible for limited gene flow between existing populations. Nematodes play a potentially important role in the micro-habitat of guano piles and have been recorded in large numbers from overseas caves (Decu 1986). Nematodes are also believed to be one of the first colonisers of new bat caves, being deposited via urine and faeces (Decu 1986), however, very few nematodes have been recorded from guano in Australian caves (Moulds 2004).

Colonisation directly from the surface - Colonisation directly via the soil/cave interface was first proposed by Juberthie *et al.* (1980) via the mesovoid shallow substratum (MSS) found in non-calcareous rocks in Europe. The MSS is the network of small cracks and voids separated from the surface, forming an intermediate habitat between soil and cave faunas (Juberthie 2000). This habitat is found in all temperate regions of the world and is, commonly situated in the lower levels of scree slopes. The intermediate habitat formed by the MSS provides an interface for already dark adapted, deep soil dwelling species, allowing them to move into the cave environment via soil overlaying limestone (Gers 1998). Soil-dwelling species may migrate, via the MSS, into cave guano deposits due to the virtually inexhaustible food supply they provide. This process would enable the colonisation of new guano deposits without the need for active migration of individuals between locations.

Terrestrial dispersal - Long distance terrestrial dispersal of species is potentially viable for some species capable of surviving in surface habitats. *Brises acuticornis* (Tenebrionidae) is recorded from epigean and hypogean habitats and may use rabbit or wombat burrows for shelter during the day, thus assisting in long-range dispersal (Mathews 1986). This mode of dispersal may allow for the migration of epigean species into cave guano deposits. This is the simplest mode of colonisation for subterranean guano deposits with many guano associated species having nearby surface populations. Immigrants may therefore colonise guano deposits via existing epigean dispersal strategies without the need for specialised dispersal methods.

Subterranean migration - Migration of species through micro- and mesocaverns may enable new guano deposits in caves near to other previously colonised deposits to be successfully exploited. Migration of troglobitic species through small subterranean cavities was recognised by Howarth (1972, 1973, 1983) as a mechanism for short-range dispersal in Hawaiian lava fields, and it could potentially be used by guano dependent troglophilic species. This is dependent on the close proximity of caves and the limestone containing a suitable amount of micro- and mesocaverns. Migration by guano arthropods using this method is likely to be restricted to movements within approximately 10 km, as postulated in this study for populations of *Protochelifer naracoortensis* in the Naracoorte Caves (see Chapter 4).

5.4.3 Potential endemism

Endemism of guano species within individual caves, has, in the past been assigned without a full understanding of the distribution of the Australian guano fauna. This is apparent for the maternal chamber of Bat Cave, Naracoorte, where previous studies (Hamilton-Smith 2000, Moulds 2003), identified ‘several endemic species’ in the maternity chamber. A checklist of Australia’s guano invertebrates (Moulds 2004) reduced this to only a single possibly endemic species, *Protochelifer naracoortensis*, that has subsequently been identified in three other caves within the Naracoorte Cave World Heritage Area (see Chapter 4), however, this species can still be regarded as a short range endemic species as defined by Harvey (2002).

Table 5.5. Possibly endemic guano dependent species in Australia. These species all show known restricted distributions and a significant degree of guano dependence.

State	Order	Genus and Species	Cave and Guano Dependance	Cave
QLD	Pseudoscorpionida	*Sathrochthonius webbi*	Tb, Gp	Holy Jump Lava Cave (BM1)
QLD	Coleoptera	*Choleva australis*	Tp, Gp	Royal Arch Cave (CH9)
QLD	Coleoptera	*Omorgus costatus*	Tp, Gp?	Johannsens Cave (J1-2)
NSW	Pseudoscorpionida	*Oratemnus cavernicola*	Tp, Gp?	Jump Up Cave, Gray Range
NSW	Pseudoscorpionida	*Sundochernes guanophilus*	Tp2, Gb	Fig Tree Cave (W148)
NSW	Pseudoscorpionida	*Tyrannochthonius cavicola*	Tp2, Gb	Grill Cave (B44)
NSW	Acarina	*Neotrombidium gracilipes*	Tp2, Gb	Fig Tree Cave (W148)
NSW	Acarina	*Hypoaspis annectans*	Tp, Gp	Carrai Bat Cave (SC5)
Nullarbor	Pseudoscorpionida	*Cryptocheiridium australicum*	Tp2, Gp	Murra-El-Elevyn Cave (N47)
Nullarbor	Isopoda	*Abedaioscia troglodytes*	Tb, Gp?	Pannikin Plain Cave (N49)
Nullarbor	Coleoptera	*Quedius luridipennis*	Tp?, Gp	Abrakurrie Cave (N3)
VIC	Pseudoscorpionida	*Pseudotyrannochthonius hamiltonsmithi*	Tp2, Gp	Mount Widderin Cave (H1)
VIC	Coleoptera	*Achosia lanigera*	Tp?, Gp	Wilson Cave (EB4)

Several species have been identified as having restricted distributions and guano dependence, although none can yet be positively identified as endemic to specific caves (Table 5.5). The restricted distribution of all species listed in Table 5.5 must be regarded as tentative. More extensive collecting, both above and below ground, must be undertaken before their distributions can be confirmed. This is especially true for troglophilic species, as epigean occurrence of these species will affect their endemic status. The degree of a species’ dependence on guano will also affect its potential as an endemic taxon and more information is required to confirm the biology of most species. Taxa currently recorded from single caves or isolated areas are more likely to prove to be endemic when they are guano dependent. To date only Fig Tree Cave (W148) (Wombeyan, NSW) is known to contain two species showing both restricted distribution and guano dependence (Table 5.5). However, given the problems with taxonomy, limited field collecting, and evidence of cryptic species, endemism is likely to be much more common than indicated by Table 5.5.

Chapter 6: General discussion - Australian cavernicolous guano associated arthropods

6.1 Conservation and management of cavernicolous guanophilic invertebrate communities

The management of guano associated invertebrate communities is not a difficult issue in most cases despite the sometimes diverse invertebrate assemblages present. Guano associated communities rely on the adequate protection of guano producing animals and the caves they inhabit, ensuring the continual or seasonal presence of fresh guano (Gnaspini 2005). The protection of micro-organisms that are the basis of most guano food webs is vital. Removal of guano for use as a nitrogen rich fertiliser can also dramatically impact on invertebrate populations as habitat is destroyed, and micro-habitats altered, impacting on the bacteria and fungi that form the basis of guano food webs. The compaction of guano deposits by trampling reduces the surface area and aeration of guano, essential for the survival of quiescent species and larvae residing below the guano surface. Compaction can make guano unusable to bacteria and fungi. All these issues are essential to the conservation of guano communities.

The protection of bat breeding and over-wintering sites is perhaps the most important and obvious step in the protection of guano associated arthropod communities (Elliot 2000; Hamilton-Smith and Eberhard 2000). Breeding and over-wintering sites provide the largest, most continuous and predictable input of guano that is essential to the maintenance of diverse guano communities. The protection of cave-dwelling bats and their habitat shall be only dealt with briefly here as it is the subject of many published articles (Martin *et al.* 2003; Elliot 2005; Murray and Kunz 2005). The restriction of human visitation to known bat maternity sites during birthing periods is vital to minimise impact on the population. Disturbance of pups in the weeks after birthing can result in increased mortality from falling and, consequently, minimal disturbance is crucial in maintaining the integrity of bat populations (Murray and Kunz 2005).

Fresh guano contains the highest species richness in temperate caves (see Chapters 2 and 3) and its removal stops the succession of bacteria and fungi crucial to the lowest trophic levels of the food web. Substantial removal of guano, either fresh or desiccated, dramatically decreases or destroys guano associated communities, primarily by reducing available food but also via excessive disturbance (Gnaspini 2005). Limited removal of guano, if conducted without disturbance to bat colonies, may not prove detrimental to guano invertebrates but should be avoided or discouraged whenever possible.

Compaction is the largest factor in the destruction of all sedimentary and organic cave floor micro-habitats (Hamilton-Smith and Eberhard 2000; Juberthie 2000). This form of degradation is directly associated with the level of human traffic through a cave. Compaction of guano deposits through human visitation destroys essential micro-habitats in the upper layers of deposits making them unusable to virtually all organisms. Compaction of guano deposits also dramatically reduces surface area, slowing or halting breakdown of chitin and other major guano constituents by bacteria and fungi. This can be catastrophic to guano invertebrate communities as these organisms form the base of the food web making nutrients available to mycetophages and their predators.

Encouraging suitable epigean landuse to allow natural hydrology processes is essential in maintaining species richness, as this is directly linked to the moisture content of hypogean substrates. For example, the clearing of native vegetation and its replacement with pine plantation significantly reduces surface water recharge to caves (Hamilton-Smith and Eberhard 2000) and reduces the level of regional water tables. Pollution of groundwater that contacts guano deposits can also adversely affect guano communities by reducing, or completely destroying, natural populations of micro-organisms.

Maintaining natural cave airflow is important to all cave-dwelling communities as desiccation of subterranean habitats is potentially destructive to all hypogean communities. The premature desiccation of guano reduces the turnover and succession of micro-organisms and therefore limits the arthropod communities that can utilise the resource. The majority of cavernicolous and guanobitic taxa are hydrophilic and require a moist habitat to survive, so abnormal flows of dry air can rapidly kill large populations of cave invertebrates.

Guano communities in arid habitats have fewer hydrophilic species and are generally far less abundant and transient in their distribution (Moulds 2005).

The impact of invasive species is a potentially significant factor for the conservation of guano dependent ecosystems. Invasive non-native species can have possibly drastic impacts on guano ecosystems and alter the fine dynamics of an invertebrate community. The presence of several invasive species (*Porcellio scaber*, *Hypogastrura* spp., *Thrips imaginis*) within Bat and Starlight Caves is potentially significant although the species are generally present in low abundances. Such species in sufficient numbers could however have an adverse impact on pre-existing invertebrate communities. This requires further investigation in Bat Cave to determine if a link exists between the presence of invasive species and the apparent decline in the abundance of the native cockroach *Neotemnopteryx australis*.

6.1.1 Management

The conservation of guano associated cave communities within managed parks and reserves is easily achieved in most cases due to the highly specific nature of the habitat concerned. Bat sites are generally easily identified and access is commonly already restricted. Due to the unpleasant smell and health issues (e.g. *Histoplasmosis*) associated with guano deposits the general public are not inclined, nor should be encouraged, to enter cave areas regularly occupied by large bat colonies. Fortunately, this lack of popularity greatly assists the survival of guano invertebrate communities. In such cases where regular access is unavoidable track marking should be maintained to minimise compaction and disturbance of guano micro-habitats. This is especially important for irregular roost sites located in tourist caves where small but important guano deposits can support invertebrate communities.

In Australia, caves on private land or on freely accessible public land that contain bat colonies are most commonly wintering torpor sites. These sites often engender little interest by owners. Appropriate education by local caving groups or nearby cave managers is the best way to ensure these sites are protected and left undisturbed. In areas where caves are situated away from actively managed sites or on freely accessible land, discouraging visits by casual tourists should be a primary concern for conservation and hence guano deposits and their fauna. Interpretive signs at entrances explaining the needs of bats (and caves) are an effective way to keep most casual visitors away.

6.2 General discussion

Karst and caves in Australia remain relatively poorly known biologically compared with other terrestrial ecosystems. Guano associated arthropods comprise a substantial component of total subterranean biodiversity in Australia. Few studies of guano ecosystems have been conducted relative to other hypogean ecosystems, despite their diverse communities well suited to research in community ecology. The evolution of these complex ecosystems is very different to the resource poor ecosystems dominated by troglobites and therefore warrants particular attention.

The first quanitative information characterising micro-habitats associated with cavernicolous guano deposits was documented by Harris (1970) and Poulson (1972) and involved pH, temperature and moisture content of guano piles in temperate regions. The extensive and detailed data obtained from this study (Chapters 2 and 3) show guano micro-habitats are highly variable and change rapidly over short distances. This is vital for the future understanding of these ecosystems as micro-habitat dictates broader patterns of diversity and abundance found within guano deposits. The relationship between species richness and micro-habitat is complex, and further detailed study at small spatial scales is required to fully understand this relationship. The correlation between fresh guano deposition, pH and moisture content obscures these relationships, and more detailed ecological experiments are required to determine which of these factors is ultimately determining the species richness in any individual micro-habitat. The limiting factor of many micro-habitats with regard to species richness and abundance is also yet to be fully understood and is clearly demonstrated by the relationships between Simpson’s diversity index values and the environmental variables measured here. The numerous low diversity values associated with all environmental variables indicates a single, or most probably, several limiting factors are present. Other environmental variables beside the three measured in this study are undoubtedly influencing invertebrate community structure and need to be identified in future studies to provide a fuller picture of guano associated invertebrate ecosystems.

This study has demonstrated that differences in cave morphology exert a significant influence on environmental conditions in guano deposits, and the subsequent composition of invertebrate communities. The importance of airflow and cave hydrology cannot be under-estimated when investigating arthropod community structure and should be considered in every study. The need for accurate cave maps is also vital, not only for spatial analysis, but also for the interpretation of environmental variables within each cave.

Genetic divergence between invertebrate species from guano caves should be further investigated as it may shed new light on speciation and potential dispersal mechanisms. The colonisation of cavernicolous guano deposits by epigean species can also be used as a model for speciation between populations in close proximity but separated by significant environment and behavioural barriers.

The diversity of Australian guano associated arthropods is considerable and shows the diversity and adaptability of arthropods to exploit novel resources and habitats. The factors controlling this diversity are different to those affecting purely cave dependent populations and species. Biogeographic patterns are emerging from the scant data available indicating differences across climatic gradients. Further sampling is required before meaningful conclusions can be reached. It is, however, interesting to note the multiple invasions of guano and cave environments by some widespread common surface dwelling species such as *Ptinus exluans* (Coleoptera: Anobiidae) and *Monopis crocicapitella* (Lepidoptera: Tineidae). Climatic regions in Australia control much of the diversity for guano associated arthropods Changes in abundance and behaviour of bats, combined with rainfall and humidity patterns undoubtedly influence arthropod community structure. Temperate southern Australian bat caves, primarily represented by large maternity colonies of *Miniopterus* spp. support diverse and abundant communities enabling practical ecological study of community structure and its relationship with guano micro-habitat. The presence of high individual species abundances compared with other hypogean communities is likely to provide better statistical support for testing ecological hypotheses.

The use of subterranean guano ecosystems as model systems for community ecology is potentially very powerful, due to the absence of many variables associated with epigean habitats. A stable temperature and humidity, the removal of diurnal and seasonal cycles, and the relatively small number of species, combined with the absence of large immigration events makes these ecosystems an excellent choice for ecological experiments. The experimental manipulation of guano arthropod communities is now easily achieved using the results from this study to predict the species richness associated with different micro-habitat conditions. The mosaic of guano micro-habitats, although complicating analysis is relatively easy to predict and can be utilised in future project designs.

Opportunities for future research in this field are immense with only limited knowledge existing for most karst areas. The ecological classification for many species is poorly known and further *in situ* observations are required to increase knowledge in this area. The microbiology of guano deposits also remain very poorly known in Australia, as well as for overseas caves. The study of hypogean guano ecosystems should, however, be encouraged as there is significant potential for many areas of biological research within such communities.

References

Adams, M., Baverstock, P. R., Watts, C. H. S. and Reardon, T. B. (1987). Electrophoretic resolution of species boundaries in Australian Microchiroptera. *I. Eptesicus* (Chiroptera, Vespertilionidae). *Australian Journal of Biological Sciences* **40**: 143-162.

Austin, A. D. and Dangerfield, P. C. (1992). Synopsis of Australasian Microgastrinae (Hymenoptera: Braconidae) with a key to genera and description of new species. *Invertebrate Taxonomy* **6**: 1-76.

Barr, T. C. J. (1968). Cave ecology and the evolution of troglobites. *Evolutionary Biology 2*. Dobzhansky, T., Hect, M. and Steere, W. New York, Appleton-Century-Crofts. **2:** 35-102.

Baudinette, R. V., Wells, R. T., Sanderson, K. J. and Clarke, B. (1994). Microclimatic conditions in maternity caves of the bent-wing bat, *Miniopterus schreibersii*: an attempted restoration of a former maternity site. *Wildlife Research* **21**: 607-619.

Beier, M. (1966). On the Pseudoscorpionidea of Australia. *Australian Journal of Zoology* **14**: 275-303.

Beier, M. (1967). Some Pseudoscorpionidea from Australia, chiefly from caves. *Australian Zoologist* **14**: 199-205.

Beier, M. (1968). Some cave-dwelling Pseudoscorpionidea from Australia and New Caledonia. *Records of the South Australian Museum* **15**: 757-765.

Beier, M. (1969). Neue Pseudoskorpione aus Australien. *Annalen des Naturhistorischen Museums in Wien* **73**: 171-187.

Beier, M. (1975). Neue Pseudoskorpione aus Australien und Neu-Guinea. *Annalen des Naturhistorischen Museums in Wien* **78**: 203-213.

Bellati, J. (2001). Guanophilic invertebrate diversity and seasonality in Bat Cave at Naracoorte, South Australia. Department of Applied and Molecular Ecology. Adelaide, University of Adelaide**:** 1-81.

Bellati, J., Austin, A. D. and Stevens, N. B. (2003). Arthropod diversity of Bat Cave, Naracoorte Caves World Heritage Area, South Australia. *Records of the South Australian Museum, Monograph Series* **7**: 257-265.

Blyth, J., Jasinska, E., Mutter, L., English, V. and Tholen, P. (2002). Threatened wildlife of the Yanchep Caves. *Landscope* **17**: 34-40.

Boult, P. J. and Hibburt, J. E., Eds. (2002). *The petroleum geology of South Australia. Otway Basin*. Petroleum Geology of South Australia Series. Adelaide, Department of Primary Industries and Resources.

Boutin, C. (2004). Organisms: classification. *Encyclopedia of caves and karst science*. Gunn, J. London, Fitzroy Dearborn**:** 548-550.

Bradbury, J. H. and Williams, W. D. (1997). Amphipod (Crustacea) diversity in underground waters in Australia: an Aladdin's Cave. *Memiors of the Museum of Victoria* **56**: 513-519.

Bradbury, J. H. (2000). Western Australian stygobiont amphipods (Crustacea: Paramelitidae) from the Mt Newman and Millstream regions. *Records of the Western Australian Museum, Supplement* **60**: 1-102.

Brown, S. P. and Wells, R. T. (2000). A middle Pleistocene vertebrate fossil assemblage from Cathedral Cave, Naracoorte, South Australia. *Transactions of the South Australian Museum* **124**: 91-104.

Cade, B. S. and Noon, B. R. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* **1**: 412-420.

Calder, D. R. and Bleakney, J. S. (1965). Microarthropod ecology of a porcupine-inhabited cave in Nova Scotia. *Ecology* **46**: 895-899.

Camassa, M. M. (2004). Food resources. *Encyclopedia of caves and karst science*. Gunn, J. London, Fitzroy Dearborn**:** 365-368.

Cardinal, B. R. and Christidis, L. (2000). Mitochondrial DNA and morphology reveal three geographically distinct lineages of the large bentwing bat (*Miniopterus schreibersii*) in Australia. *Australian Journal of Zoology* **48**: 1-19.

Christiansen, K. A. (1962). Proposition pour la classification des animaux cavernicoles. *Spelunca Mem.* **2**: 76-78.

Churchill, S. (1998). *Australian Bats*. Sydney, Reed New Holland.

Colless, D. H. and McAlpine, D. K. (1991). Diptera. *The insects of Australia*. Naumann, I. D., Carne, P. B., Lawerence, J. F.*et al*. Melbourne, Melbourne University Press. **2:** 717-786.

Cooper, S. J. B., Hinze, S., Leys, R., Watts, C. H. S. and Humphreys, W. F. (2002). Islands under the desert: molecular systematics and evolutionary origins of stygobitic beetles (Coleoptera: Dytiscidae) from central Western Australia. *Invertebrate Systematics* **16**: 589-598.

Culver, D. C. (1982). *Cave Life. Evolution and ecology*, Harvard University press, Cambridge, MA.

Culver, D. C., Kane, T. C. and Fong, D. W. (1995). *Adaptation and natural selection in caves: the evolution of Gammarus minus*. Cambridge MA, Harvard University Press.

Culver, D. C. and Wilkens, H. (2000). Chapter 20. Critical review of the relevant theories of the evolution of subterranean animals. *Ecosystems of the world. Subterranean Ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 381-398.

Decu, V. (1986). Some considerations on the bat guano synusia. *Travaux de l'Institut de Spéologie "Emile Racovitza"* **25**: 41-51.

Dufrene, M. and Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**: 345-366.

Eberhard, S. M. and Spate, A. (1995). Cave invertebrate survey: toward an atlas of NSW cave fauna. NSW heritage assistance program NEP 94765**:** 1-112.

Eberhard, S. M. and Humphreys, W. F. (2003). The crawling, creeping and swimming life of caves. *Beneath the surface. A natural history of Australian caves*. Finlayson, B. and Hamilton-Smith, E. Sydney, UNSW Press**:** 127-147.

Elliot, W. R. (2000). Conservation of the North American cave and karst biota. *Ecosystems of the world. Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elevier. **30:** 665-689.

Elliot, W. R. (2005). Protecting caves and cave life. *Encyclopedia of caves*. Culver, D. C. and White, W. B. San Diego, California, Elsevier**:** 458-467.

Felsenstein, J. (1993). PHYLIP (Phylogeny Inference Package). Version 3.5c.

Ferreira, R. L. and Martins, R. P. (1998). Diversity and distributions of spiders associated with bat guano piles in Mirrinho Cave (Bahia State, Brazil). *Diversity and Distributions* **4**: 235-241.

Ferreira, R. L. and Martins, R. P. (1999). Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. *Tropical Zoology* **12**: 231-252.

Fletcher, M. W. (1975). Microbial ecology of bat guano. *Cave Research Foundation* **1975 Annual Report**: 51-53.

Folmer, O. M., Black, W., Hoeh, R., Lutz, R. and Vrijenhoek, R. (1994). DNA primers for amplification of mitichondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294-299.

GentraSystems. (2005). DNA purification from a single fly. http://www.gentra.com/documents.asp (Accessed 25 January 2005).

Gers, C. (1998). Diversity of energy fluxes and interactions between arthropod communities: from soil to cave. *Acta Oecologica* **19**: 205-213.

Gill, E. D. (1948). Structure and origin of Guano Cave, near Warrnambool, Victoria. *Victorian Naturalist* **65**: 186-191.

Gillieson, D. (1997). *Caves: Processes, development and management*. Oxford, Blackwell.

Gnaspini, P. (1992). Bat guano ecosystems. A new classification and some considerations, with special references to Neotropical data. *Mémoires de Biospéologie* **19**: 135-138.

Gnaspini, P. and Trajano, E. (2000). Guano communities in tropical caves. *Ecosystems of the world. Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 251-268.

Gnaspini, P. (2005). Guano communities. *Encyclopedia of caves*. Culver, D. C. and White, W. B. San Diego, California, Elsevier**:** 276-283.

GraphPad (2002). GraphPad Prism. Version 3.03.

Haack, R. A. and Wilkinson, R. C. (1987). Phoresy by *Dendrochernes* pseudoscorpions on Cerambycidae (Coleoptera) and Aulacidae (Hymenoptera) in Florida. *American Midland Naturalist* **117**: 369-373.

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows. Version 7.0.1.

Hamilton-Smith, E. and Adams, D. J. H. (1966). The alleged obligate ectoparasitism of *Myotyphlus jasoni* (Matth.) (Coleoptera Staphylinidae). *Journal of the Entomological Society of Queensland* **5**: 44-45.

Hamilton-Smith, E. (1967). The Arthropoda of Australian caves. *Journal of the Australian Entomological Society* **6**: 103-118.

Hamilton-Smith, E. (1971). The classification of cavernicoles. *Bulletin of the National Speleological Society* **33**: 63-66.

Hamilton-Smith, E., Flavel, S. and Reardon, T. B. (1997). Potential wealth and great optimism: mining bat guano in the Flinders Ranges. *21st biennial conference of the Australian Speleological Federation*, Quorn, South Australia, Australian Speleological Federation.

Hamilton-Smith, E. (2000). Report on current changes in biodiversity of the Bat Cave, Naracoorte World Heritage Area., Internal report for the Department of Environment and Heritage, South Australia.

Hamilton-Smith, E. and Eberhard, S. (2000). Conservation of cave communities in Australia. *Ecosystems of the world. Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 647-664.

Harris, J. A. (1970). Bat guano cave environment. *Science* **169**: 1342-1343.

Harris, J. A. (1971). Dynamics of a bat-guano cave ecosystem with particular reference to the guano mite *Uroobovella coprophila* (Womersley). Brisbane, University of Queensland.

Harris, J. A. (1973). Structure and dynamics of a cave population of the guano mite, *Uroobovella coprophila* (Womersley). *Australian Journal of Zoology* **21**: 239-275.

Harvey, M. S. (1981). A checklist of the Australian Pseudoscorpionida. *Bulletin of the British Arachnological Society* **5**: 237-252.

Harvey, M. S. (1984). The genus *Nannochelifer* Beier, with a new species from the Coral Sea (Pseudoscorpionida, Cheliferidae). *Journal of Arachnology* **12**: 291-296.

Harvey, M. S. (1991). *Catalogue of the Pseudoscorpionida*. Manchester, Manchester University Press.

Harvey, M. S. (1992). The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). *Invertebrate Taxonomy* **6**: 1373-1435.

Harvey, M. S. and Parnaby, H. E. (1993). Records of pseudoscorpions associated with bats. *Australian Mammologist* **16**: 39-40.

Harvey, M. S. (2002). Short-range endemism among the Australian fuana: some examples from non-marine environments. *Invertebrate Systematics* **16**: 555-570.

Hawes, R. S. (1939). The flood factor in the ecology of caves. *Journal of Animal Ecology* **8**: 1-5.

Hickman, V. V. (1974). Notes on the biology of *Ptinus exulans* Erichson (Coleoptera: Ptinidae). *Journal of the Entomological Society of Australia (N.S.W.)* **8**: 7-14.

Higgins, E. T. and Petterd, W. F. (1883). Description of a new cave-inhabiting spider, together with notes on mammalian remains from recently discovered caves in the Chudleigh district. *Papers and Proceedings of the Royal Society of Tasmania* **1882**: 191-192.

Hill, A. L., Ed. (1966). *Biological notes*. Mullamullang Cave Expeditions 1966. Adelaide, Cave Exploration Group South Australia.

Hill, M. O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**: 427-431.

Hoch, H. (1988). A new cavernicolous planthopper species (Homoptera: Fulgoroidea: Cixiidae) from Mexico. *Mitteilungen der Schweizerischen entomologischen Gesellschaft* **61**: 295-302.

Hoch, H. (1990). Cavernicolous Meenoplidae of the genus *Phaconeura* (Homoptera: Fulgoroidea) from Australia. *Bishop Museum Occasional Papers* **30**: 188-203.

Hoch, H. (1993). A new troglobitic planthopper species (Homoptera: Fulgoroidea: Meenoplidae) from Western Australia. *Records of the Western Australian Museum* **16**: 393-398.

Hoch, H. and Howarth, F. G. (1999). Multiple cave invasions by species of the planthopper genus Oliarus in Hawaii (Homoptera: Fulgoroidea: Cixiidae). *Zoological Journal of the Linnean Society* **127**: 453-475.

Hopper, S. D. and Gioia, P. (2004). The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual review of Ecology, Evolution and Systematics* **35**: 623-650.

Horst, R. (1972). Bats as primary producers in an ecosystem. *Bulletin of the National Speleological Society* **34**: 49-54.

Howarth, F. G. (1972). Cavernicoles in lava tubes on the island of Hawaii. *Science* **175**: 325-326.

Howarth, F. G. (1973). The cavernicolous fauna of Hawaiian lava tubes, 1. Introduction. *Pacific Insects* **15**: 139-151.

Howarth, F. G. (1983). Ecology of cave arthropods. *Annual review of Entomology* **28**: 365-389.

Howarth, F. G. (1987). The evolution of non-relictual tropical troglobites. *International Journal of Speleology* **16**: 1-16.

Howarth, F. G. (1988). Environmental ecology of north Queensland caves: or why are there so many troglobites in Australia. *17th Biennial Australian Speleological Federation Tropicon Conference*, Lake Tinaroo, Far North Queensland, Australian Speleological Federation.

Howarth, F. G. and Stone, F. D. (1990). Elevated carbon dioxide levels in Bayliss Cave, Australia: Implications for the evolution of obligate cave species. *Pacific Science* **44**: 207-218.

Howarth, F. G. (2003). Cave insects. *Encyclopedia of Insects*. Resh, V. H. and Carde, R. T. San Diego, Elsevier. **1:** 1-1266.

Howarth, F. G. and Hoch, H. (2005). Adaptive shifts. *Encyclopedia of caves*. Culver, D. C. and White, W. B. San Diego, Elsevier**:** 17-24.

Huelsenbeck, J. P. and Ronquist, F. (2001). MrBayes 3. Bayesian Analysis of Phylogeny. Version 3.0b4.

Humphreys, W. F. (1991). Experimental re-establishment of pulse-driven populations in a terrestrial troglobite community. *Journal of Animal Ecology* **60**: 609-623.

Humphreys, W. F. (2000a). Background and glossary. *Ecosystems of the world. Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 3-14.

Humphreys, W. F. (2000b). The hypogean fauna of the Cape Range Peninsula and Barrow Island, northwestern Australia. *Ecosystems of the world. Subterranean Ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** Chapter 30.

Humphreys, W. F. (2001). Groundwater calcrete aquifers in Australian arid zone: the context to an unfolding plethora of stygal biodiversity. *Records of the Western Australian Museum* **Supplement 64**: 63-83.

Humphreys, W. F. and Eberhard, S. (2001). Subterranean fauna of Christmas Island, Indian Ocean. *Helictite* **37**: 59-73.

Humphreys, W. F. (2005). Diversity patterns in Australia. *Encyclopedia of caves*. Culver, D. C. and White, W. B. San Diego, California, Elsevier. **1:** 183-196.

Hunt, G. S. (1993). A new cavernicolous harvestmen from lava tube caves in tropical Australia (Arachnida: Opiliones: Phalangodidae). *Memoirs of the Queensland Museum* **33**: 135-163.

Hutchinson, G. E. (1950). Survey of contemporary knowledge of biogeochemistry. 3. The biogeochemistry of vertebrate excretion. *Bulletin of the American Museum of Natural History* **96**: 1-554.

Juberthie, C., Delay, B. and Bouillon, M. (1980). Extension du milieu souterrain en zone non calcaire: description d'un nouveau milieu et du son peuplement par les coleopteres troglobies. *Mémoires de Biospéologie* **7**: 19-52.

Juberthie, C. (2000a). The diversity of the karstic and pseudokarstic hypogean habitats in the world. *Ecosystems of the world. Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 17-39.

Juberthie, C. (2000b). Conservation of subterranean habitats and species. *Ecosystems of the world. Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 691-700.

Kane, T. C. and Richardson, R. C. (2005). Natural selection. *Encyclopedia of caves*. Culver, D. C. and White, W. B. San Diego, California, Elsevier. **1:** 409-411.

Koenker, R. and Bassett, G. (1978). Regression quantiles. *Econometrica* **46**: 33-50.

Koon, L. C. and Cranbrook, E. (2002). *Swiftlets of Borneo. Builders of edible nests*, Natural History Publications (Borneo).

Kumar, S., Tamura, K. and Nei, M. (2004). MEGA3: Integrated software for Molecular Evolutionary Genetics Analysis and sequence alignment. Version 3.0.

Lamprecht, G. and Weber, F. (1992). Spontaneous locomotion behaviour in cavernicolous animals: the regression of the endogenous circadian system. *The natural history of biospeleology*. Camacho, A. I. Madrid, Spain, National Museum of Natural Sciences**:** 225-262.

Langecker, T. G. (2000). The effects of continuous darkness on cave ecology and cavernicolous evolution. *Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 135-157.

Lawrence, J. F. and Britton, E. B. (1991). Coleoptera (Beetles). *The insects of Australia*. Naumann, I. D., Carne, P. B., Lawerence, J. F.*et al*. Melbourne, Melbourne University Press. **2:** 543-683.

Lea, A. M. (1910). On some Tasmanian cave-inhabiting beetles. *Tasmanian Naturalist* **2**: 53-58.

Lewis, I. D. (1976). *South Australian Cave Reference Book*. Adelaide, Cave Exploration Group South Australia.

Maa, T. C. (1971). Studies in Batflies (Diptera: Streblidae: Nycteribiidae). *Pacific Insects Monographs* **28**: 1-247.

Magurran, A. E. (1988). *Ecological diversity and its measurement*. Cambridge, Cambridge University Press.

Martin, B. J. (1975). Bat guano arthropod communities. *Cave Research Foundation* **1975 Annual Report**: 54-55.

Martin, B. J. (1977). The influence of patterns of guano renewal on bat guano arthropod communities, Cave Research Foundation. **1976 Annual Report:** 36-42.

Martin, K. W., Leslie, D. M., Payton, M. E., Puckette, W. L. and Hensley, S. L. (2003). Internal cave gating for the protection of colonies of the endangered gray bat (*Myotis grisescens*). *Acta Chiropterologica* **5**: 143-150.

Mathews, E. G. (1986). A revision of the troglophilic genus *Brises* Pascoe, with a discussion of the Cyphaleini (Coleoptera: Tenebrionidae). *Records of the South Australian Museum* **19**: 77-90.

McCune, B. and Mefford, M. J. (1999). PC-ORD for Windows. 4.10.

McCune, B. and Grace, J. B. (2002). *Analysis of ecological communities*. Gleneden Beach, MjM Software Design.

Medway, L. (1962). The swiftlets (*Collocalia*) of Niah Cave, Sarawak. Part 2 Ecology and the regulation of breeding. *Ibis* **104**: 228-245.

Moore, B. P. (1967). New Australian cave Carabidae (Coleoptera). *Proceedings of the Linnean Society of New South Wales* **91**: 179-184.

Moulds, T. A. (2003). Arthropod ecology of Bat Cave, Naracoorte, South Australia. *Proceedings of the 24th Biennial Conference of the Australian Speleological Federation*, Bunbury WA, Australian Speleological Federation.

Moulds, T. A. (2004). Review of Australian cave guano ecosystems with a checklist of guano invertebrates. *Proceedings of the Linnean Society of New South Wales* **125**: 1-42.

Moulds, T. A. (2005). Diversity and biogeography of subterranean guano arthropod communities of the Flinders Ranges, South Australia. *Proceedings of the Linnean Society of New South Wales* **126**: 125-132.

Murray, S. W. and Kunz, T. H. (2005). Bats. *Encyclopedia of caves*. Culver, D. C. and White, W. B. San Diego, California, Elsevier**:** 39-45.

Naumann, I. D. (1991). Hymenoptera. *The Insects of Australia*. Naumann, I. D., Carne, P. B., Lawerence, J. F.*et al*. Melbourne, Melbourne University Press. **2:** 916-1000.

Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89**: 583-590.

Norris, K. R. (1996). General Biology. *The Insects of Australia*. Naumann, I. D., Carne, P. B., Lawerence, J. F.*et al*. Melbourne, Melbourne University Press. **1:** 68-108.

Page, R. D. M. (1996). TREEVIEW: an application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* **12**: 357-358.

Park, O. and Barr, T. C. J. (1961). Some observations on a cave cricket (Abstr.). *Bulletin of the Entomological Society of America* **7**: 144.

Peck, S. B. (1976). The effect of cave entrances on the distribution of cave inhabiting terrestrial arthropods. *International Journal of Speleology* **8**: 309-321.

Peet, R. K. (1974). The measurement of species diversity. *Annual review of Ecology and Systematics* **5**: 285-307.

Posada, D. and Crandall, K. A. (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817-818.

Poulson, T. L. and White, W. B. (1969). The cave environment. *Science* **165**: 971-981.

Poulson, T. L. (1972). Bat guano ecosystems. *Bulletin of the National Speleological Society* **34**: 55-59.

Poulson, T. L. (1992). The Mammoth Cave ecosystem. *The natural history of biospeleology*. Camacho, A. I. Madrid, Spain, National Museum of Natural Sciences**:** 569-611.

Poulson, T. L. and Lavoie, K. H. (2000). The trophic basis of subsurface ecosystems. *Ecosystems of the world. Subterranean ecosystems*. Wilkens, H., Culver, D. C. and Humphreys, W. F. Amsterdam, Elsevier. **30:** 231-249.

Poulson, T. L. (2005). Food sources. *Encyclopedia of caves*. Culver, D. C. and White, W. B. San Diego, California, Elsevier. **1:** 255-263.

Racovitza, E. G. (1907). Essai sur les problemes biospeologiques. *Arch. zool. exp. et gen.* **36**: 371-488.

Rainbow, W. J. (1904). Studies in Australian Araneidae III. *Records of the Australian Museum* **5**: 326-336.

Rainbow, W. J. (1905). Studies in Australian Araneidae IV. *Records of the Australian Museum* **6**: 9-12.

Rainbow, W. J. (1907). Two new species of Australian Collembola. *Records of the Australian Museum* **6**: 313-314.

Richards, A. M. (1971). An ecological study of the cavernicolous fauna of the Nullarbor Plain Southern Australia. *Journal of the Zoological Society of London* **164**: 1-60.

Richardson, B. J., Baverstock, P. R. and Adams, M. (1986). *Allozyme electrophoresis. A handbook for animal systematics and population studies*. San Diego, Academic Press.

Robinson, G. S. and Nielsen, E. S. (1993). *Tineid genera of Australia*. Canberra, CSIRO Entomology.

Sanderson, K. J. (2001). Bats and cave fauna in Naracoorte Caves in the 1990s. *South Australian Naturalist* **75**: 8-10.

Sanderson, K. J. and Bourne, S. (2002). Cave temperatures at Naracoorte Caves. *Helictite* **38**: 7-10.

Scharf, F. S., Juanes, F. and Sutherland, M. (1998). Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* **79**: 448-460.

Schiner, J. R. (1854). Fauna der Adelsberger, Lueger- und Magdalener-grotte. *Die grotten und hohlen von Adelsberg, Lueg, Planina und Lass*. Schmidl, A. Wien, Braunmuller**:** 231-272.

Shimodaira, H. and Hasegawa, M. (1999). Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* **16**: 1114-1116.

Snow, D. W. (1975). Oilbirds, cave-living birds of South America. *Studies in Speleology* **2**: 257-264 +257 plates.

Soulier-Perkins, A. (2005). Phylogenetic evidence for multiple invasions and speciation in caves: the Australian planthopper genus *Solonaima*

(Hemiptera: Fulgoromorpha: Cixiidae). *Systematic Entomology* **30**: 281-288.

Studier, E. H., Lavoie, K. H., Wares II, W. D. and Linn, J. A. M. (1986). Bioenergetics of the cave cricket, *Hadenoecus subterraneus*. *Comparative Biochemistry and Physiology* **84A**: 431-436.

Studier, E. H., Sevick, S. H., Ridley, D. M. and Wilson, D. E. (1994). Mineral and nitrogen concentration in faeces of some Neotropical bats. *Journal of Mammalogy* **75**: 674-680.

Swofford, D. L. (2000). PAUP* Phylogenetic Analysis Using Parsimony - and other methods. Version 4.0b10.

Trajano, E. and Gnaspini, P. (1991). Notes on the food webs in caves of southeastern brazil. *Memoires de Biospeologie* **18**: 75-79.

Trajano, E. (1996). Movements of cave bats in southeastern Brazil, with emphasis on the population ecology of the common vampire bat, Desmodus rotundus (Chiroptera). *Biotropica* **28**: 121-129.

Tubb, J. A. (1937). Reports of the expedition of the McCoy Society for field investigation and research (Lady Julia Percy Island). 19. Arachnida. *Proceedings of the Royal Society of Victoria (new series)* **49**: 412-421.

Upton, M. S. (1991). *Methods for collecting, preserving, and studying insects and allied forms*. Brisbane, The Australian Entomological Society.

Watts, C. H. S. and Humphreys, W. F. (1999). Three new genera and five new species of Dytiscidae (Coleoptera) from underground waters in Australia. *Records of the South Australian Museum* **32**: 121-142.

Watts, C. H. S. and Humphreys, W. F. (2000). Six new species of *Nirridessus* and *Tjirtudessus* (Dytiscidae: Coleoptera) from underground waters in Australia. *Records of the South Australian Museum* **33**: 127-144.

Webb, J., Grimes, K. G. and Osbourne, R. A. L. (2003). Black holes: caves in the Australian landscape. *Beneath the surface. A natural history of Australian caves.* Finlayson, B. and Hamilton-Smith, E. Sydney, University of New South Wales Press**:** 1-52.

Weygoldt, P. (1969). *The biology of pseudoscorpions*. Cambridge, Harvard University Press.

Whittaker, R. H. (1965). Dominance and diversity in land plant communities. *Science* **147**: 250-260.

Winton, L. J. (1922). Report on the guano deposits held by Nitrogen Limited at Arcoota and Buckalowie Creeks, Counties Hanson and Granville, out of Hundreds. *Mining Review (Adelaide)* **36**: 57-61.

Womersley, H. and Domrow, R. (1959). A new Asternolaelaps from Australia (Acarina: Ichthyostomatogasteridae). *Records of the South Australian Museum* **13**: 355-358.

Womersley, H. (1960). A new coprophilous Uropodid mite, Cilliba coprophila sp. nov. from a bat cave in South Australia (Acarina: Cillibidae). *Records of the South Australian Museum* **13**: 471-479.

Womersley, H. (1963a). Two new species of Acarina from guano from Australian bat caves. *Transactions of the Royal Society of South Australia* **86**: 147-154.

Womersley, H. (1963b). A new larval Neotrombidium (Acarina: Leeuwenhoekidae) from bat guano. *Records of the South Australian Museum* **14**: 473-476.

Wygodzinsky, P. W. (1950). Reduvioidea from New South Wales. *Proceedings of the Linnean Society of New South Wales* **75**: 81-88.

Yen, A. L. and Milledge, G. A. (1990). Invertebrates of the Buchan-Murrindal area cave systems. Melbourne, Department of Conservation and Environment**:** 1-38.

Zeh, D. W. and Zeh, J. A. (1992). Dispersal-generated sexual selection in a beetle-riding pseudoscorpion. *Behavioural Ecology and Sociobiology* **30**: 135-142.

Zeh, J. A., Zeh, D. W. and Bonilla, M. M. (2003). Phylogeography of the harlequin beetle-riding pseudoscorpion and the rise of the Isthmus of Panama. *Molecular Ecology* **12**: 2759-2769.

Zimmer, M. and Topp, W. (1998). Microorganisms and cellulose digestion in the gut of the woodlouse *Porcellio scaber*. *Journal of Chemical Ecology* **24**: 1397 - 1408.

Appendix 1: Review of Australian cave guano ecosystems with a checklist of guano invertebrates.

Moulds, T. A. (2004). Review of Australian cave guano ecosystems with a checklist of guano invertebrates. *Proceedings of the Linnean Society of New South Wales* **125**: 1-42.

Moulds, T.A. (2004) Review of Australian cave guano ecosystems with a checklist of guano invertebrates.
Proceedings of the Linnean Society of New South Wales 125 pp. 1-42

NOTE: This publication is included on pages 163-204 in the print copy of the thesis held in the University of Adelaide Library.

Appendix 2: Arthropod ecology of Bat Cave, Naracoorte, South Australia.

Moulds, T.A. (2003). Arthropod ecology of Bat Cave, Naracoorte, South Australia. *Proceedings of the 24th Biennial Conference of the Australian Speleological Federation*, Bunbury WA, Australian Speleological Federation.

Moulds, T.A. (2003) Arthropod ecology of Bat Cave, Naracoorte, South Australia. *Proceedings of the 24th Biennial Conference of the Australian Speleological Federation, Bunbury, WA. Australian Speleological Federation.*

Appendix 3: Bat Cave arthropod abundances

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
10-12 Oct 2002	1	Bottom	0	0	0	0	0	0	0	6	0	0	0	0	0
10-12 Oct 2002	2	Bottom	0	5	0	0	1	0	0	8	1	0	0	0	0
10-12 Oct 2002	3	Bottom	0	3	0	0	3	0	0	12	0	0	0	0	0
10-12 Oct 2002	4	Bottom	1	32	0	0	1	0	0	13	1	0	0	0	0
10-12 Oct 2002	5	Bottom	0	2	0	0	0	0	1	2	0	0	0	0	0
10-12 Oct 2002	6	Bottom	0	12	0	0	2	0	0	4	0	1	0	0	0
10-12 Oct 2002	7	Bottom	3	0	0	0	0	2	0	0	0	0	0	0	0
10-12 Oct 2002	8	Bottom	4	2	0	0	3	0	0	13	0	0	0	0	0
10-12 Oct 2002	9	Bottom	27	16	0	0	2	2	0	7	2227	0	0	0	0
10-12 Oct 2002	10	Bottom	4	7	0	0	1	1	1	2	1	0	0	0	0
10-12 Oct 2002	11	Bottom	2	3	0	0	0	0	0	2	9	0	0	0	0
10-12 Oct 2002	12	Bottom	1	0	0	0	1	0	0	7	0	1	0	0	0
10-12 Oct 2002	13	Bottom	1	0	0	0	2	0	1	1	0	0	0	0	0
10-12 Oct 2002	14	Bottom	3	1	0	0	1	1	2	0	0	1	0	0	0
10-12 Oct 2002	15	Bottom	2	1	0	0	0	1	1	0	0	0	0	0	0
10-12 Oct 2002	16	Bottom	2	0	0	0	0	0	1	3	1	0	0	1	0
10-12 Oct 2002	17	Bottom	0	0	0	0	0	0	0	1	1	0	0	0	0
10-12 Oct 2002	18	Bottom	0	3	0	0	1	0	3	8	0	0	0	0	0
10-12 Oct 2002	1	Top	1	0	1	0	1	0	0	9	2	0	0	0	0
10-12 Oct 2002	2	Top	7	0	0	0	2	0	1	18	0	0	0	0	0
10-12 Oct 2002	3	Top	18	16	0	0	3	1	0	51	6	0	1	1	0
10-12 Oct 2002	4	Top	6	1	1	0	0	1	1	23	132	0	0	0	1
10-12 Oct 2002	5	Top	0	0	0	0	0	0	1	8	22	0	0	0	0
10-12 Oct 2002	6	Top	3	0	0	0	1	0	2	19	3	0	0	1	0
10-12 Oct 2002	7	Top	22	9	0	0	1	8	0	25	14	0	3	0	0
10-12 Oct 2002	8	Top	0	0	0	0	0	2	0	10	13	0	0	0	0
10-12 Oct 2002	9	Top	39	0	0	0	0	1	1	1	3020	0	0	0	0
10-12 Oct 2002	10	Top	1	0	0	0	0	1	1	9	704	0	0	0	0
10-12 Oct 2002	11	Top	49	3	0	0	0	0	7	0	10641	2	3	0	0
10-12 Oct 2002	12	Top	9	0	0	0	0	0	1	7	27	0	1	0	0
10-12 Oct 2002	13	Top	9	0	0	0	0	0	0	6	228	0	0	0	0
10-12 Oct 2002	14	Top	25	2	0	0	1	0	0	11	0	1	0	0	0
10-12 Oct 2002	15	Top	5	0	0	0	0	0	1	3	2	0	0	0	1
10-12 Oct 2002	16	Top	18	0	0	0	0	0	2	2	55	56	0	0	0
10-12 Oct 2002	17	Top	1	0	0	0	0	0	0	1	0	0	0	0	0
10-12 Oct 2002	18	Top	0	0	0	0	0	0	1	2	3	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
25-27 Nov 2002	1	Bottom	0	0	0	0	0	0	0	7	0	0	0	0	0
25-27 Nov 2002	2	Bottom	1	18	0	0	3	0	0	5	0	0	0	0	0
25-27 Nov 2002	3	Bottom	0	0	0	0	0	0	0	7	0	1	0	0	0
25-27 Nov 2002	4	Bottom	1	73	0	0	1	0	0	13	1	0	0	0	0
25-27 Nov 2002	5	Bottom	0	0	0	0	1	1	0	4	3	0	0	0	0
25-27 Nov 2002	6	Bottom	1	5	0	0	1	0	1	3	2	0	0	0	0
25-27 Nov 2002	7	Bottom	10	37	0	0	3	2	0	3	1	0	0	0	0
25-27 Nov 2002	8	Bottom	2	8	0	0	0	0	0	20	1	0	0	0	0
25-27 Nov 2002	9	Bottom	39	139	0	0	12	2	1	9	8360	0	0	0	0
25-27 Nov 2002	10	Bottom	8	36	0	0	8	2	3	8	12	0	0	0	0
25-27 Nov 2002	11	Bottom	8	77	0	0	3	3	8	6	89	0	0	0	0
25-27 Nov 2002	12	Bottom	1	6	0	0	3	0	3	7	1	0	0	0	0
25-27 Nov 2002	13	Bottom	1	0	0	0	0	0	0	1	2	0	0	0	0
25-27 Nov 2002	14	Bottom	2	37	0	0	3	0	1	4	0	0	0	0	0
25-27 Nov 2002	15	Bottom	3	5	0	0	3	0	2	2	0	0	0	0	0
25-27 Nov 2002	16	Bottom	0	0	0	0	1	0	4	2	0	0	0	0	0
25-27 Nov 2002	17	Bottom	0	1	0	0	0	0	0	5	0	0	0	0	0
25-27 Nov 2002	18	Bottom	2	0	0	0	2	0	3	7	7	0	0	0	0
25-27 Nov 2002	1	Top	6	0	0	0	0	0	1	12	4	0	0	0	0
25-27 Nov 2002	2	Top	5	1	0	0	8	0	0	26	3	0	0	0	0
25-27 Nov 2002	3	Top	2	7	0	0	11	0	0	54	27	0	1	0	0
25-27 Nov 2002	4	Top	36	6	1	0	0	0	0	10	9420	0	1	7	0
25-27 Nov 2002	5	Top	1	1	0	0	1	0	1	2	640	0	1	0	0
25-27 Nov 2002	6	Top	5	0	0	0	1	0	0	15	19	0	0	1	0
25-27 Nov 2002	7	Top	58	59	0	0	7	11	0	77	35	0	7	0	0
25-27 Nov 2002	8	Top	7	7	0	0	0	1	0	31	35	0	0	0	0
25-27 Nov 2002	9	Top	27	1	0	0	0	3	1	2	51200	0	4	0	0
25-27 Nov 2002	10	Top	14	0	0	0	0	3	0	8	643	0	0	0	0
25-27 Nov 2002	11	Top	70	1	0	0	0	2	1	2	73600	12	12	0	0
25-27 Nov 2002	12	Top	30	0	1	0	0	1	0	15	960	0	0	0	0
25-27 Nov 2002	13	Top	19	0	0	2	3	0	1	1	1440	1	0	0	0
25-27 Nov 2002	14	Top	19	0	0	0	0	0	0	8	58	0	0	0	0
25-27 Nov 2002	15	Top	30	3	0	0	0	1	0	2	3	0	2	0	0
25-27 Nov 2002	16	Top	38	0	0	0	0	0	1	2	119	36	0	0	0
25-27 Nov 2002	17	Top	7	1	0	0	2	0	0	1	1	0	0	0	0
25-27 Nov 2002	18	Top	7	0	0	0	2	0	0	1	359	0	1	1	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
5-7 Feb 2003	1	Bottom	2	0	0	0	1	0	1	2	0	0	0	0	0
5-7 Feb 2003	2	Bottom	1	5	0	0	0	0	0	2	0	0	0	0	0
5-7 Feb 2003	3	Bottom	0	0	0	0	0	0	0	1	0	0	0	0	0
5-7 Feb 2003	4	Bottom	0	1	0	0	1	0	1	4	0	0	0	0	0
5-7 Feb 2003	5	Bottom	0	0	0	0	1	0	0	0	0	0	0	0	0
5-7 Feb 2003	6	Bottom	2	0	0	0	0	0	0	0	1	0	0	0	0
5-7 Feb 2003	7	Bottom	15	1	0	0	1	1	0	1	0	0	0	0	0
5-7 Feb 2003	8	Bottom	5	0	0	0	0	3	1	4	0	0	0	0	0
5-7 Feb 2003	9	Bottom	16	0	0	0	2	0	2	0	1900	1	0	0	0
5-7 Feb 2003	10	Bottom	8	3	0	0	6	2	0	0	5	1	0	0	0
5-7 Feb 2003	11	Bottom	8	1	0	0	4	1	2	1	4	0	0	0	0
5-7 Feb 2003	12	Bottom	0	0	0	0	1	0	0	1	1	0	0	0	0
5-7 Feb 2003	13	Bottom	0	0	0	0	0	0	0	0	0	0	1	0	0
5-7 Feb 2003	14	Bottom	3	6	0	0	1	0	1	6	0	0	0	0	0
5-7 Feb 2003	15	Bottom	0	0	0	0	0	0	1	5	0	0	0	0	0
5-7 Feb 2003	16	Bottom	2	0	0	0	3	0	0	0	0	0	1	0	0
5-7 Feb 2003	17	Bottom	0	0	0	0	1	0	1	1	0	0	0	0	0
5-7 Feb 2003	18	Bottom	0	0	0	0	5	0	4	3	2	0	0	0	0
5-7 Feb 2003	1	Top	5	0	0	0	3	0	1	0	4	0	0	0	0
5-7 Feb 2003	2	Top	17	0	0	0	1	0	0	0	0	3	7	0	0
5-7 Feb 2003	3	Top	36	1	0	0	4	0	0	32	9	15	9	3	0
5-7 Feb 2003	4	Top	12	0	0	0	1	0	0	3	9500	0	1	4	0
5-7 Feb 2003	5	Top	6	0	0	0	3	0	0	0	94	0	1	0	0
5-7 Feb 2003	6	Top	4	1	0	0	7	0	1	26	11	0	1	0	0
5-7 Feb 2003	7	Top	47	10	0	0	1	2	0	3	73	0	12	0	0
5-7 Feb 2003	8	Top	8	0	0	0	1	2	1	8	27	5	0	0	0
5-7 Feb 2003	9	Top	7	0	0	0	1	2	1	0	7540	1	4	0	0
5-7 Feb 2003	10	Top	15	0	0	0	1	0	1	1	4540	0	0	0	0
5-7 Feb 2003	11	Top	32	0	0	54	0	0	2	0	5760	2	4	0	0
5-7 Feb 2003	12	Top	12	1	0	0	1	1	0	3	780	0	1	0	0
5-7 Feb 2003	13	Top	22	0	0	0	0	0	1	2	4620	1	1	0	0
5-7 Feb 2003	14	Top	13	0	0	0	0	1	2	9	17	0	1	0	0
5-7 Feb 2003	15	Top	7	1	0	0	1	0	0	7	1	0	1	0	0
5-7 Feb 2003	16	Top	9	0	1	0	4	0	0	19	2980	0	1	0	0
5-7 Feb 2003	17	Top	4	0	0	0	0	0	1	0	3	1	0	0	0
5-7 Feb 2003	18	Top	2	0	0	0	0	0	1	7	27	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
3-5 April 2003	1	Bottom	0	1	0	0	0	0	0	3	1	0	0	0	0
3-5 April 2003	2	Bottom	0	7	0	0	0	0	1	9	0	0	0	0	0
3-5 April 2003	3	Bottom	0	0	0	0	1	0	1	5	0	0	0	0	0
3-5 April 2003	4	Bottom	0	8	0	0	0	0	0	5	0	0	0	0	0
3-5 April 2003	5	Bottom	0	0	0	0	1	0	0	1	0	0	0	0	0
3-5 April 2003	6	Bottom	0	0	0	0	1	0	0	3	0	0	0	0	0
3-5 April 2003	7	Bottom	0	6	0	0	1	0	0	6	0	0	0	0	0
3-5 April 2003	8	Bottom	3	16	0	0	1	2	0	24	1	0	0	0	0
3-5 April 2003	9	Bottom	5	19	0	0	4	0	0	7	99	0	0	0	0
3-5 April 2003	10	Bottom	4	29	0	0	2	1	1	10	1	0	0	0	0
3-5 April 2003	11	Bottom	5	65	1	0	4	2	3	8	10	0	0	0	0
3-5 April 2003	12	Bottom	0	7	0	0	1	0	1	2	1	0	0	0	0
3-5 April 2003	13	Bottom	0	0	0	0	0	0	1	0	3	0	0	0	0
3-5 April 2003	14	Bottom	0	26	0	0	5	1	0	3	0	0	0	0	1
3-5 April 2003	15	Bottom	0	8	0	0	1	0	0	6	0	0	0	0	0
3-5 April 2003	16	Bottom	0	0	0	0	0	0	2	1	0	0	0	0	0
3-5 April 2003	17	Bottom	0	0	0	0	1	0	3	2	1	0	0	0	0
3-5 April 2003	18	Bottom	0	2	0	0	1	0	0	11	3	0	0	0	0
3-5 April 2003	1	Top	1	0	0	0	2	0	0	9	4	0	0	0	0
3-5 April 2003	2	Top	3	0	0	0	9	0	0	20	2	0	2	0	0
3-5 April 2003	3	Top	4	0	0	0	2	0	1	12	4	0	6	1	0
3-5 April 2003	4	Top	4	1	1	0	1	0	0	4	1640	0	2	0	0
3-5 April 2003	5	Top	2	0	0	0	0	0	0	8	22	0	0	0	0
3-5 April 2003	6	Top	6	0	0	0	1	0	1	17	1	0	0	0	0
3-5 April 2003	7	Top	17	48	1	0	2	2	0	26	39	0	14	0	0
3-5 April 2003	8	Top	18	0	0	0	0	1	0	18	24	0	0	0	0
3-5 April 2003	9	Top	7	0	1	2	0	0	0	2	540	0	4	0	0
3-5 April 2003	10	Top	5	0	0	1	1	0	1	4	1320	1	0	0	0
3-5 April 2003	11	Top	24	1	2	15	0	1	0	0	620	1	1	0	0
3-5 April 2003	12	Top	10	0	0	0	2	2	0	10	620	0	1	0	0
3-5 April 2003	13	Top	9	0	0	1	2	0	0	6	5020	0	1	0	0
3-5 April 2003	14	Top	9	1	0	0	0	1	0	17	138	0	0	0	0
3-5 April 2003	15	Top	6	2	0	0	2	0	1	16	2	0	1	0	0
3-5 April 2003	16	Top	22	0	0	0	0	0	0	1	107	9	0	21	0
3-5 April 2003	17	Top	2	0	0	0	0	0	0	4	2	0	0	0	0
3-5 April 2003	18	Top	2	1	0	0	1	0	2	8	40	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
6-8 June 2003	1	Bottom	0	1	0	2	0	0	1	4	0	0	0	0	0
6-8 June 2003	2	Bottom	1	32	0	0	0	0	0	3	0	0	0	0	0
6-8 June 2003	3	Bottom	0	2	0	0	1	0	1	5	0	0	0	0	0
6-8 June 2003	4	Bottom	0	79	0	0	0	0	0	0	1	0	0	0	0
6-8 June 2003	5	Bottom	0	1	0	0	0	1	1	0	0	0	0	0	0
6-8 June 2003	6	Bottom	0	9	0	0	1	0	0	6	0	0	0	0	0
6-8 June 2003	7	Bottom	0	246	0	0	0	3	0	3	0	0	0	0	0
6-8 June 2003	8	Bottom	1	46	0	0	0	6	0	10	0	0	0	0	0
6-8 June 2003	9	Bottom	1	531	4	0	1	6	0	7	0	0	0	0	0
6-8 June 2003	10	Bottom	2	40	0	0	0	8	0	2	0	0	0	0	0
6-8 June 2003	11	Bottom	0	332	0	0	0	5	4	5	0	0	0	0	0
6-8 June 2003	12	Bottom	0	9	0	0	1	1	1	0	0	0	0	0	0
6-8 June 2003	13	Bottom	0	2	0	0	0	0	0	1	2	0	0	0	0
6-8 June 2003	14	Bottom	0	68	0	0	1	3	0	0	0	0	0	0	0
6-8 June 2003	15	Bottom	0	16	0	0	0	1	1	4	0	0	0	0	0
6-8 June 2003	16	Bottom	0	3	0	0	0	1	2	3	0	0	0	0	0
6-8 June 2003	17	Bottom	0	0	0	0	0	0	0	7	0	0	0	0	0
6-8 June 2003	18	Bottom	0	2	0	0	0	1	1	1	1	0	0	0	0
6-8 June 2003	1	Top	0	3	0	0	0	3	2	7	0	0	0	0	0
6-8 June 2003	2	Top	3	15	1	0	3	1	3	10	1	0	1	0	0
6-8 June 2003	3	Top	1	143	2	0	1	3	2	33	3	0	0	1	0
6-8 June 2003	4	Top	1	2	0	0	0	0	4	4	12	0	0	2	0
6-8 June 2003	5	Top	0	3	0	0	0	1	0	0	5	0	0	0	0
6-8 June 2003	6	Top	2	24	1	0	2	0	3	7	1	0	0	0	0
6-8 June 2003	7	Top	29	155	0	0	0	18	0	15	0	0	0	0	0
6-8 June 2003	8	Top	1	34	0	0	0	3	1	7	39	0	0	0	0
6-8 June 2003	9	Top	12	71	4	4	0	4	2	5	10	0	0	0	0
6-8 June 2003	10	Top	7	88	0	0	0	0	2	11	54	0	0	0	0
6-8 June 2003	11	Top	50	12	14	29	0	12	1	10	1	2	0	0	0
6-8 June 2003	12	Top	32	116	0	0	0	7	1	29	50	0	0	0	0
6-8 June 2003	13	Top	1	4	0	12	0	0	1	3	78	0	0	0	0
6-8 June 2003	14	Top	2	67	1	0	0	1	1	13	10	0	0	0	0
6-8 June 2003	15	Top	2	53	0	0	0	2	0	23	2	0	0	0	0
6-8 June 2003	16	Top	4	45	0	0	0	0	3	12	15	2	0	0	0
6-8 June 2003	17	Top	0	14	0	0	0	1	0	6	0	0	0	0	0
6-8 June 2003	18	Top	1	5	0	0	0	0	0	4	1	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
1-3 August 2003	1	Bottom	0	5	0	0	0	0	0	6	0	0	0	0	0
1-3 August 2003	2	Bottom	0	72	0	0	0	1	1	3	0	0	0	0	0
1-3 August 2003	3	Bottom	0	0	0	0	0	0	0	0	0	0	0	0	0
1-3 August 2003	4	Bottom	0	53	0	0	2	0	0	7	0	0	0	0	0
1-3 August 2003	5	Bottom	0	0	0	0	0	0	0	1	0	0	0	0	0
1-3 August 2003	6	Bottom	0	8	0	0	0	0	0	3	0	0	0	0	0
1-3 August 2003	7	Bottom	1	106	0	0	0	0	0	15	0	0	0	0	0
1-3 August 2003	8	Bottom	5	2	0	0	0	0	0	7	0	0	0	0	0
1-3 August 2003	9	Bottom	2	6	0	0	0	0	3	6	5	0	0	0	0
1-3 August 2003	10	Bottom	4	10	0	0	2	0	0	3	0	0	0	0	0
1-3 August 2003	11	Bottom	0	4	0	0	2	0	0	8	2	0	0	0	0
1-3 August 2003	12	Bottom	1	3	0	0	1	0	0	2	0	0	0	0	0
1-3 August 2003	13	Bottom	0	1	0	0	2	0	3	0	0	0	0	0	0
1-3 August 2003	14	Bottom	4	51	0	0	5	1	2	5	0	0	0	0	0
1-3 August 2003	15	Bottom	0	14	0	0	0	0	0	7	0	0	0	0	0
1-3 August 2003	16	Bottom	1	10	0	0	0	1	3	3	0	0	0	0	0
1-3 August 2003	17	Bottom	0	1	0	0	1	0	0	4	0	0	0	0	0
1-3 August 2003	18	Bottom	2	4	0	0	0	0	3	0	1	0	0	0	0
1-3 August 2003	1	Top	1	47	0	0	0	0	0	24	0	0	0	0	0
1-3 August 2003	2	Top	3	139	1	0	1	1	0	16	0	0	0	0	0
1-3 August 2003	3	Top	0	20	0	0	0	0	1	54	9	0	0	0	0
1-3 August 2003	4	Top	1	89	0	0	0	0	1	31	56	0	0	0	0
1-3 August 2003	5	Top	1	13	1	0	0	0	1	11	3	0	0	0	0
1-3 August 2003	6	Top	6	68	1	0	3	0	0	30	5	0	0	0	0
1-3 August 2003	7	Top	3	9	0	0	0	3	0	7	3	0	0	1	0
1-3 August 2003	8	Top	1	0	0	0	0	0	1	4	12	0	0	0	0
1-3 August 2003	9	Top	2	27	0	1	0	1	0	12	31	0	0	0	0
1-3 August 2003	10	Top	2	0	0	0	0	0	0	5	14	0	0	0	0
1-3 August 2003	11	Top	13	39	7	6	0	2	0	90	33	0	0	0	0
1-3 August 2003	12	Top	6	35	0	0	0	0	1	22	29	0	0	0	0
1-3 August 2003	13	Top	3	22	0	1	0	0	0	5	107	0	0	0	0
1-3 August 2003	14	Top	8	90	0	0	1	0	1	46	11	0	0	0	0
1-3 August 2003	15	Top	3	82	0	0	0	1	2	34	1	0	2	0	0
1-3 August 2003	16	Top	3	88	0	0	0	1	0	17	32	0	0	0	0
1-3 August 2003	17	Top	1	19	0	0	0	0	0	14	1	0	0	0	0
1-3 August 2003	18	Top	1	5	0	0	0	0	0	3	9	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
9-11 Oct 2003	1	Bottom	3	11	0	0	0	0	0	8	0	0	0	0	0
9-11 Oct 2003	2	Bottom	14	69	0	0	1	0	0	5	1	0	0	0	0
9-11 Oct 2003	3	Bottom	2	8	0	0	3	0	1	1	0	0	0	0	0
9-11 Oct 2003	4	Bottom	0	24	0	0	1	0	0	13	0	0	0	0	0
9-11 Oct 2003	5	Bottom	0	8	0	0	1	0	0	2	0	0	0	0	0
9-11 Oct 2003	6	Bottom	0	10	0	0	3	0	0	8	1	0	0	0	0
9-11 Oct 2003	7	Bottom	17	13	0	0	0	0	0	10	0	0	0	0	0
9-11 Oct 2003	8	Bottom	7	0	0	0	0	2	0	15	0	0	0	0	0
9-11 Oct 2003	9	Bottom	84	59	1	0	3	1	1	14	0	0	0	0	0
9-11 Oct 2003	10	Bottom	14	24	0	0	1	0	0	4	0	0	0	0	0
9-11 Oct 2003	11	Bottom	21	3	0	0	1	0	0	2	0	0	0	0	0
9-11 Oct 2003	12	Bottom	0	0	0	0	0	0	0	2	0	0	0	0	0
9-11 Oct 2003	13	Bottom	0	2	0	0	1	0	0	3	1	0	0	0	0
9-11 Oct 2003	14	Bottom	1	0	0	0	1	0	1	4	0	1	0	0	0
9-11 Oct 2003	15	Bottom	12	1	0	0	1	0	0	2	0	0	0	0	0
9-11 Oct 2003	16	Bottom	4	0	0	0	0	0	2	3	0	0	0	0	0
9-11 Oct 2003	17	Bottom	0	1	0	0	1	0	0	13	1	0	0	0	0
9-11 Oct 2003	18	Bottom	0	1	0	0	1	0	6	6	0	0	0	0	0
9-11 Oct 2003	1	Top	18	3	0	0	0	0	0	59	0	0	0	0	0
9-11 Oct 2003	2	Top	45	0	0	0	1	0	0	22	1	0	0	0	0
9-11 Oct 2003	3	Top	33	2	0	0	0	0	0	58	3	0	1	0	0
9-11 Oct 2003	4	Top	7	1	0	0	2	0	1	26	104	0	0	1	0
9-11 Oct 2003	5	Top	6	0	0	0	0	0	0	1	2	0	0	0	0
9-11 Oct 2003	6	Top	9	0	0	0	1	0	1	21	2	0	1	0	0
9-11 Oct 2003	7	Top	81	1	1	0	2	1	0	34	1	0	2	1	0
9-11 Oct 2003	8	Top	7	0	0	0	1	0	0	4	1	0	0	0	0
9-11 Oct 2003	9	Top	48	0	0	1	0	0	0	4	100	0	0	0	0
9-11 Oct 2003	10	Top	14	0	0	0	3	0	0	16	17	0	0	0	0
9-11 Oct 2003	11	Top	126	3	1	107	0	0	4	1	11	0	0	0	0
9-11 Oct 2003	12	Top	55	0	0	0	0	0	0	47	7	0	0	1	0
9-11 Oct 2003	13	Top	19	0	0	0	0	0	0	10	784	0	0	0	0
9-11 Oct 2003	14	Top	25	0	0	0	0	0	1	13	2	0	0	0	0
9-11 Oct 2003	15	Top	29	0	0	0	1	0	2	194	1	0	0	0	0
9-11 Oct 2003	16	Top	2	0	0	0	5	0	0	23	485	0	0	0	0
9-11 Oct 2003	17	Top	1	1	0	0	1	0	0	15	2	0	0	0	0
9-11 Oct 2003	18	Top	3	0	0	0	0	0	1	1	26	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
19-21 Nov 2003	1	Bottom	3	0	0	0	0	0	0	3	0	0	0	0	0
19-21 Nov 2003	2	Bottom	11	7	0	0	1	0	0	6	0	0	0	0	0
19-21 Nov 2003	3	Bottom	1	3	0	0	0	0	0	4	0	0	0	0	0
19-21 Nov 2003	4	Bottom	4	6	0	0	0	0	1	3	0	0	0	0	0
19-21 Nov 2003	5	Bottom	0	0	0	0	1	1	1	1	3	0	0	0	0
19-21 Nov 2003	6	Bottom	2	12	0	0	4	0	2	4	0	0	0	0	0
19-21 Nov 2003	7	Bottom	6	10	0	0	0	3	0	3	2	0	0	0	0
19-21 Nov 2003	8	Bottom	1	5	0	0	1	2	0	12	3	0	0	0	0
19-21 Nov 2003	9	Bottom	41	5	0	0	9	0	1	0	15	0	0	0	0
19-21 Nov 2003	10	Bottom	4	11	0	0	3	0	0	9	4	0	0	0	0
19-21 Nov 2003	11	Bottom	16	44	0	0	1	5	1	2	2	0	0	0	0
19-21 Nov 2003	12	Bottom	0	2	0	0	1	0	0	4	1	0	0	0	0
19-21 Nov 2003	13	Bottom	2	0	0	0	0	0	3	3	9	0	0	0	0
19-21 Nov 2003	14	Bottom	5	2	0	0	1	1	4	2	0	0	0	0	0
19-21 Nov 2003	15	Bottom	2	0	0	0	2	0	2	0	1	0	0	0	0
19-21 Nov 2003	16	Bottom	1	3	0	0	2	0	6	2	0	0	0	0	0
19-21 Nov 2003	17	Bottom	0	4	0	0	0	0	0	4	10	0	0	0	0
19-21 Nov 2003	18	Bottom	1	3	0	0	1	0	5	8	3	0	0	0	0
19-21 Nov 2003	1	Top	18	0	0	0	3	0	2	45	1	0	0	0	0
19-21 Nov 2003	2	Top	4	1	0	0	2	0	0	19	7	0	1	0	0
19-21 Nov 2003	3	Top	2	5	0	0	1	0	0	51	18	0	0	0	0
19-21 Nov 2003	4	Top	44	0	0	0	0	0	0	6	1300	0	1	1	0
19-21 Nov 2003	5	Top	5	0	0	0	1	0	0	4	17	0	0	1	0
19-21 Nov 2003	6	Top	4	4	0	0	3	0	0	14	6	0	2	1	0
19-21 Nov 2003	7	Top	121	11	2	0	4	20	0	26	8	0	2	0	0
19-21 Nov 2003	8	Top	7	0	0	0	0	4	2	12	109	0	0	0	0
19-21 Nov 2003	9	Top	77	1	1	1	0	3	3	0	3760	0	1	0	0
19-21 Nov 2003	10	Top	11	0	0	0	0	0	2	1	312	0	0	0	0
19-21 Nov 2003	11	Top	41	0	0	0	0	3	5	1	11000	5	1	0	0
19-21 Nov 2003	12	Top	17	0	0	0	0	3	3	11	543	0	1	0	0
19-21 Nov 2003	13	Top	4	0	0	7	1	2	2	1	1180	0	0	0	0
19-21 Nov 2003	14	Top	44	2	0	0	1	2	2	4	4	0	0	0	0
19-21 Nov 2003	15	Top	15	2	0	0	5	2	1	19	7	0	0	0	1
19-21 Nov 2003	16	Top	25	2	0	1	1	1	0	8	17	0	0	0	0
19-21 Nov 2003	17	Top	2	1	0	0	0	0	0	0	7	0	0	0	0
19-21 Nov 2003	18	Top	2	0	0	0	0	1	1	0	178	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
5-7 Feb 2004	1	Bottom	1	0	0	0	0	0	0	2	0	0	0	0	0
5-7 Feb 2004	2	Bottom	1	1	0	0	0	0	0	18	0	0	0	0	0
5-7 Feb 2004	3	Bottom	0	0	0	0	0	0	0	1	0	0	0	0	0
5-7 Feb 2004	4	Bottom	1	4	0	0	2	0	0	3	1	0	0	0	1
5-7 Feb 2004	5	Bottom	0	1	0	0	0	0	2	1	0	0	0	0	0
5-7 Feb 2004	6	Bottom	1	2	0	0	1	0	0	0	0	0	0	0	0
5-7 Feb 2004	7	Bottom	20	0	0	0	0	0	0	1	0	0	0	0	0
5-7 Feb 2004	8	Bottom	0	2	0	0	0	1	0	22	0	0	0	0	0
5-7 Feb 2004	9	Bottom	3	14	0	0	6	0	0	5	849	0	0	0	0
5-7 Feb 2004	10	Bottom	7	9	0	0	0	1	0	2	4	0	0	0	0
5-7 Feb 2004	11	Bottom	5	11	0	0	2	0	0	1	10	0	0	0	0
5-7 Feb 2004	12	Bottom	0	0	0	0	0	0	0	5	6	0	0	0	0
5-7 Feb 2004	13	Bottom	0	0	0	0	0	0	0	2	2	0	0	0	0
5-7 Feb 2004	14	Bottom	0	2	0	0	0	0	1	1	0	0	0	0	0
5-7 Feb 2004	15	Bottom	0	0	0	0	0	0	3	0	0	0	0	0	0
5-7 Feb 2004	16	Bottom	1	0	0	0	0	0	1	5	1	0	0	0	0
5-7 Feb 2004	17	Bottom	0	0	0	0	0	0	0	7	6	0	0	0	0
5-7 Feb 2004	18	Bottom	1	1	0	0	4	0	1	9	3	0	0	0	1
5-7 Feb 2004	1	Top	7	2	0	0	3	0	1	19	8	0	0	0	1
5-7 Feb 2004	2	Top	17	0	0	0	0	0	0	11	6	0	1	0	8
5-7 Feb 2004	3	Top	3	5	0	0	1	0	0	120	90	0	0	1	5
5-7 Feb 2004	4	Top	8	2	1	0	1	0	0	9	1740	0	0	2	0
5-7 Feb 2004	5	Top	4	0	0	0	1	0	0	1	46	0	0	0	0
5-7 Feb 2004	6	Top	5	0	0	0	0	0	0	0	6	0	0	0	1
5-7 Feb 2004	7	Top	36	17	0	0	9	1	0	9	11	0	0	0	16
5-7 Feb 2004	8	Top	5	1	0	1	1	0	0	7	870	0	0	0	1
5-7 Feb 2004	9	Top	8	1	0	4	0	1	0	1	42500	0	0	0	1
5-7 Feb 2004	10	Top	4	2	1	0	0	0	0	5	480	0	0	0	0
5-7 Feb 2004	11	Top	24	0	0	0	1	0	0	5	16000	3	0	0	1
5-7 Feb 2004	12	Top	21	0	0	0	0	0	1	19	298	0	0	0	3
5-7 Feb 2004	13	Top	7	0	0	6	0	0	0	3	3223	0	0	0	2
5-7 Feb 2004	14	Top	7	0	0	0	1	0	0	49	7	0	0	0	0
5-7 Feb 2004	15	Top	2	4	1	0	5	0	0	38	7	0	0	0	0
5-7 Feb 2004	16	Top	16	0	0	0	0	0	0	2	4800	0	0	0	0
5-7 Feb 2004	17	Top	2	0	0	0	0	0	1	3	7	6	0	0	0
5-7 Feb 2004	18	Top	1	0	0	0	0	0	0	12	91	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
9-11 April 2004	1	Bottom	1	1	0	0	0	0	0	4	0	0	0	0	0
9-11 April 2004	2	Bottom	4	17	0	0	4	0	0	4	0	0	0	0	0
9-11 April 2004	3	Bottom	0	0	0	0	0	0	0	9	0	0	0	0	0
9-11 April 2004	4	Bottom	7	24	0	0	2	0	0	11	0	0	0	0	0
9-11 April 2004	5	Bottom	0	0	0	0	0	0	0	9	0	0	0	0	0
9-11 April 2004	6	Bottom	0	2	0	0	5	0	0	3	1	0	0	0	0
9-11 April 2004	7	Bottom	21	8	0	0	5	1	0	6	2	0	1	0	0
9-11 April 2004	8	Bottom	0	2	1	0	3	1	0	20	5	0	0	0	0
9-11 April 2004	9	Bottom	24	18	0	0	9	0	0	8	538	0	0	0	0
9-11 April 2004	10	Bottom	6	3	0	0	3	0	2	3	5	0	0	0	0
9-11 April 2004	11	Bottom	8	1	0	0	3	2	1	2	5	0	0	0	0
9-11 April 2004	12	Bottom	0	2	0	0	0	0	0	3	2	0	0	0	0
9-11 April 2004	13	Bottom	0	0	0	0	0	0	0	6	2	0	0	0	0
9-11 April 2004	14	Bottom	1	4	0	0	2	0	1	5	0	1	0	0	0
9-11 April 2004	15	Bottom	4	0	0	0	1	0	1	3	0	0	0	0	0
9-11 April 2004	16	Bottom	1	0	0	0	0	0	1	0	1	0	0	0	0
9-11 April 2004	17	Bottom	0	0	0	0	3	0	1	8	0	0	0	0	0
9-11 April 2004	18	Bottom	0	0	1	0	1	0	3	10	0	0	0	0	0
9-11 April 2004	1	Top	18	1	0	0	2	0	1	30	3	0	1	0	0
9-11 April 2004	2	Top	15	2	0	0	3	0	0	47	1	0	4	0	0
9-11 April 2004	3	Top	11	2	1	0	4	0	2	14	1	1	1	0	0
9-11 April 2004	4	Top	16	0	0	0	1	0	0	21	827	0	3	1	0
9-11 April 2004	5	Top	1	0	0	0	0	1	0	8	20	0	0	0	0
9-11 April 2004	6	Top	6	0	0	0	0	0	0	28	2	1	2	1	0
9-11 April 2004	7	Top	125	14	0	0	9	4	0	146	3	0	8	0	0
9-11 April 2004	8	Top	4	2	0	0	1	0	0	34	219	0	0	0	0
9-11 April 2004	9	Top	13	0	0	0	0	0	0	0	11067	0	0	0	0
9-11 April 2004	10	Top	4	0	0	0	0	0	0	7	134	0	1	0	0
9-11 April 2004	11	Top	28	0	0	25	0	0	1	0	5380	4	1	0	0
9-11 April 2004	12	Top	16	1	0	0	1	0	1	27	114	0	1	0	0
9-11 April 2004	13	Top	5	0	0	0	2	0	2	6	882	0	0	1	0
9-11 April 2004	14	Top	12	0	1	0	0	0	0	66	6	0	3	0	0
9-11 April 2004	15	Top	9	1	2	0	3	0	0	49	7	0	0	0	0
9-11 April 2004	16	Top	22	2	0	0	11	0	2	15	892	3	0	0	0
9-11 April 2004	17	Top	1	0	0	0	0	0	0	10	4	0	0	0	0
9-11 April 2004	18	Top	0	0	0	0	2	0	0	14	10	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
4-6 June 2004	1	Bottom	0	11	0	0	0	0	0	2	0	0	0	0	0
4-6 June 2004	2	Bottom	17	20	0	0	0	2	0	46	1	0	0	0	0
4-6 June 2004	3	Bottom	1	6	0	0	0	0	0	11	0	0	0	0	0
4-6 June 2004	4	Bottom	0	120	0	0	1	0	0	9	0	0	0	0	0
4-6 June 2004	5	Bottom	0	12	0	0	1	0	0	3	0	0	0	0	0
4-6 June 2004	6	Bottom	0	29	0	0	3	0	0	9	0	0	0	0	0
4-6 June 2004	7	Bottom	6	50	0	0	0	2	2	4	1	0	0	0	0
4-6 June 2004	8	Bottom	2	13	0	0	0	0	0	6	1	0	0	0	0
4-6 June 2004	9	Bottom	7	216	0	0	5	1	1	10	25	0	0	0	0
4-6 June 2004	10	Bottom	6	118	0	0	4	1	1	6	5	0	0	0	0
4-6 June 2004	11	Bottom	4	79	0	0	0	1	1	0	0	0	0	0	0
4-6 June 2004	12	Bottom	0	5	0	0	0	0	0	6	5	0	0	0	0
4-6 June 2004	13	Bottom	0	0	0	0	0	2	2	2	0	0	0	0	0
4-6 June 2004	14	Bottom	0	49	0	0	0	0	0	1	0	0	0	0	0
4-6 June 2004	15	Bottom	1	10	0	0	1	0	0	4	1	0	0	0	0
4-6 June 2004	16	Bottom	0	4	0	0	0	0	0	5	2	0	0	0	0
4-6 June 2004	17	Bottom	0	3	0	0	0	0	0	7	3	0	0	0	0
4-6 June 2004	18	Bottom	1	5	0	0	0	1	3	6	0	0	0	0	0
4-6 June 2004	1	Top	9	3	0	0	0	0	0	15	0	0	0	0	0
4-6 June 2004	2	Top	0	56	0	0	1	0	0	3	0	0	0	0	0
4-6 June 2004	3	Top	10	211	0	0	0	1	1	91	18	0	0	1	0
4-6 June 2004	4	Top	9	6	3	0	0	0	0	30	156	0	0	0	0
4-6 June 2004	5	Top	5	1	0	0	2	2	2	13	8	0	0	0	0
4-6 June 2004	6	Top	0	14	0	0	1	1	1	63	3	0	0	1	0
4-6 June 2004	7	Top	47	37	1	0	3	1	1	53	1	0	0	0	0
4-6 June 2004	8	Top	2	47	0	0	0	0	0	14	49	0	0	0	0
4-6 June 2004	9	Top	9	1	0	2	0	3	3	1	2960	0	0	0	0
4-6 June 2004	10	Top	6	9	0	0	0	0	1	11	58	0	0	0	0
4-6 June 2004	11	Top	25	0	1	26	0	1	1	3	1094	0	0	0	0
4-6 June 2004	12	Top	19	31	2	0	0	1	1	23	114	0	0	1	0
4-6 June 2004	13	Top	4	2	0	2	0	0	0	17	190	0	0	0	0
4-6 June 2004	14	Top	4	59	1	0	0	4	4	32	5	0	0	0	0
4-6 June 2004	15	Top	3	4	0	0	0	3	3	36	6	0	0	0	0
4-6 June 2004	16	Top	12	61	1	1	2	0	0	54	413	0	0	0	0
4-6 June 2004	17	Top	2	8	0	0	0	1	2	7	2	0	0	0	0
4-6 June 2004	18	Top	1	5	0	0	0	1	1	6	4	0	0	0	0

Date	Guano Pile	Sample	Histeridae	Anobiidae	Cryptophagidae	Jacobsoniidae	Carabidae	Braconidae	*Monopis*	Pseudoscorpionida	Urodinychidae	Phoridae	Nycteribiidae	Isopoda	Arachnida: Tick
1-3 August 2004	1	Bottom	2	5	0	0	0	0	0	9	0	0	0	0	0
1-3 August 2004	2	Bottom	2	18	0	0	1	0	0	8	0	0	0	0	0
1-3 August 2004	3	Bottom	4	3	0	0	0	0	1	9	1	0	0	0	0
1-3 August 2004	4	Bottom	2	27	0	0	0	0	0	25	0	0	0	0	0
1-3 August 2004	5	Bottom	0	5	0	0	0	0	0	12	0	0	0	0	0
1-3 August 2004	6	Bottom	1	6	0	0	2	0	0	1	1	0	0	0	0
1-3 August 2004	7	Bottom	14	32	0	0	0	0	0	2	0	0	0	0	0
1-3 August 2004	8	Bottom	10	1	0	0	1	0	0	19	0	0	0	0	0
1-3 August 2004	9	Bottom	44	61	0	0	3	0	1	4	35	0	0	0	0
1-3 August 2004	10	Bottom	8	27	0	0	2	0	0	5	6	0	0	0	0
1-3 August 2004	11	Bottom	28	71	0	0	4	0	0	8	25	0	0	0	0
1-3 August 2004	12	Bottom	2	1	0	0	1	0	0	4	0	0	0	0	0
1-3 August 2004	13	Bottom	2	3	0	0	2	0	1	2	11	0	0	0	0
1-3 August 2004	14	Bottom	2	2	1	0	9	0	0	0	0	0	0	0	0
1-3 August 2004	15	Bottom	4	7	0	0	0	0	0	8	0	0	0	0	0
1-3 August 2004	16	Bottom	0	2	0	0	1	0	0	4	2	0	0	0	0
1-3 August 2004	17	Bottom	1	3	0	0	1	0	0	10	1	0	0	0	0
1-3 August 2004	18	Bottom	1	22	0	0	2	0	1	7	1	0	0	0	0
1-3 August 2004	1	Top	0	4	0	0	2	0	1	158	0	0	0	0	0
1-3 August 2004	2	Top	10	45	2	0	1	0	1	93	1	0	0	0	0
1-3 August 2004	3	Top	29	2	0	0	0	0	0	85	6	0	0	0	0
1-3 August 2004	4	Top	21	2	0	0	3	0	0	39	353	0	0	0	0
1-3 August 2004	5	Top	0	8	0	0	0	0	0	46	4	0	0	0	0
1-3 August 2004	6	Top	4	2	0	0	2	0	1	98	3	0	0	0	0
1-3 August 2004	7	Top	73	6	1	0	6	5	0	65	5	0	0	0	0
1-3 August 2004	8	Top	4	2	0	0	0	0	2	12	5	0	0	0	0
1-3 August 2004	9	Top	30	0	0	3	1	0	1	4	5950	0	0	0	0
1-3 August 2004	10	Top	1	6	0	0	0	0	2	15	5	0	0	0	0
1-3 August 2004	11	Top	116	1	0	6	0	0	0	1	24100	0	0	0	0
1-3 August 2004	12	Top	26	2	0	0	5	1	0	34	16	0	0	0	0
1-3 August 2004	13	Top	13	16	0	0	8	0	0	38	282	0	0	0	0
1-3 August 2004	14	Top	21	35	0	0	1	0	1	47	5	0	0	0	0
1-3 August 2004	15	Top	15	5	2	0	5	0	0	45	3	0	0	1	0
1-3 August 2004	16	Top	21	0	0	2	2	0	2	5	53	1	0	0	0
1-3 August 2004	17	Top	2	10	0	0	2	0	0	9	1	0	0	0	0
1-3 August 2004	18	Top	2	1	0	0	0	0	0	3	7	0	0	0	0

Appexdix 4: Bat Cave environmental data

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
10-12 Oct 2002	1	Bottom	50.22	5.5	0.1
10-12 Oct 2002	2	Bottom	44.24	6.0	0.0
10-12 Oct 2002	3	Bottom	59.17	6.0	0.2
10-12 Oct 2002	4	Bottom	44.47	5.5	0.3
10-12 Oct 2002	5	Bottom	56.23	6.5	0.9
10-12 Oct 2002	6	Bottom	50.27	5.0	0.7
10-12 Oct 2002	7	Bottom	42.39	6.5	19.7
10-12 Oct 2002	8	Bottom	56.14	5.5	18.7
10-12 Oct 2002	9	Bottom	36.43	6.0	12.0
10-12 Oct 2002	10	Bottom	46.68	4.5	1.0
10-12 Oct 2002	11	Bottom	56.55	5.5	1.6
10-12 Oct 2002	12	Bottom	50.14	5.5	14.0
10-12 Oct 2002	13	Bottom	63.47	5.5	3.6
10-12 Oct 2002	14	Bottom	43.72	6.5	4.7
10-12 Oct 2002	15	Bottom	58.09	6.0	0.1
10-12 Oct 2002	16	Bottom	62.18	6.0	1.8
10-12 Oct 2002	17	Bottom	57.51	6.5	0.5
10-12 Oct 2002	18	Bottom	60.26	8.5	1.8
10-12 Oct 2002	1	Top	68.86	9.0	5.9
10-12 Oct 2002	2	Top	64.76	6.5	2.2
10-12 Oct 2002	3	Top	44.47	7.5	0.1
10-12 Oct 2002	4	Top	59.03	5.5	29.7
10-12 Oct 2002	5	Top	69.10	8.5	18.4
10-12 Oct 2002	6	Top	62.51	5.5	6.8
10-12 Oct 2002	7	Top	65.27	7.0	10.2
10-12 Oct 2002	8	Top	68.91	5.0	0.4
10-12 Oct 2002	9	Top	72.55	7.0	119.0
10-12 Oct 2002	10	Top	57.62	6.5	26.9
10-12 Oct 2002	11	Top	57.93	7.5	141.9
10-12 Oct 2002	12	Top	52.22	5.5	46.4
10-12 Oct 2002	13	Top	73.36	5.5	17.9
10-12 Oct 2002	14	Top	71.10	5.0	32.8
10-12 Oct 2002	15	Top	68.91	5.5	1.6
10-12 Oct 2002	16	Top	70.34	5.0	17.9
10-12 Oct 2002	17	Top	68.66	10.5	0.1
10-12 Oct 2002	18	Top	53.16	5.0	13.8

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
25-27 Nov 2002	1	Bottom	44.87	5.5	4.2
25-27 Nov 2002	2	Bottom	31.03	6.5	4.3
25-27 Nov 2002	3	Bottom	50.85	5.5	4.6
25-27 Nov 2002	4	Bottom	31.51	6.5	4.7
25-27 Nov 2002	5	Bottom	50.00	5.5	6.0
25-27 Nov 2002	6	Bottom	44.44	5.5	4.6
25-27 Nov 2002	7	Bottom	36.36	9.5	5.2
25-27 Nov 2002	8	Bottom	46.91	5.5	4.3
25-27 Nov 2002	9	Bottom	26.00	9.0	10.5
25-27 Nov 2002	10	Bottom	37.50	7.5	4.6
25-27 Nov 2002	11	Bottom	36.14	6.5	5.3
25-27 Nov 2002	12	Bottom	39.76	7.0	4.2
25-27 Nov 2002	13	Bottom	51.79	5.5	6.8
25-27 Nov 2002	14	Bottom	34.92	7.0	5.4
25-27 Nov 2002	15	Bottom	44.19	6.5	6.5
25-27 Nov 2002	16	Bottom	51.72	5.5	6.1
25-27 Nov 2002	17	Bottom	46.55	5.0	4.5
25-27 Nov 2002	18	Bottom	50.00	6.0	6.1
25-27 Nov 2002	1	Top	57.38	8.0	10.1
25-27 Nov 2002	2	Top	46.81	6.5	4.9
25-27 Nov 2002	3	Top	36.62	7.5	5.1
25-27 Nov 2002	4	Top	51.61	9.0	26.2
25-27 Nov 2002	5	Top	54.10	6.5	20.0
25-27 Nov 2002	6	Top	53.26	7.5	35.2
25-27 Nov 2002	7	Top	48.48	6.5	7.9
25-27 Nov 2002	8	Top	56.41	8.0	14.7
25-27 Nov 2002	9	Top	70.81	9.0	54.1
25-27 Nov 2002	10	Top	54.87	9.0	23.7
25-27 Nov 2002	11	Top	70.15	9.0	71.0
25-27 Nov 2002	12	Top	61.84	9.0	23.0
25-27 Nov 2002	13	Top	70.67	9.0	33.9
25-27 Nov 2002	14	Top	61.22	9.0	45.9
25-27 Nov 2002	15	Top	59.69	9.5	21.1
25-27 Nov 2002	16	Top	64.49	9.5	18.1
25-27 Nov 2002	17	Top	52.17	7.0	8.6
25-27 Nov 2002	18	Top	46.43	9.0	26.8

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
5-7 Feb 2003	1	Bottom	50.64	5.5	0.1
5-7 Feb 2003	2	Bottom	28.00	5.5	0.2
5-7 Feb 2003	3	Bottom	51.56	5.5	2.6
5-7 Feb 2003	4	Bottom	37.88	5.0	0.3
5-7 Feb 2003	5	Bottom	54.87	5.0	0.5
5-7 Feb 2003	6	Bottom	48.28	5.5	1.5
5-7 Feb 2003	7	Bottom	41.38	8.5	6.8
5-7 Feb 2003	8	Bottom	30.00	5.0	0.2
5-7 Feb 2003	9	Bottom	26.67	9.0	5.4
5-7 Feb 2003	10	Bottom	36.36	7.5	1.1
5-7 Feb 2003	11	Bottom	32.79	6.0	0.5
5-7 Feb 2003	12	Bottom	35.29	7.0	0.2
5-7 Feb 2003	13	Bottom	51.97	5.0	2.3
5-7 Feb 2003	14	Bottom	39.29	6.5	1.0
5-7 Feb 2003	15	Bottom	44.00	5.5	2.5
5-7 Feb 2003	16	Bottom	46.34	5.5	2.4
5-7 Feb 2003	17	Bottom	47.49	5.0	0.0
5-7 Feb 2003	18	Bottom	55.38	5.5	1.6
5-7 Feb 2003	1	Top	61.21	6.0	6.0
5-7 Feb 2003	2	Top	64.44	9.5	27.4
5-7 Feb 2003	3	Top	66.67	9.5	92.2
5-7 Feb 2003	4	Top	56.41	9.5	23.6
5-7 Feb 2003	5	Top	63.22	7.5	8.7
5-7 Feb 2003	6	Top	52.63	5.5	4.5
5-7 Feb 2003	7	Top	51.05	5.5	2.1
5-7 Feb 2003	8	Top	54.17	9.5	8.7
5-7 Feb 2003	9	Top	69.61	9.5	54.7
5-7 Feb 2003	10	Top	50.00	9.0	8.8
5-7 Feb 2003	11	Top	67.53	7.0	69.7
5-7 Feb 2003	12	Top	51.22	8.0	11.6
5-7 Feb 2003	13	Top	63.93	5.5	28.9
5-7 Feb 2003	14	Top	50.00	7.5	8.4
5-7 Feb 2003	15	Top	55.82	7.0	10.1
5-7 Feb 2003	16	Top	55.56	9.0	0.5
5-7 Feb 2003	17	Top	59.93	6.5	5.6
5-7 Feb 2003	18	Top	42.86	8.5	3.0

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
3-5 April 2003	1	Bottom	48.60	5.5	0.0
3-5 April 2003	2	Bottom	29.58	5.5	0.1
3-5 April 2003	3	Bottom	54.32	5.0	0.8
3-5 April 2003	4	Bottom	37.84	5.5	0.5
3-5 April 2003	5	Bottom	53.52	5.0	0.4
3-5 April 2003	6	Bottom	47.92	5.5	0.7
3-5 April 2003	7	Bottom	34.21	5.5	1.3
3-5 April 2003	8	Bottom	45.16	5.5	0.1
3-5 April 2003	9	Bottom	29.41	9.0	4.7
3-5 April 2003	10	Bottom	51.79	8.5	0.3
3-5 April 2003	11	Bottom	30.77	7.0	0.8
3-5 April 2003	12	Bottom	36.99	7.5	0.3
3-5 April 2003	13	Bottom	50.62	5.5	1.8
3-5 April 2003	14	Bottom	34.48	6.5	0.8
3-5 April 2003	15	Bottom	34.92	5.5	1.9
3-5 April 2003	16	Bottom	43.90	8.0	2.8
3-5 April 2003	17	Bottom	49.47	5.5	0.2
3-5 April 2003	18	Bottom	46.67	5.5	2.1
3-5 April 2003	1	Top	61.64	7.0	4.8
3-5 April 2003	2	Top	48.89	7.0	1.5
3-5 April 2003	3	Top	45.83	9.5	43.9
3-5 April 2003	4	Top	57.41	8.5	19.0
3-5 April 2003	5	Top	61.25	7.0	7.8
3-5 April 2003	6	Top	54.84	7.5	13.0
3-5 April 2003	7	Top	56.00	7.5	2.5
3-5 April 2003	8	Top	47.87	8.5	9.5
3-5 April 2003	9	Top	70.83	9.5	52.6
3-5 April 2003	10	Top	33.33	7.0	9.9
3-5 April 2003	11	Top	74.39	9.5	73.8
3-5 April 2003	12	Top	54.76	8.5	8.8
3-5 April 2003	13	Top	65.17	9.0	20.5
3-5 April 2003	14	Top	54.17	9.0	7.3
3-5 April 2003	15	Top	52.83	8.0	7.4
3-5 April 2003	16	Top	80.30	9.5	96.6
3-5 April 2003	17	Top	55.38	6.5	5.4
3-5 April 2003	18	Top	68.18	9.5	2.2

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
6-8 June 2003	1	Bottom	47.46	5.5	0.0
6-8 June 2003	2	Bottom	34.97	5.5	0.1
6-8 June 2003	3	Bottom	52.94	5.0	0.3
6-8 June 2003	4	Bottom	34.62	5.5	0.0
6-8 June 2003	5	Bottom	53.21	5.0	0.3
6-8 June 2003	6	Bottom	48.26	5.5	0.2
6-8 June 2003	7	Bottom	34.85	6.5	0.0
6-8 June 2003	8	Bottom	45.57	5.0	0.0
6-8 June 2003	9	Bottom	29.90	7.5	0.1
6-8 June 2003	10	Bottom	39.47	5.5	0.1
6-8 June 2003	11	Bottom	33.91	6.5	0.0
6-8 June 2003	12	Bottom	38.36	6.5	0.2
6-8 June 2003	13	Bottom	50.00	5.5	0.0
6-8 June 2003	14	Bottom	31.82	6.0	0.0
6-8 June 2003	15	Bottom	43.24	5.5	0.1
6-8 June 2003	16	Bottom	44.78	7.0	0.0
6-8 June 2003	17	Bottom	49.63	5.0	0.4
6-8 June 2003	18	Bottom	50.27	5.5	0.5
6-8 June 2003	1	Top	60.14	5.5	0.0
6-8 June 2003	2	Top	51.85	5.5	0.3
6-8 June 2003	3	Top	50.00	7.5	0.2
6-8 June 2003	4	Top	60.33	6.5	0.3
6-8 June 2003	5	Top	64.42	5.5	0.1
6-8 June 2003	6	Top	57.58	5.5	0.3
6-8 June 2003	7	Top	55.56	6.5	0.3
6-8 June 2003	8	Top	55.56	6.5	0.4
6-8 June 2003	9	Top	64.74	7.0	1.0
6-8 June 2003	10	Top	50.00	7.0	0.0
6-8 June 2003	11	Top	70.06	5.5	2.0
6-8 June 2003	12	Top	54.26	7.0	0.1
6-8 June 2003	13	Top	61.24	6.0	0.0
6-8 June 2003	14	Top	50.57	5.5	0.2
6-8 June 2003	15	Top	48.65	7.0	0.0
6-8 June 2003	16	Top	57.58	6.5	0.2
6-8 June 2003	17	Top	56.04	6.0	0.0
6-8 June 2003	18	Top	49.75	6.0	0.1

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
1-3 August 2003	1	Bottom	46.50	4.5	0.1
1-3 August 2003	2	Bottom	23.29	5.5	0.0
1-3 August 2003	3	Bottom	52.25	4.5	0.1
1-3 August 2003	4	Bottom	35.29	4.5	0.0
1-3 August 2003	5	Bottom	44.74	4.5	0.0
1-3 August 2003	6	Bottom	44.16	6.0	0.0
1-3 August 2003	7	Bottom	24.39	6.5	0.0
1-3 August 2003	8	Bottom	45.67	5.0	0.2
1-3 August 2003	9	Bottom	30.14	6.5	1.0
1-3 August 2003	10	Bottom	37.70	6.0	3.0
1-3 August 2003	11	Bottom	30.36	6.5	0.0
1-3 August 2003	12	Bottom	36.54	5.5	0.1
1-3 August 2003	13	Bottom	45.19	5.5	0.2
1-3 August 2003	14	Bottom	40.21	6.0	0.0
1-3 August 2003	15	Bottom	43.18	5.5	0.0
1-3 August 2003	16	Bottom	41.46	6.0	0.3
1-3 August 2003	17	Bottom	49.43	4.5	0.4
1-3 August 2003	18	Bottom	47.31	5.5	0.1
1-3 August 2003	1	Top	53.54	5.5	0.1
1-3 August 2003	2	Top	46.88	5.5	0.0
1-3 August 2003	3	Top	37.78	6.0	0.0
1-3 August 2003	4	Top	48.91	5.5	0.0
1-3 August 2003	5	Top	55.04	5.5	0.0
1-3 August 2003	6	Top	53.09	5.5	0.0
1-3 August 2003	7	Top	56.31	6.5	0.0
1-3 August 2003	8	Top	52.83	5.5	0.2
1-3 August 2003	9	Top	54.55	6.5	10.6
1-3 August 2003	10	Top	51.82	7.0	0.5
1-3 August 2003	11	Top	62.58	5.5	15.6
1-3 August 2003	12	Top	50.35	6.5	0.6
1-3 August 2003	13	Top	55.86	5.5	0.3
1-3 August 2003	14	Top	54.17	6.5	0.0
1-3 August 2003	15	Top	48.98	6.5	0.3
1-3 August 2003	16	Top	62.82	5.5	0.1
1-3 August 2003	17	Top	53.40	5.5	0.3
1-3 August 2003	18	Top	46.74	6.0	0.0

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
9-11 Oct 2003	1	Bottom	57.30	5.0	2.7
9-11 Oct 2003	2	Bottom	45.71	5.5	0.8
9-11 Oct 2003	3	Bottom	68.31	5.0	0.8
9-11 Oct 2003	4	Bottom	31.51	5.5	0.8
9-11 Oct 2003	5	Bottom	52.89	5.5	0.8
9-11 Oct 2003	6	Bottom	50.30	5.5	1.6
9-11 Oct 2003	7	Bottom	52.94	7.5	2.2
9-11 Oct 2003	8	Bottom	39.74	5.0	0.8
9-11 Oct 2003	9	Bottom	62.50	7.5	3.4
9-11 Oct 2003	10	Bottom	45.45	5.5	1.0
9-11 Oct 2003	11	Bottom	61.72	6.0	1.2
9-11 Oct 2003	12	Bottom	39.02	5.5	0.9
9-11 Oct 2003	13	Bottom	64.66	5.0	0.9
9-11 Oct 2003	14	Bottom	38.10	6.5	10.9
9-11 Oct 2003	15	Bottom	56.15	7.5	15.5
9-11 Oct 2003	16	Bottom	45.78	6.5	1.3
9-11 Oct 2003	17	Bottom	75.77	5.0	1.1
9-11 Oct 2003	18	Bottom	35.42	5.5	1.3
9-11 Oct 2003	1	Top	53.63	6.5	1.1
9-11 Oct 2003	2	Top	46.43	8.0	0.8
9-11 Oct 2003	3	Top	76.84	7.5	0.8
9-11 Oct 2003	4	Top	40.66	7.0	3.3
9-11 Oct 2003	5	Top	62.64	7.0	1.9
9-11 Oct 2003	6	Top	40.74	7.5	1.6
9-11 Oct 2003	7	Top	62.94	7.0	2.0
9-11 Oct 2003	8	Top	52.24	6.5	1.2
9-11 Oct 2003	9	Top	58.51	9.0	44.7
9-11 Oct 2003	10	Top	37.68	8.0	2.6
9-11 Oct 2003	11	Top	58.56	8.0	81.1
9-11 Oct 2003	12	Top	57.02	8.5	3.3
9-11 Oct 2003	13	Top	61.90	7.0	4.7
9-11 Oct 2003	14	Top	46.25	7.5	120.5
9-11 Oct 2003	15	Top	54.36	8.0	108.3
9-11 Oct 2003	16	Top	51.55	6.5	37.7
9-11 Oct 2003	17	Top	57.14	5.5	1.6
9-11 Oct 2003	18	Top	50.00	6.5	3.1

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
19-21 Nov 2003	1	Bottom	46.85	5.0	0.9
19-21 Nov 2003	2	Bottom	28.24	7.0	0.8
19-21 Nov 2003	3	Bottom	44.44	4.5	1.2
19-21 Nov 2003	4	Bottom	36.49	5.5	2.0
19-21 Nov 2003	5	Bottom	45.45	4.5	0.9
19-21 Nov 2003	6	Bottom	42.86	5.5	1.2
19-21 Nov 2003	7	Bottom	34.62	6.5	1.0
19-21 Nov 2003	8	Bottom	42.06	5.5	0.7
19-21 Nov 2003	9	Bottom	34.15	8.0	3.2
19-21 Nov 2003	10	Bottom	38.64	7.0	1.4
19-21 Nov 2003	11	Bottom	33.33	6.5	0.9
19-21 Nov 2003	12	Bottom	40.96	7.5	3.1
19-21 Nov 2003	13	Bottom	52.44	5.5	1.8
19-21 Nov 2003	14	Bottom	34.04	7.0	1.2
19-21 Nov 2003	15	Bottom	44.55	5.5	2.3
19-21 Nov 2003	16	Bottom	46.59	7.0	0.8
19-21 Nov 2003	17	Bottom	45.36	5.5	0.4
19-21 Nov 2003	18	Bottom	49.04	5.5	0.6
19-21 Nov 2003	1	Top	57.36	7.0	6.2
19-21 Nov 2003	2	Top	61.47	6.5	1.3
19-21 Nov 2003	3	Top	42.86	7.5	1.0
19-21 Nov 2003	4	Top	57.24	9.0	114.7
19-21 Nov 2003	5	Top	57.43	7.5	20.1
19-21 Nov 2003	6	Top	55.34	5.5	5.4
19-21 Nov 2003	7	Top	61.36	8.5	6.3
19-21 Nov 2003	8	Top	57.48	8.5	10.6
19-21 Nov 2003	9	Top	73.21	9.5	44.7
19-21 Nov 2003	10	Top	53.00	8.5	16.0
19-21 Nov 2003	11	Top	72.07	10.0	63.6
19-21 Nov 2003	12	Top	63.82	9.0	17.5
19-21 Nov 2003	13	Top	65.55	8.0	22.5
19-21 Nov 2003	14	Top	67.67	9.0	21.5
19-21 Nov 2003	15	Top	60.14	7.5	0.6
19-21 Nov 2003	16	Top	69.23	7.0	0.5
19-21 Nov 2003	17	Top	54.55	6.0	0.4
19-21 Nov 2003	18	Top	52.88	7.0	0.4

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
5-7 Feb 2004	1	Bottom	48.13	5.5	0.7
5-7 Feb 2004	2	Bottom	34.31	5.5	0.8
5-7 Feb 2004	3	Bottom	48.78	5.0	0.9
5-7 Feb 2004	4	Bottom	39.46	5.5	0.7
5-7 Feb 2004	5	Bottom	48.08	5.5	3.2
5-7 Feb 2004	6	Bottom	45.07	5.5	3.9
5-7 Feb 2004	7	Bottom	40.78	8.0	16.4
5-7 Feb 2004	8	Bottom	42.05	5.0	5.2
5-7 Feb 2004	9	Bottom	31.67	8.0	7.4
5-7 Feb 2004	10	Bottom	34.41	7.5	1.6
5-7 Feb 2004	11	Bottom	32.97	7.5	1.8
5-7 Feb 2004	12	Bottom	38.75	5.5	0.6
5-7 Feb 2004	13	Bottom	48.72	5.5	2.3
5-7 Feb 2004	14	Bottom	36.70	6.5	1.1
5-7 Feb 2004	15	Bottom	41.94	6.5	3.3
5-7 Feb 2004	16	Bottom	48.53	7.0	3.5
5-7 Feb 2004	17	Bottom	51.11	5.5	1.1
5-7 Feb 2004	18	Bottom	45.45	4.5	2.9
5-7 Feb 2004	1	Top	57.14	7.0	12.9
5-7 Feb 2004	2	Top	68.35	9.0	106.1
5-7 Feb 2004	3	Top	44.33	7.5	2.1
5-7 Feb 2004	4	Top	64.18	9.0	17.2
5-7 Feb 2004	5	Top	61.93	7.5	16.4
5-7 Feb 2004	6	Top	58.82	6.5	11.4
5-7 Feb 2004	7	Top	59.27	8.5	11.4
5-7 Feb 2004	8	Top	55.38	7.5	16.3
5-7 Feb 2004	9	Top	68.49	9.0	69.0
5-7 Feb 2004	10	Top	50.33	8.0	8.5
5-7 Feb 2004	11	Top	71.71	8.5	92.7
5-7 Feb 2004	12	Top	60.18	8.5	12.8
5-7 Feb 2004	13	Top	65.00	7.5	24.6
5-7 Feb 2004	14	Top	64.55	8.5	12.2
5-7 Feb 2004	15	Top	54.90	7.0	0.5
5-7 Feb 2004	16	Top	64.63	8.5	55.4
5-7 Feb 2004	17	Top	46.91	5.5	3.3
5-7 Feb 2004	18	Top	51.39	7.0	1.4

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
9-11 April 2004	1	Bottom	46.36	5.5	0.8
9-11 April 2004	2	Bottom	23.60	5.5	0.5
9-11 April 2004	3	Bottom	48.48	5.0	1.0
9-11 April 2004	4	Bottom	38.71	5.0	0.7
9-11 April 2004	5	Bottom	50.00	5.0	1.2
9-11 April 2004	6	Bottom	45.45	5.5	0.8
9-11 April 2004	7	Bottom	39.02	7.0	2.4
9-11 April 2004	8	Bottom	43.37	5.0	0.3
9-11 April 2004	9	Bottom	28.00	8.0	5.9
9-11 April 2004	10	Bottom	37.68	6.5	0.8
9-11 April 2004	11	Bottom	31.96	7.0	1.2
9-11 April 2004	12	Bottom	39.45	5.0	1.4
9-11 April 2004	13	Bottom	50.43	5.5	2.6
9-11 April 2004	14	Bottom	58.56	7.5	6.3
9-11 April 2004	15	Bottom	46.73	6.5	1.7
9-11 April 2004	16	Bottom	46.55	5.5	3.0
9-11 April 2004	17	Bottom	46.93	4.5	1.2
9-11 April 2004	18	Bottom	45.98	5.0	2.6
9-11 April 2004	1	Top	56.58	6.5	6.7
9-11 April 2004	2	Top	58.74	7.5	3.5
9-11 April 2004	3	Top	36.00	8.0	3.5
9-11 April 2004	4	Top	62.11	8.5	13.4
9-11 April 2004	5	Top	62.66	6.5	10.4
9-11 April 2004	6	Top	57.67	6.5	3.6
9-11 April 2004	7	Top	58.02	7.5	5.6
9-11 April 2004	8	Top	51.41	6.5	6.8
9-11 April 2004	9	Top	68.33	9.0	71.6
9-11 April 2004	10	Top	50.49	7.5	10.5
9-11 April 2004	11	Top	74.44	9.0	101.3
9-11 April 2004	12	Top	55.28	7.5	14.7
9-11 April 2004	13	Top	55.61	7.5	19.4
9-11 April 2004	14	Top	37.93	5.5	1.3
9-11 April 2004	15	Top	53.33	7.5	2.5
9-11 April 2004	16	Top	56.32	7.0	0.5
9-11 April 2004	17	Top	53.39	5.5	6.6
9-11 April 2004	18	Top	48.51	6.0	2.4

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
4-6 June 2004	1	Bottom	42.31	5.0	0.1
4-6 June 2004	2	Bottom	24.32	5.0	0.1
4-6 June 2004	3	Bottom	50.00	5.0	0.2
4-6 June 2004	4	Bottom	39.56	5.0	0.3
4-6 June 2004	5	Bottom	50.00	4.5	0.0
4-6 June 2004	6	Bottom	44.21	5.5	0.1
4-6 June 2004	7	Bottom	38.33	6.5	0.2
4-6 June 2004	8	Bottom	43.94	5.5	0.2
4-6 June 2004	9	Bottom	25.64	7.5	0.5
4-6 June 2004	10	Bottom	32.65	6.0	0.2
4-6 June 2004	11	Bottom	31.03	6.5	0.3
4-6 June 2004	12	Bottom	32.61	6.0	0.6
4-6 June 2004	13	Bottom	48.96	5.5	0.1
4-6 June 2004	14	Bottom	39.06	6.5	0.3
4-6 June 2004	15	Bottom	43.04	5.5	0.1
4-6 June 2004	16	Bottom	45.33	6.0	0.0
4-6 June 2004	17	Bottom	42.98	4.5	0.3
4-6 June 2004	18	Bottom	48.98	5.5	0.6
4-6 June 2004	1	Top	56.41	5.5	0.2
4-6 June 2004	2	Top	59.41	6.0	0.1
4-6 June 2004	3	Top	38.46	7.5	0.1
4-6 June 2004	4	Top	42.22	7.0	0.1
4-6 June 2004	5	Top	60.93	6.0	0.1
4-6 June 2004	6	Top	52.46	6.5	0.6
4-6 June 2004	7	Top	58.65	6.5	0.2
4-6 June 2004	8	Top	44.33	6.5	0.2
4-6 June 2004	9	Top	65.26	7.5	1.0
4-6 June 2004	10	Top	49.54	7.0	0.3
4-6 June 2004	11	Top	70.23	5.5	2.3
4-6 June 2004	12	Top	50.53	7.5	0.4
4-6 June 2004	13	Top	61.33	6.5	0.4
4-6 June 2004	14	Top	55.41	6.5	0.0
4-6 June 2004	15	Top	48.39	7.0	0.1
4-6 June 2004	16	Top	54.14	6.5	0.4
4-6 June 2004	17	Top	51.24	6.5	0.0
4-6 June 2004	18	Top	48.11	6.5	0.1

Date	Guano Pile	Sample	Water content *in situ*	pH	Fresh Guano wet weight
1-3 August 2004	1	Bottom	45.24	5.5	0.3
1-3 August 2004	2	Bottom	25.37	6.0	0.3
1-3 August 2004	3	Bottom	45.35	4.5	1.2
1-3 August 2004	4	Bottom	35.94	5.0	1.0
1-3 August 2004	5	Bottom	43.59	5.0	1.5
1-3 August 2004	6	Bottom	38.36	5.0	1.3
1-3 August 2004	7	Bottom	29.85	6.5	0.8
1-3 August 2004	8	Bottom	39.78	5.0	1.5
1-3 August 2004	9	Bottom	21.05	7.0	1.9
1-3 August 2004	10	Bottom	38.46	6.0	0.8
1-3 August 2004	11	Bottom	33.33	6.5	1.0
1-3 August 2004	12	Bottom	42.86	6.0	0.8
1-3 August 2004	13	Bottom	52.43	5.5	1.0
1-3 August 2004	14	Bottom	42.11	5.5	0.9
1-3 August 2004	15	Bottom	49.41	5.5	1.8
1-3 August 2004	16	Bottom	45.12	6.0	0.9
1-3 August 2004	17	Bottom	53.13	5.5	0.6
1-3 August 2004	18	Bottom	48.60	5.5	0.8
1-3 August 2004	1	Top	55.66	6.0	0.5
1-3 August 2004	2	Top	58.49	6.0	0.6
1-3 August 2004	3	Top	60.16	9.0	28.6
1-3 August 2004	4	Top	47.95	6.5	1.0
1-3 August 2004	5	Top	59.84	6.0	1.5
1-3 August 2004	6	Top	56.07	6.5	2.0
1-3 August 2004	7	Top	61.22	6.5	1.4
1-3 August 2004	8	Top	52.33	6.0	1.3
1-3 August 2004	9	Top	65.81	8.0	13.7
1-3 August 2004	10	Top	49.02	7.5	0.8
1-3 August 2004	11	Top	70.67	7.0	53.6
1-3 August 2004	12	Top	50.62	7.5	1.3
1-3 August 2004	13	Top	58.14	6.5	1.4
1-3 August 2004	14	Top	57.84	6.5	0.8
1-3 August 2004	15	Top	54.84	7.5	12.8
1-3 August 2004	16	Top	65.73	9.0	20.5
1-3 August 2004	17	Top	52.04	6.0	0.9
1-3 August 2004	18	Top	59.46	7.0	0.8

Appendix 5: Starlight Cave species abundances

Date	Guano Pile	Sample	Histerid	Anobid	Cryptophagidae	Jacobsoniidae	Carabidae	Ichnuemonidae	*Monopis*	Collembola	Staphylinidae
28-30 Nov 2002	1	**Bottom**	2	11	2	0	0	2	1	0	1
28-30 Nov 2002	2	**Bottom**	1	3	0	0	0	0	0	0	0
28-30 Nov 2002	3	**Bottom**	63	78	0	0	0	0	8	0	0
28-30 Nov 2002	4	**Bottom**	46	158	1	0	0	1	8	0	0
28-30 Nov 2002	5	**Bottom**	4	9	1	0	0	0	0	0	0
28-30 Nov 2002	1	**Top**	91	161	1	0	0	7	2	0	21
28-30 Nov 2002	2	**Top**	60	66	0	0	0	1	0	0	0
28-30 Nov 2002	3	**Top**	48	10	0	0	0	2	1	0	0
28-30 Nov 2002	4	**Top**	12	73	0	0	0	0	6	0	0
28-30 Nov 2002	5	**Top**	28	56	0	0	0	16	0	0	2
5-7 Aug 2003	1	**Bottom**	1	9	0	0	0	0	0	1	0
5-7 Aug 2003	2	**Bottom**	5	482	0	1	0	1	0	0	2
5-7 Aug 2003	3	**Bottom**	4	312	0	0	0	0	0	1	1
5-7 Aug 2003	4	**Bottom**	2	1604	1	0	0	1	1	0	0
5-7 Aug 2003	5	**Bottom**	20	481	0	0	2	0	26	0	1
5-7 Aug 2003	1	**Top**	4	28	39	0	0	0	0	1	0
5-7 Aug 2003	2	**Top**	9	672	0	0	0	1	2	0	4
5-7 Aug 2003	3	**Top**	0	633	0	1	0	1	0	5	0
5-7 Aug 2003	4	**Top**	0	1685	0	0	0	0	0	0	0
5-7 Aug 2003	5	**Top**	8	708	0	0	0	1	3	1	0
22-24 Nov 2003	1	**Bottom**	3	28	0	1	0	2	17	0	0
22-24 Nov 2003	2	**Bottom**	13	190	0	0	0	0	3	0	5
22-24 Nov 2003	3	**Bottom**	5	127	0	0	0	0	5	0	0
22-24 Nov 2003	4	**Bottom**	57	855	0	0	0	0	4	0	0
22-24 Nov 2003	5	**Bottom**	152	158	0	0	0	6	51	0	0
22-24 Nov 2003	1	**Top**	27	112	25	0	0	9	20	0	16
22-24 Nov 2003	2	**Top**	8	38	1	1	0	1	3	0	2
22-24 Nov 2003	3	**Top**	6	87	0	1	0	1	4	4	1
22-24 Nov 2003	4	**Top**	3	321	0	0	0	1	0	0	0
22-24 Nov 2003	5	**Top**	83	877	0	0	0	13	11	0	1
4-6 Aug 2004	1	**Bottom**	0	27	0	0	0	0	3	0	0
4-6 Aug 2004	2	**Bottom**	1	450	1	0	0	0	2	0	1
4-6 Aug 2004	3	**Bottom**	0	128	0	0	0	0	2	2	1
4-6 Aug 2004	4	**Bottom**	6	243	0	0	0	0	3	1	0
4-6 Aug 2004	5	**Bottom**	3	70	0	0	0	0	1	0	0
4-6 Aug 2004	1	**Top**	1	66	13	0	0	0	6	0	1
4-6 Aug 2004	2	**Top**	4	377	0	2	0	0	1	0	2
4-6 Aug 2004	3	**Top**	3	508	0	1	0	1	3	1	1
4-6 Aug 2004	4	**Top**	0	208	0	0	0	0	0	0	0
4-6 Aug 2004	5	**Top**	0	162	1	0	0	0	1	0	1

Date	Guano Pile	Sample	Pseudoscorpionida	Cunaxidae	Urodinychid	Macrochelidae	Spinturnicidae	Sciaridae	Phoridae	Sphaeroceridae	Nycteribiidae
28-30 Nov 2002	1	**Bottom**	0	3	2	0	0	9	0	0	0
28-30 Nov 2002	2	**Bottom**	0	6	0	0	0	0	0	0	0
28-30 Nov 2002	3	**Bottom**	1	5	0	0	0	0	0	0	0
28-30 Nov 2002	4	**Bottom**	3	1	0	0	0	0	0	0	0
28-30 Nov 2002	5	**Bottom**	2	1	0	0	0	0	0	0	0
28-30 Nov 2002	1	**Top**	5	2	1	0	0	15	186	2	0
28-30 Nov 2002	2	**Top**	1	19	0	0	0	0	0	0	0
28-30 Nov 2002	3	**Top**	0	6	0	0	0	0	0	0	0
28-30 Nov 2002	4	**Top**	6	1	0	0	0	0	0	0	0
28-30 Nov 2002	5	**Top**	4	0	0	0	0	0	0	0	0
5-7 Aug 2003	1	**Bottom**	0	0	0	0	0	0	2	0	0
5-7 Aug 2003	2	**Bottom**	2	0	0	0	0	0	0	0	0
5-7 Aug 2003	3	**Bottom**	0	5	0	0	0	1	0	0	0
5-7 Aug 2003	4	**Bottom**	0	4	0	0	0	0	0	0	0
5-7 Aug 2003	5	**Bottom**	0	12	0	0	0	0	0	0	2
5-7 Aug 2003	1	**Top**	1	4	2	1	0	16	84	6	0
5-7 Aug 2003	2	**Top**	2	58	0	0	0	0	0	0	0
5-7 Aug 2003	3	**Top**	0	0	0	0	0	0	2	0	0
5-7 Aug 2003	4	**Top**	1	2	0	0	0	0	0	0	0
5-7 Aug 2003	5	**Top**	0	1	0	1	0	0	0	0	0
22-24 Nov 2003	1	**Bottom**	0	2	0	1	0	0	4	0	1
22-24 Nov 2003	2	**Bottom**	4	24	0	2	0	0	0	0	0
22-24 Nov 2003	3	**Bottom**	1	2	0	0	0	0	1	1	1
22-24 Nov 2003	4	**Bottom**	2	0	1	0	0	0	0	1	0
22-24 Nov 2003	5	**Bottom**	0	0	0	0	0	0	0	0	2
22-24 Nov 2003	1	**Top**	4	0	10	0	0	0	13	0	113
22-24 Nov 2003	2	**Top**	6	140	0	0	0	0	0	1	0
22-24 Nov 2003	3	**Top**	4	30	0	7	0	0	0	0	2
22-24 Nov 2003	4	**Top**	4	1	0	0	0	0	0	0	0
22-24 Nov 2003	5	**Top**	0	0	0	0	0	0	0	1	0
4-6 Aug 2004	1	**Bottom**	0	0	0	0	0	1	0	0	0
4-6 Aug 2004	2	**Bottom**	1	2	0	1	0	0	0	0	0
4-6 Aug 2004	3	**Bottom**	0	2	0	2	0	1	0	0	0
4-6 Aug 2004	4	**Bottom**	2	0	0	0	0	0	0	0	0
4-6 Aug 2004	5	**Bottom**	2	1	0	0	0	0	0	0	0
4-6 Aug 2004	1	**Top**	1	10	10	0	0	9	46	34	0
4-6 Aug 2004	2	**Top**	1	2	1	1	8	0	0	0	0
4-6 Aug 2004	3	**Top**	1	1	1	2	0	0	0	0	2
4-6 Aug 2004	4	**Top**	2	0	0	0	0	0	0	0	0
4-6 Aug 2004	5	**Top**	1	3	3	0	2	0	0	0	0

Date	Guano Pile	Sample	Tnomisidae	Isopoda	Leiodidae	Elatridae	Bostrichidae	Curculionidae	*Thrips imaginis*	Lygaeoidea	Rhaphidophoridae
28-30 Nov 2002	1	**Bottom**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	2	**Bottom**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	3	**Bottom**	0	0	0	0	0	1	0	1	1
28-30 Nov 2002	4	**Bottom**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	5	**Bottom**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	1	**Top**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	2	**Top**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	3	**Top**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	4	**Top**	0	0	0	0	0	0	0	0	0
28-30 Nov 2002	5	**Top**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	1	**Bottom**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	2	**Bottom**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	3	**Bottom**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	4	**Bottom**	0	1	0	0	0	0	0	0	0
5-7 Aug 2003	5	**Bottom**	1	0	0	0	0	0	0	0	0
5-7 Aug 2003	1	**Top**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	2	**Top**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	3	**Top**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	4	**Top**	0	0	0	0	0	0	0	0	0
5-7 Aug 2003	5	**Top**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	1	**Bottom**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	2	**Bottom**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	3	**Bottom**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	4	**Bottom**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	5	**Bottom**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	1	**Top**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	2	**Top**	0	0	1	0	0	0	0	0	0
22-24 Nov 2003	3	**Top**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	4	**Top**	0	0	0	0	0	0	0	0	0
22-24 Nov 2003	5	**Top**	1	0	0	1	1	1	0	0	0
4-6 Aug 2004	1	**Bottom**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	2	**Bottom**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	3	**Bottom**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	4	**Bottom**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	5	**Bottom**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	1	**Top**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	2	**Top**	0	0	0	0	0	0	0	3	0
4-6 Aug 2004	3	**Top**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	4	**Top**	0	0	0	0	0	0	0	0	0
4-6 Aug 2004	5	**Top**	1	0	0	0	0	0	0	1	0

Appendix 6: Starlight Cave Environmental Data

Date	Guano Pile	Sample	Moisture content In Situ guano %	Fresh Guano Wet weight	pH
28-30 Nov 2002	1	**Bottom**	41.3	0.1	8.5
28-30 Nov 2002	2	**Bottom**	20.0	0.7	7.5
28-30 Nov 2002	3	**Bottom**	32.3	2.1	8.0
28-30 Nov 2002	4	**Bottom**	20.2	0.2	6.5
28-30 Nov 2002	5	**Bottom**	18.6	0.3	6.5
28-30 Nov 2002	1	**Top**	43.0	19.7	9.5
28-30 Nov 2002	2	**Top**	39.7	10.3	9.0
28-30 Nov 2002	3	**Top**	41.4	7.4	9.5
28-30 Nov 2002	4	**Top**	27.3	0.5	6.5
28-30 Nov 2002	5	**Top**	14.7	1.5	6.5
5-7 Aug 2003	1	**Bottom**	42.5	0	6.5
5-7 Aug 2003	2	**Bottom**	28.0	0.1	7.0
5-7 Aug 2003	3	**Bottom**	30.9	0.1	7.5
5-7 Aug 2003	4	**Bottom**	25.0	0	6.5
5-7 Aug 2003	5	**Bottom**	13.4	0.1	6.0
5-7 Aug 2003	1	**Top**	49.0	0.1	8.5
5-7 Aug 2003	2	**Top**	41.1	0.5	8.5
5-7 Aug 2003	3	**Top**	34.8	0.2	8.5
5-7 Aug 2003	4	**Top**	25.9	0.1	5.0
5-7 Aug 2003	5	**Top**	13.9	0.2	6.0
22-24 Nov 2003	1	**Bottom**	39.4	0.2	7.0
22-24 Nov 2003	2	**Bottom**	23.6	1.5	6.5
22-24 Nov 2003	3	**Bottom**	32.1	1.5	7.5
22-24 Nov 2003	4	**Bottom**	17.3	0.3	6.5
22-24 Nov 2003	5	**Bottom**	20.0	0.3	6.0
22-24 Nov 2003	1	**Top**	39.3	0.1	9.0
22-24 Nov 2003	2	**Top**	47.0	18.5	9.5
22-24 Nov 2003	3	**Top**	40.3	1.8	8.5
22-24 Nov 2003	4	**Top**	26.7	0.2	6.5
22-24 Nov 2003	5	**Top**	16.8	16.7	6.5
4-6 Aug 2004	1	**Bottom**	40.3	0.1	6.0
4-6 Aug 2004	2	**Bottom**	25.0	0.1	6.0
4-6 Aug 2004	3	**Bottom**	34.5	0.1	6.5
4-6 Aug 2004	4	**Bottom**	33.3	0	6.5
4-6 Aug 2004	5	**Bottom**	22.1	0.2	5.5
4-6 Aug 2004	1	**Top**	50.5	6.1	9.0
4-6 Aug 2004	2	**Top**	36.2	1.4	8.5
4-6 Aug 2004	3	**Top**	35.3	0.2	7.0
4-6 Aug 2004	4	**Top**	29.5	0	6.0
4-6 Aug 2004	5	**Top**	14.8	0.7	6.0

Appendix 7: Allozyme raw scores for pseudoscorpions

Locality	Gotc	Gpi	Gpt	Idhc	Mdhm	Mdhc	Mpi	ndpk	Np	Ntak
Starlight Cave	b	a	c	d	b	a	b	a	b	a
Starlight Cave	b	a	c	d	b	a	b	a	b	a
Starlight Cave	b	a	c	d	b	a	b	a	b	a
Starlight Cave	b	a	c	d	b	a	b	a	b	a
Starlight Cave	b	a	c	d	b	a	b	a	b	a
Starlight Cave	b	a	c	d	b	a	b	a	b	a
Starlight Cave	b	a	c	d	b	a	b	a	b	a
Bat Cave maternity	e	a	b	d	b	b	d	b	d	-
Bat Cave maternity	e	a	b	d	b	b	d	b	d	a
Bat Cave maternity	d	a	b	d	b	b	d	b	d	a
Bat Cave maternity	de	a	b	d	b	b	d	b	d	a
Bat Cave maternity	de	a	b	d	b	b	d	b	d	a
Bat Cave flyway	d	a	b	d	b	b	d	b	d	a
Bat Cave flyway	de	a	bc	d	b	b	d	b	d	a
Bat Cave flyway	d	a	b	d	b	b	d	b	d	a
Bat Cave flyway	de	a	b	d	b	b	d	b	d	a
Bat Cave entrance	-	a	b	bd	b	b	d	b	d	a
Bat Cave entrance	d	a	b	d	b	b	d	b	d	a
Bat Cave entrance	d	a	b	d	b	b	de	b	d	a
Bat Cave entrance	d	a	b	d	b	b	d	b	d	a
Robertsons Cave entrance	d	a	b	d	b	b	d	b	d	-
Robertsons Cave entrance	d	a	b	d	b	b	d	b	d	-
Robertsons Cave entrance	d	a	b	d	b	b	d	b	d	a
Robertsons Cave entrance	d	a	b	d	b	b	d	b	d	a
Robertsons Cave entrance	d	a	b	d	b	b	d	b	d	a
Robertsons Cave entrance	d	a	b	d	b	b	d	b	d	a
Robertsons Cave maternity	d	a	b	d	b	b	d	b	d	a
Robertsons Cave maternity	de	a	b	d	b	b	d	b	d	a
Robertsons Cave maternity	d	a	b	d	b	b	d	b	d	a
Robertsons Cave maternity	de	a	b	d	b	b	d	b	d	a
Robertsons Cave maternity	de	a	b	d	b	b	d	b	d	a
Robertsons Cave maternity	d	a	b	d	b	b	d	b	d	a
Fox Cave	d	a	b	d	b	b	d	b	d	a
Fox Cave	d	a	b	d	b	b	d	b	d	a
Fox Cave	d	a	b	d	b	b	d	b	d	a
Murrawijinie No.3 Cave	-	a	b	c	b	b	d	b	d	a
Murrawijinie No.3 Cave	-	a	b	c	b	b	d	b	d	a
Murrawijinie No.3 Cave	-	a	b	c	b	b	d	b	d	ab
Murrawijinie No.3 Cave	-	a	b	d	b	b	d	b	d	a
Murrawijinie No.3 Cave	c	a	b	cd	b	b	d	b	d	a
Warbla Cave lake	ce	b	b	b	b	b	d	b	d	a
Warbla Cave lake	-	ab	b	d	b	b	d	b	d	a
Warbla Cave lake	e	ab	b	d	b	b	d	b	d	a
Warbla Cave rockpile	c	b	b	d	b	b	de	b	d	a
Warbla Cave rockpile	-	a	b	d	b	b	d	b	d	a
Warbla Cave rockpile	e	ab	b	d	b	b	de	b	d	a
Warbla Cave rockpile	ce	b	b	d	b	b	de	b	d	a
Warbla Cave rockpile	-	a	b	d	b	b	d	b	d	a
Warbla entrance	-	a	b	d	b	b	d	b	d	a
Warbla entrance	ce	a	b	d	b	b	-	b	d	a
Warbla entrance	e	a	b	d	b	b	de	b	d	a
Warbla entrance	ce	ab	b	d	b	b	de	b	d	a
Murra-El-Elevyn Cave	a	b	d	a	a	c	a	c	a	c
Murra-El-Elevyn Cave	a	b	e	a	a	c	a	c	a	c
Murra-El-Elevyn Cave	a	b	e	a	a	c	a	c	a	c
Murra-El-Elevyn Cave	a	b	e	a	a	c	a	c	a	c
Murra-El-Elevyn Cave	a	b	e	a	a	c	a	c	-	c
Gran Gran Cave	b	a	a	d	b	b	c	a	c	-

Appendix 8: Diversity and Biogeography of Subterranean Guano Arthropod Communities of the Flinders Ranges, South Australia.

Moulds, T. A. (2005). Diversity and biogeography of subterranean guano arthropod communities of the Flinders Ranges, South Australia. *Proceedings of the Linnean Society of New South Wales* **126**: 125-132.

Moulds, T.A. (2005): Diversity and biogeography of subterranean guano arthropod communities of the Flinders Ranges, South Australia.
Proceedings of the Linnean Society of New South Wales v. 126, pp. 125-132

NOTE: This publication is included on pages 247 - 256 in the print copy of the thesis held in the University of Adelaide Library.

Appendix 9: The first Australian record of subterranean guano-collecting ants.

Moulds, T. A. (2006). The first Australian record of subterranean guano-collecting ants. *Helictite* **39**: 3-4.

Moulds, T.A. (In press). The first Australian record of subterranean guano-collecting ants. *Helictite* **39**.

Moulds, T.A. (2006): The first Australian record of subterranean guano-collecting ants.
Helictite v. 39 (1) pp. 3-4