

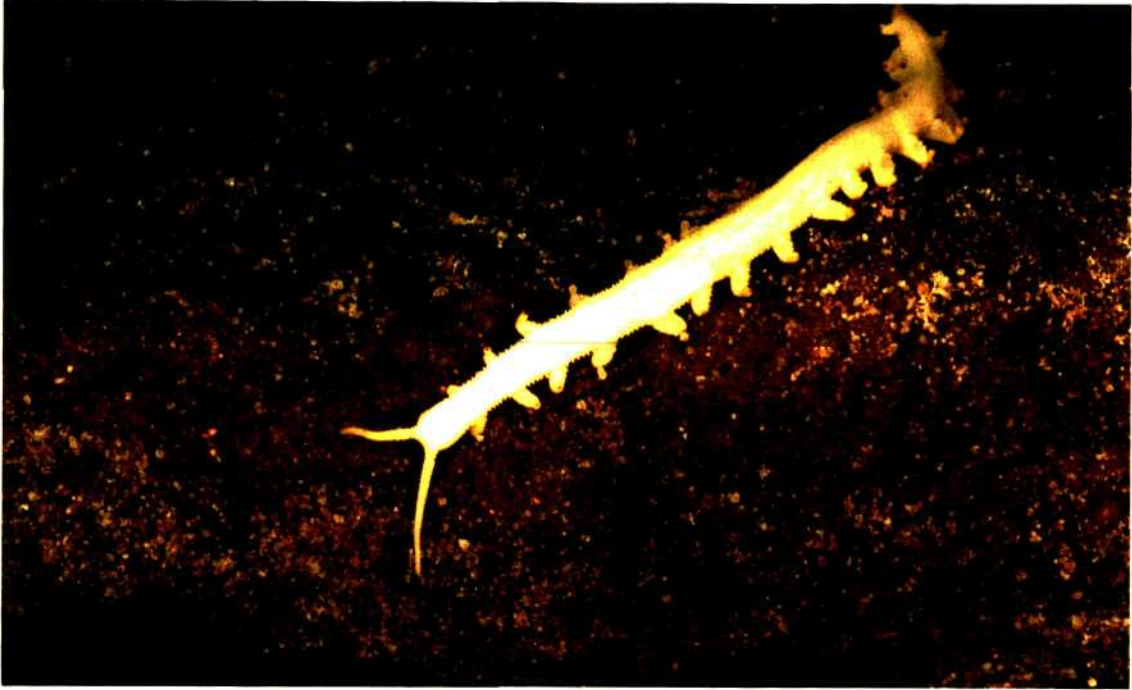
**ECOLOGICAL ASPECTS AND CONSERVATION OF THE
INVERTEBRATE FAUNA OF THE SANDSTONE CAVES OF
TABLE MOUNTAIN, CAPE TOWN**

By

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Submitted in partial fulfilment of the academic requirements for the degree of Master of
Science in the Department of Entomology, University of Natal.

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Peripatopsis alba Lawrence 1932, a rare troglobitic onychophoran endemic to the Table Mountain caves (length approximately 7 cm).

DECLARATION

The research reported on in this thesis, is the result of my own investigations. All assistance received has been fully acknowledged. The thesis has not, in its entirety or in part, been submitted for a degree at any other university or institution.



Norma J. Sharratt

30/9/1998

Date

TABLE OF CONTENTS

ABSTRACT	vii
ACKNOWLEDGEMENTS	viii
1. INTRODUCTION	1
2. STUDY SITE AND METHODS	8
2.1. Description of the study sites	8
2.1.1. Wynberg cave	9
2.1.2. Bats' cave	12
2.2. Species identification	13
2.3. Data collection	13
2.3.1. Determination of species abundance	13
2.3.2. Environmental data	14
2.3.3. Biological and behavioural data	16
2.4. Data analysis	17
2.4.1. Determination of species diversity, richness and evenness	17
2.4.2. Determination of spatial distribution patterns	18
2.4.2.1. Hierarchical clustering	18
2.4.2.2. Ordination	19
2.4.2.3. Tests for significant differences between groups	19
2.4.3. Determination of the effect of the environment on community patterns	19
3. FAUNAL COMPOSITION OF THE CAPE PENINSULA CAVES	21
3.1. The fauna	22
3.1.1. Mollusca	23
3.1.2. Platyhelminthes	33
3.1.3. Oligochaeta	33
3.1.4. Onychophora	33

3.1.5. Crustacea	34
3.1.6. Acarina	35
3.1.7. Pseudoscorpionidae	36
3.1.8. Araneae	36
3.1.9. Opiliones	38
3.1.10. Chilopoda	38
3.1.11. Diplopoda	39
3.1.12. Symphyla	40
3.1.13. Diplura	40
3.1.14. Collembola	40
3.1.15. Thysanura	41
3.1.16. Orthoptera	41
3.1.17. Dermaptera	42
3.1.18. Blattodea	42
3.1.19. Diptera	42
3.1.20. Coleoptera	43
3.1.21. Lepidoptera	44
3.2. Discussion	45
3.2.1. Faunal composition in a global context	45
3.2.2. Distribution of fauna within the caves	48
3.3. Origins and evolution	49
3.4. Conclusion	52
4. SPECIES DIVERSITY AND ABUNDANCE	53
4.1. Population abundance	61
4.2. Species richness	64
4.3. Diversity	67
4.4. Evenness	68
4.5. Biomass	68
4.6. Factors affecting community structure	69
4.7. Distribution of abundances	72
4.8. Conclusion	77

5. COMMUNITY DISTRIBUTION PATTERNS	78
5.1. Wynberg cave	79
5.2. Bats' cave	83
5.3. Taxa responsible for community patterns	87
5.4. Discussion	91
5.5. Conclusion	95
6. ENVIRONMENTAL FACTORS AFFECTING CAVERNICOLE DISTRIBUTION AND ABUNDANCE	97
6.1. Factors affecting overall cave communities	99
6.2. Factors affecting entrance communities	104
6.3. Factors affecting deep zone communities	111
6.4. Factors affecting troglobite distribution and abundance	113
6.5. Discussion	116
6.6. Conclusion	120
7. LIFE HISTORY AND DIET OF SELECTED SPECIES	122
7.1. Seasonal fluctuations in abundance	122
7.1.1. Discussion	132
7.2. Diet of cavernicoles	135
7.2.1. Discussion	139
7.3. Conclusion	140
8. CONSERVATION IMPLICATIONS	142
9. SUMMARY	147
10. CONCLUSION	152
11. REFERENCES	155

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1. Introduction

The subterranean biome is one of rigidly-defined environmental conditions that are somewhat foreign to human experience, making it a near-impossibility for ecological work to be done without intrusion and disturbance of conditions and/or communities. Inaccessibility further hampers ecological work. It has been estimated, for example, that for most karst areas of the world, only 10% open out onto the surface (Curl 1958). Most caves therefore remain unexplored and unstudied. Cave habitats are clearly far more extensive than humans perceive them to be. The subterranean biome includes a great diversity of dark spaces that may be occupied by animals (Peck 1990). In addition to large passageways that are humanly navigable, there is a vast network of cracks, channels and voids inaccessible to humans. These spaces are commonly referred to as microcaverns or mesocaverns (Howarth and Stone 1990; Howarth 1993), microcaverns being less than a millimetre (e.g. between soil grains) and mesocaverns being between one and 20 cm in diameter (e.g. crevices, spaces in leaf litter) (Peck 1990; Howarth 1993). This prevents biologists from entering and effectively studying their inhabitants. Ironically, Howarth (1982, 1983, 1988, 1993) found that many troglobites in Hawaiian lava tubes prefer to inhabit mesocaverns, only occurring in larger passageways under suitable conditions. It may be that answers to many of the ecological questions about cave fauna lie within these networks of cracks and crevices (Howarth 1983). Cave habitats, therefore, need to be redefined in terms of their invertebrate inhabitants.

The vast majority of cave research has been conducted in temperate limestone caves (mainly in North America and Europe), tropical limestone caves and lava tubes (mainly in Hawaii and Australia). In contrast, relatively few studies on cave ecology have dealt with temperate sandstone caves. Braack's (1989) study of a guano cave in the Kruger National Park is the sole ecological study of a sandstone cave in South Africa. Most of the non-taxonomic literature on South African caves is descriptive (e.g. Grindley 1956, 1957, 1961, 1975, 1976; Martini 1990; Martini *et al.* 1990; Irish 1991; Irish *et al.* 1991; Truluck 1994), contributing little to our knowledge of the ecology of South African caves.

The Cape Peninsula caves comprise a system of temperate sandstone caves on the Cape Peninsula mountains at elevations of approximately 500m to 750m above sea level. Table

Mountain forms the northernmost part of the Cape Peninsula mountain chain which extends for approximately 50km. The Cape Peninsula has a mediterranean climate with warm, dry summers and cool, wet winters. Mean annual temperatures are between 16°C and 18°C and the mean annual rainfall is between 400mm and 600mm (Moore 1994). Temperatures within the Table Mountain caves average approximately 10°C, this approximating the mean annual temperatures on the summit of the mountain.

The Peninsula caves are formed in pseudokarst areas on Palaeozoic Peninsula Formation quartzitic sandstone of the Table Mountain Group (Moore 1994; Marker and Swart 1995). Pseudokarst is a geomorphic term relating to the physical structure of landscapes developed on rocks considered to be insoluble, but exhibiting characteristics of water-eroded landscapes (i.e. karst) (Clarke 1997). In the Peninsula caves, weathering is largely chemical, water only being of importance in washing out debris from cracks and joints in the parent sandstone (P.G.F. Coley, unpublished report 1976). Weathering occurs along vertical fault lines initially formed by earth movements. No large speleothems occur in the caves but small silicious stalactite nodules occur on the ceiling and walls (Marker and Swart 1995).

Two main pseudokarst cave areas occur on the Peninsula:

- The Table Mountain caves are vertical caves occurring at elevations of approximately 750m above sea level along the Back Table overlooking Orange Kloof. Seven main caves (Bats', Wynberg, Giants', Metro, Climbers', Smugglers' and Vivarium) and a number of minor caves occur here. Collectively they form the world's third largest sandstone cave system (J. Grindley pers. comm.). The Table Mountain pseudokarst area is a maximum of approximately 12km long and 6km wide (Marker and Swart 1995).
- The Kalk Bay and Silvermine caves occur between elevations of 450 and 500m above sea level on the southern Peninsula. They are relatively shallow horizontally-orientated caves with level sandy floors. Over 70 known caves have been reported from the Kalk Bay and Silvermine area (Marker and Swart 1995), most being relatively small and in close proximity to one another. The Kalk Bay/Silvermine pseudokarst area is a maximum of approximately 15km long and 6km wide (Marker and Swart 1995).

The Cape Peninsula is rich in biodiversity and has a high degree of faunal and floral endemism (Jackson 1994; Picker and Samways 1996). The Peninsula caves support several species of endemic invertebrates, thereby making a significant contribution to the biodiversity and conservation status of the area as a whole. Picker and Samways (1996) considered 14 endemic invertebrate species (out of a total of 111) to be cavernicolous (i.e. cave-dwelling). This proportion is, in fact, far higher, as several endemic epigeal species are also able to survive and reproduce in the caves. Furthermore, a number of new species have been discovered which may be Peninsula endemics.

Troglobites exhibit a high degree of endemism. This has been explained in terms of the 'Pleistocene-effect theory' (Vandel 1965; Barr 1968, 1973, 1985; Mitchell 1969; Poulson and White 1969; Peck 1981; Culver 1982; Sbordoni 1982; Barr and Holsinger 1985; Holsinger 1988; Endrödy-Younga 1988). Ancestral forms are thought to have 'taken refuge' in the stable, humid cave habitats during periods of inclement climatic conditions (Endrödy-Younga 1983). In Europe and North America, the origin of cave faunas is ascribed to glacial events. In South Africa, northerly migration of the African continent during the break-up of Gondwanaland had a similar effect, surface conditions becoming hotter and drier (Tyson 1989). Surface populations became dramatically reduced or extinct and cave populations became genetically and geographically isolated, subsequently evolving troglomorphic adaptations. Similarly, aquatic troglobites are thought to have become restricted to caves when streams were diverted or restricted during periods of surface drought (Barr and Holsinger 1985). Characteristics of refuge species include: rarity, restricted distributions and endemism, absence of close epigeal relatives, taxonomic uniqueness and well-developed troglomorphy (Howarth 1987).

All endemic cavernicoles in Peninsula caves exhibit these characteristics to a greater or lesser degree. Furthermore, because of their isolation in caves during the breakup of Gondwanaland, refuge species in the Cape Peninsula caves are also Gondwanan relicts. Many are highly cave-adapted, phylogenetically unique and rare with restricted distributions. For example, the rare onychophoran, *Peripatopsis alba*¹, and the spelaeogriphacean, *Spelaeogriphus lepidops* are both blind and depigmented species that are restricted to two or three caves on Table

¹ Species authors and dates of description are given in Table 1.

Mountain. The latter is one of only two known extant species within the order Spelaeogriphacea, a second species occurring in Brazil (Brusca and Brusca 1990). Similarly the isopod *Protojanira leleupi* and the amphipod *Paramelita barnardi* are endemic to caves in the Kalk Bay Mountains (Grindley 1975). Several other examples of endemic, cave-adapted Gondwanan relicts exist in the caves. These include the only african rhabdophorid (*Speleiacris tabulae*), two opilionids (*Speleosiro argasiformes* and *Speleomontia cavernicola*), a pseudoscorpion (*Cthoniella cavernicola*), an isopod (*Trichoniscus tabulae*), a chilopod (*Cryptops stupendus*), two araneads (*Lepthyphantes rimicola* and *Crozetulus scutatus*) and a polydesmid (*Harpethrix caeca*). New species discovered during the course of this study may be further additions to this list.

Howarth (1973, 1981, 1987, 1988, 1993) and Deeleman-Reinhold and Deeleman (1980) observed that not all troglobites are relictual. Howarth (1988) proposed that cave adaptations could evolve by 'adaptive shift' in habitual or frequent accidentals. In situations where food resources are abundant, frequent accidentals may be able to exploit these resources and survive in caves, offering opportunities for parapatric speciation (as opposed to extinction and isolation implied by the 'Pleistocene-effect' theory) (Howarth 1988). Evidence for evolution by 'adaptive shift' in Cape Peninsula caves is explored in Chapter 3.

The restricted distributions and rarity of many relictual troglobitic species have prompted several studies of dispersal, colonisation, gene flow and speciation (e.g. Barr 1968, 1985; Poulson and White 1969; Sbordoni 1982; Barr and Holsinger 1985; Poulson 1986; Holsinger 1988) and led to caves being considered as 'islands' of genetically distinct populations (Barr 1968; Culver 1970, 1971, 1982, 1986; Culver *et al.* 1973; Crawford 1981). For cavernicoles, caves can be regarded as 'islands' of habitable patches surrounded by uninhabitable non-cavernous areas. Therefore, continuous limestone areas may contain many caves, each of which can be considered to be an island. Karst areas separated from other karst areas by non-cavernous rock can also be considered as islands (Culver *et al.* 1973). In each case, migration rates between 'islands' are negligible.

Because of their rarity and restricted distributions in island-like habitats, cave animals are particularly vulnerable to even temporary or local environmental disturbances. Numerous endangered troglobites exist (Richards 1971; Tuttle 1977; Howarth 1982; McCracken 1989;

Arita 1993). However, management recommendations cannot be made unless something is known of their specific ecological requirements. Ecological studies need to be done to determine which factors limit troglobite distribution, which disturbances can be regarded as significant and how they would affect communities (Howarth 1983). Knowledge of the diversity and abundance of cave communities is essential for detecting population fluctuations and for monitoring populations for conservation purposes.

The cave environment is a relatively rigorous and stressful one (Howarth 1983). It is characterised by complete darkness, relatively constant temperatures (near the average annual surface temperature), continually wet surfaces, constant high relative humidities (near saturation), high carbon dioxide levels, low oxygen levels and an absence of many temporal environmental cues used by surface species (Barr 1968; Howarth 1980, 1983). Because of the lack of primary production in caves, most food input is allochthonous, and caves are usually considered nutrient-poor (Poulson and White 1969; Barr and Kuehne 1971; Peck 1978, 1990; Culver 1982; Poulson 1986; Aalbu 1989). Plant debris and organic material is blown in or washed in, while visitors (usually bats) bring in food in the form of guano or carcasses which are utilised by scavengers and predators.

Cavernicoles have evolved a number of behavioural, morphological and physiological adaptations to cope with this stressful environment. These include eye reduction or loss, depigmentation, attenuation of appendages, thinning of the cuticle, lowered metabolism and loss of circadian rhythms (Barr 1968). Reproductive adaptations include aseasonal 'K'-type adaptive strategies, reduced fecundity and increased generation times (Alexander 1968; Barr 1968; Poulson 1977, 1981; Carchini *et al.* 1994). Behavioural adaptations have also been recorded (Christiansen 1961, 1965; Christiansen and Culver 1969) but are seldom considered in studies of cave fauna (Howarth 1993). Terrestrial cavernicoles can be categorised according to their degree of cave adaptation and cave-dependence (Howarth 1983).

Troglobites are defined as being obligate cave species that are unable to survive in epigeal environments. Troglaphiles are facultative species that live and reproduce in caves but may also survive in similar dark, humid microhabitats on the surface. Troglaxenes spend only part of their life cycles in caves, periodically returning to surface environments to feed. Finally accidentals are species that occur in caves but are unable to survive and reproduce there. Because of the difficulty involved in assigning categories, most scientists rely on the degree

of troglomorphic specialisation as an indicator of cave-dependence, assuming that highly adapted species would not to be able to survive in epigeal environments (Christiansen 1962; Vandel 1965; Barr 1968; Poulson and White, 1969; Howarth 1981).

A number of authors have looked at factors that might affect diversity and abundance patterns of troglobites, such as food availability, habitat diversity, stability and predictability (Christiansen *et al.* 1961; Poulson and Culver 1969; Poulson and White 1969; Culver *et al.* 1973; Christiansen and Bullion 1978; Chapman 1979; Braack 1989). A large amount of work has also focussed on environmental factors that limit troglobite distribution within caves. Troglobite distribution has been found to be correlated with the physical environment to a greater or lesser degree (Chapman 1979; Howarth 1988; Howarth and Stone 1990) and the question frequently asked is whether a predictive model for troglobite distribution can be found that will fit all caves. In practice, however, a complexity of factors has been shown to be involved, these varying between caves. Relative humidity appears to be the primary limiting factor for cavernicoles (Vandel 1965; Barr 1968; Mitchell 1968; Poulson and White 1969; Barr and Kuehne 1971; Bull and Mitchell 1972; Peck 1978; Peck and Lewis 1978; Howarth 1980, 1981, 1983, 1988), with temperature, moisture and food also being regarded as limiting in a number of caves (Barr 1968; Poulson and White 1969; Barr and Kuehne 1971; Peck 1978, 1990; Culver 1982; Sbordoni 1982; Poulson 1986; Aalbu 1989).

The bulk of biospelaological work on the Peninsula caves has been taxonomic, with a limited amount of literature referring to the biology of cave fauna. No quantitative ecological analyses have been undertaken and the ecology of cave communities was not well understood. Faunal collections commenced at the beginning of this century, this being followed by a series of taxonomic papers (e.g. Barnard 1916, 1932; Peringuey 1916; Attems 1928; Hesse 1929; Karny 1929; Lawrence 1931, 1932, 1935, 1962b, 1964; Gordon 1957; Dybas 1960; Grindley 1963). Grindley (1956, 1957, 1961, 1975, 1976) wrote a number of descriptive papers commenting on aspects of the biology and behaviour of the major taxa. Grindley (1975) and Grindley and Hessler (1971) reported on the biology and respiratory mechanisms in *Spelaeogriphus*, while Carchini *et al.* (1991a) looked at the biology of the rhabdophorid, *Speleiacris tabulae*. Rhabdophorids play an important role in the trophic ecology of caves and often occur in relatively high numbers. However, biological and ecological studies of rhabdophorids have mostly been conducted on *Dolichopoda* in Europe

(e.g. Carchini *et al.* 1982, 1983, 1991b, 1994; Di Russo *et al.* 1991), *Hadenoeus* and *Ceuthophilus* in North America (Hubbel and Norton 1978; Northup and Crawford 1991) and *Pallidotettix nullarborensis* Richards in Australia (Richards 1969, 1971). Further ecological and biological work on *Speleiacris tabulae* would be of great value for comparative purposes.

Conservation considerations are clearly a priority in the Table Mountain caves, considering their profound contribution to biodiversity. Moreover, many species are rare and phylogenetically unique with limited and specialised habitat requirements. However, ecological knowledge of the cave communities is a prerequisite for the implementation of conservation measures. Therefore, the aims of this study were:

- To achieve an updated taxonomic inventory of Peninsula cavernicoles, with an assessment of how dependent individual species are on caves, and a discussion of biotopes and zoogeography.
- To determine species abundance, richness and diversity in Bats' and Wynberg caves (Table Mountain) and to investigate factors that affect diversity.
- To establish how cavernicoles are spatially distributed within the Table Mountain caves.
- To determine the effect of the environment on distribution and abundance patterns. That is, which environmental conditions were important determinants of community patterns and which factors can be used to predict the presence of troglobites in Peninsula caves, or passageways within these caves.
- To establish whether temporal changes in abundance (both overall and for specified life cycle stages) occur over a 12-month period, with particular reference to *Speleiacris tabulae*.
- To comment on food preferences and trophic relationships of the faunal communities, and to provide specific behavioural observations for selected species.
- To assess the levels of threat to cave species and communities so that appropriate conservation measures can be taken.

2. Study sites and methods

2.1. Description of the study sites

The study was conducted in two caves on Table Mountain, Cape Town (33° 59'S, 18° 23'E). Bats' and Wynberg caves were selected for their accessibility, ease of exploration, size and depth, the presence of bats, availability of water and their putative biological importance. Both are vertical caves running along a sandstone ridge at an elevation of approximately 750m above sea level on the northern slopes above Orange Kloof. They are the most frequently-visited caves on Table Mountain and the assessment of human impact on their ecology is therefore a priority.

Qualitative faunal surveys and collections were also conducted in 31 randomly-chosen caves in the Kalk Bay and Silvermine Mountains (34° 07'S, 18° 26'E). These are all relatively shallow, horizontally-orientated caves approximately 20m to 70m long at elevations of 400m to 500m. Because of their apparent structural, environmental and faunal similarities and their proximity to one another, they were considered collectively as the Kalk Bay caves.

The Table Mountain caves are structurally more complex than the Kalk Bay caves, having clearly recognizable twilight, entrance, dark, transitional and deep zones. Boundaries between cave zones tend to be dynamic, shifting with seasons and major climatic changes. In Bats' and Wynberg caves, zonal boundaries were delimited subjectively according to the criteria suggested by Howarth (1993):

- The twilight zone extends from the boundary of photosynthetic plants to total darkness.
- The entrance zone is the area of overlap between surface and underground environments and includes the twilight zone¹.
- The transitional zone receives no light but is still affected by fluctuating surface conditions.

¹Because of the small entrances and vertical nature of the sandstone caves, the twilight zone was considered to be a subdivided part of the entrance zone. The boundary between the two zones is variable and ill-defined and the twilight zone was considered to be that part of the entrance zone receiving sufficient illumination for photosynthesis in vascular plants. The remainder of the entrance zone received sufficient illumination for photosynthesis in bryophytes.

- The deep zone exhibits relatively stable environmental conditions, temperatures approximating mean annual surface temperatures and relative humidities approaching saturation.
- The dark zone incorporates both deep and transitional zones, both of which receive no light.

2.1.1. Wynberg cave

Wynberg cave is 300m long and reaches a maximum depth of 50m (Burman 1954). It consists of a series of horizontal galleries at varying depths with five small entrances opening along the vertical fault line (Figure 1).

As the cave is so extensive, only a section was examined. A transect was extended into the cave from the main entrance to the deep zone via transitional zone passages (Figure 1). Passage lengths in entrance, transitional and deep zones were approximately 25m, 40m and 90 m respectively. The entrance and transitional zones were separated by a boulder choke followed by a four-metre vertical drop. Similarly, the transitional and deep zones were separated by a 'corkscrew' and 10m drop.

The entrance zone of Wynberg cave incorporates a relatively small twilight zone (approximately 10m) which is exposed to precipitation and received infalls of plant debris. Temperatures in the entrance zone varied between 10.84°C and 13.33°C and relative humidities between 87.33% and 92.25%. The transitional zone consists of a relatively extensive set of horizontal passageways approximately one to five metres wide with rocky floors. They extend to considerable depths in parts and temperatures and relative humidities ranged from 10.64°C to 11.66°C and from 90.67% to 97.5% respectively. The deep zone consists of a sand- and gravel-covered passage running along the bottom of the cave (Figure 1). For the most part, surfaces remained wet, while in winter (July to September) heavy rains caused minor flooding in parts (the maximum water depth being approximately 15cm). Temperatures and relative humidities were not entirely constant, varying between 10.5°C and 10.74°C and between 98.12% and 98.8% respectively.

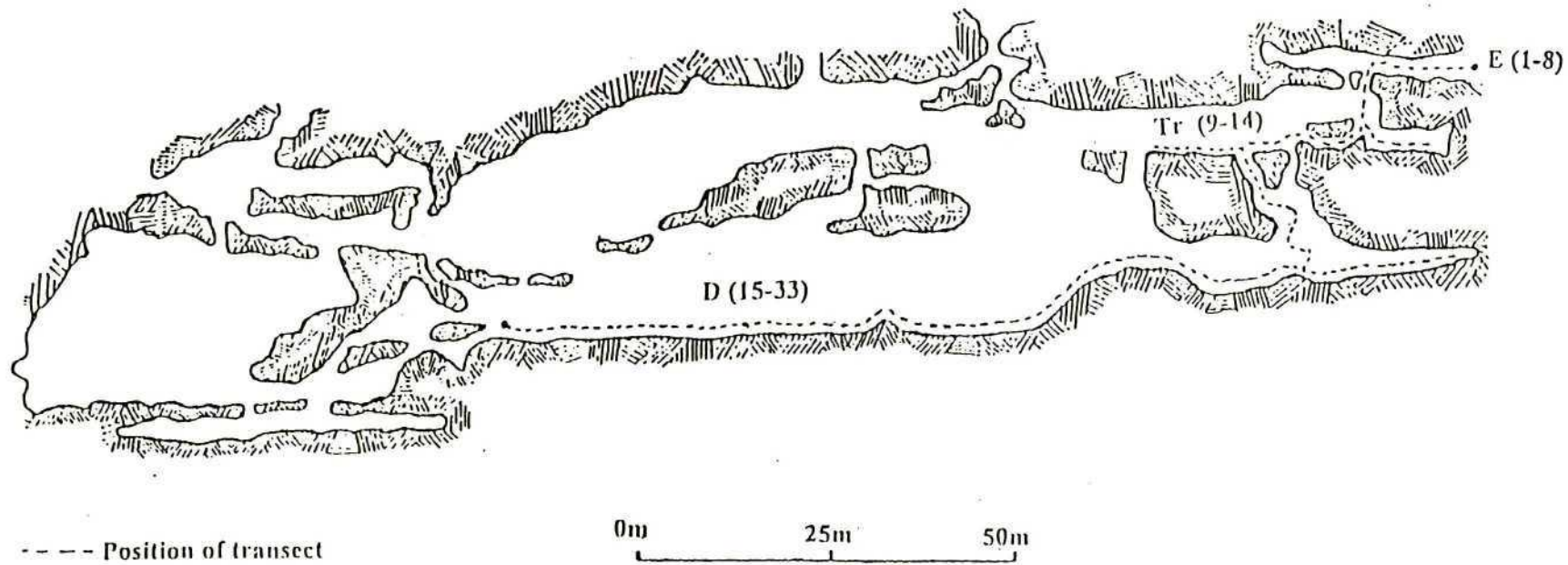


Figure 1. Sectional view of Wynberg cave showing position of the transect and delimitation of zones (from Burman 1954). Quadrat numbers are indicated in brackets. E = entrance zone, Tr = transitional zone and D = deep zone.

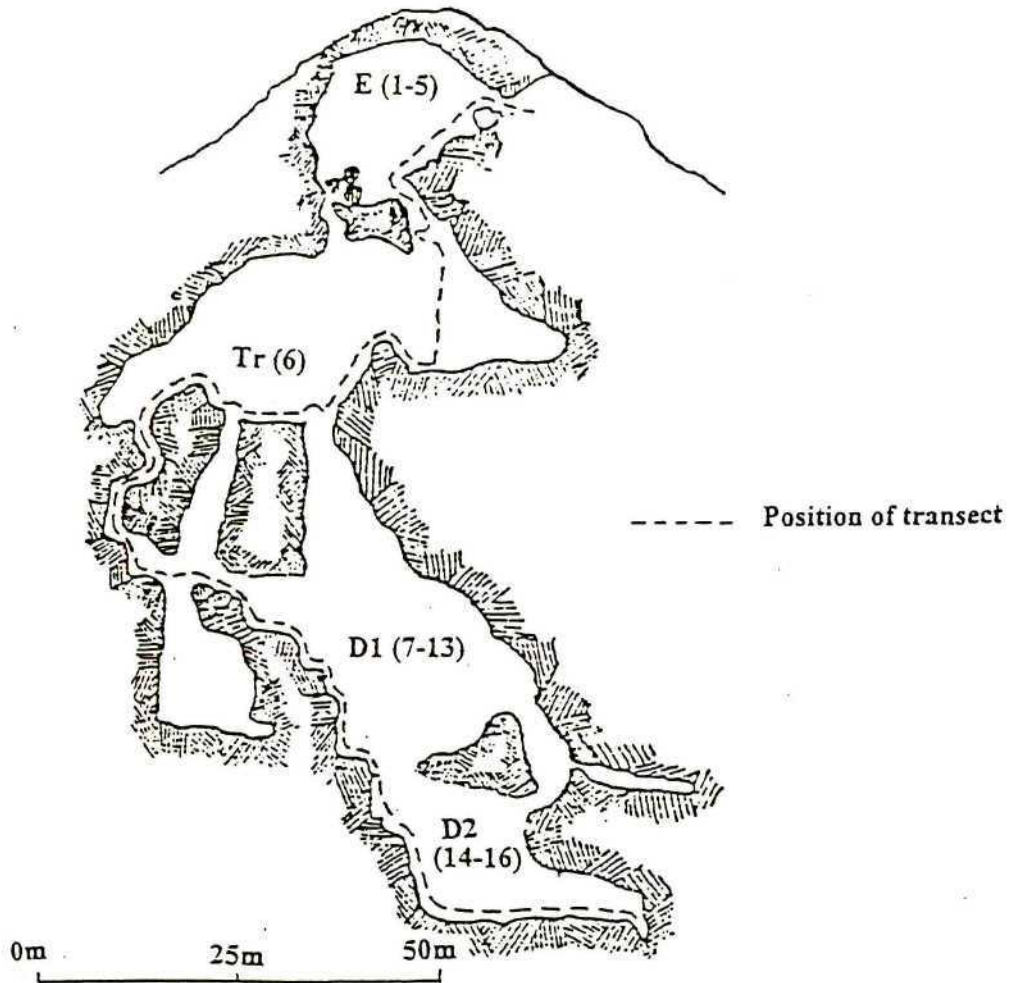


Figure 1. Sectional view of Bats' cave showing position of the transect and delimitation of zones (from Burman 1951). Quadrat numbers are indicated in brackets. E = entrance zone, Tr = transitional zone and D = deep zone.

Microchiropteran bat species recorded from Wynberg cave included *Miniopterus schreibersii natalensis* Kuhl 1819 (Meester *et al.* 1986) and *Rhinolophus capensis* Lichtenstein 1823 (Skinner and Smithers 1990). Both species are insectivorous and occurred singly, in pairs, or in small groups throughout the dark zone. They hibernated in deeper passages in winter. A small number of fruit bats (*Rousettus aegyptiacus leachii* Smith 1829) (Skinner and Smithers 1990) were occasionally encountered in entrance zones during summer.

2.1.2 Bats' cave

Bats' cave is a shorter, deeper cave, being approximately 60m in both length and width (Burman 1951) (Figure 2). It is a relatively open cave system with a large entrance chamber populated by a sizeable fruit bat colony (*Rousettus aegyptiacus leachii* Smith 1829). The entrance chamber is approximately 12m high and wide. It is well-lit with an extensive twilight zone and a small section that is directly exposed to sun and precipitation. Bat guano is abundant, but patchily distributed in mounds. Plant debris is also abundant and fluctuations in environmental conditions are relatively pronounced, temperatures varying between 10.48°C and 13.17°C and relative humidities between 82.33% and 94.88%.

Two small openings lead from the entrance into the underlying dark zone which consists of three chambers (Figure 2). A small chamber occurs directly below the first drop and was considered to represent the transitional zone. The second and third chambers were both considered to be deep zone chambers (D1 and D2 in Figure 2), but the exact boundary between transitional and deep zones was not clearly definable. Slight fluctuations in environmental conditions occurred, temperatures ranging between 9.98°C and 10.4°C and relative humidities between 97.76% and 98.25%. The second chamber (Figure 2) is relatively large with a steep, sandy slope about 35m long extending to a depth of approximately 40m. A 'corkscrew' leads to a small third chamber in the deepest part of the cave. Here the floor is sandy with rocky areas and a perennial pool is present. This was transformed into a slow-flowing stream during the winter rainy season (maximum water depth being approximately 30cm).

2.2. Species identifications

Specimens were collected, preserved in 70% ethanol and sent to the following institutions for identification: South African Museum (Cape Town), Natal Museum (Pietermaritzburg), Transvaal Museum (Pretoria), Nasionale Museum (Bloemfontein), Plant Protection Research Institute (Pretoria), California Academy of Sciences (San Francisco), Musée Royal de L’Afrique Centrale (Tervuren, Belgium). Past records, taxonomic literature (e.g. Attems 1928; Lawrence 1931, 1935, 1964, 1984; Dybas 1960; Grindley 1963; Cook 1991; Griswold 1987, 1990) and material housed in the South African Museum were also consulted. Voucher specimens will be housed in the South African Museum, Cape Town.

Identifications were taken as far as possible. Where identification to species level was not possible, the next highest identifiable taxon was used and morphospecies identified. Where confusion arose over nomenclature, the most recently-published scientifically correct name was used.

2.3. Data collection

2.3.1. Determination of species abundance

As troglobite abundances appeared to be particularly low, trapping was not considered an appropriate census technique. Pitfall trapping is notorious for causing population disturbances in caves (Vandel 1965; Peck 1975, 1976; Howarth 1981; Weinstein and Slaney 1995). Moreover, it would not be equally efficient for all species. Weinstein and Slaney (1995) further found pitfall traps (with or without bait) to be less effective than direct searching. Therefore, in the Table Mountain caves, extensive visual searching was conducted in demarkated quadrats. A sampling and replacement trapping method using wet leaf litter traps (Weinstein and Slaney 1995; Slaney and Weinstein 1996, 1997) does not impact unduly on cavernicole populations. Similarly, Yang *et al.* (1994) describe a peanut butter bait trap for the collection of gryllids. These methods should be considered in future research efforts and would be particularly useful for population studies of the raphidophorid, *Speleiacris tabulae*.

Searching was conducted in quadrats of two square metres each (subdivided into one square metre of floor and one square metre of the adjoining wall). These were marked at approximately five metre intervals along transects into each cave and were numbered sequentially from entrance to deep zone.

Thirty-three quadrats were placed in Wynberg cave and sixteen in Bats' cave. The zonal distributions of numbered quadrats are indicated in Figures 1 and 2. Visual counts were conducted in all quadrats once a month for twelve months between June 1995 and July 1996.

Quadrats varied in structural complexity (due to, for example, crevices, rocks and ledges) so that search times required per quadrat varied according to grade of complexity. To keep sampling efforts consistent from month to month, a search time was allocated to each quadrat according to its structural complexity. This varied from 10 to 25 minutes. Counting was terminated when the allocated search time had been achieved.

To convert abundance data into biomass data, adults and, where possible, immature specimens of each species were collected, oven-dried at 30°C and subsequently weighed. Because of the rarity of the fauna, only one or a few specimens were used. Exceptions were *Spermophora peninsulae* and *Speleiacris tabulae*, 10 specimens of each species and life cycle stage being used. The product of mean mass per species and number of individuals in each quadrat was obtained. From this the mean biomass per quadrat was calculated.

Visual censusing inevitably presents the problems of over-counting highly active species and under-counting inactive or inconspicuous species. Furthermore, many taxa were too small or too abundant to be counted accurately by visual censusing. These taxa were excluded from quantitative analyses of abundance data. Instead they were considered (together with the censused taxa) in analyses based on taxon presence or absence.

2.3.2. Environmental data

The following environmental data were collected from each quadrat directly after the completion of visual counts:

- Temperature and relative humidity: a clockwork hygrometer (yielding a 99% level of accuracy) was used to take readings at a distance of approximately 0.5m from any surface.
- Light: a photometric sensor sensitive to wavelengths of between 380nm and 770nm was used to measure illuminance.
- Wind: a windmeter sensitive to air currents of over 0.1 m/s was used.
- Soil water content: soil was collected in 50ml vials sealed with plumber's tape. Samples were weighed, dried in an oven at 100°C for 12 hours, and then reweighed. Percentage soil moisture was calculated on a dry weight basis.
i.e. soil water content = $(\text{wet weight} - \text{dry weight} / \text{dry weight}) * 100$.
- Soil organic content: once dried at 100°C for 12 hours, soil samples of known weight were placed in a muffle furnace at 500°C for one hour. Samples were cooled in a desiccator and reweighed. Soil organic content was calculated as percentage weight loss on ignition.
i.e. soil organic content = $(\text{pre-ignition weight} - \text{post-ignition weight} / \text{post-ignition weight}) * 100$.
- Soil energy content: soil samples were ground in a mortar and put through a 2mm wire mesh sieve. Samples of 0.5g were placed in a bomb calorimeter to obtain kJ/g values on combustion (Southwood 1995).
- Soil nitrogen content: the Kjeldahl procedure for measuring total nitrogen content was followed. This method involves the conversion of nitrogen to ammonium by digestion with concentrated sulphuric acid. The amount of nitrogen is determined by the amount of ammonia liberated by distillation of the digest with alkali. The procedure is described in Hesse (1971).

- Surface moisture: three circles of fast-absorbing hardened ashless filter paper, 7mm in diameter, were each placed on rock surfaces for ten seconds at a time. To achieve relatively representative and objective readings, the rock surface in each quadrat was divided into three, a measurement being taken from each third. The wet filter paper was placed in vials sealed with plumber's tape. Open vials of known weight were placed, with the filter paper, overnight in a 40°C oven and percentage weight loss was recorded. Percentage moisture content was calculated on a dry weight basis.
i.e. $\text{Surface moisture content} = (\text{wet weight} - \text{dry weight} / \text{dry weight}) * 100$.
- Crevice moisture: the same method was used as for the determination of surface moisture. However, circles of medium-fast qualitative filter paper 42.5cm in diameter, were used. These were each placed for 10 second intervals in three separate crevices per quadrat. Weighing, drying and calculations were the same as those described above for surface moisture determination.
- Guano, plant debris, moss, lichen and crevice availability were scored as follows: 1 = 1-20% quadrat cover; 2 = 21 - 40% cover; 3 = 41 - 60% cover; 4 = 61 - 80% cover; 5 = 81-100% cover. Crevices were defined as being cracks in the rock of between one and 20cm wide. This is equivalent to Howarth's (1993) 'mesocaverns' and the two terms are used interchangeably.

2.3.3. Biological and behavioural observations

Monthly abundances of the most abundant troglobitic species (*Lepthyphantes rimicola*², *Crozetulus scutatus*, *Speleosiro argasiformes* and *Speleomontia cavernicola*) and of the troglophile, *Speleiacris tabulae*, were obtained to determine whether populations fluctuated seasonally.

During visual counts, life cycle stages of counted individuals of *Speleiacris tabulae* and *Lepthyphantes rimicola* were noted. Since and number of instars of *Speleiacris tabulae* are not known and life cycle stages could not be determined in the field, approximate size classes

² Species authors and dates of description are given in Table 1.

were used as an index of age. Size classes were assigned subjectively by eye and were allocated as follows:

- *Speleiacris tabulae*:
 - i. Small nymphs of indeterminate sex and life cycle stage: 0-0.6cm long excluding appendages.
 - ii. Medium to large nymphs of determinate sex (i.e. subadults): 0.7-1.4cm.
 - iii. Adults of recognizable sex: >1.4cm.
- *Lephtyphantes rimicola*:
 - i. Immatures: < 2mm
 - ii. Adults: >2mm

As these size classes were subjectively assigned in the field, it is likely that a degree of overlap occurred, particularly between *Speleiacris* adults and large nymphs.

All feeding and reproductive behaviours were noted during the course of the study.

Reproductive behaviours included oviposition and mating, while feeding behaviours included handling of food items, a consistent association with particular food sources (such as guano, bat carcasses and plant debris) and contents of spider webs. Bat guano was incubated in the laboratory and the emergent species were considered to be trophically dependent on it. Feeding preferences were also observed in captive *Speleiacris tabulae* kept in a constant environment cell at 94% relative humidity and 10-12°C. Individuals were kept on filter paper in aquaria and fed a variety of food items (e.g. bat guano, oats, lettuce, apple, dead insects).

During visual counts, microhabitats occupied by counted individuals were noted. These included crevices, under rocks, between rocks or boulders, on exposed surfaces and under ledges. Observations were also made of nocturnal activity patterns both within the caves and outside cave entrances.

2.4. Data analysis

The computer software package, PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Warwick 1994), was used for quantitative analyses of communities based on data collected monthly for one year in 16 and 33 quadrats in Bats' and Wynberg caves respectively. Both abundance and taxon presence or absence data were used.

2.4.1. Determination of species diversity, richness and evenness

The program, DIVERSE, was used to generate the following indices:

- Species richness (S). S = total number of species
- The number of individuals (N).
- Margalef's richness index (d). $d = (S - 1)/\log N$
- Log series index (α). $\alpha = N(1-x)/x$.
 x = individual sampling factor: $S/N = (1-x)/x[-\ln(1-x)]$
- Shannon-Wiener diversity index (H'). $H' = \sum_i p_i (\log p_i)$.
 P_i = proportion of the total count arising from the i th series.
- Simpson's dominance index (λ). $\lambda = \sum(n_i(n_i-1)/N(N-1)$
 n_i = number of individuals in the i th series.
- Hill's second index (N_2). $N_2 = 1/\lambda$
- Pielou's evenness index (J'). $J' = H'/\log S$

These indices were calculated for both abundance data and presence or absence data from each cave. In addition, data collected from entrance quadrats and dark zone quadrats were analysed separately. Therefore, diversity and abundance patterns could be compared between caves and between zones. T-tests and Wilcoxon's signed rank tests were used to test for statistically significant differences.

2.4.2. Determination of spatial distribution patterns

2.4.2.1. Hierarchical clustering

The PRIMER program, CLUSTER (Clarke and Warwick 1994), was used to achieve hierarchical clustering of quadrats according to the faunal similarities between them. Similarities were represented in a similarity matrix derived from Bray-Curtis similarity coefficients (Bray and Curtis 1957). Group average linking was used and abundance data was fourth-root transformed. Both abundance data and taxon presence or absence data were used. Results were represented in dendrograms showing Bray-Curtis similarities between quadrats.

Hierarchical clustering was also performed on the 19 most abundant censused taxa according to the quadrats they occupied. Fourth-root transformed abundance data was used to

normalise the data and results were represented in dendrograms showing Bray-Curtis similarities between taxa.

2.4.2.2. Ordination

The PRIMER program, MDS, was used to generate two-dimensional nonmetric multidimensional scaling (MDS) ordinations of quadrats in each cave (Kruskal 1964; Ludwig and Reynolds 1988; Clarke and Warwick 1994). Ordinations were based on Bray-Curtis similarities of fourth-root transformed abundance data and of taxon presence or absence data. Quadrats with similar biota were grouped together, thus providing a visual representation of community patterns.

2.4.2.3. Tests for significant differences between groups

The PRIMER program, ANOSIM (Analysis of similarities), was used to establish significant differences between quadrat groups. This test is a non-parametric permutation procedure applied to the similarity matrix underlying the community ordination, as described by Clarke and Green (1988) and Clarke and Warwick (1994). One-way analysis of similarities (Anosim) was performed on similarity matrices derived from abundance data and taxon presence or absence data in both caves. Probabilities of less than 0.5 were considered to yield significant differences.

2.4.3. Determination of the effect of the environment on community patterns

The PRIMER program, BIO-ENV (Clarke and Warwick 1994), was used to obtain weighted Spearman's rank correlation coefficients matching ranked similarity matrices of biotic data, with ranked dissimilarity matrices of environmental data. Similarity matrices were based on Bray-Curtis similarity coefficients, while dissimilarity matrices were based on Euclidean distances, obtained using the CLUSTER program. Environmental variables were log transformed. To determine whether variables were intercorrelated, separate correlation analyses considering environmental variables alone, were conducted.

The BIO-ENV procedure involves considering combinations of environmental variables in increasing levels of complexity to find the highest correlation with biotic patterns (Clarke and

Warwick 1994). The weighted Spearman's rank correlation coefficient is obtained as follows (Clarke and Ainsworth 1993):

$$\rho_w = 1 - \{6/N(N-1)\} \sum \{(r_i - s_i)^2 / r_i + s_i\}$$

$N = n(n-1)/2$ where n is the number of samples; r_i = rank similarity coefficient of the i th series of the biota matrix; s_i = rank dissimilarity coefficient of the i th series of the environmental variable matrix.

This coefficient should not be compared with standard statistical tables of Spearman's rank correlation because the ranks are not mutually independent variables (Clarke and Warwick 1994).

Environmental factors yielding strong correlations with biotic patterns were graphically represented in an MDS ordination plot. Abiotic ordinations that best matched the biotic ordination were considered to represent the variables that best explained community patterns.

The degree to which single environmental variables explained community patterns was visually represented by superimposing environmental variables (log transformed) on MDS ordinations of biota (Clarke and Warwick 1994). Environmental variables were represented as symbols of varying sizes, scaled according to magnitude. In this way, relationships of environmental variables with ordination gradients could be observed and judged as being consistent with community patterns or not.

This procedure was conducted for Bats' and Wynberg caves (considering both abundance and presence or absence data), for entrance and deep zone communities and for a number of cave-adapted species. The latter included the troglobites, *Lepthyphantes rimicola*, *Crozetulus scutatus*, *Speleosiro argasiformes*, *Speleomontia cavernicola*, *Hahnia* sp.nov., *Trichoniscus tabulae*, as well as the troglophile, *Speleiacris tabulae*. Regression analyses were conducted between these species and environmental variables, thus determining specific responses to environmental conditions.

3. Faunal composition of the Cape Peninsula caves

Previous research on the Cape Peninsula caves has emphasised the collection and identification of cave-adapted species (Lawrence 1932, 1964; Grindley 1956, 1961, 1963, 1975, 1976). This approach had certain limitations:

- The entrance and twilight zones were under-represented as collectors concentrated mainly on the dark zones.
- Collecting methods were generally restricted to visual searching, thus emphasising the larger, active and therefore conspicuous species.
- Several caves were under-represented because of their relative inaccessibility or recent discovery.

Although previous studies contributed greatly to the knowledge of the major cavernicolous taxonomic groups and their geographical distributions, the inventory was incomplete. The aim of this study was to overcome previous bias in collecting effort by consistent sampling throughout the caves. Collections and identifications were as extensive and complete as possible, embracing entrance and dark zone fauna equally. This has resulted in the discovery of new species that are possible Cape Peninsula endemics.

The updated list of Cape Peninsula cave invertebrates is given in Table 1. All known literature and museum records were incorporated (e.g. Grindley 1956, 1957, 1961, 1975, 1976, unpublished notes). Identifications were taken as far as possible, although taxonomic limitations often made identification to species impossible. This was usually due to a lack of taxonomic expertise or knowledge of a taxon (e.g. Platyhelminthes, Oniscidae and Staphylinidae). Furthermore, many taxa could only be identified by a particular gender or life cycle stage (e.g. mature males are needed to identify diplopods, while mature females are often needed to identify Araneae). Where uncertainty arose, species were grouped together in the next highest taxon and identified to morphospecies. Undescribed species have been indicated as such.

Also shown in Table 1 are geographical and zonal distributions as well as a tentative ecological classification based on troglomorphy, biotope and zonal distribution for each species. This classification is by no means definitive but is useful as a starting point for the study of the cave fauna. Modifications to this classification will occur as additional research facilitates a more detailed understanding of ecology, taxonomy, physiology and behaviour. For the most part, a subjective decision was made, particularly in cases where the epigeal distribution was not known (e.g. new species) or the species seemed to have a potential (but not proven) ability to survive above ground.

Figures 3, 4 and 5 show the representation of species (by their ranked abundances) in entrance, transitional and deep zones. Ranking is useful when population levels are low and when absolute abundance relative to sampling method has little meaning. The delimitation of zones was subjective but nevertheless serves as a guideline for ecological classification in terms of zonal distributions.

3.1. The fauna

Eighty-five species were recorded from the Cape Peninsula caves. Only three previously-recorded species, *Protojanira leleupi* (Isopoda), *Caphrotyphlus strinatii* (Staphylinidae) and *Anisocampa leleupi* (Diplura), were not found during the course of this study. Five phyla were represented. The Arthropoda accounted for 94% of the species. Of these, 32 species were Hexapoda (38%) and 29 were Chelicerata (34%). Most chelicerates belonged to the Araneae (15 species) and the Opiliones (nine species). The Myriapoda and Crustacea were also well-represented with nine and ten species respectively.

Six species new to science were collected. These included two species of Opiliones (L. Lotz pers. comm.) and one species each of Chilopoda (L. Lotz pers. comm.), Collembola (K. Christiansen pers. comm.), Dermaptera (R. Stals pers. Comm.) and Hahniidae (C. Griswold pers. comm.). The species of Machilidae was previously collected but is not yet described (J. Irish pers. comm.) and 15 species were indeterminable beyond family.

Forty-four species were found in both the Kalk Bay and Table Mountain caves. Table Mountain is, however, greatly over-represented in this study due to greater collecting effort.

Apparent distributional differences may, therefore, not be real. Nevertheless, species unique to each pseudokarst area do exist. *Paramelita barnardi* (Thurston 1973; Griffiths 1981; Cook 1991; Stewart and Griffiths 1995) and *Protojanira leleupi* (Grindley 1963) appear to be restricted to the Kalk Bay caves, while *Peripatopsis alba* (Lawrence 1932; Brinck 1956) and *Spelaeogriphus lepidops* (Gordon 1957) are Table Mountain endemics.

Twenty-one species (approximately 24.8% of the total number recorded) are apparently endemic to the Cape Peninsula (Picker and Samways 1996). These include the new and undescribed species whose distributions are poorly known (i.e. *Hahnia* sp. nov., *Schaefferia* sp. nov., *Dermaptera* sp. nov. and *Machiloides* sp.). On the other hand, *Loxosceles valida* has in the past erroneously been considered to be a Cape Peninsula endemic (N. Larsen pers. comm.). All 13 troglobitic species are Cape Peninsula endemics. Collectively they represent 12% of the total endemic invertebrate fauna of the Peninsula (Picker and Samways 1996). Five epigean endemic species (Picker and Samways 1996) were also collected in the caves.

The majority of cavernicoles were classified as trogliphiles (30% of the species). True troglobitism was, in fact, found to be relatively rare (14% of the species). Troglonexes accounted for 23% of the species and the remaining 33% were classified separately as humicoles, guanophiles and endogeans.

The cavernicolous fauna is discussed below with reference to Table 1.

3.1.1. Mollusca

Trachycystis charybdis is a widespread forest species not restricted to caves (J. Grindley, unpublished notes). It occurred mainly in the entrance zone of Bats' cave (Figure 3) and was also observed in entrance zones of Kalk Bay caves. Both adults and immatures were present, indicating an apparent ability to breed in cave entrances. However, they are not troglomorphic and are clearly opportunistic epigean species utilising the accumulation of decaying plant matter in cave entrances.

Table 1. Invertebrate fauna of the caves of the Cape Peninsula showing geographical distributions (T=Table Mountain caves; K=Kalk Bay Mountain caves), endemism to the Cape Peninsula (E=endemic), tentative eco-evolutionary categories and zonal distributions (Ent=entrance zone, Tr=transitional zone; D=deep zone). (P=Phylum; subP=Subphylum). Erroneous names, unpublished correct names, new species and species not found during the present study are footnoted.

Taxon	Species	Geographical Distribution	Ecological Classification	Zonational Distribution		
				Ent	Tr	D
P: MOLLUSCA (van Bruggen 1970)						
Endodontidae	<i>Trachycystis charybdis</i> Benson 1851	T K	Humicole / Troglophile	X	X	
P: PLATYHELMINTHES						
CLASS TURBELLARIA						
Order Polycladida			Phreatobite / Accidental / Endogean			X
Planariidae	<i>Planaria</i> sp	T K				
Order Tricladida			Phreatobite / Accidental / Endogean			X
Dendrocoelidae	<i>Dendrocoelum</i> sp.					
P: ANNELIDA						
CLASS OLIGOCHAETA (Pickford 1937)						
Lumbricidae	<i>Bimastus parvus</i> Eis 1956	T K	Endogean	X	X	X
Megascolecidae	<i>Microchaetus benhami</i> Michaelsen 1913	T K	Endogean	X	X	X
	<i>Acanthodrilus (Eodrilus)</i> Peringuey Michaelsen 1913	T	Endogean	X	X	X
P: ONYCHOPHORA (Brinck 1956)						
Peripatopsidae	<i>Peripatopsis alba</i> Lawrence 1932	T (E)	Troglobite			X
P: ARTHROPODA						
SubP: CRUSTACEA						
Order Amphipoda (Cook 1991)						
Talitridae	<i>Talitriator setosa</i> Barnard 1940	T K	Endogean / Humicole	X	X	
	<i>Talitriator cylindriceps</i> Barnard 1940	T	Endogean / Humicole	X		
	<i>Talitriator macronyx</i> Barnard 1940	T	Endogean / Humicole	X	X	

Table 1 continued.

Taxon	Species	Geographical Distribution	Ecological Classification	Zonational Distribution			
				Ent	Tr	D	
	Paramelitidae*	<i>Paramelita barnardi</i> Thurston 1973	K (E)	Stygobite			X
Order Spelaeogriphacea		<i>Paramelita capensis</i> † (Barnard 1916)	T	Stygophile			X
		<i>Spelaeogriphus lepidops</i> Gordon 1957	T (E)	Stygobite			X
Order Isopoda (Barnard 1932)							
Suborder Oniscoidea							
	Trichoniscidae	<i>Trichoniscus tabulae</i> Barnard 1932	T K (E)	Troglobite		X	X
Suborder Asellota	Oniscidae	(2 spp. indet.)	T K	Endogean / Humicole	X	X	
	Protojaniridae	<i>Protojanira leleupi</i> Grindley 1963‡	K (E)	Stygobite			X
SubP: CHELICERATA							
CLASS ARACHNIDA							
Order Acarina		(1 sp. indet.)	T K		X	X	X
Order Pseudoscorpionidae							
	Cthoniidae	<i>Cthoniella cavernicola</i> Lawrence 1935	T K	Troglobite			X
Order Araneae (Lawrence 1964; Brignoli 1981)							
	Tetragnathidae	<i>Pachygnatha</i> sp.	T K	Troglophile / trogloxene	X	X	
	Phyxelididae	<i>Malaika longipes</i> § (Purcell 1904)	T K (E)	Troglophile	X	X	X
	Segestriida	<i>Ariadna</i> sp.	T	Occasional trogloxene	X		
	Agelenidae	(1 sp. indet.)	T	Occasional trogloxene	X		

* Formerly Gammaridae.

† Formerly *Gammarus capensis* (Barnard 1916; Griffiths 1981).

‡ Not found during this study.

§ Synonymous with *Haemilla grindleyi* Lawrence 1964 (A. Dippenaar pers. comm.). Formerly *Auximus longipes* (Amaurobiidae) (C. Griswold 1990, 1997).

Table 1 continued.

Taxon	Species	Geographical Distribution	Ecological Classification	Zonational Distribution		
				Ent	Tr	D
Cyatholipidae	<i>Isicabu capensis</i> Griswold 1987	T	Occasional troglaxene	X	X	
Hahniidae	<i>Hahnia lobata</i> Bosmans 1981	T K	Troglophile	X	X	
	<i>Hahnia</i> sp. nov.*	T (E)?	Troglobite			X
	<i>Lepthyphantes rimicola</i> † Lawrence 1964	T K	Troglobite	X	X	X
Linyphiidae	1 sp.	T	Troglaxene	X		
Pholcidae	<i>Spermophora peninsulae</i> Lawrence 1964	T K (E)	Troglophile	X	X	X
Theridiidae	<i>Steatoda</i> sp.‡		Troglaxene	X		
Anapidae	<i>Crozetulus scutatus</i> § (Lawrence 1964)	T K (E)	Troglobite	X	X	X
Loxoscelidae	<i>Loxosceles valida</i> ** Lawrence 1964	T K (E)?††	Troglophile	X	X	X
Miturgidae	<i>Machadonia</i> sp.	T	Troglaxene	X		
Order Opiliones (Lawrence 1934)						
Suborder Palpatores						
Neopilionidae	<i>Vibone vetusta</i> Kauri 1951	T K	Troglophile	X	X	X
Suborder Cyphophthalmi						
Pettalidae	<i>Speleosiro argasiformes</i> Lawrence 1931	T K (E)	Troglobite	X	X	X
Suborder Laniatores						
Acropsopilionidae	<i>Rhampsinitus</i> sp. nov.‡‡	T K (E)?	Troglaxene	X		
Adaeidae	<i>Cryptadaeum capense</i> Lawrence 1931	T K	Troglaxene	X		
Triaenonychidae	<i>Adaeum</i> sp. nov.§§	T K (E)?	Troglophile / Troglaxene	X		
	<i>Speleomontia cavernicola</i> Lawrence 1931	T K (E)	Troglobite	X	X	X
	<i>Paramontia liposoma</i> Lawrence 1931		Troglaxene	X		
	<i>Rostromontia granulifer</i> Lawrence 1931	T K (E)	Troglaxene	X		

* Probably a new species (C. Griswold pers. comm.).

† Incorrectly assigned to this genus. A new genus may need to be created (R. Jocque pers. comm.).

‡ Probably *S. capensis* (N. Larsen pers. comm.).§ Formerly *Speleodermes scutatus* (Lawrence 1964; Brignoli 1981).

** Likely to be a drymusid (A. Dippenaar pers. comm.).

†† May not be restricted to the Peninsula (N. Larsen pers. comm.).

‡‡ Probably a new species (L. Lotz pers. comm.).

§§ Probably a new species (L. Lotz pers. comm.).

Table 1 continued.

Taxon	Species	Geographical Distribution	Ecological Classification	Zonational Distribution		
				Ent	Tr	D
	<i>Rostrumontia capensis</i> Lawrence 1931	T K (E)	Trogloxene	X		
SubP: MYRIAPODA						
CLASS CHILOPODA						
(Attems 1928; Lawrence 1955)						
Order Lithobiomorpha						
	Henicopidae	<i>Paralamyctes spenceri</i> Pocock 1901	T K	Troglophile	X	X X
Order Scolopendromorpha						
	Cryptopidae	<i>Cryptops stupendus</i> Attems 1928	T K (E)	Troglophile / Troglobite		X?
Order Geophilomorpha						
	Lithobiidae	<i>Walesobius excrescens</i> Attems 1928	T	Humicole / Litericole	X	
	Schendylidae	1 sp.nov.*	T	Humicole / Litericole	X	X
CLASS SYMPHYLA (Attems 1926)						
	<i>Hanseniella capensis</i> (Hansen 1903) [†]	T	Endogean / Humicole	X	X	
CLASS DIPLOPODA (Silvestri 1910; Lawrence 1984)						
Order Polydesmida						
	Dalodesmidae	<i>Harpethrix caeca</i> Lawrence 1962 (1 sp. indet.)	T K (E) T K	Troglophile Humicole	X X	X X
	Spirostreptidae	(1 sp. indet.)	T K	Accidental	X	
Order Sphaerotherida						
	Sphaerotheriidae	<i>Sphaerotherium weberi</i> Silvestri 1910	K	Accidental / Humicole	X	
SubP: HEXAPODA						
Order Diplura						
	Campodeidae	(1 sp. indet.) <i>Anisocampa leleupi</i> Conde 1962 [‡]	T T	? Troglobite		X X

*Probably a new species (L. Lotz pers. comm.).

† Formerly *Scutigrella capensis* (Hansen 1903; Bagnall 1913).

‡ Not found during this study.

Table 1 continued.

Taxon	Species	Geographical Distribution	Ecological Classification	Zonational Distribution		
				Ent	Tr	D
Order Collembola	<i>Schaefferia (Typhlogastrura) sp.nov.*</i>	T (E)?	Troglophile / Guanophile	X	X	
Hypogastruridae						
Entomobryidae						
Entomobryinae	<i>Entomobrya sp.</i>	T K	Trogloxene / Humicole			X
Isotomidae	<i>Isotoma botubilis</i> group: <i>Isotoma sp. / Isotomurus sp.</i>	T	Accidental / Humicole	X		
Order Thysanura (Wygodzinsky 1955)						
Machilidae	<i>Machiloides sp. †</i>	T K (E)?	Troglophile / Troglloxene	X		
CLASS INSECTA						
Order Orthoptera						
Rhopidophoridae (Hesse 1929)	<i>Speleiacris tabulae</i> Peringuey 1916	T K (E)	Troglophile	X	X	X
Order Dermaptera	(1 sp.indet.)	T K	Toglobite / Troglloxene?	X	X	X
	1 sp. nov.	T (E)?	Troglobite			X
Order Blattodea (Princis 1963)	(1 sp. indet.)	T	Accidental	X		
Order Diptera						
Tipulidae (Wood 1952)	<i>Conosia sp.</i>	T K	Troglophile / Guanophile	X	X	X
Psychodidae (Satchell 1956)	<i>Psychoda spatulipennis</i> Satchell 1951	T K	Troglophile / Guanophile	X	X	X
Sciaridae	(1 sp. indet.)	T	Guanophile	X		
Heleomyzidae (Cogan 1971)	(1 sp. indet.)	T K	Trogloxene	X	X	X
Phoridae (Beyer 1965)	<i>Megaselia sp.</i>	T	Trogloxene / Guanophile	X	X	X
Fanniidae (van Ermden 1951)	<i>Fannia canicularis</i> Linnaeus 1761	T	Trogloxene			
Muscidae (van Ermden 1951)	<i>Morellia sp.</i>	T K	Trogloxene / Guanophile	X	X	X
Calliphoridae	<i>Calliphora croceipalpis</i> Jaenicke 1867	T	Troglophile? / Zoophage	X	X	X
Sarcophagidae	<i>Sarcophaga cruentata</i> Meigen 1826	T	Trogloxene	X	X	X

* Probably a new species (K. Christiansen pers.comm.).

† Undescribed species (J. Irish pers.comm.).

Table 1 continued.

Taxon	Species	Geographical Distribution	Ecological Classification	Zonational Distribution		
				Ent	Tr	D
Order Coleoptera						
Carabidae	<i>Plocamotrechus longulus</i> Jeannel 1926	T K	Troglophile / Guanophile	X	X	X
	<i>Scarites (Pachydontus) languidus</i> Wiedemann 1846	T	Trogloxene	X	X	X
Staphylinidae (Scheerpeltz 1973)						
Alaeocharinae	(1 sp. indet.)	T	Troglophile / Guanophile	X	X	X
Tachyporinae	(1 sp. indet.)	T	Troglophile / Guanophile	X	X	X
Leptotyphlinae	<i>Caphrotyphlus</i> sp. *	T	Troglophile / Guanophile			
Anthribidae (Frieser 1981, 1983)	<i>Phaenotheridium</i> sp.	T	Trogloxene	X		
Trogidae	<i>Trox nasutus</i> / <i>T. capensis</i> Scholtz 1980	T	Accidental			X
Cerambycidae						
Cerambycinae	(1 sp. indet.)	T	Accidental	X		
Curculionidae	(1 sp. indet.)	T	Accidental	X		
Ptiliidae	<i>Malkinella cavatica</i> Dybas 1960	T K	Troglophile / Guanophile	X	X	X
Order Lepidoptera						
	Pyalidae					
	<i>Aglossa incultalis</i> Zeller 1847	T K	Trogloxene	X		
	<i>A. cuprealis</i> Hubner 1934	T K	Trogloxene	X		
	Tineidae					
	<i>Monopis speculella</i> group:					
	<i>M. tanseans</i> Gozmany 1852	T K	Trogloxene	X		
	<i>Episcardia</i> sp. / <i>Proterospastis</i> sp.	T	Trogloxene	X		
	Lasiocampidae					
	<i>Mesoscelis</i> sp.†	K	Accidental	X		

* Not found during this study.

† Undescribed species (M. Krüger pers.comm.).

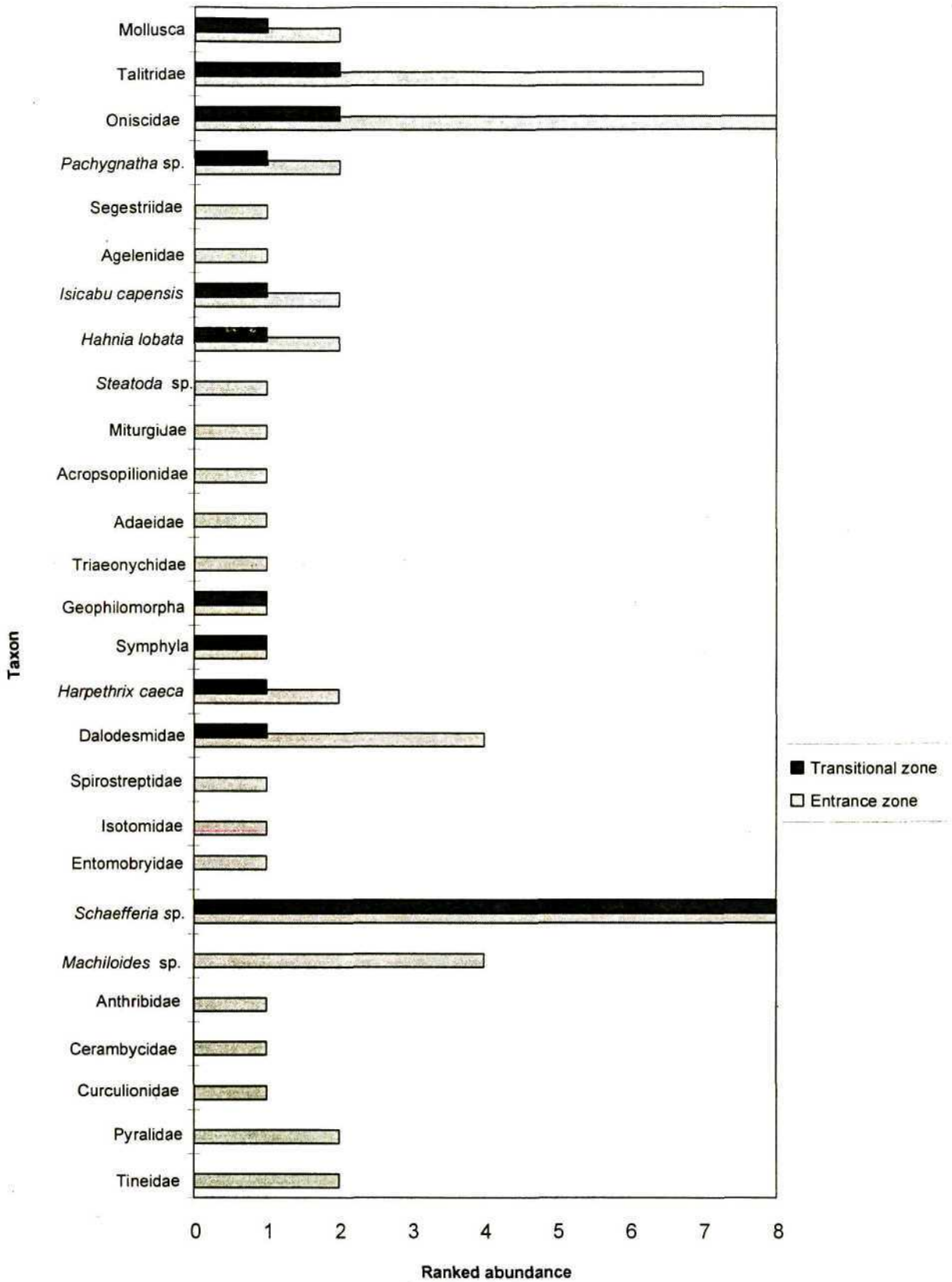


Figure 3. Ranked abundances of taxa present in entrance and transitional zones but absent from deep zones within the Table Mountain caves (1 = 1-10; 2 = 6-10; 3 = 11-15; 4 = 16-20; 5 = 21-25; 6 = 26-30; 7 = 31-35; 8 > 35 individuals).

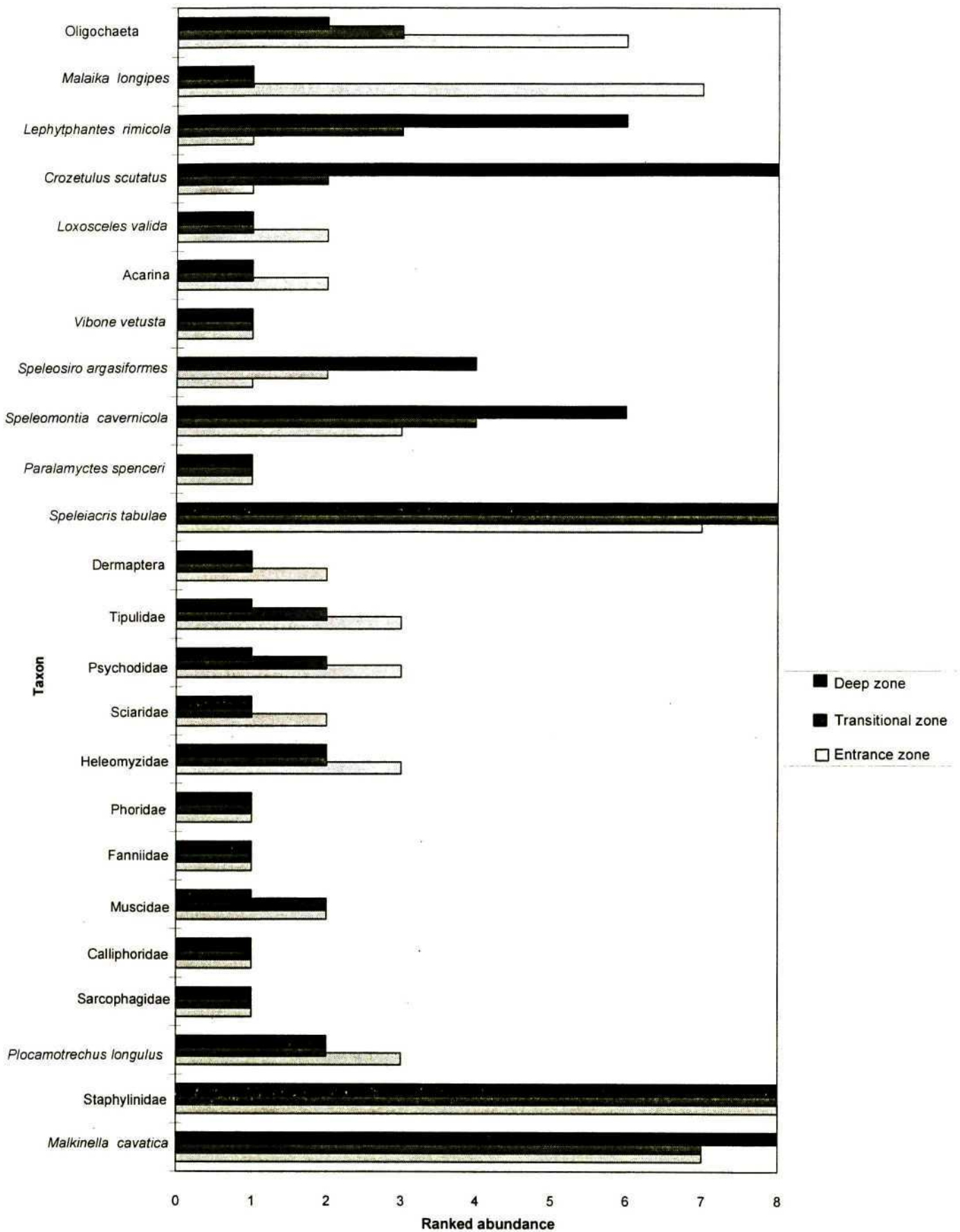


Figure 4. Ranked abundances showing zonal distribution of taxa occurring in all three zones of the Table Mountain caves (1 = 1-5; 2 = 6-10; 3 = 11-15; 4 = 16-20; 5 = 21-25; 6 = 26-30; 7 = 31-35; 8 > 35 individuals).

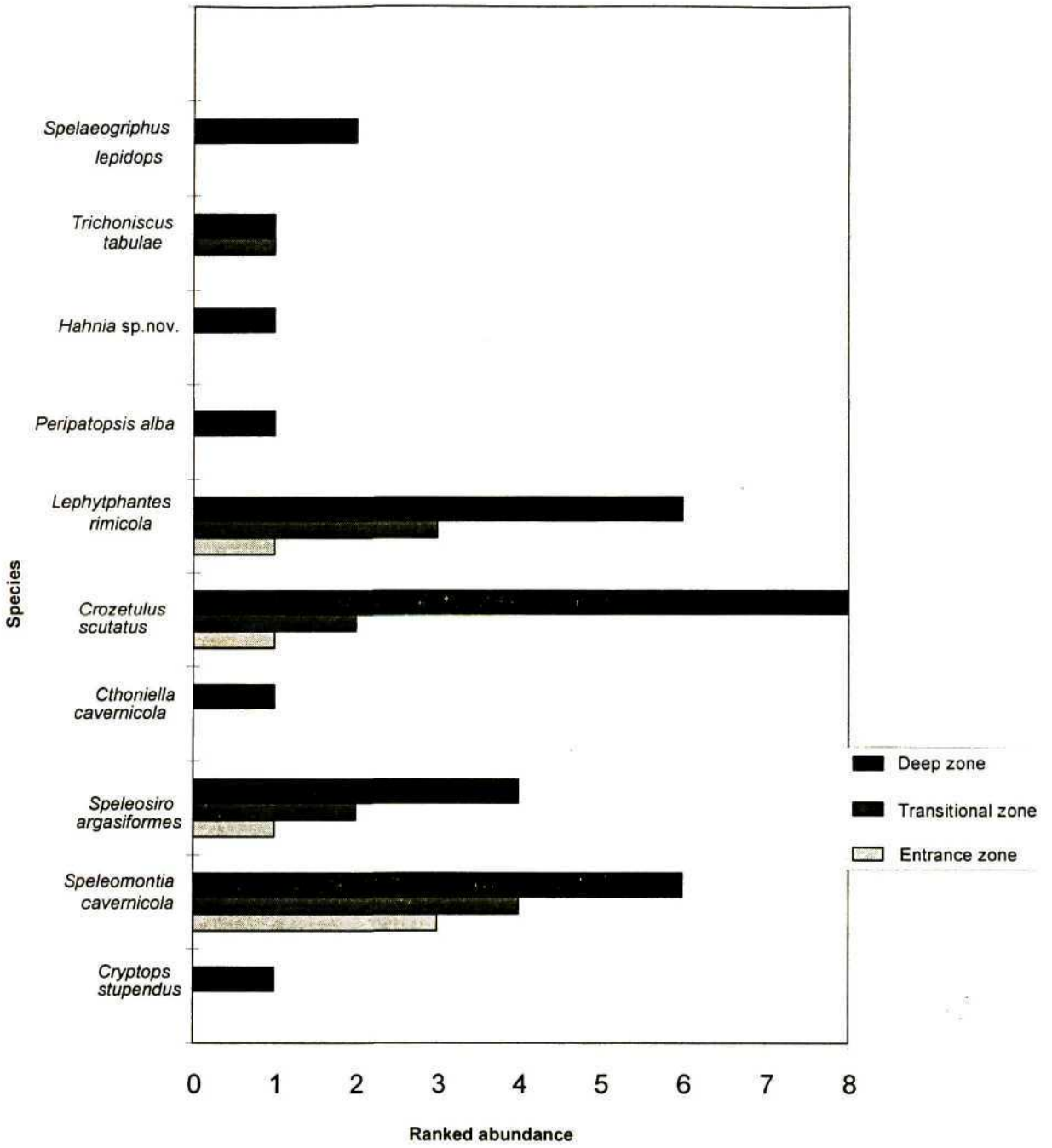


Figure 5. Ranked abundances of troglobitic species showing their zonal distributions in the Table Mountain caves (1 = 1-5; 2 = 6-10; 3 = 11-15; 4 = 16-20; 5 = 21-25; 6 = 26-30; 7 = 31-35; 8 > 35 individuals).

3.1.2. Platyhelminthes

Turbellarian flatworms were collected from winter-flowing streams in Bats' and Wynberg caves as well as from a pool in Oread Halls, a Kalk Bay cave. Dissection is normally required for identification of tricladids (Gourbault 1994) so species identification is tentative (J. Grindley, unpublished notes). Nevertheless, both species are unpigmented and negatively phototactic. Such adaptations, however, are common in interstitial fauna (or phreatobites) (Motas and Tanasachi 1946) as well as in true cave fauna. It is therefore impossible to assign them to a clear ecological category but it is likely that they are surface species washed into the caves during periods of flooding.

3.1.3. Oligochaeta

Three species were collected. They are all cosmopolitan species which also occur in surface soil layers (J. Grindley, unpublished notes). They were most abundant in entrance zones, although both adult and immature stages were collected throughout the caves (Figure 4). They showed a marked seasonal abundance, being most common in summer as streams subsided. This suggests that they were washed in with the stream water. In fact, it is not unusual for oligochaetes to passively find their way into caves where they establish permanent populations in the organically rich sediment. For example, species of *Bimastus* are often considered troglophilic (Dumnicka and Juberthie 1994). They are, however, no more than troglophiles or troglonexes exploiting an available food resource. Vandel (1965) considered cavernicolous oligochaetes to be endogeans and not part of the true cave fauna. Nevertheless, their dependence on organic material and humus for feeding and reproduction make them an important link in the food chain, as they, in turn, provide a reliable food source for cavernicolous predators (Dumnicka and Juberthie 1994).

3.1.4. Onychophora

Peripatopsis alba is a troglobitic species occurring only in the deeper caves of Table Mountain (Figure 5). It is very rare and only four individuals (three in Wynberg cave and one in Bats' cave) were seen during the study period. All occurred in the deep zone under stones or on damp walls (Newlands and Ruhberg 1978). Troglomorphy is marked and includes complete depigmentation, anophthalmy and attenuation of appendages (Lawrence 1932; Brinck 1956; Grindley 1957, 1961). Previous attempts to maintain *P. alba* outside the cave

have failed (Brinck 1956; Grindley 1957, 1961). Troglotism is rare in Onychophora, the only other species being *Spelaeoperipatus spelaeus* in Jamaica (Peck 1975, 1994) and a possible third species in North Queensland, Australia (Howarth 1988). Two troglaphiles and two troglaxenes occur in New Zealand and Tasmania (Ruhberg 1994; Clarke 1997).

Peripatopsis alba is considered to be a Gondwanan relict that 'took refuge' in the relatively damp and cool climate of the Western Cape during the period of climatic change associated with the breakup of Gondwanaland (Brinck 1956; Lawrence 1962a). Cave-adaptation apparently occurred subsequent to isolation in caves, as its closest epigeal relative,

Peripatopsis moseleyi (also a Gondwanan relict) is pigmented and ophthalmic. It is clear that *P. alba* has a very restricted range and specialised habitat requirements, so that even slight fluctuations in environmental conditions could have disastrous consequences for the population.

3.1.5. Crustacea

The crustacean fauna includes both aquatic groups (Paramelitidae, Spelaeogriphaceae and Protojaniridae) and terrestrial groups (Talitridae, Oniscidae and Trichoniscidae).

Of the aquatic species *Spelaeogriphus lepidops*, *Protojanira leleupi* and *Paramelita barnardi* are troglotites or, more accurately, stygotites, as they frequent only hypogean groundwaters (Holsinger 1994). Stygotites are thought to have become restricted to caves when streams were diverted or restricted during periods of surface drought, and subsequently evolving troglomorphic adaptations (Barr and Holsinger 1985). In Cape Peninsula caves this would have coincided with the breakup of Gondwanaland. All Cape Peninsula stygotites are therefore Gondwanan relicts that have apparently been isolated in the caves for a long time, being completely anophthalmic and depigmented (Grindley and Hessler 1971; Grindley 1975, 1976; Coineau *et al.* 1994). The only other extant spelaeogriphacean species, *Pottiicoara brasiliensis* Pirès 1987, occurs in Brazil (Pirès 1987; Brusca and Brusca 1990), while the only other *Protojanira* species occur in South America and Sri Lanka (Sket 1982; Grosso 1992; Coineau *et al.* 1994), thus showing a typical Gondwanan distribution. Similarly, the only other troglotic paramelitids (of which there are eight genera) occur in Australia (Williams 1986). *Spelaeogriphus lepidops* is known from only three caves on Table Mountain (C. Parkins pers. comm.), while *Paramelita barnardi* and *Protojanira leleupi* are

restricted to the Kalk Bay caves. It would appear that *Protojanira leleupi* is very rare, but this study did not include intensive collecting in the Kalk Bay caves and the population would therefore require monitoring. Observed numbers of *Spelaeogriphus lepidops* in Bats' cave varied between five and 40 individuals during the course of the study.

The other aquatic species collected from the caves was *Paramelita capensis*. This is a widespread epigean species but is negatively phototactic and has an unpigmented body and eyes (Barnard 1916; Griffiths 1981; Cook 1991; Stewart and Griffiths 1995). It could therefore be regarded as a stygophile. Although a Gondwanan relict, it is clear that the species did not become isolated in caves and subsequently evolve troglomorphic adaptations.

One troglobitic terrestrial crustacean species, *Trichoniscus tabulae* (Isopoda, Trichoniscidae) was found only in the deep and transitional zones where it occurred almost exclusively in wet, narrow crevices (Figure 5). It is depigmented, has reduced eyes and is relatively large in size (Barnard 1932, 1961). It is also fairly rare, and appears to have arisen from an endogean ancestor 'pre-adapted' to cavernicolous life (Vandel 1965). Most troglobitic terrestrial isopods (53 genera) belong to the Trichoniscidae (Argano 1994).

Although 70% of terrestrial oniscoids are cavernicolous, true troglobitism is rare (Peck 1989). In fact, all the terrestrial oniscoid species of the Cape Peninsula caves occurred in entrance zones in association with leaf litter and humus (Figure 3). Where individuals occurred in transitional zones, they were associated with plant debris. The same pattern occurred in the Talitridae (Amphipoda). These are known epigean species and their presence in caves (as with the oniscoids) is explained by the accumulation of humic soil and leaf litter in entrance zones (Griffiths pers. comm.). They were therefore regarded as humicoles rather than troglaphiles.

3.1.6. Acarina

Mites belonging to the Rhagidiidae (possibly a new species) and Laelaptidae (E. Ueckermann pers. comm.) were collected mostly from soil and detritus in the entrance zones. They are probably humicoles.

3.1.7. Pseudoscorpionidae

Cthoniella cavernicola (Lawrence 1935) is a troglobitic species that was found under rocks in the deep zones of Bats' and Wynberg caves (Figure 5). Only five individuals were observed although its small size and cryptic habits made detection difficult. It is anophthalmic, partially depigmented and has slender pedipalps (Lawrence 1935). These are typical modifications of cavernicolous forms which are often difficult to distinguish from cryptic epigean species with similar morphological adaptations (Heurtault 1994). *Cthoniella* is a Cape Peninsula endemic considered to be a Gondwanan relict (Lawrence 1935). *C. cavernicola* apparently 'took refuge' in the caves during the breakup of Gondwanaland, subsequently becoming cave-adapted (Picker and Samways 1996). Its closest relative, *Cthoniella heterodonta*, is an ophthalmic and pigmented epigean species that apparently did not 'take refuge' in caves during periods of climatic change (Newlands and Ruhberg 1978). No intermediate troglomorphy is evident. Troglobitism is common in the Cthoniidae but this is the only troglobitic species of *Cthoniella* (Heurtault 1994).

3.1.8. Araneae

The Araneae contributed significantly to the cavernicolous fauna with 15 species being recorded. Of these, three are troglobitic, two are possible troglloxenes, while the remaining ten are troglophiles. Although cave araneads are more diverse in tropical caves (Vandel 1965), Ribera and Juberthie (1994) point out that "it is extremely rare not to find at least one aranead troglophile or troglobite in a cave."

Endemic species that are considered troglobitic include:

- *Crozetus scutatus* (Anapidae), formerly *Speleodermes scutatus* (Lawrence 1964).
- *Lephtyphantes rimicola* (Linyphiidae), incorrectly assigned to this genus. It is probably a monotypic species within a new genus (R. Jocque pers. comm.).
- *Hahnia* sp.nov. (Hahniidae), a new species (C. Griswold pers. comm.).

All three species occurred mainly in the deep zones (Figure 5) although only *Hahnia* sp.nov. was restricted to it. This species is completely depigmented and eyeless and was found in narrow crevices in the deepest parts of the caves. No blind cave hahniids have yet been recorded from Africa (A. Dippenaar pers. comm.). In fact, hahniids are rarely found in caves, the only recorded troglobitic hahniids being three species of *Iberina* (in Spain and France,

Roumania and Chile) (Ribera and Juberthie 1994) and a possible new species in Brazil (Trajano and Sánchez 1994). Therefore, the occurrence of a highly adapted troglobite in the Table Mountain caves is surprising. *Lephtyphantes rimicola* and *Crozetulus scutatus* both occurred in transitional and deep zones (Figure 5). The former tended to occur in cracks while the latter was more common between rocks on the cave floor. Both species are depigmented with poorly-developed eyes (Lawrence 1964). Once again, all three species (most notably *Hahnia*) have the well-developed troglomorphy and restricted distributions typical of relictual species.

Endemic aranead species that are considered troglaphiles include:

- *Malaika longipes* (Phyxelididae), formerly *Haemilla grindleyi* (Amaurobiidae) (Lawrence 1939, 1964; Griswold 1990, 1997).
- *Spermophora peninsulae* (Pholcidae) (Lawrence 1964).
- *Loxosceles valida* (Loxoscelidae) which apparently also occurs off the Cape Peninsula (N. Larsen pers. comm.).

These species were common in the entrance zones (Figure 4), occasionally occurring in transitional zones. This is typical of cavernicolous Pholcidae (Ribero and Juberthie 1994). In Bats' cave they were almost entirely absent from the dark zone, while in Wynberg cave individuals of all three species were found in the deep zone where conditions were favourable. (Reasons for this are discussed in Chapters 4 and 6.) All three species have been observed in similar epigeal environments (such as in crevices in forests and ravines) and are undoubtedly troglaphiles. Cavernicolous species of *Spermophora* have been recorded from Tasmania, New Guinea (Ribera and Juberthie 1994), Argentina (Juberthie *et al.* 1994) and Kenya (*Spermophora minotaura*) (Lawrence 1964), thus showing a Gondwanan distribution.

All other Araneae were collected from entrance zones where they occurred either as troglaphiles or troglaxenes. Most are epigeal species that are common in cave entrances. *Hahnia lobata* (Hahniidae) is possibly troglaphilic, as it was common in transitional as well as entrance zones (Figure 3). Other species that occasionally occurred in the transitional zone were *Pachygnatha* sp. (Tetragnathidae) and *Isicabu capensis* (Cyatholopidae). The segestriid, selenopid, miturgid and agelenid were either accidentals or regular troglaxenes. Agelenids are frequent entrance residents (Ribera and Juberthie 1994), while miturgids of the genus

Phanotea have been recorded from caves in Kwa-Zulu Natal (*Phanotea natalensis*, *Phanotea simoni*), as well as in the Cango and Guano caves, Cape Province (*P. peringueyi* and *P. gowri*) (Lawrence 1964). The segestriid, selenopid and *Machadonia* sp. are epigeal species not normally found in caves (Filmer 1995).

3.1.9. Opiliones

Eighty species of Opiliones worldwide are considered troglobitic (Rambla and Juberthie 1994). Two of these are endemic to the Cape Peninsula caves: *Speleosiro argasiformes* (Pettalidae) and *Speleomontia cavernicola* (Triaeonychidae) (Lawrence 1931). *Speleosiro argasiformes* is the only troglobitic species of Pettalidae, a family consisting of mostly eyeless species with a Gondwanan distribution (Rambla and Juberthie 1994). The Pettalidae has one species in Chile, three in South Africa, two in Sri Lanka and 28 in Australia and New Zealand (Rambla and Juberthie 1994). The Triaeonychidae also have a Gondwanan distribution with 17 troglobitic species (Rambla and Juberthie 1994). *Speleomontia cavernicola* is partially depigmented but ophthalmic (Lawrence 1931; Grindley 1976) and tended to occur in crevices. *Speleosiro argasiformes*, on the other hand, mostly occurred under rocks where it has been observed feeding on oligochaetes. Both species occurred throughout the caves but were prevalent in the dark zones (Figure 5).

Seven other species of Opiliones were collected. Only *Vibone vetusta* was found in the dark zones and is probably trogliphilic. It occurred throughout the caves (Figure 4). The remaining species occurred infrequently and sporadically in entrance zones and appear to be occasional troglloxenes. Two species are possibly new to science (L. Lotz pers. comm.). They belong to the genera *Rhampsinitus* and *Adaeum*. *Rostrumontia granulifer* and *Rostrumontia capensis* are epigeal species endemic to the Cape Peninsula (Picker and Samways 1996).

3.1.10. Chilopoda

There are an estimated 55 species of troglobitic Chilopoda worldwide (Vandel 1965). Of these, four belong to the genus *Cryptops* (Negrea and Minelli 1994), including *Cryptops stupendus* (Scolopendromorpha) from the Cape Peninsula caves (Attems 1959). *Cryptops stupendus* has elongate antennae and appendages and weak pigmentation (Attems 1928). However, its troglobitic status is in some doubt as it has been sighted in similar dark, damp,

cryptic habitats (e.g. overhangs and grottoes) on Table Mountain (Lawrence 1962a; N. Larsen pers. comm.). Nevertheless, Grindley (unpublished notes) reported a “conspicuous absence” of the species during his cave survey in 1956, while the present study yielded no specimens and only one unconfirmed sighting in the deep zone of Wynberg cave. Clearly this species is very rare, possibly becoming increasingly so. The reason for this is uncertain and a matter of concern.

By far the most abundant chilopod in the caves was *Paralamyctes spenceri* (Lithobiomorpha). This is a cosmopolitan epigeal species but was present throughout the caves (Figure 4), both as immatures and as adults (Attems 1928). This indicates an apparent ability to breed in caves and, therefore, a trogliphilic association. Most troglitic Chilopoda occur within the Lithobiomorpha but no other species of *Paralamyctes* have been recorded from caves (Negrea and Minelli 1994). *P. spenceri* is clearly not a refuge species and it is likely that the species is utilising rich food resources within the caves and thus evolving by adaptive shift.

Two species of Geophilomorpha were collected from the entrance zone of Bats’ cave. The schendylid is apparently new to science (L. Lotz pers. comm.), while *Walesobius excrescens* (Lithobiidae) is a cosmopolitan epigeal species usually occurring in leaf litter and humus (Attems 1928). The latter has tentatively been classified as a humicole.

3.1.11. Diplopoda

Harpethrix caeca (Lawrence 1962b) (Dalodesmidae) is a cavernicolous polydesmid species endemic to Cape Peninsula caves (Picker and Samways 1996). It occurred mostly in entrance and transitional zones (Figure 3). Although it has been regarded as a troglite in the past (Grindley 1956, 1961, 1976), it has also been observed in similar dark, damp epigeal habitats (H. Robertson pers. comm.) and is almost certainly a trogliphile. It is partially depigmented and anophthalmic but lacks the modifications of typical troglitic diplopods (i.e. decalcification of the integument, attenuation of legs and antennae and increased body size) (Mauries 1994). It is considered to be a Gondwanan relict that ‘took refuge’ in caves at the time of the breakup of Gondwanaland. The only other species within the genus occurs in epigeal environments in montane forest in the Western Cape (Lawrence 1962b, 1984).

Most cavernicolous diplopods are epigean cryptophiles that also occur in caves (Mauries 1994). This seems to be true of the species of Dalodesmidae found in leaf litter and humus of entrance zones, often occurring in high numbers. They have been tentatively classified as humicoles. The isolated records of Sphaerotheriidae and Spirostreptidae collected from Bats' cave entrance, suggest they are accidentals or occasional troglonexes. *Sphaerotheridium weberi* is an epigean species endemic to the Cape Peninsula (Picker and Samways 1996).

3.1.12. Symphyla

A few isolated individuals of *Hanseniella capensis* were collected from the entrance and transitional zones of Bats' cave (Figure 3). In general, the Symphyla are endogeans with no truly cavernicolous species (Juberthie-Jupeau 1994). Although depigmentation and anophthalmy predisposes them to cave life, herbivorous feeding habits limit them to epigean and entrance habitats (Vandel 1965). *Hanseniella capensis* is probably more abundant than this study suggests, as the collecting methods used were inadequate for an accurate census of endogeans and humicoles. Species of *Hanseniella* have also been reported from caves in Tasmania (Eberhard *et al.* 1991).

3.1.13. Diplura

The troglotic *Anisocampa leleupi* (Condé 1955) is known from Bats' cave and is the only cavernicolous genus recorded from the Ethiopian region (Bareth and Pagès 1994). The present study yielded an individual campodeid collected from the deep zone of Wynberg cave. However, lack of taxonomic expertise has hindered taxonomic clarity and it is uncertain whether this is, in fact, *A. leleupi*, a new cavernicole, or an endogean.

3.1.14. Collembola

At least one new species was collected from the Table Mountain caves: the hypogastrurid *Schaefferia (Typhlogastrura)* sp.nov. (K. Christiansen pers. comm.). This species was abundant in guano-rich areas, being particularly prevalent on the fruit bat guano in Bats' cave entrance (Figure 3). The Hypogastruridae tend to be very abundant in caves and the genus *Schaefferia* differs markedly from surface forms, indicating ancient origins (Vandel 1965). It seems likely that the Table Mountain species is troglophilic but it has tentatively been

regarded as a guanophile because of limited knowledge. Only two troglobitic species of Collembola have been recorded from the Ethiopian region, both occurring in Madagascar (Wilson 1982).

The isotomids collected from the entrance of Wynberg cave were probably accidental detritivores (K. Christiansen pers. comm.), while *Entomobrya* sp. is an epigean species with no marked troglomorphy and is probably a troglaxene (K. Christiansen pers. comm.). The latter species was collected from the transitional zone of Wynberg cave and from Lower Aladdin cave in the Kalk Bay cave system. Once again, the sampling method was inadequate for the census of small inconspicuous species, humicoles and endogeans. Further collecting is likely to yield additional species of Collembola, as well as of Diplura.

3.1.15. Thysanura

Only three species of Thysanura in the world are regarded as truly cavernicolous (Vandel 1965; Mendes 1994). In general, they are troglaxenes which do not penetrate beyond the transitional zone (Vandel 1965). This is certainly true for the undescribed species of *Machiloides* (J. Irish pers. comm.) which only occurred on walls in the outer twilight zones (Figure 3). Troglomorphy included elongate antennae and caudal styles. They were observed in both the Table Mountain and Kalk Bay Mountain caves but are thought to be endemic to the Cape Peninsula (J. Irish pers. comm.). Three other species of *Machiloides* have been recorded from caves in Spain (Roca 1976).

3.1.16. Orthoptera

Speleiacris tabulae is the only rhabdophorid recorded from Africa (Hesse 1929; Karny 1929, 1931; Grindley 1956). It is endemic to the caves of the Cape Peninsula and is considered a Gondwanan relict that 'took refuge' in the caves during periods of inclement surface conditions (Karny 1931). It belongs to the tribe Macropathini, a primitive group with a Gondwanan distribution, the other species occurring in Patagonia, the Falkland Islands, New Zealand and Australia (Karny 1931; Carchini *et al.* 1991a). *Speleiacris tabulae* is clearly the most frequently encountered and conspicuous invertebrate species in the caves and therefore the most abundant and reliable food source for predators. It was common throughout the zones (Figure 4). The eyes are reduced but functional, depigmentation is

partial, the legs, antennae and palps are attenuated and it has tibial spines for gripping wet surfaces as well as a 'K'-type reproductive strategy (Grindley 1956; Carchini *et al.* 1991a). Uncertainty exists over the ecological status of raphidophorids, as several species forage outside the caves at night (Richards 1969, 1971; Hamilton-Smith 1971; Di Russo *et al.* 1991; Carchini *et al.* 1994). This was not observed in *Speleiacris tabulae*, but individuals have been seen in similar cryptic epigeal habitats (H. Robertson; J. Grindley pers. comm.). It must therefore be considered a troglophile.

3.1.17. Dermaptera

Two species were collected, one of which is considerably depigmented and is new to science (R. Stals pers. comm.). No cavernicolous dermapterans had previously been recorded from Africa (Brindle and Oromi 1994).

3.1.18. Blattodea

A single individual was collected from a crevice in the entrance zone of Wynberg cave. This is an epigeal species whose occurrence in the cave was probably fortuitous.

3.1.19. Diptera

Cavernicolous Diptera are rare, and most are troglaxenes or guanophages¹ (Vandel 1965). This was found to be true of the dipterans in Cape Peninsula caves. However, the terms 'guanophile' and 'guanobia' are preferred, as it was often impossible to distinguish between a nutritional dependence on the guano itself, or a secondary association with it. Matile (1994) proposed that cave-dwelling Diptera be classified independently as follows: troglobites; trogliphiles; subtroglyphiles (regular troglaxenes); troglaxenes; zoophages and guanophages. Intermediate forms exist and considerable overlap can occur between categories, thus making accurate classification very difficult.

All dipterans were encountered in both entrance and deep zones during summer, apparently using the cave as a shelter from hot, dry surface conditions. They were absent from the dark zones in winter. The Psychodidae, Tipulidae, Muscidae and Phoridae occurred mostly in entrance zones (Figure 4) and were guanophilic. Guano from insectivorous bats had sciarids

and phorids associated with it. The tipulid, *Conosia* sp. and the psychodid, *Psychoda spatulipennis*, were present in both Kalk Bay and Table Mountain caves throughout the year. They could be regarded as troglaphiles or subtroglyphiles. Their association with rich guano deposits may indicate evolution by 'adaptive shift'. On the other hand, the Muscidae, Phoridae, Sciaridae, Fannidae and Heleomyzidae were not regularly encountered and are either troglaxenes or guanophiles. The apparent absence of species from the Kalk Bay caves (Table 1) is almost certainly a result of undersampling.

Zoophages included one species of Nycteribiidae from Wynberg cave (parasitic on insectivorous bats) and larval Calliphoridae on a fruit bat carcass in Bats' cave. This ability to breed in caves implies that zoophages could simultaneously be classified as troglaphiles but, strictly speaking, are not part of the cave fauna *per se* (Vandel 1965). Adult Calliphoridae and Sarcophagidae were encountered in the deep zones during the hot summer months, either as troglaxenes or zoophages.

3.1.20. Coleoptera

No troglotic Coleoptera occur in South Africa (S. Endrödy-Younga pers. comm.). This is possibly because coleopterans were able to survive changes in surface conditions associated with the breakup of Gondwanaland and did not withdraw into cave 'refugiae' (S. Endrödy-Younga pers. comm.). Nevertheless, two species were well-represented in the cave community: *Malkinella cavatica* (Ptiliidae) and *Plocamotrechus longulus* (Carabidae). Both species appear to opportunistically utilise rich guano-related food resources within the caves and are likely to be evolving cave adaptations by 'adaptive shift'. *M. cavatica* was originally collected by Dybas (1960) from fruit bat guano in Cango cave, Oudtshoorn. In the Table Mountain caves they were found to be most abundant in areas of high guano concentrations. In the Kalk Bay caves they have only been found in Boomslang cave, the only cave with a sizeable fruit bat colony. They are anophthalmic, partially depigmented and one of only three cavernicolous Ptiliidae worldwide, the other two being species of *Ptenidium* (Vandel 1965). However, despite being classified as a troglote by Vandel (1965) it would be more accurately regarded as a guanophile. It occurred in all three zones (Figure 4) but its ability to survive outside of caves is not known.

¹ Guanophages occur in caves because their larvae feed on bat guano. They show few morphological

Similarly, *Plocamotrechus longulus* occurs throughout the caves (Figure 4), usually under rocks. It is common in all the Cape Peninsula caves and is apparently able to reproduce underground (carabid larvae have been collected but not identified to species level). However, *Plocamotrechus longulus* is an epigean species opportunistically utilising the guano-associated food resource in caves (S. Endrödy-Younga pers. comm.). It is best regarded as a guanophile although a troglophilic association seems likely.

A third group, the Staphylinidae, were an important component of the cave fauna. They were often very abundant in guano-rich areas and are guanophiles that are possibly evolving a cave association by 'adaptive shift'. They were common in all three zones (Figure 4) and are apparently able to complete their life cycles underground. Two species (indeterminable) were collected. A third species, *Caphrotyphlus strinatii* (Leptotyphlinae), was collected by Grindley (unpublished notes) and identified by Coiffait (1977) but this species was not collected during the course of this study.

Other Coleoptera collected were either opportunistic visitors (e.g. *Scarites* sp. and *Trox* sp.) or accidentals (Curculionidae, Cerambycidae and Anthribidae) and not part of the cave fauna proper.

3.1.21. Lepidoptera

Pyralid and tineid moths were observed exclusively in cave entrances as regular troglaxenes (Figure 3). Cavernicolous Lepidoptera are typically troglaxenes forming part of the 'parietal association' in entrance zones (Vandel 1965). The identification of the two species of *Aglossa* (Pyralidae) needs confirmation by dissection of the genitalia (M. Kruger pers. comm.). *Aglossa cuprealis* is thought to be an introduced species (M. Kruger pers. comm.) and has also been recorded from caves in France (Turquin 1994). The two tineid species belong to two species complexes: *Monopis speculella* group (probably *M. transeans*) and a group containing the genera *Episcardia* and *Proterospastis*. Five other species of *Monopis* have been recorded from caves in Europe and Australia (Richards 1971; Skalski 1972).

modifications and usually occur in entrance zones (Matile 1994).

The lasiocampid female collected from Boomslang cave (Kalk Bay Mountains) is an undescribed species of the epigean genus *Mesoscelis* (M. Kruger pers. comm.). It is, however, an accidental, collected not far from the cave entrance.

3.2. Discussion

3.2.1. Faunal composition in a global context

Cave faunas of the world have been discussed by Vandel (1965) and Juberthie and Decu (1994). The faunal composition of the Table Mountain caves appears to be fairly typical of caves worldwide. That is, most cavernicolous animals are arthropods and, of these, most are araneads (Vandel 1965). Cavernicolous fauna most commonly comprise Opiliones, Amphipoda, Isopoda, Diplopoda, Chilopoda, Pseudoscorpionidae, Collembola, Diptera and Carabidae, all of which occur in the Table Mountain caves. Vandel (1965) lists 33 arthropod orders containing cavernicoles. Of these, 13 orders are completely absent from the Table Mountain caves, all being uncommon in cave habitats worldwide. They include the Scorpionidae, Ricinulei, Copepoda, Myctacea, Branchiopoda, Mysidacea, Decapoda, Pauropoda, Blattodea (barring one accidental), Psocoptera, Neuroptera, Hymenoptera, Trichoptera and Hemiptera. Of the non-arthropod phyla represented in caves, the Turbellaria, Oligochaeta and Mollusca are common cave inhabitants. Five non-arthropod phyla that have been reported from caves elsewhere, were absent from the Table Mountain caves (Porifera, Coelenterata, Nemertea, Nematoda and Rotifera) (Vandel 1965). At the genus level, only *Lepthyphantes*, *Paramelita*, *Schaefferia*, *Loxosceles*, *Cryptops*, *Trichoniscus*, *Machiloides* and *Monopis* have been recorded as cavernicoles elsewhere.

Although no direct comparisons with other karstic regions is possible because of differences in geographical areas, the Cape Peninsula caves appear to be relatively depauperate by world standards, possibly because they are temperate and sandstone in nature. This study recorded only 85 species from approximately 80 caves, while Clarke (1997) recorded 643 invertebrate species from a total of 492 limestone caves in Tasmania; Peck (1992) recorded 250 species from 54 caves in Alabama, while in France, 639 troglobitic species have been recorded (Juberthie and Ginet 1994). However, compared with other caves in Southern Africa, the Cape Peninsula caves are by far the most faunistically diverse and abundant.

Comprehensive biospelaological surveys are scarce for Southern African caves but comparisons with faunal reports from the Congo Caves (Grindley unpublished report), a cave in the Kruger National Park (Braack 1989), several Namibian caves (Martini 1990; Martini *et al.* 1990; Irish 1991; Irish *et al.* 1991) and the Chimanimani caves in Zimbabwe (Truluck 1994) reveal a dearth of troglobitism. Most cave-adapted species are amphipods, occurring in groundwaters and caves in Namibia and South Africa (C. Griffiths pers. comm.; Martini 1990). They include five species, each within the Ingolfiellidae and Sternophysingidae, but no other species of *Paramelita*. Cave-adapted nicolettiids have been collected from Efflux cave near Oudtshoorn (J. Irish pers. comm.) and from Dragon's Breath cave and Pofadderat in Namibia (Irish *et al.* 1991). The aranead *Cangoderces lewisi* occurs in the Congo caves (Filmer 1995).

High temperatures and low humidities in most Southern African caves make them less than ideal troglobitic habitats. For example, temperatures in the Kruger National Park cave (Braack 1989) and Namibian caves are over 20°C, while relative humidities are often below 70% (Martini 1990; Irish *et al.* 1991). Their faunas therefore differ greatly from those of the Table Mountain caves. They consists mostly of cockroaches (e.g. *Gyna* sp. in the Kruger National Park cave), gryllids (in Namibian caves), tenebrionids, reduviids and formicids (the Kruger National Park cave, Namibian and Chimanimani caves) (Braack 1989; Martini 1990; Martini *et al.* 1990; Irish *et al.* 1991; Truluck 1994).

Very little data exists for caves in the southern part of the Western Cape (such as the De Hoop caves near Bredasdorp and the caves near Oudtshoorn). Similar climatic influences would conceivably result in similar cave faunas and further research may reveal this to be true. However, initial surveys conducted during this study indicate few faunal similarities with caves at Cape Point, De Hel (both sandstone caves) and De Hoop (limestone caves).

Therefore, it seems that the cave fauna of the Cape Peninsula shows far greater affinities with South American cave fauna than it does with other caves in Africa. This is, perhaps, not surprising considering the relictual origin of many Cape Peninsula cavernicoles. For example, cavernicolous hahniids also occur in Chile and Brazil (Juberthie and Di Russo 1994; Trajano and Sánchez 1994); *Spermophora* has been recorded from Argentina (Juberthie *et al.* 1994),

while *Auximus* has been recorded from Argentina and Uruguay (Strinati 1994). *Loxosceles* and the only other known spelaeogriphacean have been recorded from Brazil (Trajano and Sánchez 1994). On the other hand, only one Cape Peninsula cave genus, *Loxosceles*, has been recorded from both the Peninsula caves and other southern African caves. *Loxosceles vonwereidei* is recorded from Marchen cave and Wondergat, Namibia (Irish *et al.* 1991), while *Loxosceles speluncarum* is recorded from Apies River cave, Pretoria (Lawrence 1964). Other African records include *Spermophora*, with *Spermophora minotaura* being recorded from Kenya (Lawrence 1964).

Several studies of temperate limestone cave faunas are documented. e.g. Clarke (1988, 1997) studied Tasmanian caves, Juberthie and Ginet (1994) reported on French caves, Jefferson (1994) and Juberthie and Decu (1994) looked at British and Irish cave faunas respectively, while Chapman (1979) studied the fauna of Otter Hole, Wales. Direct comparisons with these studies are not possible because of biogeographical differences in cavernous areas, altitude and rainfall, all of which affect faunal lists (Peck 1990). Nevertheless certain trends become evident:

- The Araneae make the most significant contribution to cave faunas. In the Northern Hemisphere theridiids and leptonetids predominate, while in Tasmania and South Africa, most cavernicolous araneads are amaurobiids (Juberthie and Ginet 1994; Clarke 1997).
- The occurrence of troglobitic species of Onychophora, Spelaeogriphacea, Hahniidae and a troglophilic Ptiliidae, make the Table Mountain cave fauna highly unusual.
- The Table Mountain caves have a relative paucity of collembolans, pseudoscorpions, diplopods and carabids which are often common in other caves. Moreover, aquatic gastropods and decapods are completely absent from the Table Mountain caves. This is probably due to the acidity of subterranean water in sandstone areas, compared with the relative alkalinity of limestone-associated water (Davies and Day 1984). Furthermore, the Table Mountain caves are well above the groundwater table, thus explaining the relative paucity of aquatic species compared with, for example, limestone caves in France, where 218 aquatic troglobites have been recorded in total (Juberthie and Ginet 1994).

3.2.2. Distribution of fauna within the caves

Vandel (1965) identified six cave biotopes and their six synusia. The biotopes and their associated fauna recognizable in the Table Mountain caves include: soil with associated endogeans; guano with associated guanophiles; aquatic environments inhabited by stygobionts; crevices and natural cavities inhabited by troglaphiles and troglobites and cave entrances with guanophiles, endogeans, humicoles and troglaxenes.

The guanophiles, humicoles and endogeans were distributed according to the distribution of their food resources. For the most part they were present in the Table Mountain caves because of food or habitat requirements, rather than cave-dependence. Humicoles and endogeans often exhibit similar morphological adaptations to cavernicoles (Vandel 1965), making it difficult to distinguish between the two categories. Guanophiles, on the other hand, usually occur in very high numbers but show few morphological adaptations to caves (Howarth 1983). Humicoles in the Table Mountain caves included mostly talitrid amphipods, oniscid isopods, dalodesmid diplopods and mites, while oligochaetes were the most common endogeans. Guanophiles included *Schaefferia* sp.nov. (Collembola), larval dipterans, staphylinids, carabids and *Malkinella cavatica* (Ptiliidae). All were directly or indirectly dependent on bat guano. Many of the guanophiles, endogeans and humicoles are apparently able to reproduce in the Table Mountain caves (e.g. oligochaetes, staphylinids, talitrids, oniscids, *Malkinella cavatica*, *Plocamotrechus longulus*, tipulids, psychodids) indicating that they could simultaneously be classified as troglaphiles or troglaxenes.

Sixty-five species were collected from entrance zones (75% of the total cave fauna). Species that were restricted to entrance and transitional zones (Figure 3) included mostly troglaphiles and troglaxenes (13 species), accidentals (five species), humicoles (seven species) and guanophiles (*Schaefferia* sp.nov.). The regular troglaxenes (e.g. dipterans, lepidopterans, coleopterans and arachnids) that frequented entrance zones constituted the parietal association (Leruth 1939; Vandel 1965). Species restricted to the deep zones were mostly troglobites (*Peripatopsis alba*, *Paramelita barnardi*, *Spelaeogriphus lepidops*, *Protojanira leleupi*, *Hahnia* sp. nov., *Cthoniella cavernicola*) (Table 1, Figure 5). *Trichoniscus tabulae* extended its range into the transitional zone, while *Speleosiro argasiformes*, *Speleomontia*

cavernicola, *Crozetulus scutatus* and *Lepthyphantes rimicola* occurred throughout the caves (Figure 5). This places some doubt on whether they are troglobites at all. However, if one considers their preference for cryptic microhabitats (tight crevices or under rocks) it may well be that the humidity within these small spaces is stable and high enough to support them in an unstable macrohabitat (thus serving as a micro-cave within a macro-cave).

This microhabitat preference may also be the factor that enables certain troglophilic species to extend their ranges into suitably humid epigean microhabitats (such as crevice habitats in forests) as has been reported for *Speleiacris tabulae*, *Cryptops stupendus* and *Haemilla caeca* (N. Larsen pers. comm.). This, however, cannot be verified until we know the full extent of the mesocaverns and the role they play in invertebrate dispersal. The question that needs to be addressed is “what defines a cave entrance?” Most definitions hinge on their accessibility to humans. For a cavernicolous arthropod, however, it may merely be any opening that allows it to cross over into an epigean (micro)habitat. Therefore, in terms of cavernicolous invertebrates, these ‘micro-entrances’ are of greater significance than larger man-sized entrances for dispersal into epigean microhabitats.

Twenty-nine species occurred throughout the caves (Figure 4), indicating that they are fairly open systems with a large degree of overlap between zones. Epigean or entrance species were able to survive in the dark zones when conditions were favourable (e.g. Diptera in the warm, dry summer months). Through-cave distributions are also shown by endogeans, while winter-flowing streams bring in debris, accidentals and possibly phreatobites into the deep zones.

Cave community abundance and distribution patterns, and the environmental factors affecting them, are explored further in Chapters 5 and 6.

3.3. Origins and Evolution

Strong evidence exists for evolution of the Table Mountain cave fauna according to the ‘Pleistocene-effect’ theory (Barr 1968, 1985; Culver 1982; Barr and Holsinger 1985; Holsinger 1988). That is, troglobitism evolved in species that became isolated in caves by ‘taking refuge’ during periods of inclement surface conditions. All Cape Peninsula troglobites exhibit characteristics typical of refuge species:

- Pronounced endemism to the Cape Peninsula caves. *Spelaeogriphus lepidops* and *Peripatopsis alba* are restricted to the Table Mountain caves, while *Protojanira leleupi* and *Paramelita barnardi* only occur in the Kalk Bay caves. *Hahnia* sp.nov. and *Dermaptera* sp.nov. are only known from the Table Mountain caves.
- Few or no surface relatives. e.g. *Spelaeogriphus lepidops*.
- Well-developed troglomorphy. *Peripatopsis alba*, *Spelaeogriphus lepidops*, *Dermaptera* sp.nov. and *Hahnia* sp.nov. are depigmented and anophthalmic.
- Relative rarity. *Peripatopsis alba*, *Cthoniella cavernicola*, *Cryptops stupendus*, *Dermaptera* sp.nov. and *Protojanira leleupi* appear to be very rare.

Because the inclement conditions that drove this process coincided with the breakup of Gondwanaland, refuge species were also Gondwanan relicts. A Gondwanan distribution was shown by *Triaeonychidae*, *Patellidae*, *Cthoniella*, *Paramelitidae* and *Peripatopsis*.

Of the troglophiles, *Speleiacris tabulae* is clearly a refugial Gondwanan relict, being the only rhabdiphorid in Southern Africa and a Cape Peninsula endemic.

Several relictual troglobites still have putative surviving epigean relatives outside the caves (i.e. non-refugial relictual species). For example, *Peripatopsis balfouri* is the pigmented epigean relative of *Peripatopsis alba*, *Cthoniella heterodonta* is the epigean pigmented relative of *Cthoniella cavernicola* and *Purcellia illustrans* is the epigean relative of *Speleosiro argasiformes*. Pigmented, epigean relatives of *Trichoniscus tabulae* and *Hahnia* sp. nov. also occur on the Peninsula (Barnard 1960; Lawrence 1964; Bosmans 1981).

Several troglophiles appear to be more recent invaders. They occur in most caves on the Cape Peninsula, do not have very specialised troglomorphies, tend to occur in twilight zones and may have epigean relatives (e.g. *Loxosceles valida*, *Paralamyctes spenceri*, *Malaika longipes*, *Harpethrix caeca*, *Spermophora peninsulae*, *Machiloides* sp.nov.).

The most recent invaders are likely to be guanophiles and endogeans which inhabit caves to exploit favourable food resources or habitats. They generally show few or no troglomorphies and are often opportunistic epigean species. In Wynberg cave, bat guano is a constant and voluminous food source in the deep zone. Therefore, it is perhaps conceivable that certain

guanophilic species that exploit this resource may be evolving by 'adaptive shift'. For example, *Malkinella cavatica*, *Plocamotrechus longulus* and the Staphylinidae are able to reproduce in the deep zone but do not possess marked troglomorphies. *Malkinella cavatica* is apparently restricted to caves.

The wide distribution of troglaphiles across the Cape Peninsula is almost certainly a function of the interconnectivity of caves and the dispersal ability of the individual species, suitable epigeal microhabitats possibly also being important for dispersal. Limits to underground dispersal are known to have resulted in significant geographic isolation (Holsinger 1988). The restricted distribution of troglolithes has led to caves being compared with islands in terms of biogeography and evolution (Barr 1968; Culver 1970, 1971, 1982; Culver *et al.* 1973; Crawford 1981). Species that are small and abundant tend to achieve wider geographical distributions (Poulson and White 1969). Details of the extent of interconnectivity between the Cape Peninsula caves is not well known. Nevertheless, the Kalk Bay caves are small, numerous and relatively close together (often less than 100m apart) with numerous interconnected sandstone pores and cracks. Similarly, the Table Mountain caves are probably connected by mesocaverns. This would explain the similarity of their respective cave faunas. However, there is no apparent connection between the Kalk Bay caves and Table Mountain caves (these being approximately 15km apart). This possibly indicates that independent evolutionary processes are operating (or at least for the larger, less mobile species) in the two pseudokarst areas. This could be one explanation for the local endemism of *Peripatopsis alba*, *Spelaeogriphus lepidops*, *Paramelita barnardi* and *Protojanira leleupi*. Environmental differences and habitat requirements are additional factors. It may be that species common to both cave systems are those that are also able to survive in similar epigeal microhabitats (thus achieving greater dispersal potential) (e.g. *Speleiacris tabulae*). These species should therefore not be regarded as true troglolithes. If the two cave systems are, in fact, geographically isolated, genetic differentiation has probably occurred in the separated populations. That is, there may be more species involved, although morphological similarities may have prevented their distinction (Holsinger 1988).

3.4. Conclusion

The caves of the Cape Peninsula have clearly served as refugiae for Gondwanan relicts during periods of climatic change. Subsequent evolution has resulted in highly specialised troglobitic species that are both rare and endemic to the Cape Peninsula. Troglobitism, however, was found to be relatively rare and certainly not as common as previously thought. Microhabitat preference may enable certain thigmotactic species to disperse through mesocaverns, thus achieving greater geographical and local (or habitat) distributions. This would have implications for the allopatric speciation of troglobites in their island-like habitats. Genetic analyses would be useful to elucidate evolutionary processes operational in the two island-like cave systems of the Cape Peninsula. Furthermore, guanophilic species that opportunistically exploit food resources in the deep zones, may be evolving by 'adaptive shift' (Howarth 1988).

The significant contribution made by the Peninsula caves to the total number of Cape Peninsula invertebrate endemics, make them important considerations in the conservation of the Cape Peninsula as a whole. Of particular conservation importance are *Peripatopsis alba*, *Spelaeogriphus lepidops* and the troglobitic *Hahnia* sp.nov., all highly specialised, phylogenetically unique species that are unique to the Table Mountain caves. However, inadequate taxonomic and ecological knowledge seriously hampers an estimation of cave biodiversity and, therefore, conservation. Further research would undoubtedly reveal additional new and endemic species. The Kalk Bay cave fauna, in particular, needs to be surveyed extensively.

4. Species diversity and abundance

Diversity, at various scales ranging from caves to ecosystems, lies at the root of many fundamental questions in ecology. Diversity is the most frequently adopted criterion used to assess habitats for conservation (Margules and Usher 1981). Rarity and abundance are also of considerable importance (Magurran 1988). Environmental disturbances are often detected by observing changes in abundance patterns and species diversity (Southwood 1977).

Environmental monitoring makes extensive use of diversity indices and species abundance distributions, while conservation concentrates on species richness (Magurran 1988).

Therefore, to understand the ecology and conservation status of cavernicoles in the Table Mountain caves, it is necessary to know how many species there are and what their relative abundances are. In caves, relictual troglobites tend to be rare, while guanobia often have high abundances of between 100 000 and 1 000 000 per cave (Mitchell 1970).

Faunal abundances and diversities of Bats' and Wynberg caves were compared in this study. The aim was to determine which species were common and which were rare, as well as to observe overall trends in community structure. The effects of cave entrances and dark zones on these measures were also considered.

Caves are often regarded as 'natural laboratories' for ecological and evolutionary studies because they have relatively finite boundaries (Howarth 1983). However, to calculate total abundances per cave, it is necessary to know the precise area of the habitable environment (Mitchell 1970). This differs considerably from the area accessible for measurement.

Therefore, extrapolation from density figures can lead to serious underestimates of population abundance. Considering that cavernicoles utilise all available crevices and mesocaverns, the underground population is undoubtedly far more abundant than it would seem. Delay (1975), for example, found a ratio of 50:1 between mark-recapture estimates and baited trap counts of terrestrial coleopterans, indicating that a proportion of the population remained hidden in mesocaverns. Furthermore, most animals predominantly occur at the bottom of cave walls or on the floor, so that extrapolation to the entire surface area would produce an overestimation (Mitchell 1970). Therefore, for comparative purposes, abundances were expressed here as the average number of animals per quadrat.

Table 2. A comparison of mean taxon abundance and biomass per 2m² quadrat and their proportional contribution to total population abundances of Wynberg and Bats' caves. Taxa are arranged in descending order of abundance. Counts were made monthly over one year in 33 and 16 quadrats for Wynberg and Bats' caves respectively. Taxa with mean abundances that differ significantly between caves (P<0.05, using the t-test on ln(x+1) transformed data) are marked with an asterisk (*).

WYNBERG CAVE						BATS' CAVE					
	Mean no. per quadrat n=396	Standard deviation	Upper limit of range (min=0)	% of Total	Mean biomass per quadrat (mg)		Mean no. per quadrat n=192	Standard deviation	Upper limit of range (min=0)	% of Total	Mean biomass per quadrat (mg)
<i>Speleiacris tabulae</i> *	6.504	1.35	30	49.64	97.5595	<i>Speleiacris tabulae</i> *	12.056	1.08	62	44.99	180.8418
<i>Spermophora peninsulae</i> *	1.190	0.88	19	9.09	1.7857	<i>Spermophora peninsulae</i> *	4.755	1.21	40	17.75	7.1327
<i>Speleomontia cavernicola</i> *	1.071	0.79	9	8.18	3.2143	<i>Crozetulus scutatus</i> *	2.372	0.86	18	8.85	0.7117
<i>Lepthyphantes rimicola</i> *	0.877	0.7	12	6.69	0.2631	<i>Speleosiro argasiformes</i> *	1.413	0.71	14	5.27	7.0663
<i>Linyphiidae</i> sp.*	0.829	0.62	2	6.33	0.1659	<i>Malaika longipes</i> *	1.209	0.75	11	4.51	9.6735
<i>Speleosiro argasiformes</i> *	0.563	0.5	8	4.3	2.8175	<i>Lepthyphantes rimicola</i> *	1.107	0.6	9	4.13	0.3321
<i>Crozetulus scutatus</i> *	0.421	0.47	5	3.21	0.1262	<i>Speleomontia cavernicola</i> *	0.791	0.56	6	2.95	2.3724
<i>Malaika longipes</i> *	0.357	0.49	9	2.73	2.8571	<i>Plocamotrechus longulus</i> *	0.566	0.54	9	2.11	0.8495
<i>Hahnia lobata</i> *	0.181	0.32	4	1.38	0.0181	<i>Loxosceles valida</i> *	0.423	0.49	12	1.58	19.3526
<i>Machiloides</i> sp.	0.161	0.42	11	1.23	1.1089	<i>Machiloides</i> sp.	0.316	0.42	10	1.18	2.1827
<i>Vibone vetusta</i>	0.155	0.25	3	1.18	0.0155	<i>Pachygnatha</i> sp.	0.296	0.39	4	1.1	2.3673
<i>Dalodesmidae</i> sp.	0.133	0.36	10	1.01	0.5317	<i>Trachycystis charybdis</i>	0.255	0.36	5	0.95	51.0204 [#]
<i>Harpethrix caeca</i>	0.127	0.23	2	0.97	0.6349	<i>Paralamyctes spenceri</i>	0.240	0.05	1	0.89	4.7959
<i>Paralamyctes spenceri</i>	0.119	0.28	2	0.91	2.3810	<i>Vibone vetusta</i>	0.209	0.32	3	0.78	0.0209
<i>Trichoniscus tabulae</i>	0.101	0.21	2	0.77	0.6071	<i>Dermaptera</i> sp.*	0.204	0.33	7	0.76	3.0612
<i>Plocamotrechus longulus</i> *	0.075	0.24	6	0.58	0.1131	<i>Dalodesmidae</i> sp.	0.173	0.31	6	0.65	0.6939
<i>Hahnia</i> sp. nov.*	0.075	0.16	2	0.58	0.0377	<i>Harpethrix caeca</i>	0.158	0.29	4	0.59	0.7908
<i>Loxosceles valida</i> *	0.024	0.22	2	0.18	1.0881	<i>Hahnia lobata</i> *	0.056	0.16	1	0.21	0.0056
<i>Trachycystis charybdis</i>	0.020	0.02	1	0.15	4.2659 [#]	<i>Isicabu capensis</i>	0.041	0.15	2	0.15	0.0041
<i>Pachygnatha</i> sp.	0.018	0.13	2	0.14	0.1429	<i>Machadonia</i> sp.	0.026	0.12	2	0.1	0.0255
<i>Cthoniella cavernicola</i>	0.014	0.09	1	0.11	0.0028	<i>Trichoniscus tabulae</i>	0.020	0.12	2	0.08	2.3469
<i>Dermaptera</i> *sp.	0.012	0.12	2	0.09	0.1786	<i>Hanseniella capensis</i>	0.015	0.09	1	0.06	0.0306
<i>Rostrumontia granulifer</i>	0.010	0.09	1	0.08	0.0446	<i>Dermaptera</i> sp. nov.*	0.015	0.09	1	0.06	
<i>Paramontia liposoma</i>	0.010	0.1	2	0.08	0.0427	<i>Spirostreptidae</i> sp.	0.010	0.07	1	0.04	2.1939
<i>Isicabu capensis</i>	0.010	0.1	1	0.08	0.0010	<i>Rostrumontia granulifer</i>	0.010	0.05	1	0.04	0.0459
<i>Spirostreptidae</i> sp.	0.006	0.08	2	0.05	1.2798	<i>Cthoniella cavernicola</i>	0.010	0.07	1	0.04	0.0020
<i>Cryptadaeum capense</i>	0.006	0.09	1	0.05	0.0250	<i>Hahnia</i> sp.nov.*	0.010	0.07	1	0.04	0.8776
<i>Scarites languidus</i>	0.004	0.09	1	0.03	1.0119	<i>Steatoda</i> sp.	0.005	0.05	1	0.02	0.0255
<i>Peripatopsis alba</i>	0.004	0.09	1	0.03		<i>Schendylidae</i> sp.	0.005	0.05	1	0.02	0.0510
<i>Trox</i> sp.	0.002	0.04	1	0.02	0.0417	<i>Rhampsinitus</i> sp.	0.005	0.05	1	0.02	0.0230

[#]Mass includes shell.

Table 2 continued.

WYNBERG CAVE						BATS' CAVE					
	Mean no. per quadrat n=396	Standard deviation	Upper limit of range (min=0)	% of Total	Mean biomass per quadrat (mg)		Mean no. per quadrat n=192	Standard deviation	Upper limit of range (min=0)	% of Total	Mean biomass per quadrat (mg)
<i>Steatoda</i> sp.	0.002	0.04	1	0.02	0.0099	<i>Peripatopsis alba</i>	0.005	0.05	1	0.02	
<i>Selenops</i> sp.	0.002	0.04	1	0.02	0.0397	<i>Paramontia liposoma</i>	0.005	0.05	1	0.02	0.0219
<i>Rhampsinitus</i> sp.	0.002	0.04	1	0.02	0.0089	Agelenidae	0.005	0.05	1	0.02	0.0510
<i>Phaenotheridium</i> sp.	0.002	0.04	1	0.02	0.1984	<i>Adaeum</i> sp.nov.	0.005	0.05	1	0.02	0.0204
<i>Machadonia</i> sp.	0.002	0.04	1	0.02	0.0020	<i>Trox</i> sp.	0			0	0
Curculionidae sp.	0.002	0.04	1	0.02	0.0119	<i>Selenops</i> sp.	0			0	0
Cerambycidae sp.	0.002	0.04	1	0.02	0.1984	<i>Scarites languidus</i>	0			0	0
<i>Ariadna</i> sp.	0.002	0.04	1	0.02	0.0198	<i>Phaenotheridium</i> sp.	0			0	0
<i>Adaeum</i> sp.nov.	0.002	0.04	1	0.02	0.0079	Linyphiidae sp.*	0			0	0
Dermaptera sp. nov.*	0.002	0.04	1	0.02	0	Curculionidae sp.	0			0	0
Schendylidae sp.	0			0	0	<i>Cryptadaeum capense</i>	0			0	0
<i>Hanseniella capensis</i>	0			0	0	Cerambycidae sp.	0			0	0
Agelenidae	0			0	0	<i>Ariadna</i> sp.	0			0	0
Total	13.10			100	122.89	Total	26.80			100	299.11
Mean per 2m² quadrat	0.33			2.44	3.07	Mean per 2m² quadrat	0.788			2.86	8.80

*Mass includes shell.

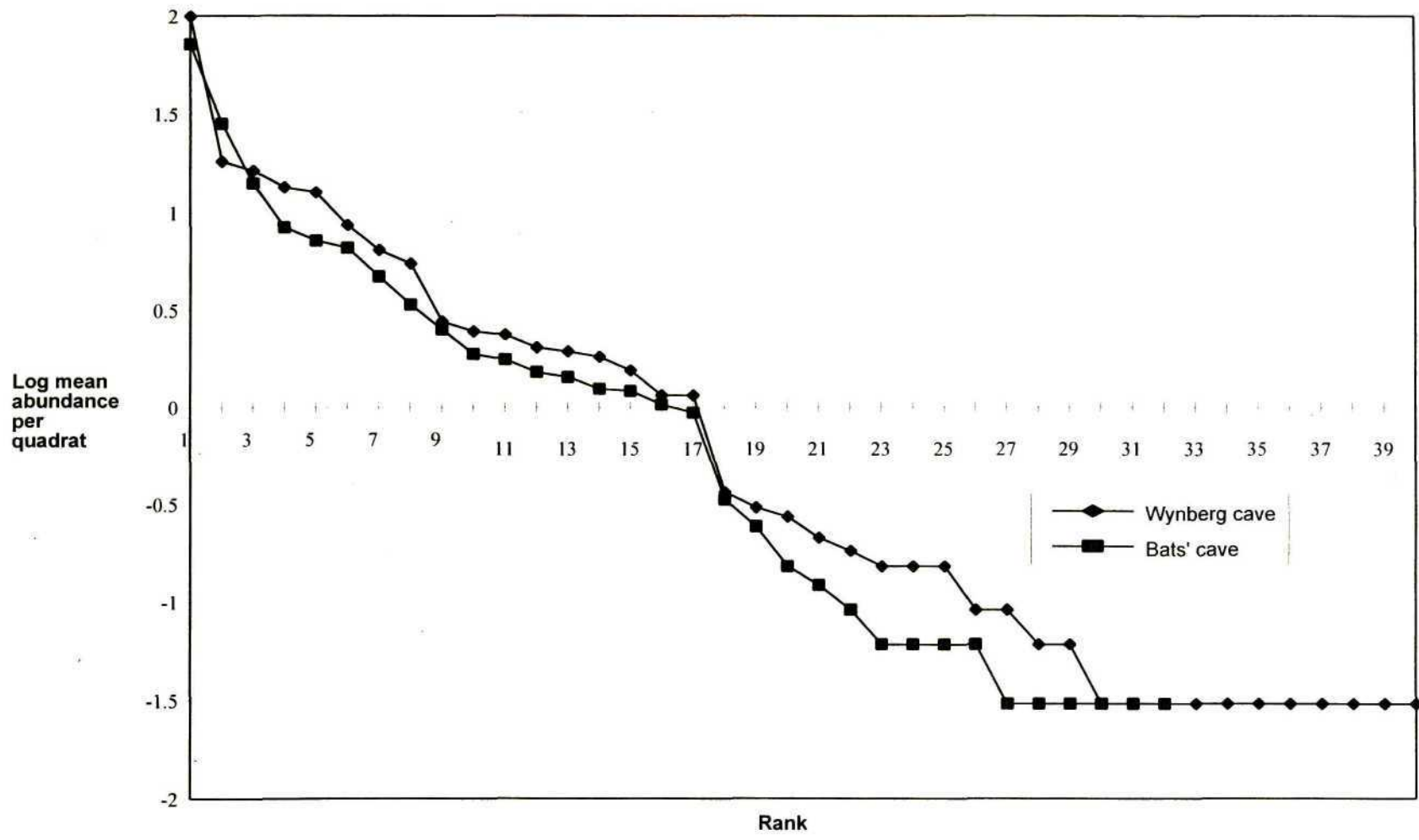


Figure 6. Rank-abundance curves for taxa counted in Bats' and Wynberg caves. Counts were made monthly for one year in 33 and 16 2m² quadrats in Wynberg and Bats' cave respectively.

Table 3. A comparison of estimates of mean abundance and biomass per 2m² quadrat for uncensused taxa in Wynberg and Bats' caves. Taxa are arranged in descending order of abundance. Counts were made monthly for one year in 33 and 16 quadrats in Wynberg and Bats' caves respectively.

WYNBERG CAVE			BATS'CAVE		
	Approx. mean no. per quadrat (n=396)	Approx. mean Biomass (mg)		Approx. mean no. per quadrat (n=192)	Approx. mean Biomass (mg)
Ptiliidae	12.90	0.00193	<i>Schaefferia</i> sp.nov.	54.69	0.00547
Staphylinidae	6.94	0.00138	Ptiliidae	39.06	0.00586
<i>Schaefferia</i> sp. nov.	2.98	0.00050	Staphylinidae	33.85	0.00677
Oniscidae	1.88	0.00189	Oniscidae	7.81	0.00391
Talitridae	0.89	0.00042	Talitridae	4.95	0.00148
Oligochaeta	0.50	0.00947	Tipulidae	2.86	0.00573
Tipulidae	0.30	0.00076	Oligochaeta	1.82	0.02734
Psychodidae	0.30	0.00042	Psychodidae	1.30	0.00143
Lepidoptera	0.15	0.00007	Lepidoptera	1.30	0.00052
Heleomyzidae	0.15	0.00004	Heleomyzidae	0.78	0.00016
Acarina	0.06	0.000005	Acarina	0.78	0.00006
Total	26.75	0.0143	Total	149.20	0.0627
Mean per quadrat	2.432	0.0013	Mean per quadrat	13.56	0.0057

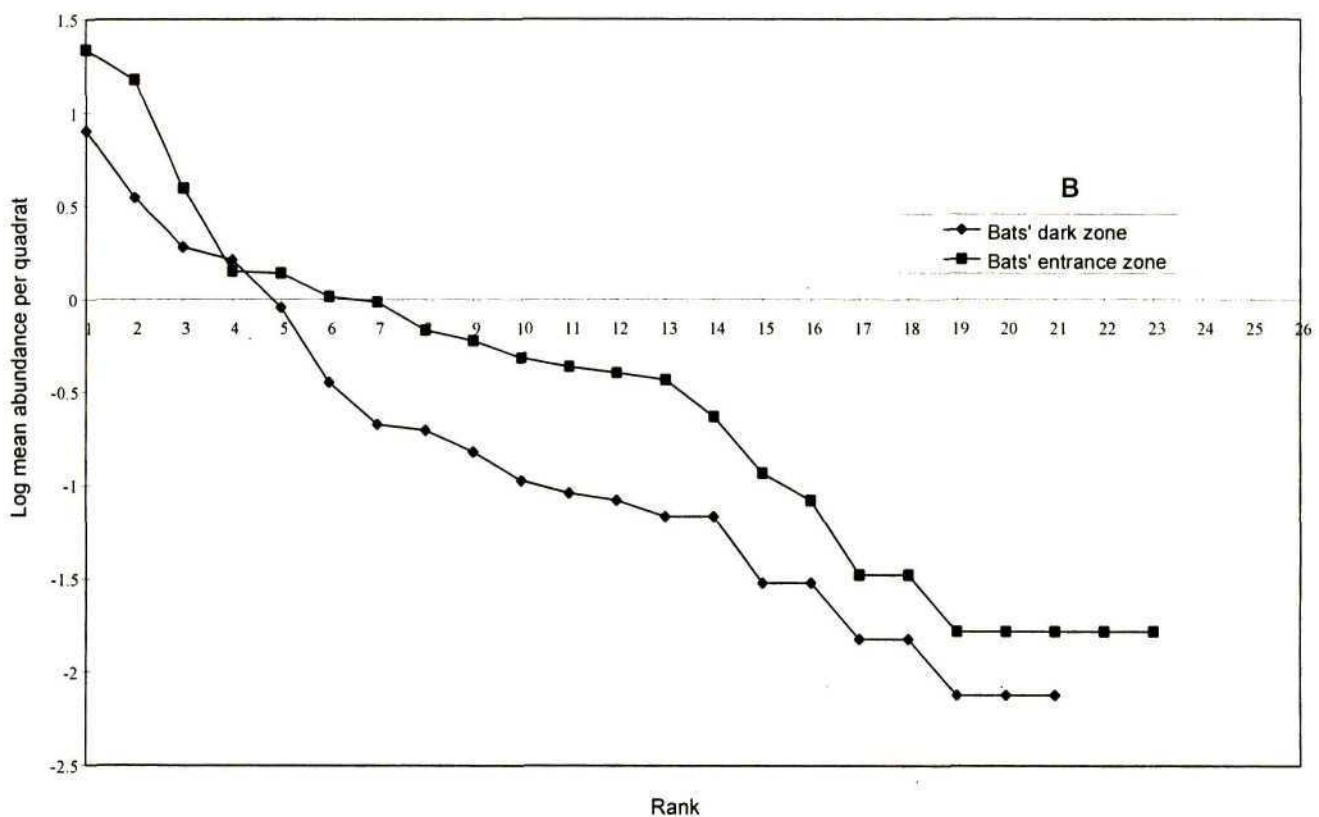
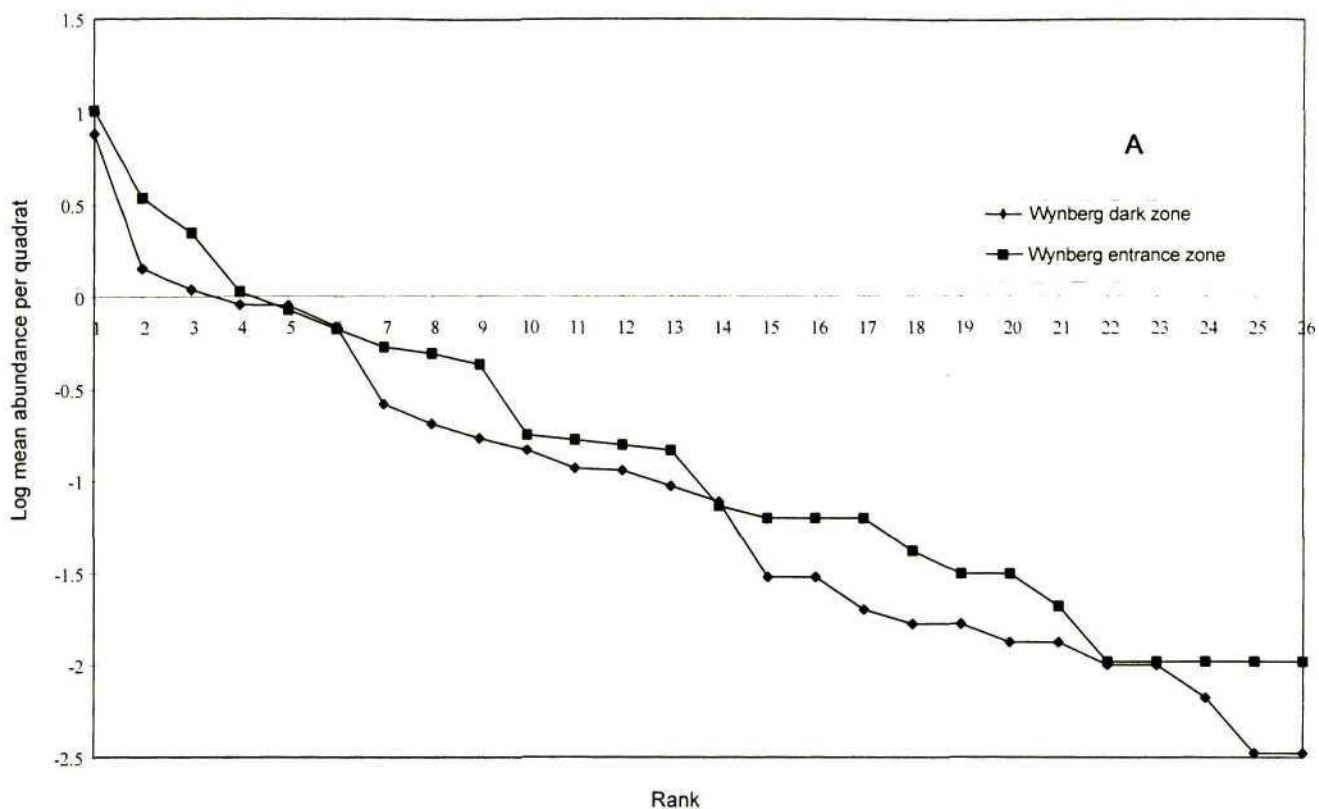


Figure 7. Rank-abundance curves for taxa counted in dark zones and entrance areas of:
A) Wynberg and B) Bats' caves. Monthly counts were conducted for one year in 11 dark zone and 5 entrance zone quadrats in Bats' cave and in 25 dark zone and 8 entrance zone quadrats in Wynberg cave (1 quadrat = 2m²).

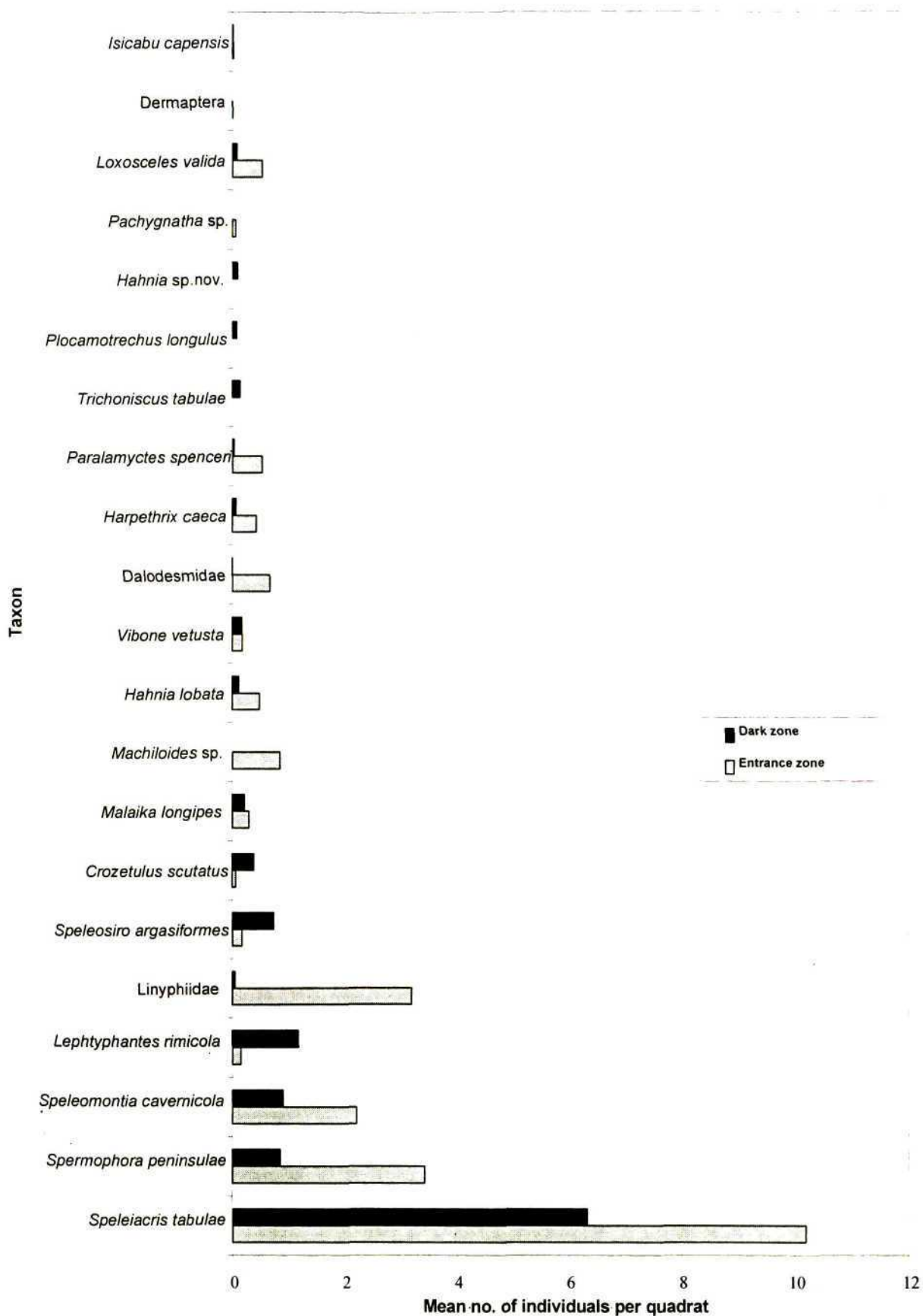


Figure 8. Mean abundances per quadrat of the most common cavernicoles in the dark zone and entrance zone of Wynberg cave. Monthly counts were made for one year in 25 dark zone and 8 entrance zone quadrats of 2m² each.

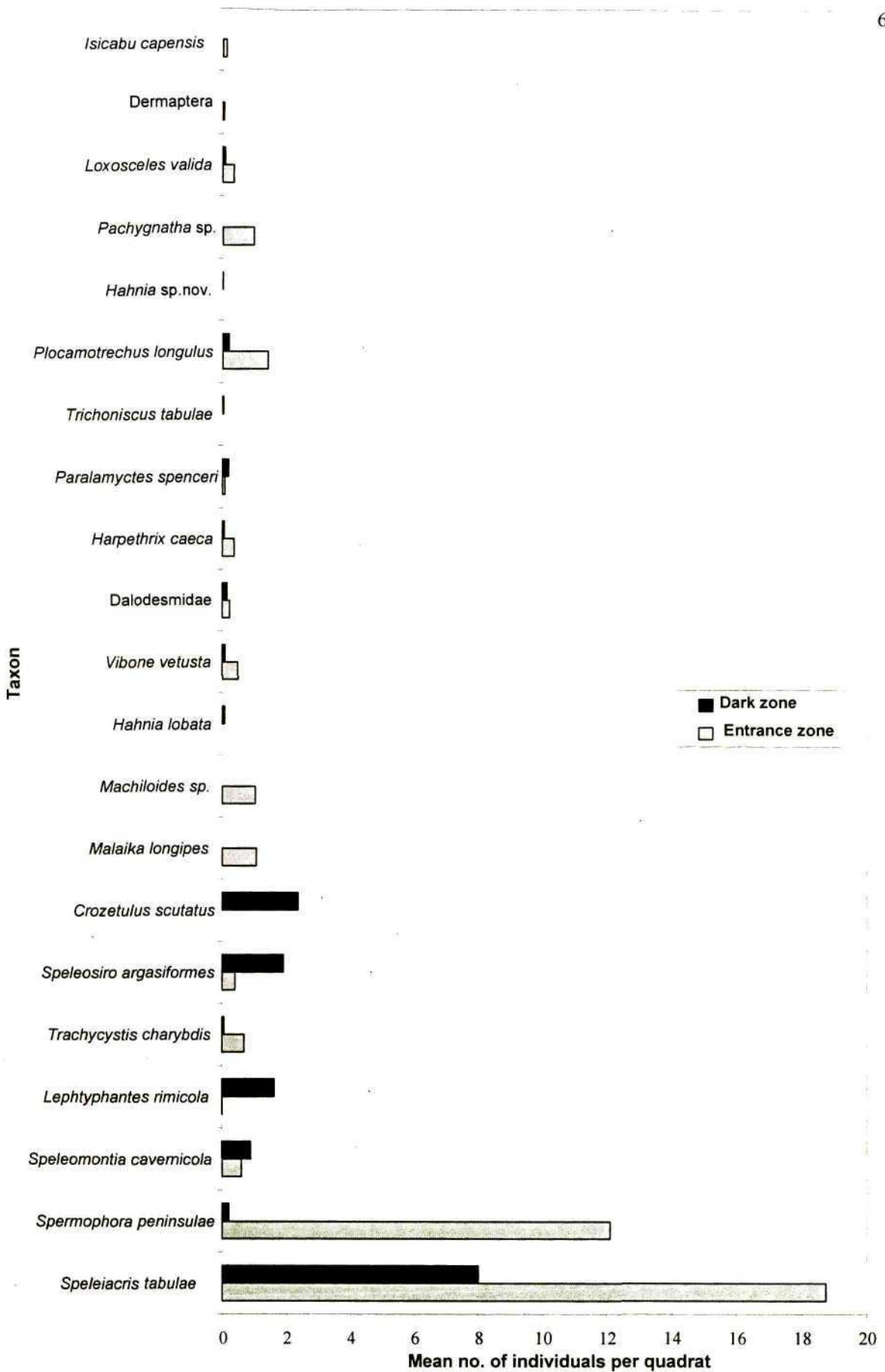


Figure 9. Mean abundances per 2m² quadrat of the most common cavernicoles in the dark zone and entrance zone of Bat's cave. Monthly counts were made for one year in 11 dark zone and 5 entrance zone quadrats.

Accuracy of counts is not only affected by cave morphology but also by the behavioural and biological features of the animal being counted. In the Table Mountain caves, count surfaces were often structurally complex with deep narrow crevices, leading to underestimates of abundance. Furthermore, small, sedentary species (e.g. *Cthoniella cavernicola*, *Crozetulus scutatus*, *Lepthyphantes rimicola*, *Isicabu capensis* and *Vibone vetusta*) may have been undercounted, while recounting of highly active species (e.g. *Speleiacris tabulae*) may in some instances have led to over-estimates of abundance.

The average number of individuals per quadrat, their biomasses and proportional contribution to the total population is given in Table 2. Species are arranged in decreasing order of abundance.

Species occurring in extremely high densities and species too small or inconspicuous for accurate counts, were excluded from quantitative analyses. i.e. guanobia, endogeans, small humicoles, aquatic and flying species. Separate comparisons of these species were made using abundance estimates (Table 3).

Table 4 gives the diversity indices calculated for the two Table Mountain caves, as well as for their respective entrance and dark zones. The corresponding rank-abundance curves are shown in Figures 6 and 7. Abundances of the most common entrance and dark zone species are compared in Figures 8 (Wynberg cave) and 9 (Bats' cave).

4.1. Population abundance

Rank-abundance curves for Bats' and Wynberg caves fitted neither the geometric nor the log-series distributions at the 95% confidence levels (Figure 6). Abundances were not normally distributed and a truncated lognormal distribution was the most likely fit (Magurran 1988).

Total mean abundance was substantially higher for Bats' cave than Wynberg cave (Table 2). Mean abundances were, however, not significantly different at the 95% level using the t-test on $\ln(x+1)$ transformed data. *Speleiacris tabulae* was by far the most abundant of the censused species (Table 2, Figure 6), contributing 49.6% and 44.99% to the total censused

populations of Wynberg cave and Bats' cave respectively. Mean *Speleiacris* abundance was significantly higher in Bats' than Wynberg cave at the 95% level of confidence (using the t-test on $\ln(x+1)$ transformed data).

Spermophora peninsulae was the second most abundant species in both caves, being significantly less abundant than *Speleiacris tabulae* and only contributing 9.09% and 17.75% to the total censused populations of Wynberg and Bats' caves respectively (Table 2, Figure 6). The mean abundance of *Spermophora* was significantly higher in Bats' cave than Wynberg cave, and significantly lower than the mean abundance of *Speleiacris tabulae* at the 99% confidence level (using the t-test on $\ln(x+1)$ transformed data).

Of the non-censused species (Table 3), the guanophilic *Schaefferia* sp.nov., ptiliids and staphylinids were estimated to be the most abundant taxa in both caves (Table 3). Once again, they appeared to be substantially more abundant in Bats' cave than Wynberg cave (most notably *Schaefferia* sp.nov.). However, as their abundances were merely estimates, no quantitative comparisons could be made and they were excluded from quantitative analyses. The Talitridae and Oniscidae were also common (Table 3), most notably in the humic soils of Bats' cave entrance.

The troglobites, *Crozetulus scutatus*, *Speleomontia cavernicola*, *Speleosiro argasiformes* and *Lephtyphantes rimicola*, and the troglophile, *Malaika longipes*, were moderately common in both caves (Table 2), contributing similar proportions (25.1% and 25.7%) to the total censused populations. However, a comparison of species abundances (Table 2) and the resulting rank-abundance curves (Figure 6) revealed that different species produced similar abundance distribution patterns in each cave. While *Speleiacris tabulae* and *Spermophora capensis* were the most common species in both caves, differences existed in the moderately common species of Opiliones and Araneae: *Speleomontia* was significantly more abundant (at the 95% level) in Wynberg cave, while *Speleosiro* had a significantly higher mean abundance in Bats' cave (using the t-test on $\ln(x+1)$ transformed data) (Table 2). Furthermore, the linyphiids (*Lephtyphantes* and an unidentified entrance species) and *Hahnia lobata* were significantly more abundant in Wynberg cave, while *Malaika longipes* and

Loxosceles valida were significantly more abundant in Bats' cave at the 95% level (using the t-test on $\ln(x+1)$ transformed data) (Table 2).

Most species were relatively rare, with fewer than 20 individuals having been counted during the study period. Wynberg cave had a larger number of rare species. Thirteen species were represented by only one or two counted individuals, this being the case for 11 species in Bats' cave (Figure 6). Both common and rare species were more abundant (in terms of mean number per quadrat) in Bats' cave, although the proportion they contributed to the total populations were similar (*Speleiacris* and *Spermophora* together accounted for 59.7% and 62% of Wynberg and Bats' cave populations respectively, while the rare species contributed 0.28% and 0.3%) (Table 2).

Peripatopsis alba was the rarest censused troglobite, two individuals having been counted in Wynberg cave and one individual in Bats' cave. *Cthoniella cavernicola* and *Hahnia* sp.nov. were also rare, each having been counted only twice in Bats' cave. *Cryptops stupendus* was undoubtedly rare with one unconfirmed sighting in Wynberg cave (excluded from quantitative analyses). The contribution of the censused terrestrial troglobites to the total populations, were similar in the two caves (2.33% in Wynberg cave and 2.13% in Bats' cave). Of these, however, the rare, relictual troglobites that were restricted to dark zones (i.e. *Hahnia* sp.nov., *Cthoniella cavernicola*, *Trichoniscus tabulae* and *Peripatopsis alba*) were more abundant in Wynberg cave (Table 2) and accounted for 1.49% of the total population, as opposed to 0.18% of the Bats' cave population. *Hahnia* sp.nov. and *Trichoniscus tabulae* were included with the moderately common species in Wynberg cave, but were rarer in Bats' cave where only four and two individuals of each species were counted respectively (Table 2).

A marked drop in abundance between the commoner and rarer species occurred in both caves (Figure 6). The commoner species (log mean abundances > -1) were species that were distributed throughout the caves, while the rarer species (log mean abundances < -1.5) generally had limited distributions and were restricted to entrance or deep zones (as discussed in Chapter 3). Once again, different species produced similar abundance distribution patterns in each cave (Table 2).

Abundance, rarity and commonality are influenced by habitat (Magurran 1988). Figure 7 compares the rank-abundance curves for entrance and dark zones in each cave while Figures 8 and 9 compare mean abundances of the most common species counted in entrance and dark zones of Wynberg and Bats' caves respectively. T-tests on $\ln(x+1)$ transformed data revealed a significantly higher mean abundance for the Bats' cave entrance fauna than for its dark zone fauna ($P < 0.05$). It was also significantly higher than the mean entrance abundance of Wynberg cave ($P < 0.05$). In Wynberg cave, abundance was also higher in the entrance zone, although this difference was not statistically significant ($P > 0.05$). Dark zone mean abundances did not differ significantly between caves ($P > 0.05$).

Common species that influenced the rank-abundance curves of entrance zones differed markedly from those species influencing dark zone rank-abundance curves (Figures 8 and 9). Furthermore, these species differed between caves. *Speleiacris tabulae* was the most abundant species in both zones of both caves. The most notable difference was the replacement of *Spermophora peninsulae* with *Crozetulus scutatus* and *Lepthyphantes rimicola* as the second most common species in the dark zones of Bats' and Wynberg caves respectively (Figures 8 and 9). In Bats' cave, *Crozetulus scutatus*, *Speleosiro argasiformes* and *Lepthyphantes rimicola* were common dark zone species, while in Wynberg cave *Lepthyphantes rimicola* and *Speleomontia cavernicola* were common. In entrance zones of both caves, *Spermophora peninsulae* was the second most common species (Figures 8 and 9). *Malaika longipes* and *Plocamotrechus longulus* were common in the entrance of Bats' cave only (Figure 9), while *Hahnia lobata* and an unidentified linyphiid species occurred almost exclusively in the entrance of Wynberg cave (Table 2, Figure 8). *Machiloides* sp. was common in both cave entrances, while *Speleomontia cavernicola* was particularly common in the entrance of Wynberg cave (Figure 8). Species that were rare were generally accidentals in entrance zones and troglobites in dark zones.

4.2. Species richness

Wynberg cave had the greater species richness, having 40 species compared with 34 in Bats' cave (Table 4, Figure 6). Figure 10 shows that this can be regarded as a representative assessment of species number, most species being present after 20 sampling units. Margalef's

Table 4. A comparison of diversity indices calculated for the whole of Bats' and Wynberg caves, and their entrance and dark zones considered separately. Abundance data was collected monthly for one year in 33 and 16 quadrats of 2m² each in Wynberg and Bats' cave respectively. Eight quadrats (Wynberg cave) and five quadrats (Bats' cave) occurred in entrance areas.

	Wynberg cave	Bats' cave	entrance zone		dark zone	
			Wynberg	Bats'	Wynberg	Bats'
Number of species (<i>S</i>)	40	34	32	26	28	23
Number of individuals (<i>N</i>)	6634	5259	2413	2947	4222	2304
Average no. per quadrat	13.20	27.40	25.14	29.82	15.41	19.20
Mean biomass per quadrat (mg)	3.07	8.80	7.94	17.40	4.42	7.89
Margalef's Richness index (<i>d</i>)	15.10	9.97	2.49	2.02	1.59	1.53
Pielou's evenness index (<i>J</i>)	0.53	0.55	0.70	0.53	0.50	0.67
Log series index (α)	6.17	5.64	5.20	3.93	4.06	3.56
Shannon-Wiener diversity index (<i>H'</i>)	1.97	1.95	1.82	1.36	1.14	1.43
Simpson's dominance index (λ)	0.21	0.22	0.22	0.41	0.52	0.32
Hill's second index (<i>N</i> ₂)	4.72	4.51	4.51	2.46	1.95	3.16

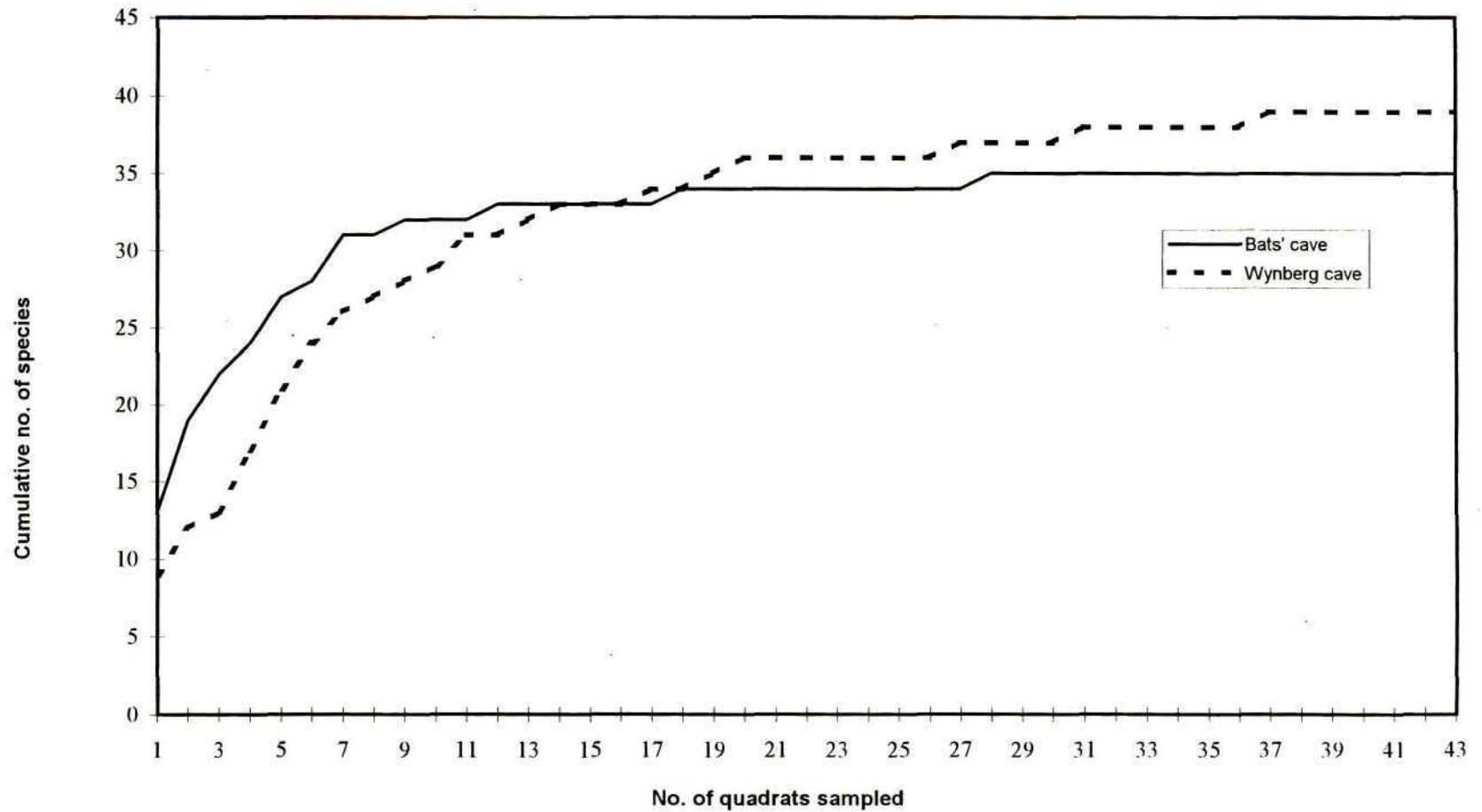


Figure 10. Species accumulation curves for sampling in 2m² quadrats in Bats' and Wynberg caves. In total, 396 and 192 quadrats were sampled in Wynberg and Bats' caves respectively. Most species were present after 20 sampled quadrats.

richness index (d) was also higher for Wynberg cave. Entrance zones were more species-rich than dark zones in both caves (Table 4, Figure 7). Analysis of Variance of $\ln(x+1)$ transformed data revealed that the difference in species richness (S) between caves was not significant, but Margalef's index was significantly higher for Wynberg cave ($P < 0.05$). Complementarity between caves, as measured by the Maczewski-Steinhaus (C) distance index (Colwell and Coddington 1995), was 0.28 with 31 species being common to both caves. This value was sufficiently close to zero to suggest that a reasonable representation of the Table Mountain cave fauna was sampled, and that the two caves had similar faunal compositions. Significant differences in richness between entrance and dark zones occurred for both caves, while differences in Margalef's index were only significant between zones in Wynberg cave.

4.3. Diversity

Depending on their emphasis on dominance or richness, diversity indices gave conflicting results. Therefore, as measures of diversity, they can only be used to monitor changes or trends. Because of the existence of a few highly abundant species (e.g. *Speleiacris tabulae* and *Spermophora peninsulae*) and a majority of relatively rare species, diversity indices based on richness rather than dominance were selected (Table 4). The log series index (α), regarded by Magurran (1988) as being the best richness-based discriminator between sites, indicated a higher diversity for Wynberg cave than Bats' cave (in both zones), and more diverse entrance zones than dark zones. The Shannon diversity index was significantly higher for Wynberg cave, while Simpson's index was significantly higher for Bats' cave ($P < 0.05$) (Analysis of Variance on $\ln(x+1)$ transformed data). Similarly, the entrance zones of the two caves differed significantly, the Shannon index being higher for Wynberg cave entrance, while Simpson's index was higher for Bats' cave entrance. This difference can be explained by Shannon-Wiener diversity index (H'), which takes evenness into account, being more sensitive to rare species, while Simpson's index is a dominance index emphasising the most common species (Magurran 1988). For this reason, it would be preferable to use the reciprocal of Simpson's index (Hill's N_2), in conjunction with the Shannon-Wiener index, as they would be more sensitive to population fluctuations of rare troglobitic species (e.g. *Peripatopsis alba* and *Cthoniella cavernicola*) and not place undue emphasis on *Speleiacris* and *Spermophora*

abundances. The differences between entrance and dark zones were not significant in either cave, nor was the difference between their dark zones.

4.4. Evenness

Bats' cave fauna generated a more even rank-abundance curve (Figure 6) and a higher value for Pielou's evenness index (Table 4). Moreover, its dark zone was more even than its entrance zone (Table 4, Figure 7). Wynberg's entrance zone was more even than its dark zone (Table 4, Figure 7) and more even than the entrance zone of Bats' cave (Table 4). Figures 3 and 4 illustrate the drop-off in abundance from *Speleiacris tabulae* to the moderately common species. This drop-off is most gradual for the entrance fauna of Wynberg cave (Figure 8) and dark zone fauna of Bats' cave (Figure 9). Analysis of Variance of $\ln(x+1)$ transformed data showed Wynberg entrance to be significantly more even ($P < 0.05$) than Bats' entrance, while the latter was significantly less even than its dark zone. However, the two zones of Wynberg cave did not differ significantly, nor did the caves differ significantly overall.

4.5. Biomass

Biomass data followed similar trends to the abundance data. i.e. Bats' cave had a higher overall mean biomass than Wynberg cave (Tables 2 and 4), and entrance zones generally had a greater mean biomass than dark zones (Table 4). Wilcoxon's signed rank test showed a significant difference between mean cave biomasses ($P = 0.005$). In both caves, entrance zone quadrats differed significantly from dark zones quadrats ($P < 0.05$). The higher mean biomass in Bats' cave suggests higher productivity in this cave.

Speleiacris tabulae was the main contributor to overall biomass by a clear margin, accounting for 79% and 60% of the total biomasses of Wynberg and Bats' caves respectively (Table 2). Although *Speleiacris* contributed markedly to both zones, the entrance zone biomasses were largely augmented by Araneae (most notably *Malaika longipes* and *Loxosceles valida*) (Figures 8 and 9) and, in Bats' cave, the mollusc, *Trachycystis charybdis*. The Araneae appeared to be major contributors to total biomass. In Bats' cave araneads accounted for 13.33% of the total biomass compared with only 3% in Wynberg cave (Table 2). Their abundances and biomasses appeared to reflect the densities of their guanophilic prey.

Therefore, the guano-rich entrance to Bats' cave had higher aranead and *Speleiacris* densities, which contributed to the higher overall cave biomass (Table 2, Figure 8). The estimated biomasses of the highly abundant guanophilic and humicolous fauna (Table 3) contributed very little to overall biomass.

4.6. Factors affecting community structure

Bats' and Wynberg caves were found to differ in faunal abundance, biomass and diversity. Bats' cave had a greater biomass and abundance per unit area, while Wynberg cave was more species-rich (Tables 2 and 4). As bat guano is the most abundant and voluminous food source in both caves, it seems likely that its distribution and abundance would have an important effect on community processes.

Bats' cave entrance is inhabited by a permanent and sizeable fruit bat colony. The bats provide a rich, concentrated guano supply that supports numerous guanophiles and their associated predators. The entrance zone is also relatively large and open (having a larger twilight zone) and environmental conditions are more unstable than within the smaller entrance zone of Wynberg cave (Table 6). In Wynberg cave, on the other hand, insectivorous bats provide a more diffuse and regular guano supply throughout the cave. Insectivorous bat guano and its associated guanophiles occur mostly in the dark zone. Therefore, the virtual absence of insectivorous bats from Bats' cave results in a relatively bat-free and guano-poor dark zone. These differences in guano distribution are reflected by measurements of soil nitrogen, energy and organic contents in entrance and deep zones of each cave (Table 6). The dark zone of Wynberg cave is also more extensive than that of Bats' cave so that a larger proportion of the cave is relatively stable (in terms of temperature, relative humidity and air currents) (Table 5). Differences in abundance and diversity between caves can be explained in terms of these differences in food availability, environmental stability and cave topography.

The factors affecting diversity and community structure in caves has been addressed by several authors (e.g. Christiansen *et al.* 1961; Poulson and Culver 1969; Poulson and White 1969; Culver 1970; Christiansen 1992; Tilman and Downing 1994). Stability, rigor and predictability are considered primary explanations for diversity (Elton 1958; Pianka 1967;

May 1973, 1981, 1984; Pimm 1982, 1984). Secondary explanations are habitat diversity (MacArthur and MacArthur 1961; Pianka 1966; MacArthur and Wilson 1967; Williamson 1981) and food availability (Margalef 1963), while tertiary explanations are predation, competition and niche overlap (Paine 1966).

Populations of cave arthropods are generally considered to be food-limited (Peck 1976). Therefore, population density and species diversity would likely to be greatest where food is most abundant. This appears to be the case for the Table Mountain caves. Both diversity and abundances were higher in entrance zones that had higher plant debris and soil nutrient contents (Table 6). This is consistent with other findings. Poulson and Culver (1969) found the diversity of terrestrial arthropods in the Flint-ridge Mammoth cave system to be positively correlated with organic content of the substrate. In Crossing Cave, Alabama, Peck (1989) found diversity to be highest a short distance into the dark zone where detritus in fall was greatest. A second peak in diversity coincided with increased amounts of *Hadenoeus* cricket guano. McKinney (1975) found that the troglobitic predatory beetles *Pseudonaphthalmus menetriesi* and *P. pubescens* became more abundant when prey density was increased by adding leaf litter. Finally, in a cave in the Kruger National Park, Braack (1989) found both species richness and abundance to be related to bat colony size (i.e. guano input) and cave zone. Culver (1970) observed that higher diversities occurred where epigean and cave faunas mixed in entrance zones.

Greater food availability allows for specialised feeding behaviours and hence, the accommodation of more species (MacArthur and Levins 1964; MacArthur 1965). According to Margalef (1963), a few opportunistic species predominate where productivity is sporadically high and many species co-exist where productivity is stable. In the Table Mountain caves, guano is the most voluminous and constant food source. Guano is typically exploited by numerous highly vagile species that are able to build up populations rapidly to exploit a temporary resource (Howarth 1983). These guanophilic species were highly abundant in the Table Mountain caves but did not contribute greatly to overall biomass (Table 3). Their inclusion in future quantitative analyses could provide a valuable insight into community processes. Associated with them were their aranead predators that contributed

significantly to overall cave biomasses (Table 2). *Speleiacris tabulae* was also most abundant in guano-rich areas.

In Bats' cave, the concentrated guano deposits in the entrance zone supported higher mean abundances and biomasses so that the rank-abundance curve for the entrance zone closely approximated that produced for the cave as a whole (Figures 6 and 7b). This suggests that the bat guano concentrations in Bats' cave entrance greatly affect the overall cave community. Furthermore, the higher mean abundance and biomass of Bats' cave implies that its productivity is greater than that of Wynberg cave. However, if productivity were the only factor shaping community structure, diversity would be expected to be greater in Bats' cave. This is clearly not the case, indicating that other factors affect diversity and species richness in Wynberg cave.

Several cave studies have found no correlation between diversity and food availability. Diversity was found to be greater in the nutrient-poor deep zones of caves in France (Christiansen and Bullion 1978) and in Otter Hole, Wales (Chapman 1979). Christiansen and Bullion (1978) attributed this to the greater stability of deep zones. Chapman (1979) found habitat diversity to be an important variable in this regard. Similarly, Braack (1989) found cave area to be important in a Kruger National Park cave. Longer caves generally have a greater number of available niches and, therefore, accommodate more species. They also have more stable environmental conditions. In the Greenbrier valley, West Virginia, Culver (1970) found rigor and predictability to be important, while the presence of predators, food, habitat diversity and stability were not.

The relationship between diversity and stability is a complicated one (MacArthur 1955; May 1974, Tilman and Downing 1994). Stability favours predictability and lowers extinction rates (Poulson and Culver 1969; Culver 1970). Furthermore, a stable environment leads to stable productivity which allows for higher predation rates. This causes decreased competition and greater diversity in the lower trophic levels (Poulson and Culver 1969). However, Mueller-Dombois and Howarth (1981) found that in Hawaiian cave ecosystems diversity was not necessarily related to stability, and they challenge the assumption that dark zones are always nutrient-poor. Howarth (1983) points out that the role of mesocaverns in food availability is

not known. In Wynberg cave, the dark zone is provided with a constant and diffuse (i.e. predictable but not highly abundant) supply of guano. This would allow many species to co-exist 'where productivity is low' (Margalef 1963). Furthermore, the seasonal stream in the bottom passageway undoubtedly plays a role in allochthonous food transmission and input. It is possible that this food source has been underestimated and is responsible for the higher overall diversity of Wynberg cave. Flooding would increase food availability and rigor but decrease stability, thus having conflicting effects on diversity. Poulson and Culver (1969), for example, found diversity in the Mammoth cave system to be correlated positively with substrate diversity and organic content, but negatively with intensity of flooding.

It has been found that the number of terrestrial cave species is strongly affected by area (Culver *et al.* 1973; Braack 1989). Clearly this is an additional factor in the Table Mountain caves. A larger cave would have greater habitat heterogeneity, thus offering more available niches to more species (Chapman 1979). A large dark zone would favour troglobitic species and would be more stable, thus reducing extinction rates and preserving rarity. This has led to caves being compared with islands (both having low immigration and extinction rates) and their communities discussed in terms of island biogeographic theories (Barr 1967; Culver 1970, 1971; Culver *et al.* 1973).

In Wynberg cave, the existence of a relatively extensive dark zone with a relatively constant food resource, means that dark zone habitat heterogeneity, stability and food availability are all greater, thus increasing species diversity. On an evolutionary time scale, this has no doubt promoted the persistence of phylogenetically unique relictual groups that became extinct elsewhere.

4.7. Distribution of abundances

The relative abundances of species differed in the two caves (Table 2, Figure 6) and the two zones (Figures 8 and 9), indicating that dark and entrance communities differed between caves. The entrance community of Bats' cave was dominated by *Speleiacris tabulae*, *Spermophora peninsulae*, *Malaika longipes* and *Plocamotrechus longulus*, while in Wynberg cave, *Speleiacris tabulae*, *Spermophora peninsulae*, Linyphiidae and *Speleomontia cavernicola* were most abundant. In the dark zones, *Speleiacris tabulae*, *Crozetulus scutatus*,

Speleosiro argasiformes and *Lephtyphantes rimicola* were most abundant in Bats' cave, while *Speleiacris tabulae*, *Lephtyphantes rimicola*, *Speleomontia cavernicola* and *Speleosiro argasiformes* were abundant in the dark zone of Wynberg cave. Differences in entrance community species can largely be explained in terms of differences in availability of bat guano and its associated fauna. This does not, however, explain the significant differences between mean abundances of dark zone troglobitic species that are not guano-dependent. Clearly, there are other factors (e.g. moisture) causing differences in the abundances of *Crozetus scutatus*, *Speleosiro argasiformes* (more abundant in Bats' cave), *Lephtyphantes rimicola*, *Hahnia* sp.nov. and *Speleomontia cavernicola* (more abundant in Wynberg cave). These factors are explored further in Chapter 6.

Speleiacris tabulae and *Spermophora peninsulae* were the most common of the censused species, accounting for 58.7% and 62.75% of Wynberg cave and Bats' cave populations respectively. *Speleiacris tabulae* accounted for almost half (49.64% and 44.99%) of the censused populations. Their population densities appear to be markedly higher than that of *Dolichopoda geniculata* (Raphidophoridae) in Valmarino cave, Italy. Carchini *et al.* (1994) found densities of 0.68 to 0.70 *Dolichopoda* individuals per square metre, compared with approximately 3.20 *Speleiacris* individuals per square metre in Wynberg cave. These differences are probably related to the warmer conditions within Table Mountain caves and greater food availability in the form of fruit bat guano (large frugivorous bats being absent from Europe). Overestimates of the Wynberg cave population may also have occurred, as the complexity of count surfaces increased actual quadrat surface areas above two square metres.

Common species were more common (in terms of mean number per quadrat) in Bats' cave, while rare species were rarer in Wynberg cave (Table 2, Figure 6). In terms of numbers of species, more common species (i.e. species having a mean abundance per quadrat of greater than one) occurred in Bats' cave (six species in Bats' cave, three in Wynberg cave), while rarer species (with mean abundances per quadrat of less than 0.05) occurred in Wynberg cave (13 species in Wynberg cave, 11 in Bats' cave).

Most species were relatively rare. Rarity in caves can be accidental or real (Poulson and White 1969). Accidental rare species include twilight zone species and aquatic interstitial

Table 5. A tentative categorization of Cape Peninsula troglobitic invertebrates according to the criteria listed in the *IUCN Red List Categories (1994)*. Total population sizes in all Peninsula caves are not known and categorization may be subject to modification with the availability of additional abundance and distribution data.

Species	Tentative category	Reason
<i>Spelaeogriphus lepidops</i>	Critically Endangered/ Endangered	Extent of occurrence < 100km ² . Area of occupancy < 10km ² .
<i>Paramelita barnardi</i>	Data Deficient / Endangered	Extent of occurrence < 5000km ² . Abundance not known.
<i>Protojanira leleupi</i>	Data Deficient / Endangered	Extent of occurrence < 5000km ² . Abundance not known (apparently rare).
<i>Trichoniscus tabulae</i>	Endangered / Vulnerable	Extent of occurrence < 5000km ² . Apparently rare.
<i>Peripatopsis alba</i>	Critically Endangered/ Endangered	Extent of occurrence < 100km ² . Apparently very rare.
<i>Cthoniella cavernicola</i>	Data Deficient / Endangered	Extent of occurrence < 5000km ² . Apparently very rare.
<i>Cryptops stupendus</i>	Data Deficient / Critically Endangered	Extent of occurrence < 5000km ² . Abundance not known (apparently very rare).
<i>Hahnia</i> sp.nov.	Data Deficient / Critically Endangered	Extent of occurrence possibly < 100km ² . Apparently rare.
Dermaptera (sp.nov.)	Data Deficient / Critically Endangered	Extent of occurrence possibly < 100km ² . Apparently very rare.
<i>Crozetulus scutatus</i>	Endangered	Moderately common but extent of occurrence < 5000km ² .
<i>Lepthyphantes rimicola</i>	Endangered	Moderately common but extent of occurrence < 5000km ² .
<i>Speleomontia cavernicola</i>	Endangered	Moderately common but extent of occurrence < 5000km ² .
<i>Speleosiro argasiformes</i>	Endangered	Moderately common but extent of occurrence < 5000km ² .
<i>Harpethrix caeca</i>	Endangered	Moderately common but extent of occurrence < 5000km ² .
<i>Schaefferia</i> sp.nov.	Endangered	Common but extent of occurrence < 5000km ² .
<i>Speleiacris tabulae</i>	Endangered	Common but extent of occurrence < 5000km ² .

species, while real rarity occurs in marginally adapted troglophiles, recently isolated troglobites or relictual troglobites (Poulson and White 1969; Culver 1986). In the Table Mountain caves, rare species were clearly either accidentals (e.g. *Trox* sp., Curculionidae) or relictual troglobites. The troglobites *Peripatopsis alba*, *Cthoniella cavernicola* and *Cryptops stupendus* were observed fewer than ten times. Similar examples of rarity have been recorded, for example, from the Appalachian Mountains, USA, where some pseudoscorpion species are known from fewer than ten individuals (Culver 1986). Similarly, in Tasmania the carabid *Goedetrechus mendumae* is known from fewer than twenty specimens (Clarke 1988, 1997).

Rarity is important in ecosystem function for one of three reasons:

- rare species may have a collectively important role,
- rarity may occur in large species at the top of the food chain (such as *Peripatopsis alba*),
or
- a rare species may fulfil an important role under adverse conditions (Lovejoy 1988, 1995).

The specialisation and limited distribution of troglobites in an island-like habitat make them particularly susceptible to even temporary or local modifications of their environment (Culver 1970, 1986). Many cave animals are considered endangered (Howarth 1982; McCracken 1989; Arita 1993) and many have become extinct (Richards 1971; Tuttle 1977). The rarity and restricted distributions of relictual troglobites in the Peninsula caves emphasises the need to establish their vulnerability to extinction. Therefore, tentative *IUCN Red List Categories* (1994) were allocated to Peninsula troglobites (Table 5). Categorisation, however, proved difficult, as certain criteria did not seem applicable to cave environments. The major problem was one of scale. In caves, the extent of the mesocaverns and cave depth are additional dimensions that need to be considered in determining area of occupancy as well as extent of occurrence. These are unfortunately seldom known. Instead, only macrocavern length and breadth are considered, leading to underestimates in area of occupancy. Therefore, immobile species that tended to occur in crevices may have been far more widespread in terms of the mesocavernous area than the macrocavernous area. To overcome the uncertainty of mesocavernous distributions of animals, extent of occurrence

was assumed to include the entire pseudokarst area where the animal occurred (i.e. Kalk Bay / Silvermine or Table Mountain), even if it was only known from one cave (accessible to humans). A further categorisation problem was the lack of abundance and distributional data from the Kalk Bay caves, and lack of previous quantitative abundance data from all Peninsula caves. Therefore, past population fluctuations could not be assessed. Population sizes and distributions of troglobitic species restricted to Kalk Bay caves also remained unassessed.

According to the *IUCN Red List Categories* (1994), *Peripatopsis alba* and *Spelaeogriphus lepidops* can be categorised as Critically Endangered because of their phylogenetic uniqueness and the extent of their occurrence being less than 100km² within Table Mountain pseudokarst (Table 5). *Spelaeogriphus lepidops*, being aquatic, has an area of occupancy of less than 10km², only occurring in perennial pools and streams. Furthermore, the population size of *Peripatopsis alba* appears to be particularly low, only four individuals having been seen during the course of this study. Future determination of the number of adult individuals is a matter of priority. *Cryptops stupendus* is undoubtedly rare, with only one unconfirmed sighting during the study period. It is likely to be Critically Endangered but until more is known of its population abundance, it should be regarded as Data Deficient. The troglobitic dermapteran and *Hahnia* sp.nov., have not been recorded from Kalk Bay caves and may therefore also be Critically Endangered on account of their restricted distributions. Further data is required for conclusive categorisation.

Being endemic to the Cape Peninsula, all troglobites and several trogliphiles should be considered Endangered (extents of occurrence <5000km²) according to the *IUCN Red List Categories* (1994) (Table 5). Their phylogenetic uniqueness as Gondwanan relicts would also enhance their threatened status. However, cave depth was not considered as an additional parameter and lack of abundance data hinders categorisation. Further research is urgently required to assess the abundance and distributions of these species, most notably, *Protojanira leleupi*, *Paramelita barnardi* (both being restricted to Kalk Bay caves and thought to be rare), *Cryptops stupendus*, *Hahnia* sp.nov., *Cthoniella cavernicola*, Dermaptera (sp.nov.) and *Trichoniscus tabulae* (all apparently very rare).

4.8. Conclusion

Differences in abundance and diversity between Bats' and Wynberg caves can largely be attributed to differences in food availability and dark zone habitat heterogeneity (or area). Bat guano was found to be the single most important factor shaping community structure. Caves and zones with high guano availability (Bats' cave and, in particular, its entrance)(Table 4) yielded a higher mean biomass and species abundance. In Wynberg cave, the relative stability and extent of the dark zone resulted in greater diversity and species richness.

As May (1995) points out, "number of species *per se* is not an accurate measure of biodiversity". Undescribed and unrecorded species are often excluded, a very real possibility in the Table Mountain caves. Biodiversity should take into account both phylogenetic uniqueness and rarity. The endemism of rare, relictual and threatened troglobites would thus contribute substantially to the biodiversity of the area as a whole. Furthermore, ecological diversity (niche breadth and habitat heterogeneity) is often allied to species diversity (Magurran 1988). May (1995) suggests that environmental or feature patterns be used as a surrogate for lower-level biodiversity. In Wynberg cave, the greater habitat heterogeneity of the dark zone means that a greater number of rare species and a greater abundance of troglobitic species can be accommodated. Therefore, in terms of conservation of the Table Mountain caves, habitat heterogeneity (or area) within the dark zone is important.

In addition, ongoing population monitoring (using richness-based indices and rank-abundance curves) should be conducted to detect possible community disturbances and abundance trends, most notably for threatened endemic species such as *Peripatopsis alba*, *Spelaeogriphus lepidops*, *Cryptops stupendus*, *Protojanira leleupi* and *Paramelita barnardi*.

5. Community distribution patterns.

Spatial distribution patterns are an important characteristic of communities and have major implications for conservation (Southwood 1977). Aggregated or clumped distribution patterns may indicate the existence of favourable biotic or abiotic conditions for survival and reproduction within a particular habitat. Only once a pattern has been established can hypotheses be generated concerning the underlying causes. Factors affecting distribution can be extrinsic (the physical environment) or intrinsic (species interactions) and, once established, these can be used for predictive purposes in conservation considerations.

Caves are highly zonal habitats (Howarth 1983), twilight, entrance and deep zones being clearly discernible in the Table Mountain caves. This zonal cave topography is reflected in the physical environment, and cavernicolous animals become segregated into communities according to these environmental conditions. Furthermore, species exploiting the same food source often form communities that interact and support food webs in the cave (Howarth 1988). These may overlap with other communities as predators and generalists exploit more than one resource, resulting in complex community associations (Howarth 1983).

To detect community distribution patterns in the Table Mountain caves, quadrats were compared in terms of taxon abundance and composition, thus producing an ordination of cave communities. The dendrograms and multidimensional scaling (MDS) ordinations based on Bray-Curtis similarities of fourth-root transformed taxon abundance data (considering only the censused taxa) are given in Figures 11 and 13 for Wynberg and Bats' caves respectively. Dendrograms and MDS ordinations based on taxon presence or absence data (including the thirteen uncensused taxa) are given in Figures 12 and 14 for Wynberg and Bats' caves respectively. The uncensused taxa included mostly very small and abundant humicoles (e.g. talitrids and oniscids) and guanophiles (e.g. staphylinids and ptiliids), as well as trogloneic dipterans and lepidopterans.

5.1. Wynberg cave

The dendrograms and MDS ordinations of Wynberg cave quadrats, compared in terms of taxon abundances (Figure 11) and taxon presence or absence (Figure 12), separated out five community groups (A to E) at the 55% similarity level. Groups reflected cave zonation to a large extent. That is, quadrats in each zone were the most similar to each other, therefore being grouped together. At the 60% similarity level, group D was subdivided into two subgroups (D1 and D2) so that groups A and D1 contained only entrance quadrats while group D2 contained transitional zone quadrats. Deep zone quadrats fell into groups B, C and E.

Quadrat grouping at the 60% similarity level in terms of taxon abundance data (Figure 11) reflected cave topography to a large extent:

- Group A contained the first three quadrats situated in the twilight zone, thus being very exposed to fluctuations in surface conditions.
- Group D1 contained the remaining entrance zone quadrats. These were physically separated from group A quadrats by a two metre vertical drop, thus having lower light intensities and being less exposed to surface conditions, but still exhibiting the environmental fluctuations and accumulation of plant matter typical of cave entrances. In the MDS plot, however, (Figure 11b) quadrat 5e appears to be equidistant from 3e and 6e, indicating it to occur on the boundary between the twilight zone quadrats, while the remaining entrance quadrats (4e, 5e, and 6e) are closer to transitional zone quadrats.
- Group D2 contained all transitional zone quadrats as well as quadrat 8e (doubt existed over the placement of this quadrat within entrance or transitional zones and it was probably situated on the entrance-transitional zone boundary). These were all dark zone quadrats separated from preceding quadrats by a cave 'corkscrew'. They exhibited slight environmental variability and debris infall.
- Group E contained the majority of deep zone quadrats, all being situated in the bottom stream passageway with a sandy floor and permanently damp walls.
- Groups B (quadrats 16d and 17d) and C (quadrats 28d, 29d and 30d) were outlying deep zone groups. Quadrats 16d and 17d occurred at the end of the bottom passageway. They

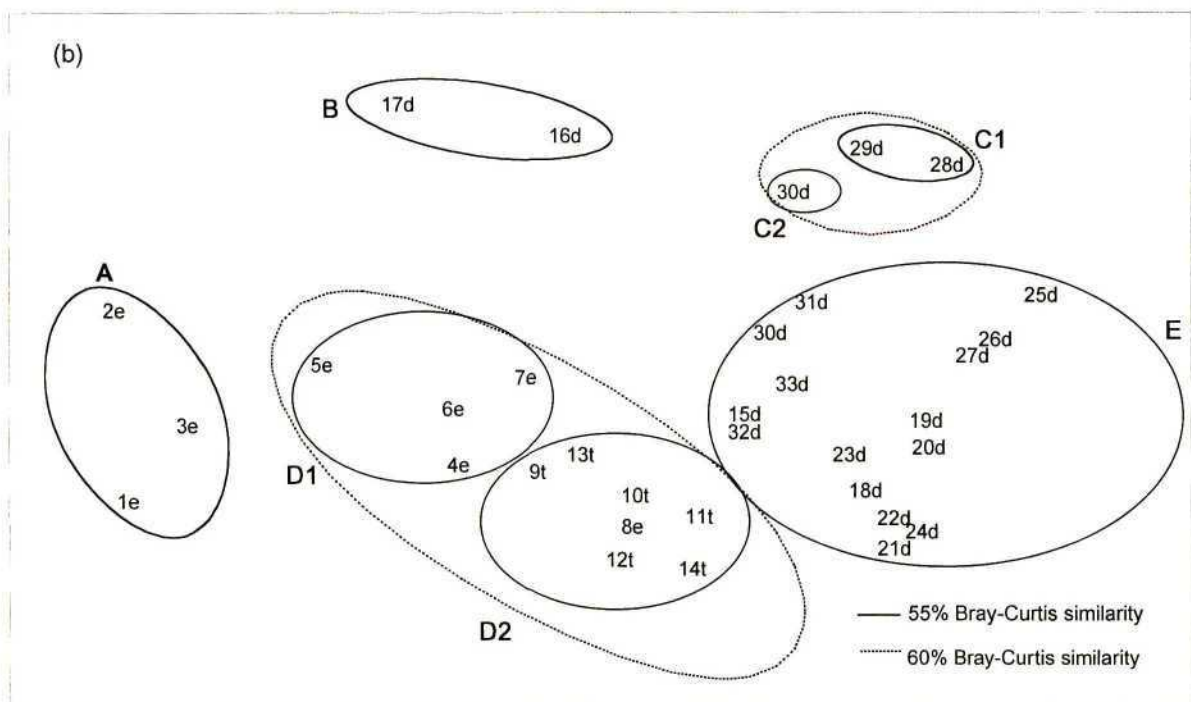
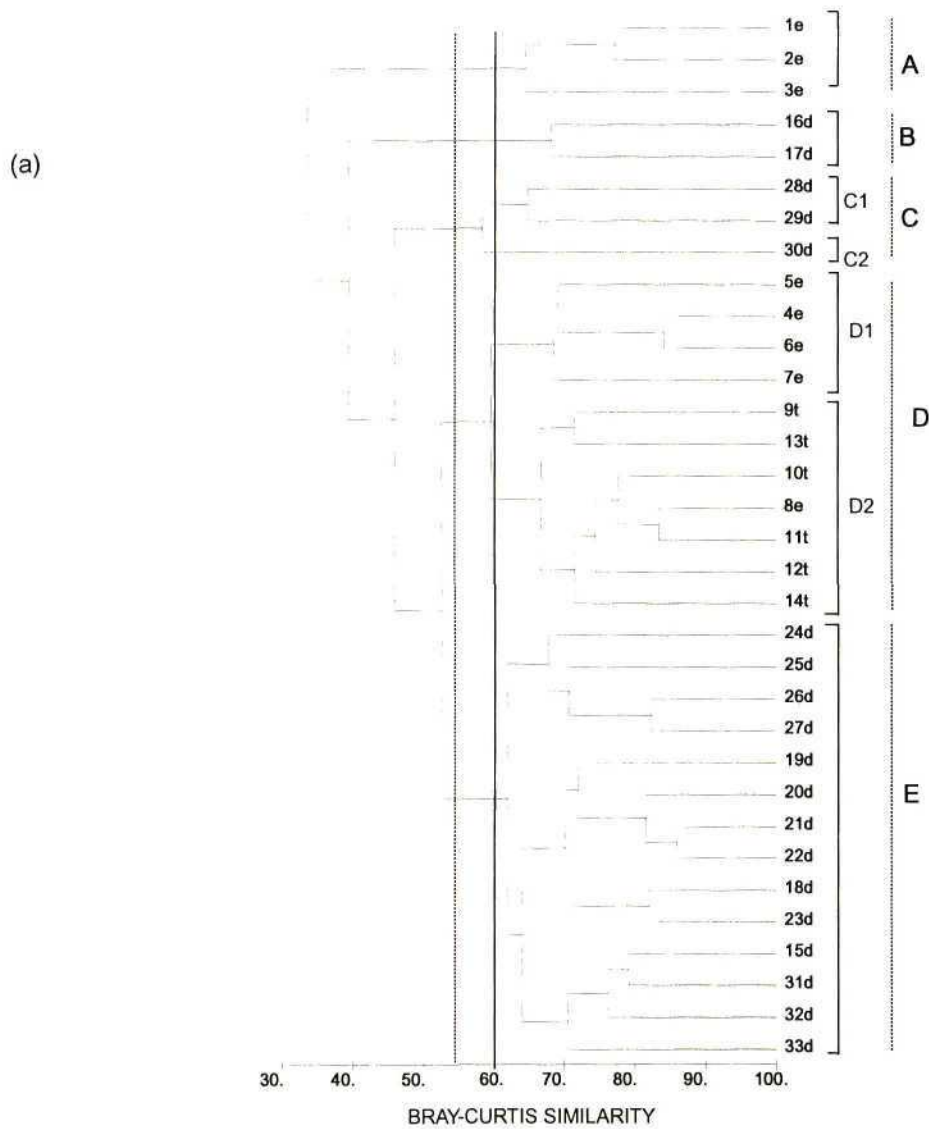


Figure 11. Dendrogram for hierarchical clustering (a) and MDS ordination plot (b) for 33 2m²-quadrats (with 12 replicates each) in Wynberg cave based on Bray-Curtis similarities of 4th-root transformed taxon abundance data. Quadrats were placed 5m apart along a transect into the cave and are numbered sequentially from the entrance (1) to deep zone (33). e=entrance zone, t=transitional zone, d=deep zone. Groups separated out at the 55% similarity level (A to E) and 60% level (A, B, C1, C2, D1, D2, E) are demarked with dotted and solid lines respectively. (stress = 0.11)

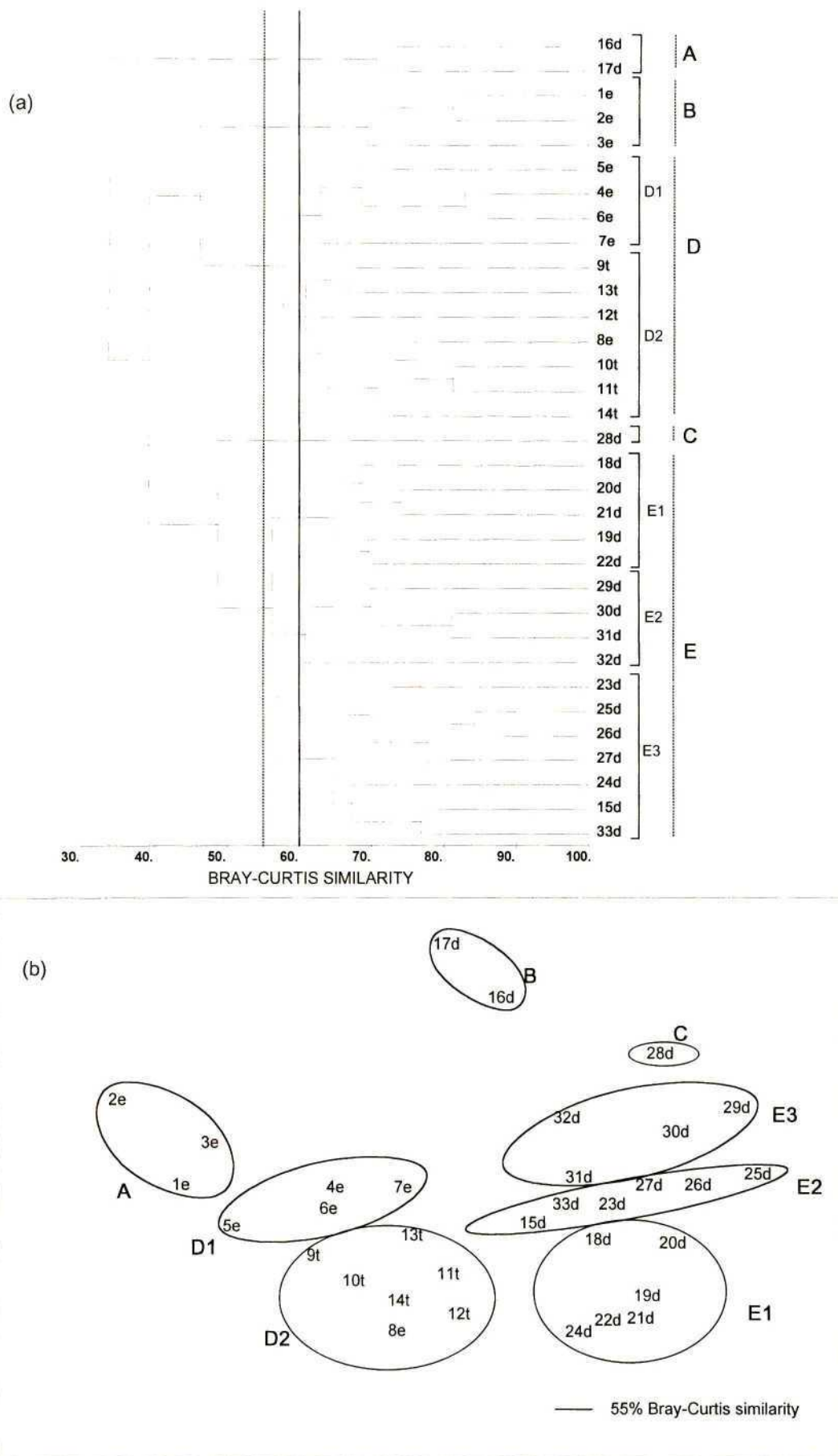


Figure 12. Dendrogram for hierarchical clustering (a) and MDS ordination plot (b) for 33 $2m^2$ -quadrats (with 12 replicates each) in Wynberg cave based on Bray-Curtis similarities of taxon presence / absence data (including censused and uncensused species). Quadrats were placed 5m apart along a transect into the cave and are numbered sequentially from the entrance (1) to deep zone (33). e=entrance zone, t=transitional zone, d=deep zone. Groups separated out at the 60% similarity level (A to E) and 55% level (A, B, C, D1, D2, E1, E2, E3) are demarkated with dotted and solid lines respectively. (Stress = 0.11)

were exposed to air currents from an overlying entrance, had rocky floors with rich deposits of guano.

In the dendrogram derived from taxon presence or absence data (Figure 12), the deep zone quadrats in group E were further subdivided into three subgroups (groups E1, E2 and E3) at the 60% similarity level. All other groups were essentially the same as discussed above (with the exception of quadrats 29d and 30d which were incorporated into group E).

One-way analysis of similarities (Anosim) on fourth-root transformed abundance data revealed significant overall differences at the 0.01% significance level, indicating the existence of distinct community distribution patterns. Communities clearly reflected cave zonation. Twilight, entrance, transitional and deep zone communities were indicated by the grouping together of quadrats within each of these zones. The existence of more than one deep zone group (groups B, C, E1, E2 and E3), however, indicated that cave zonation, although the primary factor, was not the sole factor affecting community distribution patterns.

Groups A, B and C were found not to be significantly different from one another at the 5% level (one-way Anosim on fourth-root transformed abundance data). Similarly, groups D1, D2 and E did not differ significantly from one another, but each differed significantly from groups A, B and C. This suggests that the entrance community (represented by group D1 quadrats) was more similar to the deep zone community (group E quadrats) than to the other entrance zone community (group A quadrats). Similarly, the deep zone community (group E quadrats) was more similar to entrance and transitional communities (group D1 and D2 quadrats) than to other deep zone communities (groups B and C). Therefore, although the overall delimitation of communities was strongly correlated with distance from the entrance (i.e. cave zonation), community boundaries were not clearly defined and interzonal community similarities were not explained.

The dendrogram derived from taxon presence or absence similarities (Figure 12) gave a clearer reflection of zonal communities. One-way Anosim revealed a significant difference at the 5% level, between the entrance quadrats (group D1), transitional zone quadrats (group D2) and deep zone quadrats (group E), thus representing clear entrance, transitional and deep zone communities. This can largely be explained in terms of the distribution of uncensused

humicoles and troglonexes (Figures 3 and 4, Table 1). Humicoles were common in entrance zones but were largely absent from transitional and deep zones. Their inclusion in distributional analyses, therefore, emphasised the similarity of all entrance quadrats and their dissimilarity to dark zone quadrats. Groups containing entrance quadrats (A and D1) were not significantly different. However, both differed significantly from transitional zone quadrats (D2) at the 5% level (D1 and D2 were not significantly different in the analysis of taxon abundance data). Within the deep zone (group E quadrats), the patchy distribution of bat guano and its associated guanophiles would seemingly explain the subdivision of the deep zone community. Groups E2 and E3 were not significantly different from one another at the 5% level (one-way Anosim) but both differed significantly from group E1.

5.2. Bats' cave

The dendrograms and MDS ordinations of Bats' cave communities based on abundance data (Figure 13) and taxon composition (Figure 14) show that, at the 55% similarity level, there was a clear separation of quadrats into a group containing all entrance zone quadrats (group A), and a group containing all dark zone quadrats (group B). This is indicative of the highly zonal nature of Bats' cave resulting in zonal community distribution patterns.

Topographically, the cave is relatively deep and short, so that the progression from entrance to deep zone occurs over a continuous gradient. This is reflected by the more-or-less sequential arrangement of quadrats in the dendrograms (Figures 13 and 14). Sequencing in entrance zone quadrats was the most pronounced, indicating greater homogeneity in the dark zone. Uncertainty existed over the exact demarcation of zonal boundaries. For example, quadrat six was assigned to the transitional zone but it was similar to entrance zone quadrats in having a large amount of plant debris. Therefore, in the dendrogram based on taxon presence or absence similarities (Figure 14), quadrat six was grouped with entrance zone quadrats at the 65% similarity level, while in the dendrogram derived from taxon abundance similarities (Figure 13), it was grouped with dark zone quadrats. Similarly, under extreme surface conditions (such as strong winds), slight environmental variability was detected in quadrats 7 to 12, suggesting that they could, in fact, be transitional zone quadrats. Boundaries may also have been obscured by the lumping of seasonal data.

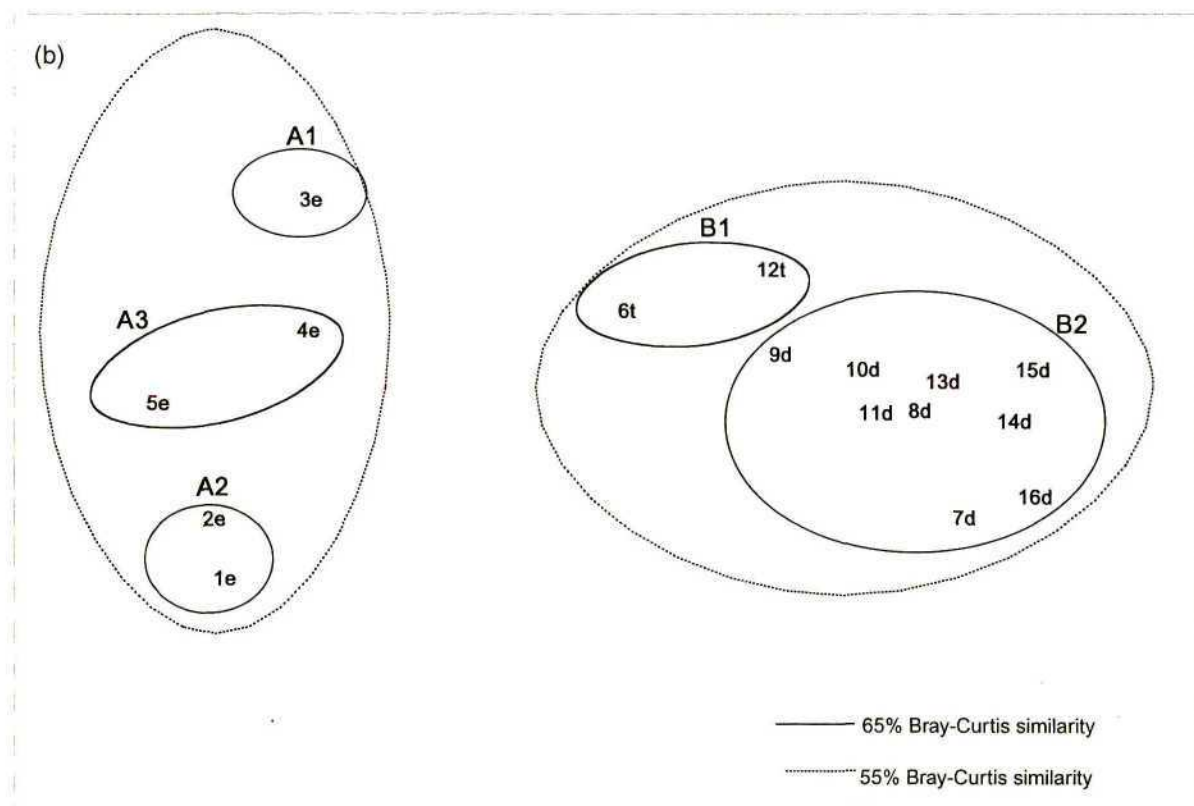
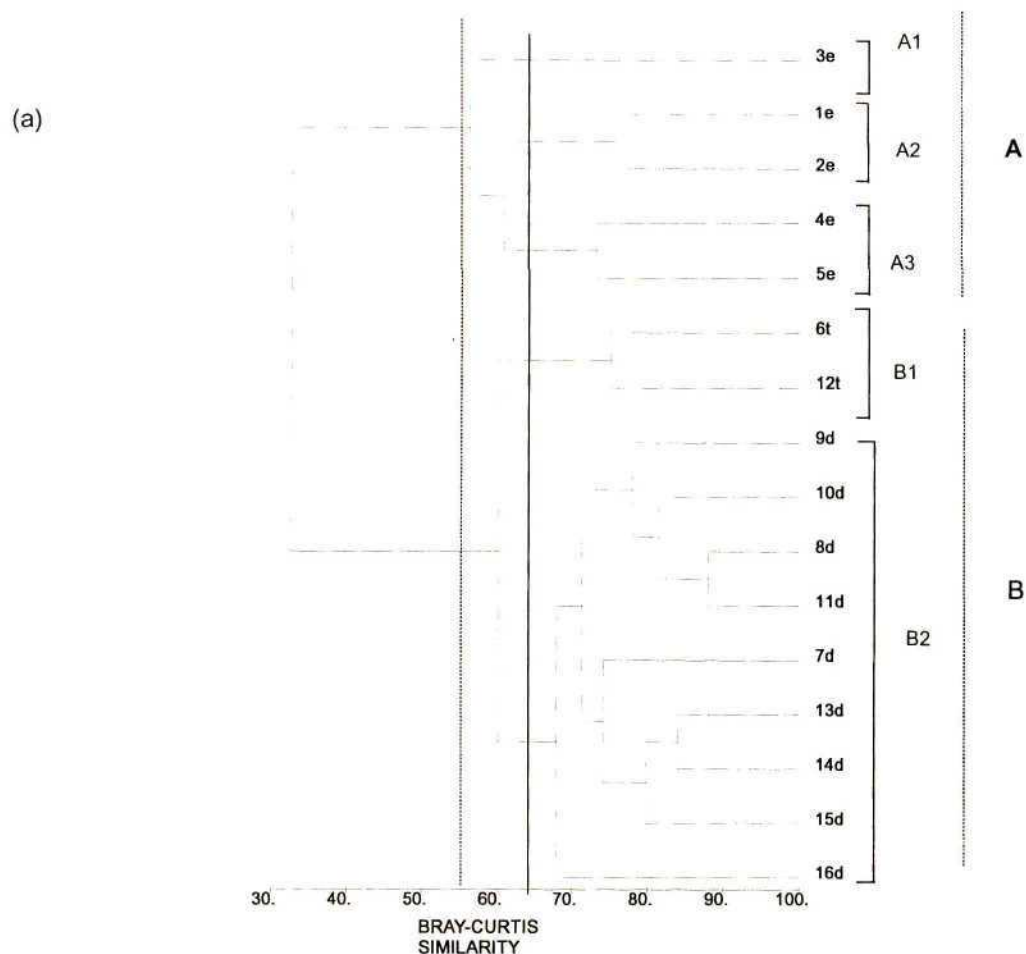


Figure 13. Dendrogram for hierarchical clustering (a) and MDS ordination plot (b) for 16 2m^2 -quadrats (with 12 replicates each) in Bats' cave based on Bray-Curtis similarities of fourth-root transformed taxon abundance data. Quadrats were placed 5m apart along a transect into the cave and are numbered sequentially from the entrance (1) to deep zone (16). e=entrance zone, t=transitional zone, d=deep zone. Groups separated out at the 55% level (A and B) and 65% similarity level (A1, 2 and 3; B1 and 2) are demarcated with dotted and solid lines respectively. (Stress = 0.07)

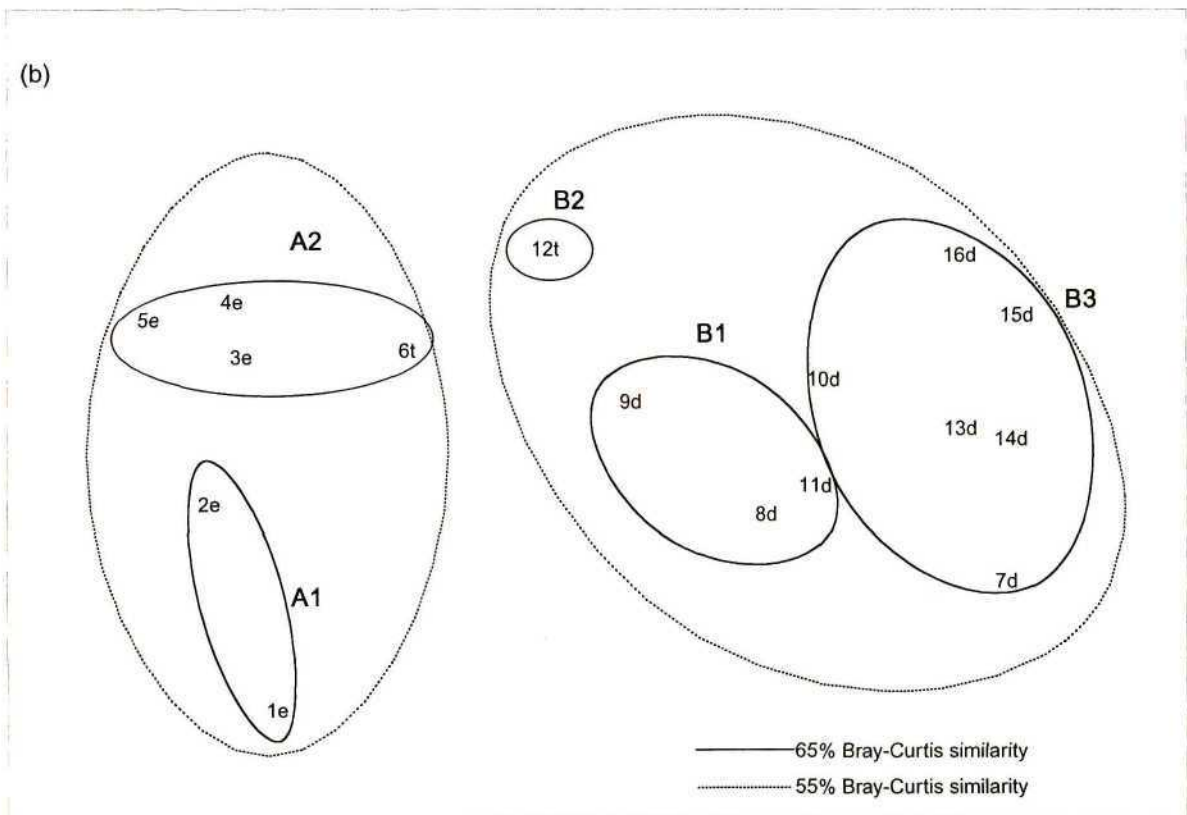
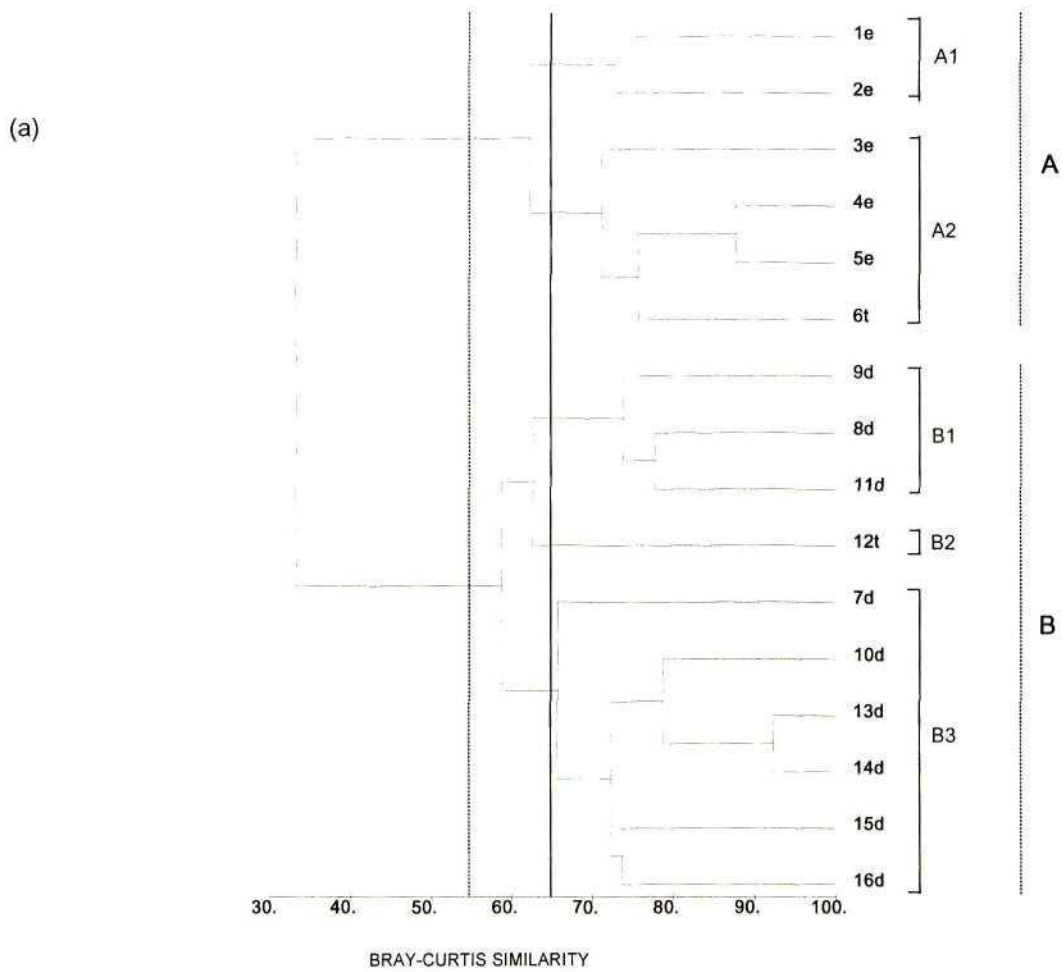


Figure 14. Dendrogram for hierarchical clustering (a) and MDS ordination plot (b) for 16 2m^2 -quadrats (with 12 replicates each) in Bats' cave based on Bray-Curtis similarities of species presence / absence data. Quadrats were placed 5m apart along a transect into the cave and are numbered sequentially from the entrance (1) to deep zone (16). e=entrance zone, t=transitional zone, d=deep zone. Groups separated out at the 55% similarity level (A and B) and 65% level (A1, A2, A3, B1, B2) are demarcated with dotted and solid lines respectively. (Stress = 0.07)

At the 65% similarity level, five groups were separated out in the dendrogram derived from abundance similarities (Figure 13). Groups largely reflected quadrat position relative to the cave entrance. This was most pronounced in the entrance zone where adjacent quadrats were most similar. The groups separated out as follows:

- Quadrats 1e and 2e (group A2) occurred in the twilight zone directly below the entrance, thus being most exposed to surface conditions.
- Quadrats 4e and 5e (group A3) were the deepest entrance zone quadrats and were least exposed to light and other surface conditions. Plant debris was abundant here. The MDS plot (Figure 13b), however, placed quadrat 4e equidistant to 3e and 5e, indicating a boundary position between the two groups.
- Quadrat 3e (group A1) was the quadrat most exposed to light and precipitation in the entrance zone. It was situated directly below a bat roost so that guano and plant debris were abundant.
- Quadrats 6t and 12t (group B1) occurred in the dark zone but received infalls of plant debris and guano from the entrance zone. They were also exposed to slight air currents and were regarded as transitional zone quadrats. The MDS plot (Figure 13b) placed 12t closer to 9d, indicating it to be less transitional than 6t.
- Group B2 contained the remaining nine dark zone quadrats. Quadrats closest together were generally the most similar. Quadrats 13d to 16d were separated from the preceding quadrats (8d to 11d) by a cave 'corkscrew' and exhibited relatively constant environmental conditions throughout the year. Quadrats 8d to 11d exhibited minor variations in environmental conditions. Quadrat 16d was situated in a stream passage experiencing winter flooding and showed very little similarity to other dark zone groups.

Hierarchical clustering of taxon presence or absence similarities (Figure 14) grouped quadrat 3e with 4e, 5e and 6t at the 65% similarity level. Within the dark zone, quadrats 8d, 9d and 11d (group B1) were segregated from group B3 (containing the remaining dark zone quadrats) and group B2 (containing quadrat 12t in the transitional zone).

One-way Anosim on fourth-root transformed abundance data revealed an overall significant difference between all groups at the 0.01% significance level, indicating the existence of clear community distribution patterns. Quadrats were grouped to suggest that community

distribution patterns were based on cave zonation. i.e. entrance quadrats were grouped together in group A, thus representing an entrance community, while deep zone quadrats in group B represented a deep zone community. These two groups were significantly different from one another at the 5% level (one-way Anosim). Transitional zone quadrats (quadrats 6t and 12t) differed from deep zone quadrats (group B2) but not from the entrance quadrats (group A) at the 5% level. Therefore, while quadrats were grouped to reflect zones, the transitional zone community was less clearly defined than entrance or deep zone communities. Communities may also have varied seasonally in which case boundaries would have been obscured by lumping of seasonal data.

Community patterns based on cave zonation were clearer in the cave ordination based on taxon presence or absence data. At the 60% similarity level three groups were separated out, all being significantly different from one another at the 5% level (using one-way Anosim). They represent an entrance community (containing primarily entrance zone quadrats), a transitional zone community (containing group B1 and B2 quadrats which exhibited slight variations in environmental conditions) and a deep zone community (containing all deep zone quadrats in group B3). This correlation with cave zonation was further associated with the zonal distribution of both guano and plant matter and, therefore, of the guanophiles and humicoles excluded from abundance data. Quadrats 3e, 4e, 5e and 6t all had dense populations of guanophiles and humicoles, therefore being grouped together in the dendrogram derived from taxon presence or absence data (Figure 14). Similarly, dark zone sub-groups (B1, B2 and B3) probably reflected the patchy distribution of guano and plant debris in the nutrient-poor dark zone (this relationship is explored further in Chapter 6).

5.3. Taxa responsible for community patterns

Having established the existence of distinct community patterns, the next step was to determine which taxa were responsible for these patterns. The 19 most abundant taxa were compared in terms of the quadrats they occupied, thus producing dendrograms based on Bray-Curtis taxon similarities (Figure 15).

In Wynberg cave, three taxon groups were separated out at the 30% similarity level (Figure 15a). Taxon groups largely reflected distribution patterns discussed in Chapters 3 and 4

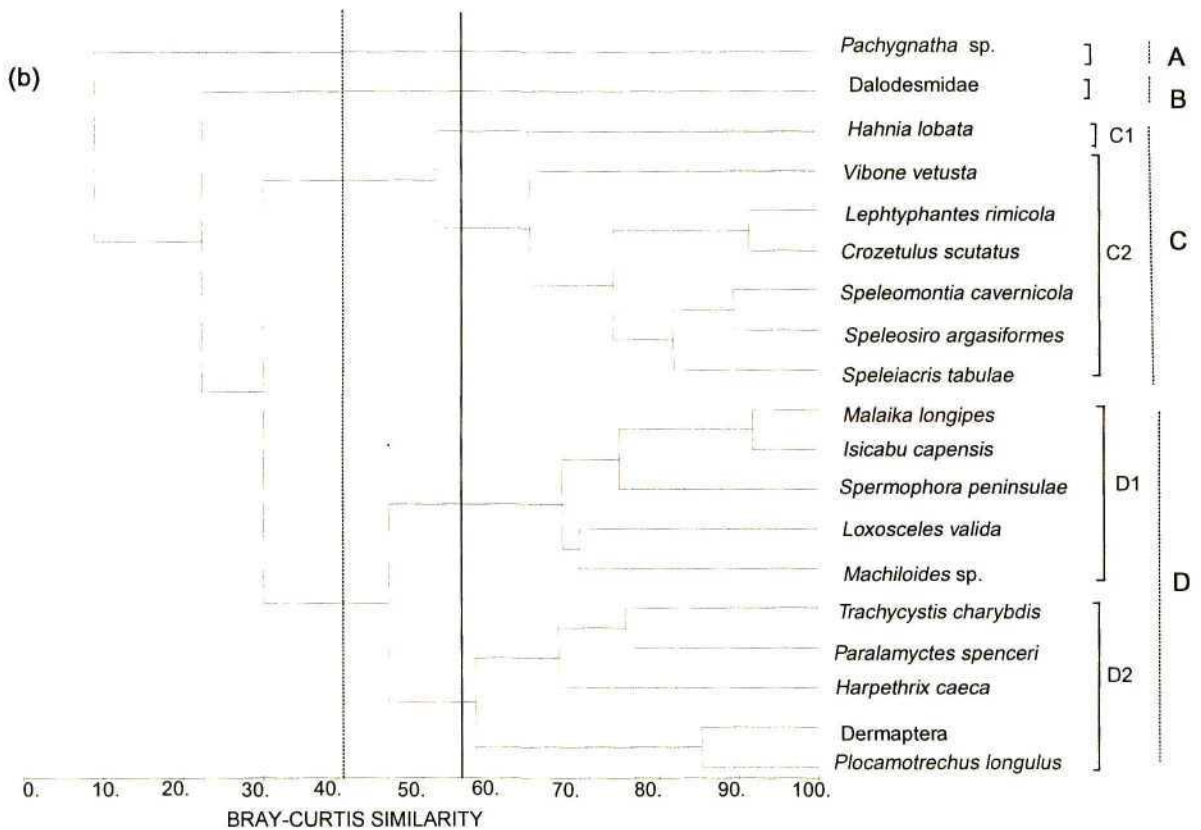
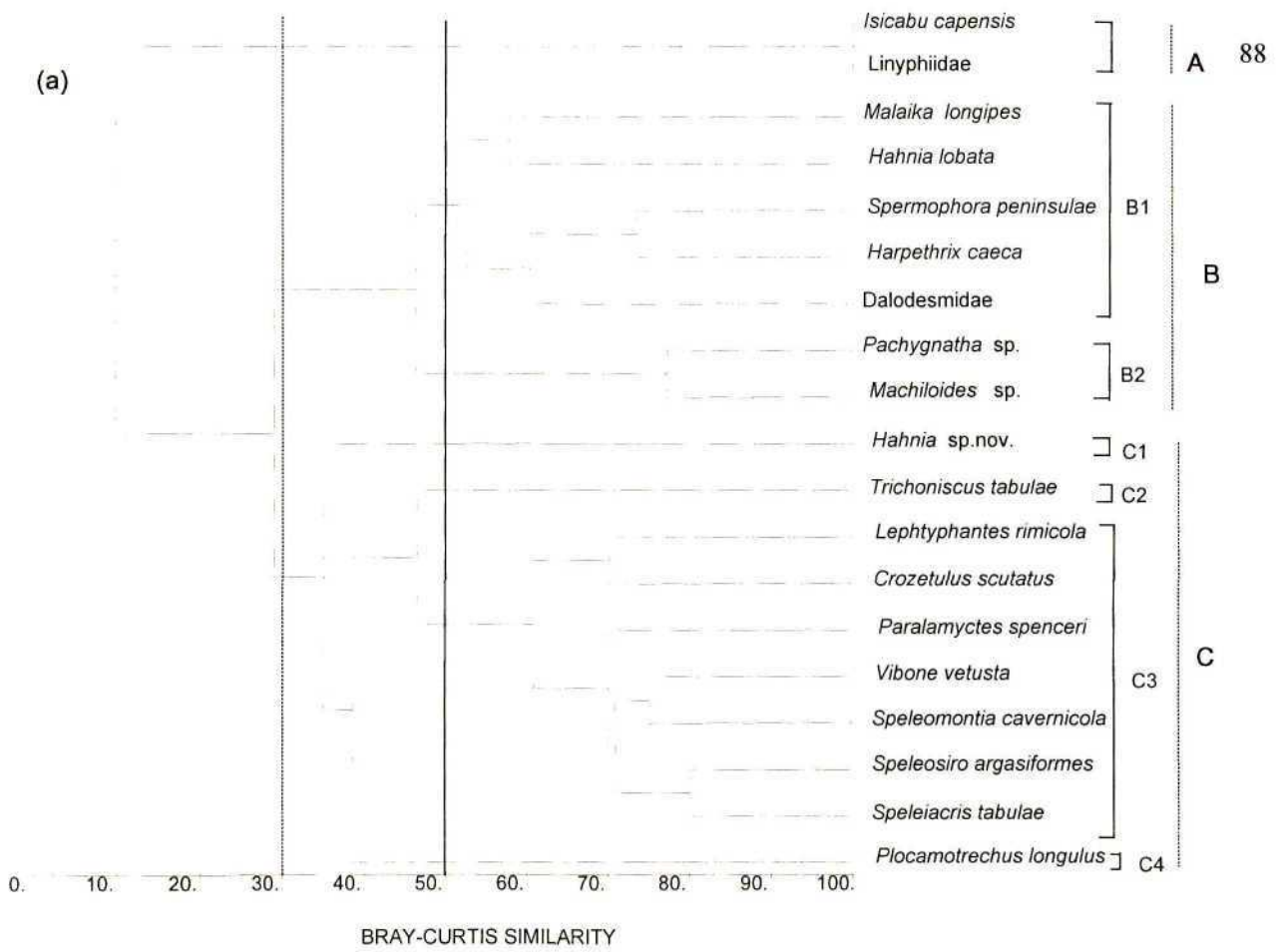


Figure 15. Dendrogram for hierarchical clustering of the 19 most abundant taxa in (a) Wynberg cave and (b) Bats' cave, based on Bray-Curtis species similarities of 4th-root transformed abundance data from 33 and 16 quadrats of 2m² each in Wynberg and Bats' caves respectively. Groups separated out at the 30% and 40% similarity levels are demarcated with dotted lines and labelled (A,B,C and D). Subgroups formed at the 50% and 55% similarity levels are demarcated with solid lines.

(Figures 3, 4, 5 and 8), as well as the degree of cave-adaptedness of taxa. One-way analysis of similarities on fourth-root transformed abundance data revealed a significant difference at the 5% level between groups A, B and C.

Group A was an outlying group comprising the troglonexic *Isicabu capensis* and Linyphiidae which occurred mainly in twilight zone quadrats (quadrats 1e, 2e and 3e). They were completely absent from the deep zone (Figure 8).

- Group B consisted of troglophiles, troglonexes and humicoles that were common in entrance zones. *Hahnia lobata*, *Harpethrix caeca*, Dalodesmidae, *Pachygnatha* sp. and *Machiloides* sp. were all absent from the deep zone (Figure 3). *Spermophora peninsulae* and *Malaika longipes* were troglophiles that occurred in all zones but predominated in entrance zones (Figures 4 and 8).
- Group C consisted of troglophiles and troglobites that were common in the dark zone. The troglobites, *Hahnia* sp.nov. and *Trichoniscus tabulae*, were restricted to the dark zone (Figures 5 and 8), while *Lephtyphantes rimicola*, *Crozetulus scutatus* and *Speleosiro argasiformes* occurred throughout the cave but predominated in the dark zone (Figures 5 and 8). The troglophilic *Speleiacris tabulae*, *Plocamotrechus longulus* and *Paralamyctes spenceri* were predators and scavengers that occurred throughout the cave (Figure 4).

At the 50% similarity level, group B (common entrance taxa) and group C (common dark zone taxa) were subdivided into two and three subgroups respectively.

- Group B1 consisted of *Pachygnatha* sp. and *Machiloides* sp. Both species predominated in the twilight zone (group A quadrats in Figure 11), the latter species being entirely restricted to this zone.
- Group B2 contained taxa that predominated in entrance and transitional zones (groups D1 and D2 quadrats in Figure 11).
- Groups C1 and C2 contained the troglobites, *Hahnia* sp.nov. and *Trichoniscus tabulae*. They were relatively rare and had marked microhabitat preferences, occurring almost exclusively in narrow, damp crevices in areas of high relative humidity. Their distribution within the deep zone was therefore affected by microhabitat availability.
- Group C4 contained the guanophilic predator, *Plocamotrechus longulus*, whose distribution in the deep zone reflected guano availability.

- Group C3 consisted of predators and scavengers that occurred throughout the dark zone.

One-way Anosim on fourth-root transformed abundance data found groups B1 and B2 to be significantly different from one another, while groups C1, C2 and C3 were not significantly different at the 5% level. In summary, taxa in groups A and B1 were prevalent in the twilight zone community, while taxa in group B2 were prevalent in entrance and transitional zone communities. Within the deep zone, additional communities defined by crevice microhabitats and guano were detected. However, these were not clearly defined communities.

In Bats' cave four groups were separated out at the 40% similarity level, again reflecting zonal distribution patterns (Figure 15b).

- *Pachygnatha* sp. is a troglaxene found exclusively in the twilight zone (Figures 3 and 9).
- The dalodesmids, being humicoles, were found in entrance and transitional zone quadrats only (Figures 3 and 9).
- Group C contained troglaphiles and troglobites. The troglobitic *Lephtyphantes rimicola* and *Crozetulus scutatus* were completely absent from the entrance zone (Figures 5 and 9), while *Speleosiro argasiformes* and *Speleomontia cavernicola* predominated in the dark zone (Figures 5 and 9). The troglaphilic *Hahnia lobata*, *Vibone vetusta* and *Speleiacris tabulae* occurred in entrance and dark zones (Figure 9).
- All species in group D were common entrance inhabitants. *Machiloides* sp., *Malaika longipes*, *Loxosceles valida* and *Isicabu capensis* were all absent from the dark zone (Figure 9).

One-way Anosim on fourth-root transformed data revealed a significant difference between groups C (common dark zone taxa) and group D (common entrance taxa) at the 5% level. This indicates that taxa were distributed in such a way as to form distinct entrance (group D taxa) and dark zone (group C taxa) communities.

At the 55% similarity level two subgroups each were separated out in groups C (common dark zone taxa) and D (common entrance taxa).

- Group C1 (containing *Hahnia lobata*) was completely absent from deep zone quadrats, preferring entrance and transitional zone habitats (Figure 3).

- Group C2 taxa occurred throughout the dark zone.
- Group D1 contained all taxa restricted to the entrance zone.
- Group D2 contained entrance and transitional zone inhabitants.

One-way Anosim on fourth-root transformed abundance data revealed a significant difference between groups D1 and D2, but not between groups C1 and C2 at the 5% level. This suggests that group D1 taxa were responsible for the entrance community, and group D2 taxa, for both entrance and transitional communities.

5.4. Discussion

The terrestrial invertebrates of the Table Mountain caves were clearly segregated into communities based on the zonal cave environment. Communities were most strongly correlated with distance from the entrance. This is clearly illustrated by the sequential arrangement of quadrats in the dendrograms (Figures 1 to 4), indicating a gradual change in community patterns with increasing cave depth. In both Bats' and Wynberg caves there were clear entrance and deep zone communities. Transitional and twilight zone communities were also detected in Wynberg cave where these zones are clearly recognizable. However, in Bats' cave, the continuum of change in the physical environment hindered the precise delimitation of the transitional zone, and therefore the transitional zone community. This sequential arrangement of quadrats in the dendrogram extends into deep zone quadrats, albeit less pronounced. This suggests that variability existed in the deep zone and that it may have been inaccurately delimited (being less extensive than indicated).

Within each zone, additional communities were detected that were not correlated with the zonal physical environment. Food utilisation and microhabitat availability were clearly additional secondary factors determining community boundaries. A community of troglobites associated with narrow, moist crevices in the dark zones, was indicated. Communities were also associated with the two most important food sources: bat guano and plant debris.

Although different taxa defined different communities, considerable overlap occurred, with generalists and predators utilising more than one food resource or zone. For example, *Speleiacris tabulae* occurred in all zones, but was more abundant in entrance zones (Figures 8

and 9). Similarly, *Plocamotrechus longulus* and *Paralamyctes spenceri* were predators overlapping with all communities, although *P. longulus* was primarily associated with guano communities. Of the 19 most abundant taxa considered, six taxa responsible for the deep zone community of Wynberg cave were also found in the entrance and transitional communities, while one species was restricted to the deep zone. In Bats' cave, four deep zone taxa were also present in entrance communities. Of the taxa defining entrance and twilight zone communities, five taxa were restricted to these zones in Wynberg cave, four taxa being restricted to them in Bats' cave. Richards (1971) similarly found that 34% of cavernicoles in Nullarbor caves utilised more than one biotope (these being twilight zone, guano and dark zone biotopes).

The clear correlation between the zonal distribution of cavernicoles and their degree of cave adaptation emphasises the effect of the physical environment on community patterns. Troglobites and troglaphiles were responsible for deep zone communities, troglaphiles for transitional zone communities and troglaxenes and troglaphiles for entrance communities. A stronger correlation was recorded from Bayliss cave, Queensland (Howarth 1988), where a community made up almost entirely of troglobites occurred in the innermost part of the cave, while troglaphiles occurred only in the outer transitional and deep zones. In the Table Mountain caves, considerable overlap occurred. Troglobites responsible for deep zone communities were also present in entrance communities (e.g. *Speleomontia cavernicola*, *Speleosiro argasiformes*, *Lephtyphantes rimicola* and *Crozetulus scutatus*). Similarly, troglaphiles responsible for transitional or entrance zone communities were also present in deep zone communities (e.g. *Malaika longipes*, *Loxosceles valida* and *Spermophora peninsulae*) (Figures 8 and 9). The zonal physical environment was, therefore, not the sole factor affecting cavernicole distribution patterns. Food availability and microenvironmental conditions were clearly additional secondary factors enabling overlap between zones.

Considering the proximity of Bats' and Wynberg caves (situated less than 500m apart) and the similarity of their physical attributes, one would expect concordance in the taxonomic composition of communities. However, there is only partial agreement due to structural and biological differences between caves. The entrance community of Bats' cave was defined by the troglaxenes, *Machiloides* sp. and *Pachygnatha* sp., and the troglaphiles, *Malaika*

longipes, *Loxosceles valida* and *Spermophora peninsulae*. All were restricted to the entrance zone of Bats' cave. In Wynberg cave, the twilight zone community was defined by the trogloneic Linyphiidae, *Isicabu capensis*, *Pachygnatha* sp. and *Machiloides* sp., the latter being restricted to this zone. Taxa responsible for entrance and transitional zone communities were largely the same, indicating considerable overlap.

No taxa were restricted to transitional zone communities in either cave, overlap occurring mainly with entrance and plant debris communities. The plant debris that fell through dorsal faults from overlying entrance zones made it increasingly difficult to delimit the transitional zone community boundaries. Taxa defining the transitional zone community were troglaphiles or humicoles. In Bats' cave, these were: *Hahnia lobata*, *Harpethrix caeca* (troglaphiles overlapping with the entrance community), Dalodesmidae, *Trachycystis charybdis* (humicoles overlapping with plant debris and entrance communities), *Plocamotrechus longulus*, Dermaptera and *Paralamyctes spenceri* (troglaphilic predators overlapping with all communities). In Wynberg cave, *Malaika longipes* and *Spermophora peninsulae* occurred throughout the cave, while *Harpethrix caeca*, *Hahnia lobata* and Dalodesmidae overlapped with entrance and plant debris communities.

Taxa defining the deep zone communities of both caves included troglobites and troglaphiles. Troglobites included: *Lepthyphantes rimicola*, *Crozetulus scutatus* (restricted to the dark zone of Bats' cave), *Speleosiro argasiformes* and *Speleomontia cavernicola* (occurring throughout the caves). Troglaphiles included *Speleiacris tabulae* and *Vibone vetusta*. In Wynberg cave, four additional species were important: *Paralamyctes spenceri* and *Plocamotrechus longulus* (predatory troglaphiles overlapping with all communities), *Hahnia* sp.nov. and *Trichoniscus tabulae* (troglobites restricted to the dark zone communities).

In addition to the physical effects of zonation on community patterns, biotic and trophic factors are also of importance in determining community patterns. The availability of nutrient resources, as well as its stability in time and space, affect the distribution of cavernicoles. For example, Peck (1976) found that in Mammoth cave, Kentucky, humicole abundance corresponded with areas of detritus infall, while guanophile and scavenger abundance corresponded with concentrations of cricket guano. Similarly, the distribution of

Pseudonaphthalmus menetresii tracked that of its patchily-distributed collembolan prey (Kane and Poulson 1976). In Bats' and Wynberg caves, communities delimited by microhabitat availability and guano were also detected from the hierarchical clustering of taxon abundance data (Figure 15). These communities overlapped with deep or entrance zone communities and were represented by troglobitic crevice fauna (*Hahnia* sp.nov. and *Trichoniscus tabulae*) and guanophiles (*Plocamotrechus longulus*) respectively.

As only the most abundant censused taxa were considered, taxon responsibility was inconclusively established, most notably for guano, plant debris and troglobitic crevice communities. Communities might be defined differently if all species were considered. The guano communities were represented by highly vagile, opportunistic and largely uncensused guanophiles (e.g. staphylinids, ptiliids, mites, collembolans and the carabid, *Plocamotrechus longulus*). The plant debris communities in the Table Mountain caves included mostly uncensused humicoles and troglaphiles that would otherwise not be able to colonise cave habitats (Barr and Kuehne 1971; Poulson and Kane 1981) e.g. talitrids, oniscids, collembolans, *Trachycystis charybdis* and Dalodesmidae.

In Bats' cave, the distribution of plant debris and bat guano was patchy and zonal, occurring mainly in the entrance zone (and transitional zone to a lesser extent). Therefore, the plant debris and guano communities overlapped with the entrance community. In Wynberg cave, however, insectivorous bat guano occurred mainly in the dark zone so that guano communities overlapped with dark zone communities. The plant debris community overlapped with twilight, entrance and, to a lesser extent, transitional zone communities. As a result of this overlap, communities were more easily defined in terms of cave zonation than food availability. However, patchy guano deposits often made it possible to detect guano communities within the relatively nutrient-poor dark zone (i.e. the overlap was not complete).

The distribution, availability and stability of food in time and space does not only affect the distribution of cavernicoles, but is also correlated with their degree of cave adaptation. Trogllobites are adapted to conditions within the dark zones where food is less available (although it may be more stable), and are only able to utilise food-rich areas if environmental conditions are favourable (Poulson 1977; Poulson and White 1969; Poulson and Kane 1981;

Chapman 1982). For example, *Spelaeorchestia koloana* was only attracted to bait if water was added (Bousfield and Howarth 1976). Entrance communities, on the other hand, are adapted to high food concentrations (Peck 1976; Howarth 1983). Therefore, larger species can extend their ranges into dark zones only where food availability is high enough to support them (Poulson and White 1969). For example, Poulson and Kane (1977) found that increasing prey density by adding manure, increased the abundance of the spider *Phanetta subterranea* and allowed it to colonise deeper zones. The more cave-adapted species, *Anthrobia monmouthia*, did not respond in this way, as it was longer-lived, could resist starvation and was better adapted to exploit deep zone resources (Poulson 1977, 1981).

Clear evidence of such food-related distribution patterns occurring in the Table Mountain caves would explain the overlap between zonal communities by cavernicoles, thus weakening the correlation of cave adaptation with the zonal physical environment. Seasonal input of food clearly affected community distributional patterns, but lumping of seasonal data would have obscured this effect. The troglophiles *Malaika longipes*, *Loxosceles valida* and *Spermophora peninsulae* defined the entrance community of Bats' cave and the transitional community of Wynberg cave. They were highly abundant in entrance zones where prey densities were high, but were almost entirely absent from the guano-poor dark zone of Bats' cave. In Wynberg cave, however, they were encountered in deep zone quadrats where guano-associated prey was abundant (Figures 8 and 9). The troglobitic *Lepthyphantes rimicola* and *Crozetulus scutatus*, on the other hand, defined deep zone communities but were also able to extend their ranges into nutrient-rich entrance zones when microhabitat availability (narrow crevices) and environmental conditions (e.g. relative humidity) were favourable (Figures 8 and 9) (factors affecting distribution are discussed further in Chapter 6).

5.5. Conclusion

In Bats' and Wynberg caves, the zonal nature of the physical environment was the primary factor governing community distribution patterns which were strongly correlated with distance from the entrance. Entrance and deep zone communities were recognizable in both caves, while twilight and transitional zone communities were also clearly defined in Wynberg cave. The effect of the zonal physical environment was further emphasised by the correlation between zonally-defined communities and their degree of cave adaptation. Troglonexes and

troglophiles were responsible for entrance and transitional zone communities, while troglophiles and troglobites were responsible for deep zone communities. Further subdivision of communities was evident, these being weakly correlated with guano, plant debris and crevice (or microhabitat) availability. Considerable overlap existed between communities defined by food availability and zonation.

Therefore, while communities appear to be primarily correlated with the zonal physical environment, biotic factors (food availability) and crevice availability cause secondary community subdivisions. The inclusion of guanophile and humicole fauna in a quantitative analysis would further elucidate food-related distribution patterns, most notably within the deep zones. The extent of the crevice community and the species defining it, also require further investigation.

6. Environmental factors affecting cavernicole distribution and abundance

Chapter 5 established the importance of the zonal physical environment in determining community distribution patterns, this being reflected by the predominance of troglobites in deep zone habitats. The deep zone environment is a rigorous and harsh one which most surface species cannot tolerate (Barr 1968; Barr and Kuehne 1971; Bull and Mitchell 1972; Howarth 1980, 1981, 1983, 1988). It is one of constant darkness, stable temperatures (near the annual average surface temperature), continually wet substrates and a constantly water-saturated atmosphere. Oxygen levels are often low, carbon dioxide levels high and food limiting (Poulson and White 1969; Howarth 1983, 1988; Aalbu 1989; Howarth and Stone 1990; Peck 1990). Troglobites are often restricted to deep zones, having very specific ecological requirements (Howarth 1988; Howarth and Stone 1990), so that any environmental modifications (even local or temporary) could result in population disturbances or disrupted distribution patterns. This vulnerability to environmental change makes it necessary to determine which environmental factor, or combination of factors, limit cavernicole distribution. These factors would present the best predictors of cavernicole distribution and abundance, both within and between caves, thus facilitating management decisions.

Environmental variables measured in entrance and deep zones of Bats' and Wynberg caves are summarised in Table 6. This clearly shows that entrance and deep zone communities were exposed to very different environmental conditions. They were therefore analysed separately from overall cave communities. Conditions also varied seasonally, a 'winter effect' (Howarth 1987) being clearly evident. Figures 21 and 22 show seasonal changes in temperature, relative humidity and soil and surface moisture. During summer (November to March), warm moist air moved into the caves along the vapour pressure gradients, resulting higher relative humidities. Cave animals were therefore able to colonize areas closer to the entrance in summer. Higher temperatures within the caves caused higher evaporation rates which, in turn, resulted in decreased soil and surface moisture (Figures 21 and 22). During winter (June to September) surface temperatures dropped below cave temperatures so that water vapour diffused out of the caves along the pressure gradients. Cave animals therefore retreated

Table 6. Environmental variables measured in entrance and deep zones of (a) Wynberg cave and (b) Bats' cave, Table Mountain. Measurements were taken monthly for 12 months in quadrats placed at five metre intervals along transects into the caves. Five and eight quadrats were placed in the entrance zones of Bats' and Wynberg caves respectively, eleven and eighteen quadrats being placed in their deep zones. Scored data was obtained as follows: 1=1-20% cover; 2=21-40%; 3=41-60%; 4=61-80%; 5=81-100% cover.

Environmental variable	Entrance zone		Deep zone	
	Mean	Range	Mean	Range
a) Wynberg cave				
Temperature (°C)	11.55	10.84-13.33	10.66	10.50-10.74
%Relative humidity	89.26	87.33-92.25	98.43	98.12-98.80
% Soil water content	8.44	11.76-57.44	24.42	7.41-43.90
% Surface moisture	5.30	1.32-14.78	11.35	0.82-56.53
% Crevice moisture	1.64	0.41-6.53	5.38	0.92-13.40
% Soil organic content	8.44	4.62-19.30	4.01	1.14-20.21
Soil nitrogen content (g/ml)	0.16	0.13-0.29	0.13	0.07-0.24
Soil energy content (J/g)	12.25	0.16-45.63	13.36	0.16-56.6
Guano (scored)	0.44	0-2	1.58	1-2.5
Plant debris (scored)	2.29	1-3	0.01	0-1
Lichen (scored)	0.29	1-4	0	0
Moss (scored)	0.21	1-4	0	0
Crevice availability (scored)	0.57	0-2	1.60	1-3
Light (lux)	0.04	0.01-0.11	0	0
Wind (m/s)	0.70	0.3-1	0	0
b) Bats' cave				
Temperature (°C)	11.85	10.48-13.17	9.99	9.78-10.40
%Relative humidity	85.63	82.33-94.88	97.76	97.54-98.25
% Soil water content	31.85	13.86-50.06	24.04	8.95-78.46
% Surface moisture	4.09	1.42-8.64	7.58	1.17-29.39
% Crevice moisture	0.78	0.24-1.59	1.77	0.47-8.32
% Soil organic content	18.87	7.63-34.12	2.89	0.76-4.94
Soil nitrogen content (g/ml)	5.41	3.49-5.98	1.03	0.37-2.94
Soil energy content (J/g)	19.05	4.95-43.02	4.21	0.01-13.00
Guano (scored)	3.0	1-4	0.3	0-1
Plant debris (scored)	2.8	2-4	0.1	0-1
Lichen (scored)	2.2	1-3	0.4	0-1
Moss (scored)	1.4	0-3	0	0
Crevice availability (scored)	3.2	1-4	2.8	1-4
Light (lux)	0.02	0-0.04	0	0
Wind (m/s)	0.28	0.1-0.4	0	0

further into caves during winter. In the Table Mountain caves this effect was dampened by winter rains which increased soil and surface moisture levels (Figures 21 and 22). The effect these seasonal changes had on the distribution of cave communities was largely obscured by the lumping of data.

Weighted Spearman's rank correlation coefficients matching environmental variables with MDS community ordinations are given in Tables 7, 8 and 9. These correlations cannot be compared with standard statistical tables of Spearman's correlation coefficient (Clarke and Warwick 1994) and do not imply causality, merely serving as a descriptive tool. Causality can only be determined by manipulative experiments (Clarke and Warwick 1994). Light and wind were found to be strongly intercorrelated in both caves ($r^2=0.87$ in Wynberg cave and $r^2=0.90$ in Bats' cave). The two variables were therefore lumped together and considered singly as 'wind/light'. In Wynberg cave both light and wind were strongly intercorrelated with temperature ($r^2=0.80$ and 0.82 respectively), while in Bats' cave, soil nitrogen content and soil organic content were both intercorrelated with relative humidity ($r^2=0.79$ and 0.75 respectively). These variables were, nevertheless, retained in the analyses.

6.1. Factors affecting overall cave communities

No single environmental variable satisfactorily explained overall distribution and abundance patterns. In both caves, these were best explained by a complex of environmental factors (Table 7). Lumping of seasonal data may further have obscured correlations. MDS ordinations of quadrats based on the 15 measured variables showed little resemblance to the MDS ordinations based on taxon abundance (Figures 16b and 17b) and yielded relatively weak correlations (Table 7). This suggests that important variables were excluded from the analysis and that all species were not necessarily uniformly influenced by the environmental variables considered.

In both Bats' and Wynberg caves, the single environmental variable showing the highest correlation with MDS ordinations based on taxon abundance data, was relative humidity (Table 7, Figures 19b and 20b). This correlation was far stronger in Bats' cave ($r^2=0.81$) than in Wynberg cave ($r^2=0.55$), suggesting that relative humidity played a diminished role

Table 7. Weighted Spearman's rank correlation coefficients matching environmental variables with community ordinations in Bats' and Wynberg caves, Table Mountain. MDS ordinations were derived from both taxon abundance and taxon presence or absence data. All data was log transformed. Environmental variables are considered (a) singly and (b) in combinations yielding the highest correlations. Bold type indicates the strongest correlation. Wind and light were strongly intercorrelated and considered as a single variable.

Bats' cave			Wynberg cave		
a) Environmental variable	Weighted Spearman's rank-correlation coefficient		Environmental variable	Weighted Spearman's rank-correlation coefficient	
	abundance data	presence /absence data		abundance data	presence /absence data
Relative humidity (%)	0.81	0.64	Relative humidity (%)	0.55	0.51
Plant debris (scored)	0.76	0.77	Lichen (scored)	0.55	0.53
Soil nitrogen content (g/ml)	0.66	0.69	Moss (scored)	0.54	0.52
Wind/light (scored)	0.59	0.57	Wind/light (scored)	0.53	0.51
Temperature (°C)	0.58	0.59	Temperature (°C)	0.50	0.45
Soil organic content (%)	0.46	0.51	Plant debris (scored)	0.38	0.41
Moss (scored)	0.55	0.40	Guano (scored)	0.33	0.38
Soil energy content (J/g)	0.32	0.24	Soil water content (%)	0.19	0.20
Guano (scored)	0.30	0.33	Surface moisture (%)	0.18	0.16
Crevice availability (scored)	0.31	0.21	Crevice moisture (%)	0.13	-0.02
Lichen (scored)	0.20	0.12	Soil organic content (%)	0.01	0.02
Soil water content (%)	-0.03	-0.00	Soil nitrogen content (g/ml)	-0.01	-0.03
Crevice moisture (%)	-0.12	-0.08	Soil energy content (J/g)	-0.03	-0.03
Surface moisture (%)	-0.21	-0.12	Crevice availability (scored)	0.07	0.03
All variables combined	0.55	0.56	All variables combined	0.44	0.42
b) Combined environmental variables			Combined environmental variables		
Relative humidity, temperature	0.83	0.73	Temperature, relative humidity, surface moisture, wind/light	0.58	0.52
Relative humidity, temperature, soil nitrogen content	0.83	0.77	Wind/light, moss, lichen	0.56	0.52
Relative humidity, soil nitrogen content	0.82	0.75	Relative humidity, wind/light, soil water content	0.56	0.51
Soil nitrogen content, plant debris	0.77	0.79	Plant debris, lichen, guano	0.56	0.53

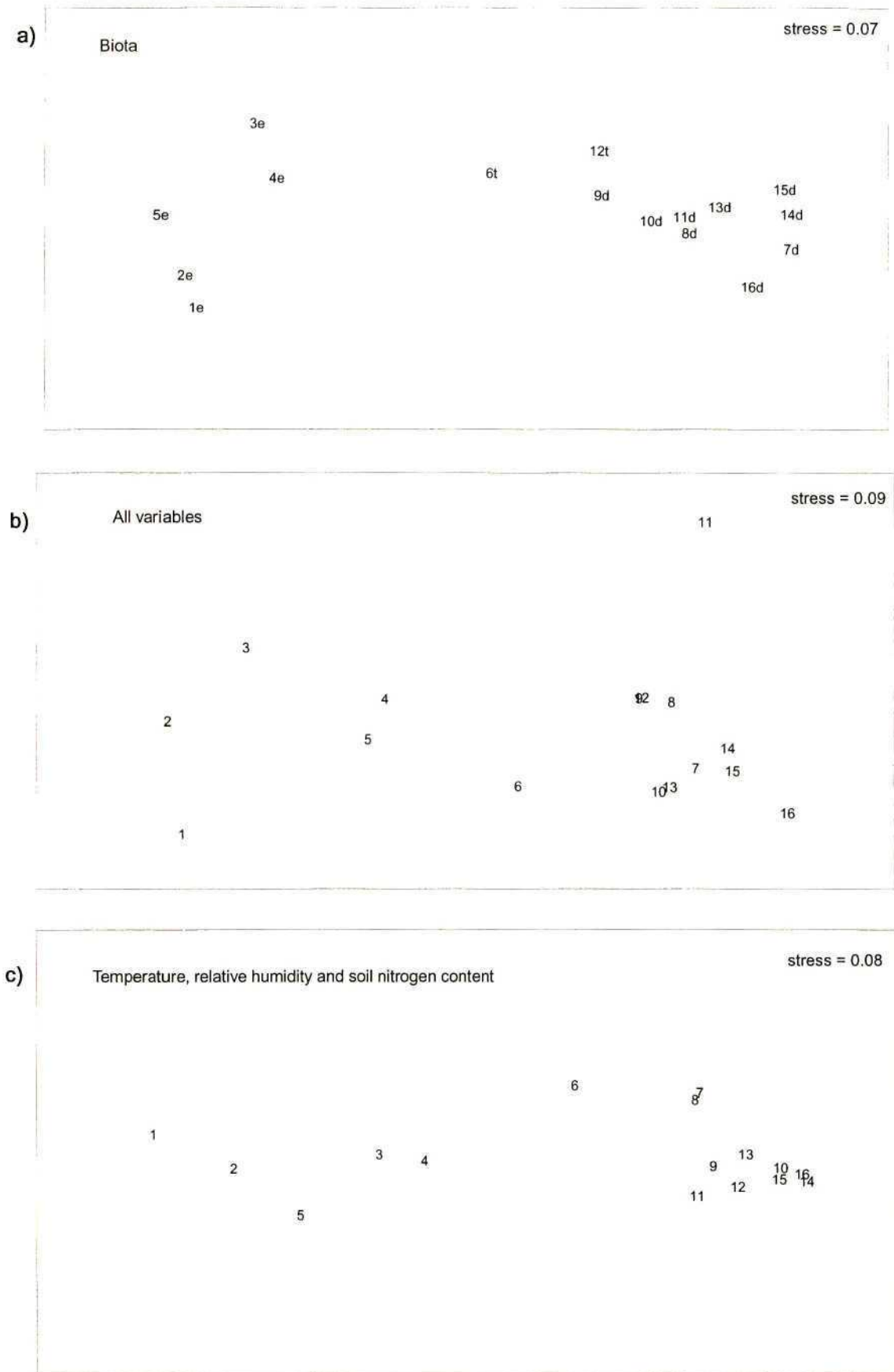


Figure 16. MDS ordinations of quadrats in Bats' cave based on (a) taxon abundance data (fourth-root transformed), (b) all 15 measured environmental variables (log transformed) and (c) variables that yielded the best match with biotic patterns: temperature, relative humidity and soil nitrogen content. Data were collected monthly for one year in 16 2m²-quadrats numbered sequentially from the entrance zone (1) to deep zone (16). e = entrance zone (quadrats 1-5); t = transitional zone (quadrats 6 and 12); d = deep zone (quadrats 7-11, 13-16).

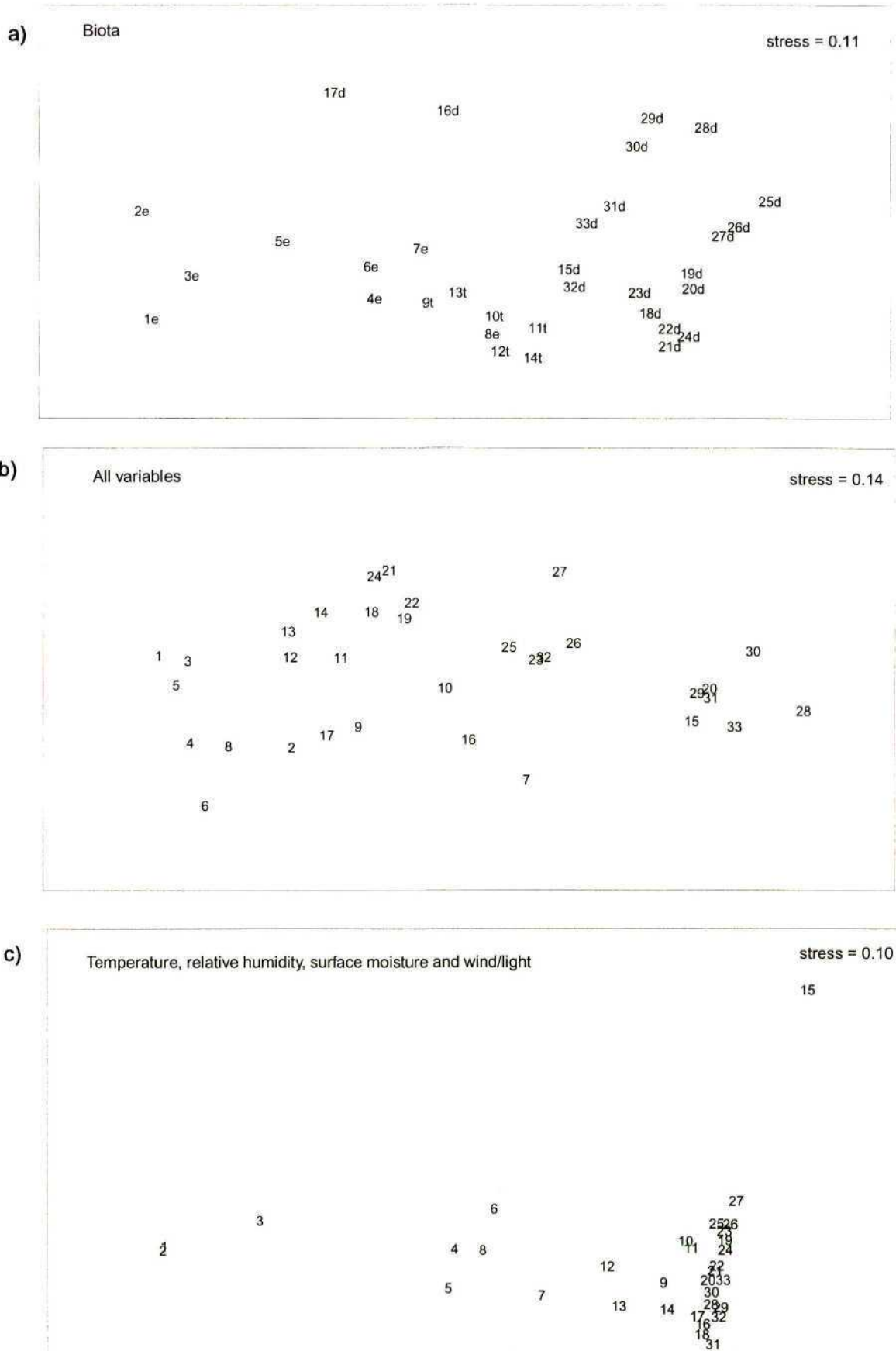


Figure 17. MDS ordinations of quadrats in Wynberg cave based on (a) taxon abundance data (fourth-root transformed), (b) all 15 measured environmental variables (log transformed) and (c) variables that yielded the best match with biotic patterns: temperature, relative humidity, surface moisture and wind/light. Wind and light were intercorrelated and regarded as a single variable. Data were collected monthly for one year in 33 2m²-quadrats numbered sequentially from the entrance (1) to deep zone (33). e = entrance zone (quadrats 1-8); t = transitional zone (quadrats 9-14); d = deep zone (quadrats 15-33).

relative to other (possibly unmeasured) conditions in Wynberg cave. This is supported by the fact that a combination of four variables yielded the highest correlation in Wynberg cave, these being temperature, relative humidity, surface moisture and wind/light ($r^2 = 0.57$). In Bats' cave, only two variables, temperature and relative humidity, showed the highest correlation ($r^2 = 0.83$) (Table 7). The more graded environmental conditions in Bats' cave, compared with the relative uniformity of conditions throughout Wynberg cave (Table 6), may have resulted in correlations being stronger in Bats' cave.

In addition to relative humidity, temperature was clearly an important factor in both caves. Soil nitrogen content was of additional importance in Bats' cave, temperature, relative humidity and soil nitrogen content yielding a correlation coefficient of 0.83.

The MDS ordinations of quadrats based on temperature, relative humidity, wind/light and surface moisture (Figure 17c), and of soil nitrogen content, temperature and relative humidity (Figure 16c), yielded fairly good matches with the biotic ordinations of Bats' and Wynberg caves respectively. However, the patterns of incremental change along transects were more pronounced in entrance and transitional zones than deep zones. Entrance and transitional communities were therefore more clearly explained by these variables than the deep zone communities. Moreover, anomalies existed in both caves, indicating that seasonal data obscured correlations or that additional factors were also involved.

Environmental variables showing the weakest correlations with biotic patterns in Bats' cave were lichen, water availability (i.e. soil water, surface moisture, crevice moisture) and crevice availability (Table 7). These correlations may have been weakened by the lumping of seasonal data. In Wynberg cave, soil organic content, soil nitrogen content and soil energy content yielded weak correlations with biotic data, in addition to crevice moisture and crevice availability. In contrast, soil organic, nitrogen and energy contents were strongly correlated with Bats' cave biota, representing the most significant difference between the two caves. Soil nutrient content therefore appears to be more limiting in Bats' cave. This may be because insectivorous bat guano has a higher nitrogen content than fruit bat guano (Strong *et al.* 1984). Therefore, the presence of insectivorous bats in the deep zone of Wynberg cave resulted in higher soil nitrogen contents in this zone (Table 6). Soil nitrogen was therefore

less limiting and showed weaker correlations with the deep zone community (Table 7). The correlation of soil nitrogen with cave communities could also indirectly have been affected by biotic and abiotic factors. Water availability (surface and crevice moisture), on the other hand, was of greater importance in Wynberg cave when considered together with temperature and relative humidity.

Rank correlation coefficients matching environmental variables with taxon presence or absence data, rather than abundance data (Table 7), showed a weaker correlation for relative humidity, while food availability (e.g. plant debris, moss, lichen and guano) were better correlated with biotic patterns. Thus in Bats' cave, the highest correlation was yielded by the combination of plant debris and soil nitrogen content ($r^2 = 0.79$), while in Wynberg cave, plant debris, lichen, moss and guano yielded the highest correlation ($r^2 = 0.53$) (Table 7).

6.2. Factors affecting entrance communities

MDS community ordinations with superimposed environmental variables are given in Figures 19 and 20. Relative humidity and temperature showed clear patterns of incremental change with increasing depth, both remaining relatively constant within deep zone quadrats (Figures 19 and 20, b and c). Wind and light clearly reflected the contrast between entrance and dark zone community patterns, both being completely absent from dark zone quadrats (Figures 19 and 20, k and l). Soil nitrogen content and soil organic content strongly matched entrance community patterns in Bats' cave, this not being evident in Wynberg cave (Figures 19 and 20, e and f). Water availability (soil, surface and crevice moisture) generally showed very little reflection of biotic patterns in both caves (Figures 19 and 20, h, i and j).

Upon removal of variables with tied values (i.e. moss, lichen), the highest correlations with Bats' cave entrance biota (Table 8) were yielded by:

- Soil nitrogen content, soil energy content and crevice moisture ($r^2 = 0.82$) (Figure 18a).
- Soil nitrogen content, soil energy content, surface moisture, guano and wind/light ($r^2 = 0.81$).

In Wynberg cave, the highest correlations were yielded by:

- Temperature, relative humidity and plant debris ($r^2 = 0.80$) (Figure 18b).
- Temperature, relative humidity, plant debris and wind/light ($r^2 = 0.79$).

Table 8. Weighted Spearman's rank correlation coefficients matching environmental variables with abundance and distribution patterns of entrance and deep zone communities in Bats' and Wynberg caves. Taxon abundance data were considered and data was log transformed. Environmental variables are considered (a) singly and (b) in combinations yielding the highest correlations. Bold type indicates the strongest correlation. Light and wind were intercorrelated and considered as a single variable in the entrance zone. Being absent in deep zones, they were excluded from deep zone data.

Entrance community				Deep zone community				
a)	Bats' cave		Wynberg cave		Bats' cave		Wynberg cave	
Relative humidity (%)	0.44	Temperature (°C)	0.73	Relative humidity (%)	0.65	Relative humidity (%)	0.29	
Guano (scored)	0.44	Relative humidity (%)	0.69	Soil organic content (%)	0.54	Surface moisture (%)	0.10	
Soil nitrogen content (g/ml)	0.41	Wind/light (m/s; lux)	0.61	Soil nitrogen content (g/ml)	0.54	Crevice availability (%)	0.09	
Crevice moisture (%)	0.34	Plant debris (scored)	0.30	Soil energy content (J/g)	0.45	Guano (scored)	0.04	
Soil energy content (J/g)	0.14	Guano (scored)	0.08	Temperature (°C)	0.30	Crevice moisture (%)	0.04	
Surface moisture (%)	-0.00	Crevice availability (scored)	0.01	Soil water content (%)	0.01	Soil water content (%)	-0.02	
Plant debris (scored)	-0.09	Soil energy content (J/g)	-0.07	Crevice availability (scored)	-0.05	Soil nitrogen content (g/ml)	-0.05	
Crevice availability (scored)	-0.10	Soil water content (%)	-0.08	Guano (scored)	-0.11	Temperature (°C)	-0.08	
Temperature (°C)	-0.17	Crevice moisture (%)	-0.11	Crevice moisture (%)	-0.19	Soil energy content (J/g)	-0.15	
Wind/light (m/s; lux))	-0.23	Soil nitrogen content (g/ml)	-0.26	Surface moisture (%)	-0.29	Soil organic content (%)	-0.16	
Soil water content (%)	-0.23	Soil organic content (%)	-0.28					
Soil organic content (%)	-0.31	Surface moisture (%)	-0.36					
b)								
Soil energy content, soil nitrogen content, crevice moisture	0.82	Temperature, relative humidity, plant debris	0.80	Relative humidity, soil energy content, surface moisture	0.74	Relative humidity, surface moisture	0.27	
Soil nitrogen content, soil energy content, surface moisture, wind/light, guano	0.81	Temperature, relative humidity, wind/light, plant debris	0.79	Relative humidity, soil energy content, soil organic content	0.74	Relative humidity, crevice availability, surface moisture	0.27	
Relative humidity, soil organic content, soil Nitrogen content, soil energy content, crevice moisture, wind/light	0.80	Temperature, relative humidity	0.77	Relative humidity, soil energy content, soil nitrogen content	0.73	Relative humidity, soil organic content, crevice moisture	0.26	

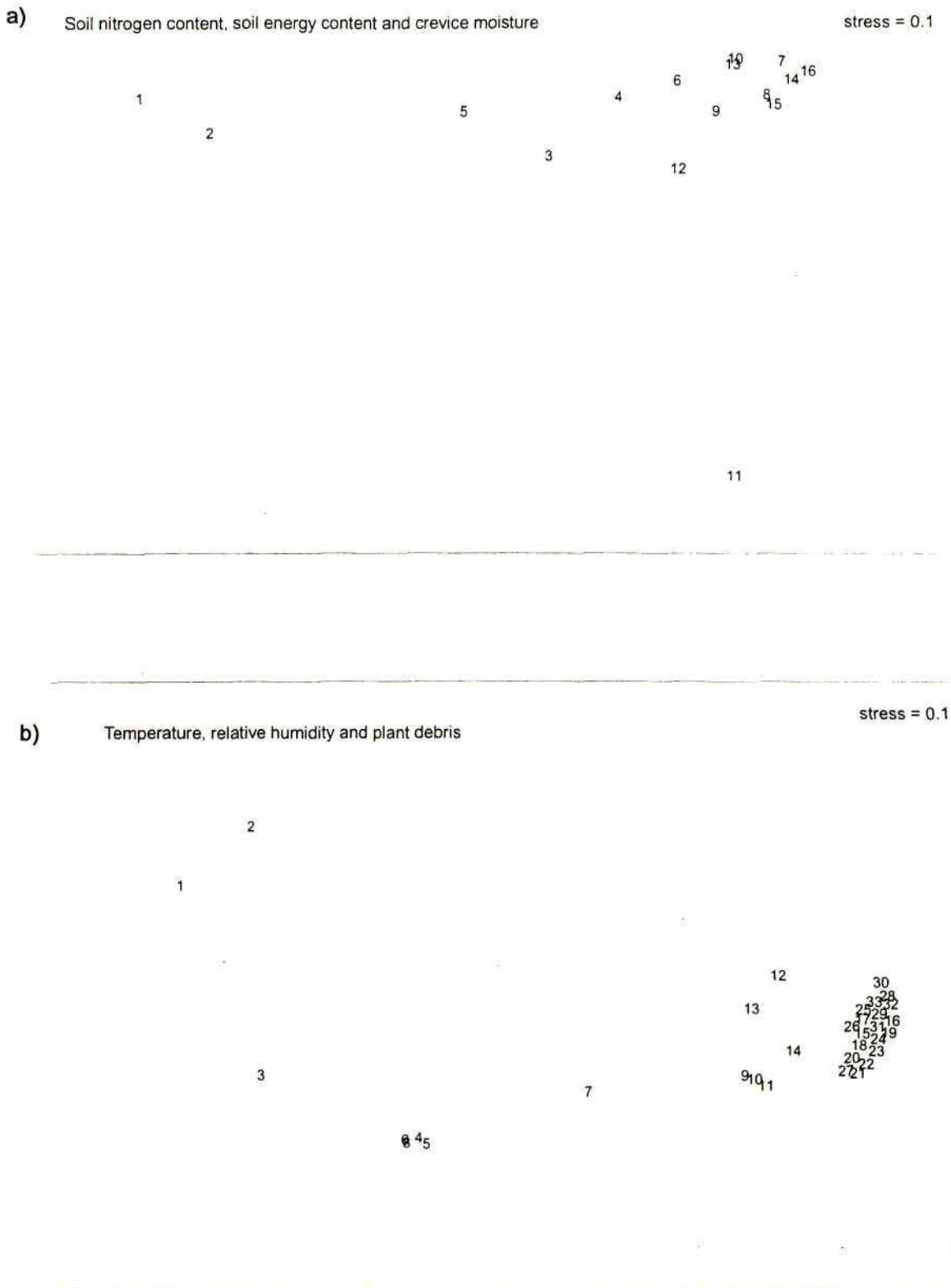


Figure 18: MDS ordination of quadrats based on environmental variables (log transformed) that yielded the strongest correlations with entrance community patterns in (a) Bats' cave (soil nitrogen content, soil energy content and crevice moisture) and (b) Wynberg cave (temperature, relative humidity and plant debris). Data were collected monthly for one year in 16 and 33 2m²-quadrats in Bats' and Wynberg caves respectively. Quadrats were numbered sequentially from entrance zones (quadrats 1-5 in Bats' cave and 1-8 in Wynberg cave) to deep zones quadrats (7-11, 13-16 in Bats' cave and 15-33 in Wynberg cave).

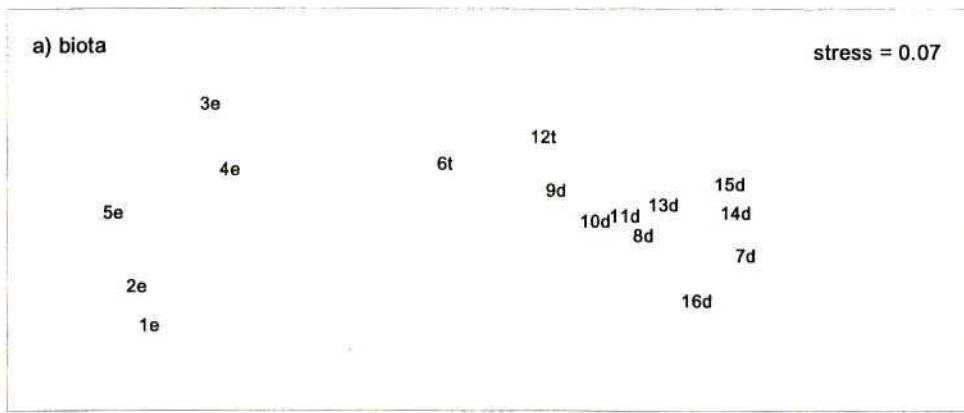


Figure 19. (a) MDS ordination of quadrats in Bats' cave based on taxon abundance data (fourth-root transformed). (b-g) Biotic ordinations with superimposed environmental variables (log transformed). Data were collected monthly for one year in 16 2m²-quadrats numbered sequentially from the entrance zone (1) to deep zone (16). e = entrance zone; t = transitional zone; d = deep zone. Symbols are scaled according to the magnitude of the measured environmental variable.



Figure 19 continued. (h-k) Bats' cave biotic ordinations with superimposed environmental data.

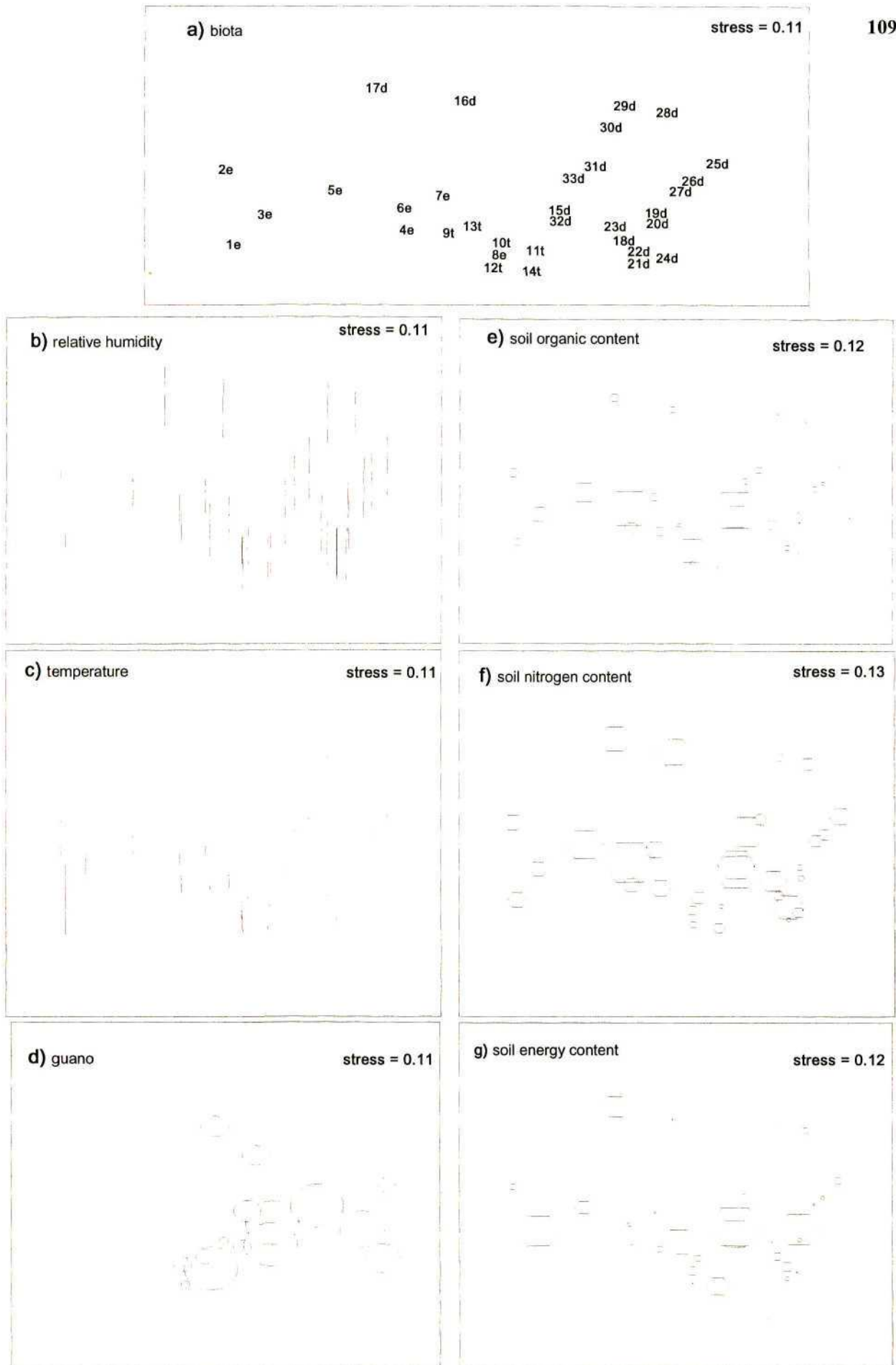


Figure 20. (a) MDS ordination of quadrats Wynberg cave based on taxon abundance data (fourth-root transformed). (b-g) Biotic ordinations with superimposed environmental variables (log transformed). Data were collected monthly for one year in 33 2m²-quadrats numbered sequentially from the entrance zone (1) to deep zone (33). e = entrance zone; t = transitional zone; d = deep zone. Symbols are scaled according to the magnitude of the measured environmental variable.

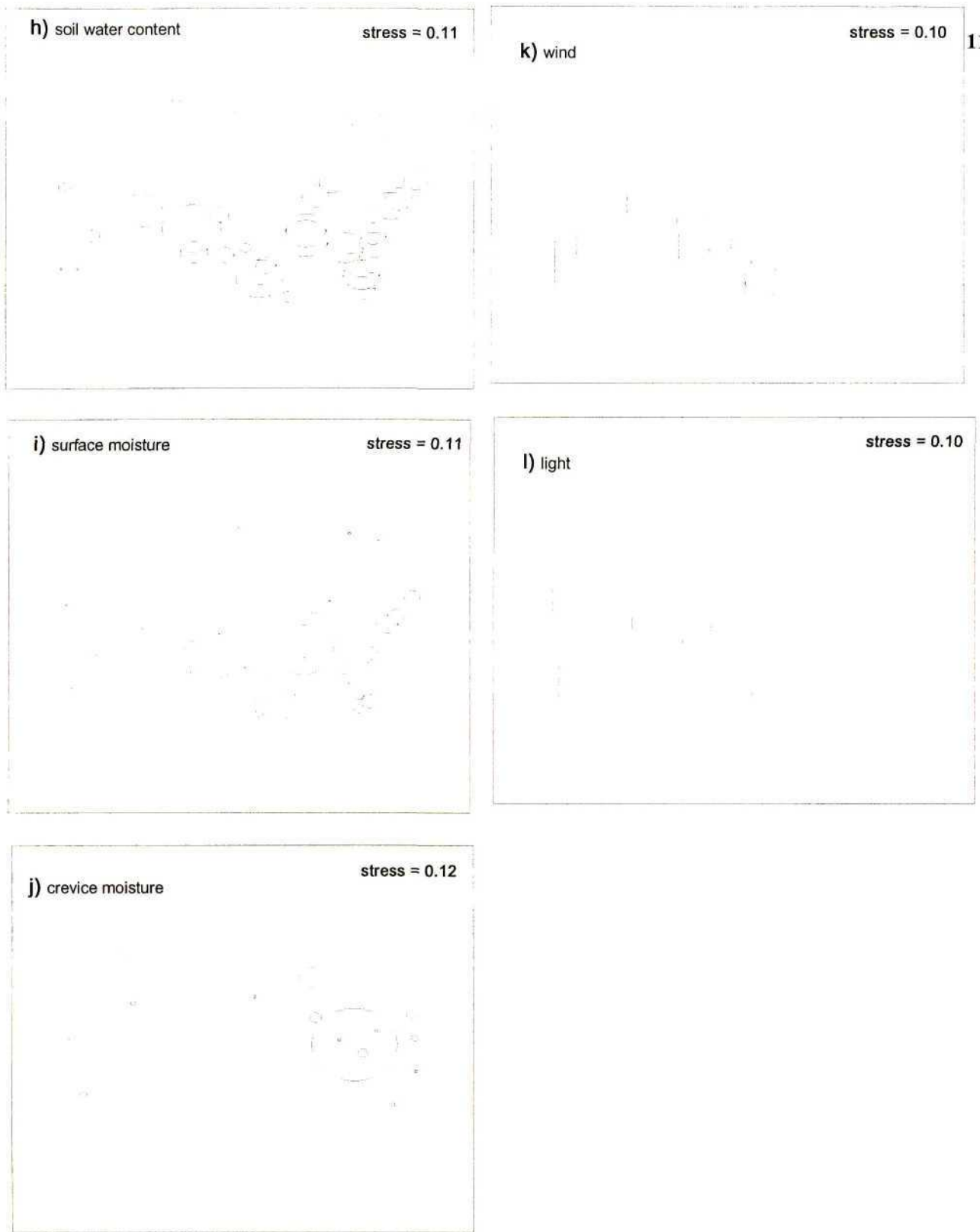


Figure 20 continued. (h-l) Wynberg cave biotic ordinations with superimposed environmental data.

The MDS ordinations of the most highly correlated variables (Figures 18a and b) showed patterns of pronounced incremental change in entrance quadrats, but bore little reflection of biotic patterns in deep zone quadrats which were tightly clustered.

Therefore, relative humidity was clearly important in determining community patterns in both cave entrances. This correlation was stronger in Wynberg cave than in Bats' cave ($r^2=0.69$ and 0.42 respectively). Temperature and plant debris showed stronger correlations with the entrance community of Wynberg cave, while soil nitrogen content, guano and soil energy content were more limiting in the entrance zone of Bats' cave. Surface and crevice moisture, however, appear to be of some importance in structuring community patterns in both cave entrances. Separate Analysis of seasonal data would further elucidate this importance of water availability.

6.3 Factors affecting deep zone communities

The Bats' cave biotic MDS ordinations with superimposed environmental variables (Figure 19) reveal that soil energy content (Figure 19g) and relative humidity (Figure 19b) match deep zone community patterns (Figure 19a) relatively well. Therefore, the deep zone quadrats, 14, 15 and 16, are characterised by low soil energy content and high relative humidities.

Wind, light and plant debris were excluded from deep zone environmental data due to tied values. Combined factors yielding the highest correlations with deep zone community patterns in Bats' cave (Table 8) were:

- Relative humidity, soil energy content and surface moisture ($r^2=0.74$).
- Relative humidity, soil organic content and soil energy content ($r^2=0.74$).
- Relative humidity, soil nitrogen content and soil energy content ($r^2=0.73$).

In Wynberg cave, weak correlations were yielded by all environmental variables (Table 8), indicating deep zone community patterns to be more complex and environmental conditions to be more uniform. Nevertheless, the highest correlation with biotic patterns was yielded by a single variable, relative humidity ($r^2=0.29$). Surface moisture, crevice availability and

Table 9. Weighted Spearman's rank correlation coefficients matching environmental variables with species ordinations of troglobitic species in Bats' and Wynberg caves. Environmental variables are considered (a) singly and (b) in combinations yielding the highest correlations. Data were log transformed and bold type indicates the overall optimum correlation. Species abundance data of the troglobites, *Trichoniscus tabulae*, *Hahnia* sp.nov., *Lepthyphantes rimicola*, *Crozetulus scutatus*, *Speleomontia cavernicola*, and *Speleosiro argasiformes*, as well as of the troglophile, *Speleiacris tabulae*, were considered. Light and wind were strongly negatively correlated with troglobites, but were removed from the analysis because of tied values.

a)	Bats' cave		Wynberg cave
Relative humidity (%)	0.66	Relative humidity (%)	0.38
Soil organic content (%)	0.55	Temperature (°C)	0.25
Soil nitrogen content (g/ml)	0.54	Crevice availability (scored)	0.25
Soil energy content (J/g)	0.42	Guano (scored)	0.02
Temperature (°C)	0.32	Soil organic content (%)	-0.05
Guano (scored)	0.10	Surface moisture (%)	-0.07
Soil water content (%)	0.01	Soil water content (%)	-0.08
Crevice availability (scored)	-0.10	Crevice moisture (%)	-0.07
Surface moisture (%)	-0.20	Soil energy content (J/g)	-0.08
Crevice moisture (%)	-0.31	Soil nitrogen content (g/ml)	-0.11
b)			
Relative humidity, soil organic content, soil nitrogen content, soil energy content, crevice availability	0.76	Relative humidity, crevice availability	0.39
Relative humidity, soil organic content, soil energy content	0.75	Relative humidity, crevice availability, guano, surface moisture	0.35

guano were also of relative importance (Table 8). The superimposition of soil nitrogen content (Figure 20f) and soil water content (Figure 20h) on the biotic MDS ordination, explain the similarity of quadrats 16 to 17 as well as of quadrats 15 to 32. All four quadrats were guano-rich, while quadrats 16 and 17 were far drier than other deep zone quadrats. It would appear, therefore, that these factors affected community patterns in these quadrats.

Therefore, while relative humidity showed the strongest correlation with deep zone community patterns in both caves, correlations were far stronger in Bats' cave. Soil nitrogen and soil energy contents were strongly correlated with Bats' cave deep zone community, while surface moisture, crevice moisture and crevice availability were of greater importance (relative to other variables) in the Wynberg cave deep zone community, although weakly correlated. These trends may be more meaningful if seasonal fluctuations are also considered.

6.4. Factors affecting troglobite distribution and abundance.

Table 4 gives the rank correlation coefficients matching environmental variables with the MDS ordinations of troglobitic species. The troglobites considered were *Trichoniscus tabulae*, *Hahnia* sp.nov., *Lepthyphantes rimicola*, *Crozetulus scutatus*, *Speleomontia cavernicola* and *Speleosiro argasiformes*. The troglophile, *Speleiacris tabulae*, was also considered. Relative humidity yielded the strongest correlation in both caves (Table 9). In Wynberg cave, correlations were very weak, probably due to the uniformity of environmental conditions. However, lumping of seasonal data may have caused correlations to become obscured. Other unconsidered variables may also have been important. The strongest correlation was yielded by relative humidity and crevice availability ($r^2= 0.39$) (Table 9). Temperature also showed a relatively strong correlation. In Bats' cave, soil organic, nitrogen and energy contents were relatively more important. The strongest correlation was yielded by these three variables combined with relative humidity and crevice availability ($r^2= 0.76$).

These trends were very similar to those derived from deep zone data in both caves (Table 8). Nevertheless, correlations in Wynberg cave were too weak for a conclusive comparison of caves. Furthermore, the larger number of variables and stronger correlations yielded in Bats' cave, compared with the weak correlations yielded by a small number of variables in Wynberg cave, may be explained by three possible factors:

Table 10. Correlation coefficients yielded by regression of environmental variables and troglobite abundance (both log transformed) in Bats' and Wynberg caves. The most abundant troglophile, *Speleiacris tabulae*, was also considered. Bold type indicates significant correlations ($P < 0.05$).

Species	Temperature	Relative humidity	Soil water content	Surface moisture	Crevice moisture	Soil organic content	Soil nitrogen content	Soil energy content	Guano	Crevice availability	Rocks
Wynberg cave											
<i>Trichoniscus tabulae</i>	-0.22	0.21	-0.25	0.31	0.51	-0.22	-0.28	0.00	0.13	0.33	0.10
<i>Hahnia</i> sp.nov.	-0.24	0.25	0.05	0.17	0.29	-0.16	-0.07	-0.24	0.24	0.31	0.06
<i>Lepthyphantes rimicola</i>	-0.22	0.21	-0.20	0.22	-0.03	-0.05	-0.16	-0.06	-0.08	-0.37	0.54
<i>Crozetulus scutatus</i>	-0.15	0.24	-0.31	0.12	-0.03	-0.27	-0.26	0.03	-0.08	0.48	0.25
<i>Speleomontia cavernicola</i>	-0.44	0.46	0.18	0.54	0.56	-0.28	-0.10	-0.06	0.40	0.24	0.02
<i>Speleosiro argasiformes</i>	-0.10	0.22	-0.13	0.11	-0.07	-0.19	-0.11	-0.08	-0.44	0.03	0.66
<i>Speleiacris tabulae</i>	-0.89	0.80	0.12	0.16	0.17	0.18	0.12	0.08	0.62	-0.15	-0.14
Bats' cave											
<i>Trichoniscus tabulae</i>	-0.37	0.24	0.08	-0.25	0.43	-0.39	-0.37	-0.58	0.01	0.33	0.25
<i>Hahnia</i> sp.nov.	-0.34	0.16	-0.46	0.01	0.09	-0.34	-0.32	0.32	0.31	0.45	0.19
<i>Lepthyphantes rimicola</i>	-0.65	0.84	-0.40	0.18	0.21	-0.60	-0.75	-0.38	0.01	0.04	-0.20
<i>Crozetulus scutatus</i>	-0.68	0.84	-0.30	-0.18	0.22	-0.59	-0.71	-0.43	-0.09	0.14	-0.12
<i>Speleomontia cavernicola</i>	-0.34	0.47	-0.11	0.50	0.37	-0.28	-0.28	-0.13	0.21	0.47	0.01
<i>Speleosiro argasiformes</i>	-0.59	0.70	-0.19	0.24	0.29	-0.56	-0.58	-0.50	-0.30	0.17	0.30
<i>Speleiacris tabulae</i>	-0.48	0.70	-0.19	-0.26	-0.18	0.09	0.21	0.19	0.49	0.02	-0.11

- intercorrelated or excluded variables, or
- greater uniformity of conditions in Wynberg cave compared with the more graded physical environment in Bats' cave which facilitated the detection of limiting factors.
- Seasonal changes were not considered. The winter effect may have been stronger in Bats' cave, while in Wynberg cave its effect may have been cancelled out by conditions in summer.

Because variables yielding the highest correlations for each species differed so strikingly between caves, species were individually correlated with environmental variables (species abundance being regarded as a dependent variable) (Table 10). It is clear that one or a few environmental variables did not explain the distribution and abundance patterns of all species. Similarities that did exist between troglobites were neither striking nor uniform. Results were also not consistent between caves. This may be because different factors were limiting in each cave, or because lumping of seasonal data as well as intercorrelated variables accentuated differences. Certain trends were, however, recognizable:

- *Trichoniscus tabulae*, *Hahnia* sp.nov., and *Crozetulus scutatus* all showed statistically significant ($P < 0.05$) positive correlations with crevice availability in Wynberg cave. *Lepthyphantes rimicola* showed a significantly negative correlation with crevice availability, but was positively correlated with rock availability ($P < 0.05$) (Microhabitat preferences of species are discussed in Chapter 7).
- *Trichoniscus tabulae* and *Speleomontia cavernicola* were significantly correlated with crevice and surface moisture ($P < 0.05$) in Wynberg cave.
- Relative humidity was important for all species, most notably, *Lepthyphantes rimicola*, *Speleosiro argasiformes*, *Speleomontia cavernicola* and *Crozetulus scutatus*. All showed significant positive correlations ($P < 0.05$) in Bats' cave.
- *Speleiacris tabulae* showed significant positive correlations ($P < 0.05$) with relative humidity and guano availability, but a significant negative correlation with temperature. This sensitivity to temperature and humidity is well-documented in biological studies of raphidophorid crickets (Richards 1969).
- *Speleiacris tabulae* showed positive correlations with soil organic, energy and nitrogen contents, while troglotic species showed strong negative correlations with these

variables. This negative correlation was significant ($P < 0.05$) for *Speleosiro argasiformes* in Bats' cave.

6.5. Discussion

The most striking result is the apparent complexity of factors affecting abundance and distribution patterns of cavernicoles in the Table Mountain caves. No single environmental factor satisfactorily explained community patterns in either cave, a complex of variables showing the strongest correlation. Correlations were generally weaker in Wynberg cave, indicating that conditions were more uniform, or that a greater complexity of unmeasured factors were involved. Lumping of seasonal data undoubtedly also obscured community patterns. Although microclimate was not considered in this study, it clearly plays a major role in the distribution of a variety of cave species (Poulson and Culver 1969; Juberthie 1969; Christiansen 1970). Inclusion of microenvironmental variables would undoubtedly yield more complex interactions (Christiansen 1970). Separate analysis of seasonal data would also further elucidate seasonal community patterns.

Relative humidity was found to be the most important environmental variable affecting community patterns in the Table Mountain caves. This agrees with findings for the vast majority of cave studies which have found a stable saturated atmosphere to be the most critical environmental factor affecting the distribution of cave animals within caves, and excluding them from surface habitats (Vandel 1965; Barr 1968; Mitchell 1968; Poulson and White 1969; Barr and Kuehne 1971; Bull and Mitchell 1972; Accordi and Sbordoni 1978; Lucarelli and Sbordoni 1978; Peck 1978; Peck and Lewis 1978; Howarth 1980, 1981, 1983, 1988). Barr (1968) and Barr and Kuehne (1971) found a strong correlation between evaporation and the presence of troglobites in Mammoth cave, Kentucky. Higher rates of water loss have been observed in cave species at lowered relative humidities (Howarth 1980; Hadley *et al.* 1981). Howarth (1980) reported a 75% reduction in longevity of the troglobitic spider, *Lycosa howarthi*, at relative humidities lowered from 100% to 90%. Finally, Richards (1971) observed that cavernicoles were able to move into epigeal habitats only when surface relative humidities were over 90%.

Although relative humidity was consistently important, other important variables showed no uniformity either within caves, between caves or between species (Tables 17, 18, 19 and 20). Relative humidity, temperature and plant debris showed stronger correlations with the entrance community of Wynberg cave, while relative humidity, surface moisture, crevice moisture and crevice availability were of greater importance in its deep zone (Table 8). In Bats' cave, on the other hand, surface moisture, crevice moisture and guano were more strongly correlated with entrance communities, while temperature and soil organic content showed stronger correlations with its deep zone community (Table 8). Soil nitrogen and energy contents were of importance in both zones. Correlations with environmental variables were stronger in entrance than in deep zone communities, most notably in Wynberg cave.

To what extent these differences between caves were true differences in limiting factors, or were influenced by cave structure or intercorrelated variables, is not clear. However, pronounced differences in cave structure would undoubtedly have influenced environmental conditions and, therefore, community patterns in each cave. Temperature, relative humidity and moisture are affected by the configuration of passageways and the position and size of the entrance (Christiansen and Bullion 1978; Howarth 1973, 1980, 1983; Tuttle and Stevenson 1978). Wynberg cave has a small entrance and an extensive deep zone. This has resulted in relatively uniform and stable conditions throughout the cave. Bats' cave, on the other hand, has a large, exposed entrance, while its deep zone extends steeply downwards from the entrance, resulting in graded changes in biotic and abiotic patterns with increasing depth. Consequently, stronger correlations between biotic and abiotic patterns were observed in Bats' cave (Tables 7 and 8). The greater stability and uniformity of conditions in Wynberg cave hindered the detection of trends in both community and environmental patterns, thus explaining the relatively weak correlations, most notably in the deep zone. It may also be that intercorrelation of highly zonal variables occurred in Bats' cave, thus yielding confounded results. That is, unmeasured variables may have been important in both caves, but were masked by measured variables in Bats' cave. Lumping of seasonal data may also have cancelled out correlations produced for summer and winter conditions, thus obscuring the winter effect.

Environmental conditions in caves are greatly influenced by entrance size and location (Howarth 1983). The large entrance to Bats' cave resulted in lower relative humidities and higher temperatures in its entrance zone. On the other hand, the smaller entrance to Wynberg cave resulted in higher relative humidities and lower temperatures (Table 6). Species requiring high relative humidities and low temperatures would only be able to extend their ranges into cave entrances where conditions allowed. These conditions are more likely to arise in Wynberg cave, temperature and relative humidity consequently becoming limiting factors affecting entrance community patterns. This would explain the occasional occurrence, often in relatively high numbers, of the troglobitic *Speleomontia cavernicola* in crevices in the entrance zone of Wynberg cave. Temperature, relative humidity and light would be most limiting in summer when conditions in the entrance zones are hotter and drier.

Crevice availability was, in fact, found to be an additional limiting factor for troglobites and deep zone communities (Tables 8 and 9). Many troglobitic species showed strong positive correlations with crevice availability, surface moisture and crevice moisture, most notably, *Speleomontia cavernicola*, *Hahnia* sp.nov. and *Trichoniscus tabulae* (Table 10). The small entrance and large, stable deep zone of Wynberg cave has resulted in more surfaces and crevices remaining permanently wet (Table 6). The gradient of moisture availability is therefore more pronounced, thus explaining the stronger correlations of these factors with troglobite and deep zone community patterns in Wynberg cave (Tables 8 and 9). One can conclude, therefore, that Wynberg cave with its higher moisture availability and relatively stable environmental conditions (relative humidity and temperature, in particular), offers more favourable conditions for troglobitic species.

The strong correlations of troglobitic species with crevice availability suggest that microhabitats and their associated microclimates may be more important determinants of troglobite community patterns than environmental conditions in humanly-navigable passages. Studies on cave insects and millipedes show that they tend to favour cool, humid microenvironments (Mitchell 1971; Bull and Mitchell 1972; Wilson 1975). Culver (1972) suggested that microhabitats serve as islands of favourable habitat surrounded by unfavourable habitat. Howarth (1982, 1983, 1988) further suggested that troglobites are adapted to exploit resources in mesocaverns, only occurring in large passageways when

environmental conditions are favourable. This certainly appears to hold true for the Table Mountain caves, most troglobites showing preferences for crevices. In addition to offering favourable microclimates, crevices may also be important for predator evasion. It is crucial, therefore, to correctly define the habitat before establishing ecological relationships.

While saturated atmospheres and the absence of light are essential criteria for cavernicole distribution, temperature, food and moisture have also been regarded as limiting in caves (Barr 1968; Poulson and White 1969; Barr and Kuehne 1971; Peck 1978, 1990; Culver 1982; Sbordoni 1982; Poulson 1986; Aalbu 1989). Abundant food resources, however, tend to favour opportunistic species rather than troglobites (Poulson and White 1969). In Bats' and Wynberg caves, community patterns derived from taxon presence or absence data showed stronger correlations with food availability than with the physical environment. This is because presence or absence data considered uncensused taxa, including the highly abundant humicoles and guanophiles. These taxa were primarily associated with their food resources that predominated in entrance zones where relative humidities were lower. This would explain the decreased importance of relative humidity as a limiting factor, and increased importance of food availability. In Bats' cave, plant debris and soil nitrogen yielded the highest correlations, while in Wynberg cave, plant debris, moss, lichen and guano were important. The dependence of the cave communities on the allochthonous input of food (most notably guano) has important conservation considerations which are discussed in Chapter 7.

Troglobitic species showed marked negative correlations with soil nitrogen content and guano (Table 10), most notably, *Lepthyphantes rimicola*, *Crozetulus scutatus* and *Speleosiro argasiformes*. Poulson and White (1969) similarly found that high food input was correlated with an absence of troglobites in a number of temperate caves. As Howarth (1987) points out, for troglobites, the total amount of food may not be as important as its spatial and temporal variability and ease of exploitation.

Soil nitrogen and energy contents showed strong positive correlations in Bats' cave, being more pronounced in entrance quadrats. They were, however, weakly correlated in Wynberg cave (Table 8). This can largely be explained by the different types, amounts and distributions of bat guano in the two caves, insectivorous bat guano having a higher nitrogen

content per unit volume (Strong *et al.* 1984). The large volume of fruit bat guano concentrated in the entrance zone of Bats' cave, yielded higher readings for soil nitrogen, energy and organic contents, as well as stronger correlations with the entrance biota (Tables 6 and 8, Figures 19 d-g). In contrast, the smaller amounts of diffusely-distributed insectivorous guano in the deep zone of Wynberg cave, resulted in the deep zone community being more strongly correlated with bat guano than the entrance community (Tables 6 and 8, Figure 20d). Despite this difference, however, both the deep zone and overall cave communities of Bats' cave showed significantly stronger correlations with these variables than those of Wynberg cave. There are four possible reasons for this:

- The irregular dispersion of large amounts of fruit bat guano in Bats' cave, facilitated the detection of limiting factors, most notably, soil nitrogen.
- Soil nutrient values and guano were intercorrelated with relative humidity.
- Concentrations of soil nitrogen in the deep zone of Bats' cave (presumably washed in from the overlying guano-rich entrance zone) may have allowed species positively correlated with nitrogen (and possibly other soil nutrients) to extend their ranges into the relatively nutrient-poor dark zone.
- The abundance of *Speleiacris tabulae*. Unlike troglobitic species, *S. tabulae* was positively correlated with guano, soil nitrogen, energy and organic contents (Table 10). Higher guano concentrations and soil nutrient contents in Bats' cave would explain the greater abundance of *S. tabulae* in this cave (Chapter 4), thus emphasising the positive correlation of its fauna with these variables, in both entrance and deep zones.

Troglobites, on the other hand, showed more pronounced negative correlations with soil nutrient content in Bats' cave than in Wynberg cave. As guano was primarily concentrated in the cave entrance, relative humidity, light and temperature would have limited their distribution, thus further emphasising the negative correlations.

6.6. Conclusion

Ecological factors associated with the distribution and abundance of cavernicoles in the Table Mountain caves are exceedingly complex. There are probably many more factors involved than were considered (e.g. oxygen and carbon dioxide levels, amount of stream-borne detritus or guano decompositional stage may all be of importance). Furthermore, real differences

appear to exist in the limiting effects of environmental variables on communities in Bats' and Wynberg caves, despite the similarity of their faunas. In general, however, relative humidity, temperature and moisture availability were of the greatest importance in both Bats' and Wynberg caves. Soil nitrogen and energy contents were far more limiting in Bats' cave, largely on account of the concentrated deposits of fruit bat guano in the entrance zone, compared with the diffuse and relatively uniform dark zone dispersion of insectivorous bat guano in Wynberg cave.

Factors affecting troglobitic species were particularly complex and varied from species to species. However, relative humidity, crevice availability and moisture availability were of the greatest importance for troglobites. It seems likely that troglobitic species remain in crevices and emerge in larger passages only when conditions are favourable. These movements are also likely to fluctuate seasonally, but data collected for summer and winter months were not separated in this analysis.

Therefore, to fully understand the factors that limit troglobite distribution and abundance, the microenvironment needs to be considered. However, similar macroenvironmental factors showed strong correlations with both troglobite and deep zone communities (Tables 8 and 9). Troglobites would therefore be expected to occur in deep zones where light and air currents are absent, temperatures are low and constant, the atmosphere is constantly saturated or nearly so, surfaces are permanently wet and nutrient availability is relatively poor. Any disturbance of these conditions would undoubtedly greatly affect troglobite communities.

7. Life history and diet of selected species

7.1. Seasonal fluctuations in abundance

Environmental stability in caves results in a complete absence of environmental cues that commonly trigger temporal life cycle adjustments in epigeal environments. This has a profound effect on life history traits and may represent a crucial factor for troglobite survival (Carchini *et al.* 1991b). The reproductive strategy characteristic of stable cave environments is that of so-called K-selected continuous breeding without diapause stages or marked seasonal changes (Alexander 1968). Troglotic species tend to decrease fecundity by laying fewer, larger eggs, or they may display a degree of neoteny (Poulson and White 1969; Howarth 1983). However, considerable variation exists between species (Poulson and White 1969; Poulson 1981; Poulson and Kane 1981).

To establish the extent to which their life cycles reflect this aseasonal pattern in the Table Mountain caves, seasonal fluctuations in abundance of the most abundant troglobites (*Crozetulus scutatus*, *Lepthyphantes rimicola*, *Speleosiro argasiformes* and *Speleomontia cavernicola*) as well as the troglophile, *Speleiacris tabulae*, were observed.

Environmental conditions of temperature, relative humidity and moisture availability (in the soil and on rock surfaces) varied seasonally in Bats' and Wynberg caves (Figures 21 and 22). Even within the deep zones, conditions were not absolutely constant (Table 6). The monthly measurements given in Figures 21 and 22 do not, in fact, represent the monthly mean, but the mean of conditions measured in each quadrat on days of sampling in each cave. Nevertheless, the cave environment remained relatively constant from one day to another and environmental fluctuations over each month were not expected to alter measurements to any extent. This, of course, does not preclude unforeseen fluctuations from having occurred and could, perhaps, explain anomalous differences in conditions between Bats' and Wynberg caves (such as the difference in the April reading of relative humidity). A number of generalisations can, however, be made:

- Temperatures were highest between February and May (peaking in March in Wynberg cave and in April in Bats' cave).

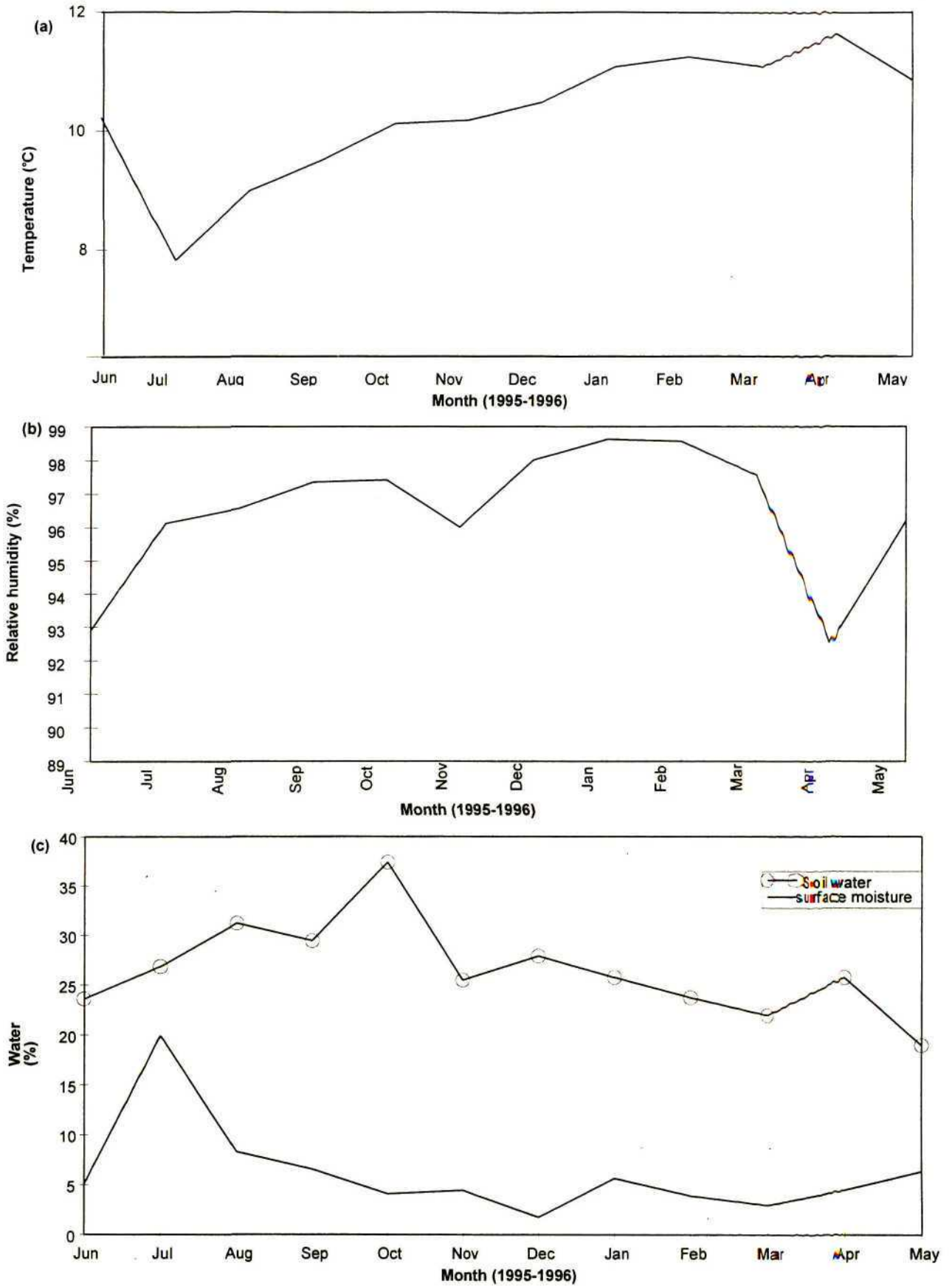


Figure 21. Monthly means per quadrat of (a) temperature, (b) relative humidity and (c) water availability (soil water content and surface moisture) in Bats' cave. Measurements were taken once a month for one year in 16 quadrats.

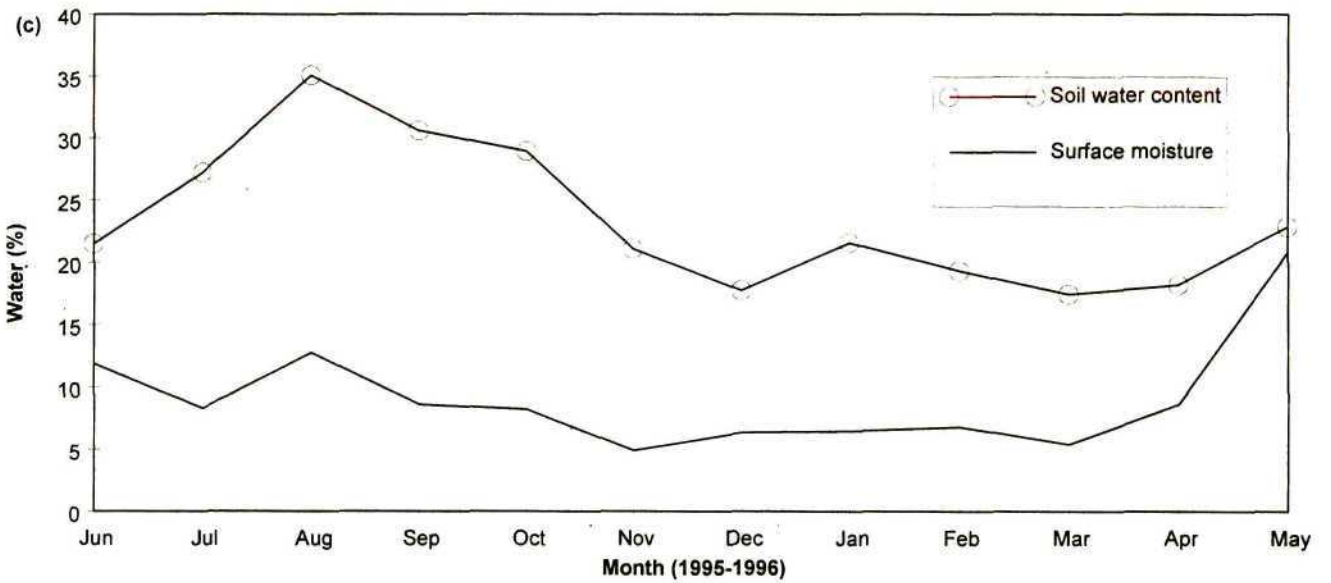
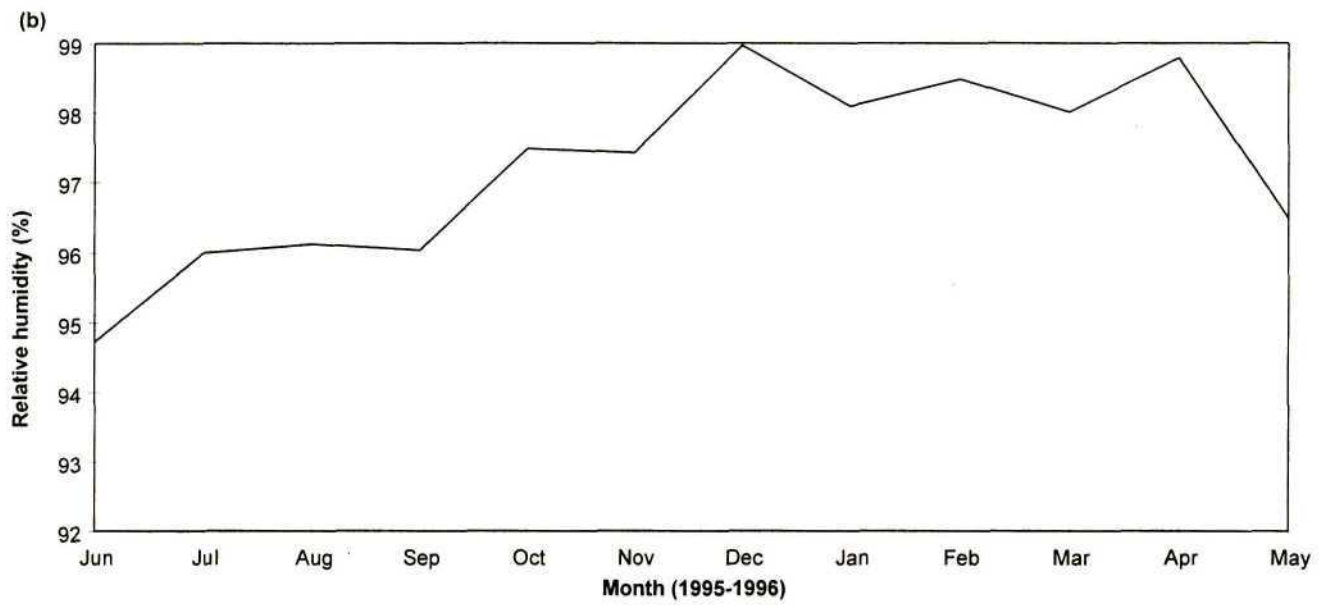
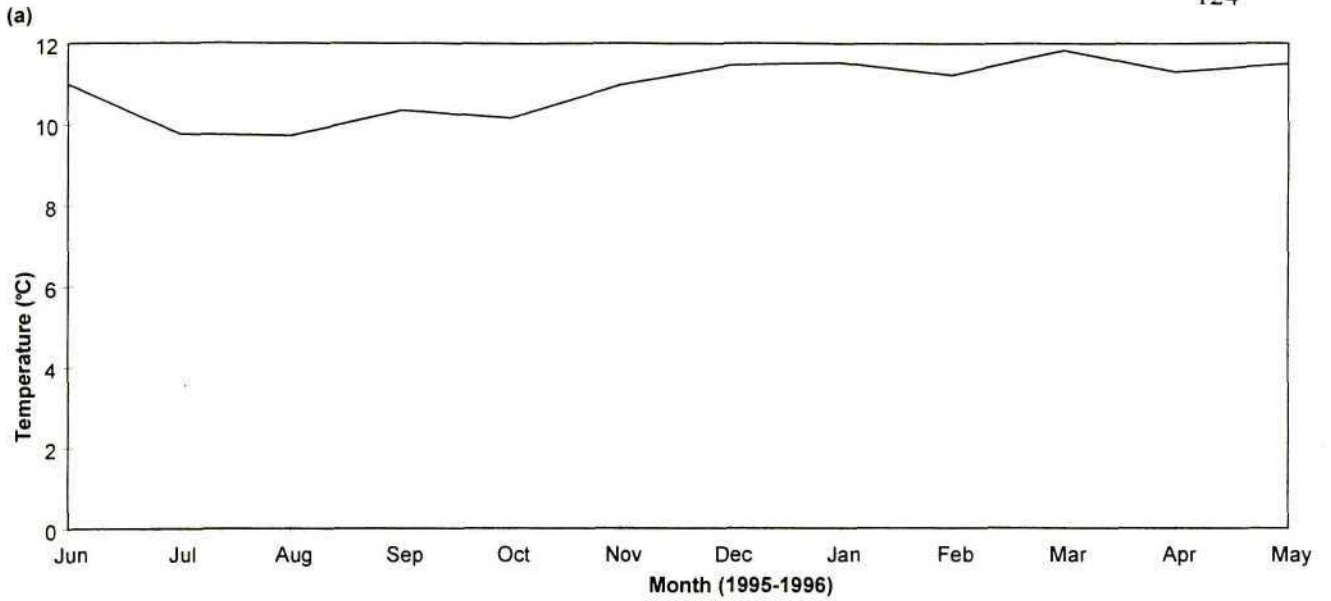


Figure 22. Monthly means per quadrat of (a) temperature, (b) relative humidity and (c) water availability (soil water content and surface moisture) in Wynberg cave. Measurements were taken once a month for one year in 33 quadrats.

- Relative humidities were greatest between December and March (peaking in December in Wynberg cave and in both January and February in Bats' cave).
- Soil water content was greatest between August and October (peaking in August in Wynberg cave and in October in Bats' cave).
- Surface moisture was greatest between May and September (peaking in May in Wynberg cave and in July in Bats' cave).
- Most environmental variables fluctuated less in Wynberg cave than in Bats' cave.

Seasonal variability in the cave environment reflected fluctuations in the surface environmental conditions, summers being hot and dry and winters being cold and wet. Although these fluctuations were dampened in the caves, they were of sufficient magnitude to act as cues to trigger seasonal changes in cavernicole abundance (Figures 23 to 27).

Lepthyphantes rimicola showed a pronounced peak in abundance in summer (November and March in Bats' cave, and October and January in Wynberg cave) (Figure 23). The population was at its lowest in the winter months (June, July and August). Large individuals (presumed to be adults or late-stage immatures) appeared in September, increased in abundance during the summer months, but were completely absent during winter (June, July and August). This strongly suggests the existence of an annual breeding cycle with one generation per year. However, because age classes were subjectively assigned in the field, some overlap may have occurred. Immature forms showed peaks in abundance in summer between February and April in both caves (as well as in January in Wynberg cave).

Crozetulus scutatus showed a peak in population size in late summer and autumn (between February and May in Wynberg cave, and between February and June in Bats' cave) (Figure 24). Abundance was lowest during winter and spring from July to November. A minor peak occurred in August. As the number of individuals considered in Wynberg cave was fairly low (297 individuals), irregular fluctuations were possibly accentuated.

Speleosiro argasiformes showed a pronounced seasonal cycle, populations peaking in summer from September to March in Bats' cave, and from December to February in Wynberg cave (Figure 25). The maximum number of individuals was counted in December

in Wynberg cave, and in January in Bats' cave. Population numbers were lowest in the winter months (June, July and August). In Wynberg cave, there was a marked decline in abundance between October and November, this not being apparent in Bats' cave. This may, once again, be as a result of too few individuals being counted in Wynberg cave (251 individuals) so that variations by only a few individuals were registered as major population fluctuations.

Population fluctuations of *Speleomontia cavernicola* were less pronounced (Figure 26). Two peaks in abundance were evident. A major peak occurred in autumn, this being between May and June in Bats' cave, and between April and May in Wynberg cave. Less pronounced peaks occurred in spring and early summer between September and December. Populations dropped in abundance in winter (July and August in Bats' cave and June and July in Wynberg cave) and again in summer (January to March in Wynberg cave and January to April in Bats' cave). There are three possible explanations for this trend: the life cycle is aseasonal, the life cycle extends over more than one year so that consecutive generations overlap, or active and conspicuous individuals were counted only, thus not reflecting overall numbers.

Figure 27 shows marked seasonal fluctuations in *Speleiacris tabulae* populations in the Table Mountain caves. Populations were most abundant in summer (October to March) and least abundant in winter (June to August) (Figures 27a and b). This variation was largely influenced by the annual increase in the number of young nymphs following oviposition (Figures 27b and c). All stages were present throughout the year.

Small nymphs showed the most pronounced seasonal fluctuations, although they appear to be produced continuously throughout the year (Figure 27c and d). Populations showed a steady increase from November onwards, being most abundant in January in both caves. Adult mating and egg-laying behaviours were observed between November and January. The number of small nymphs rose directly thereafter, possibly indicating that the eggs hatch rapidly. In Bats' cave, there was a pronounced decline in number after January. This was far more gradual in Wynberg cave, suggesting further recruitment (Figures 27 b and c).

Medium to large nymphs and adults showed very similar seasonal abundance patterns, most notably in Wynberg cave (Figure 27c and d). It is likely that a degree of overlap occurred

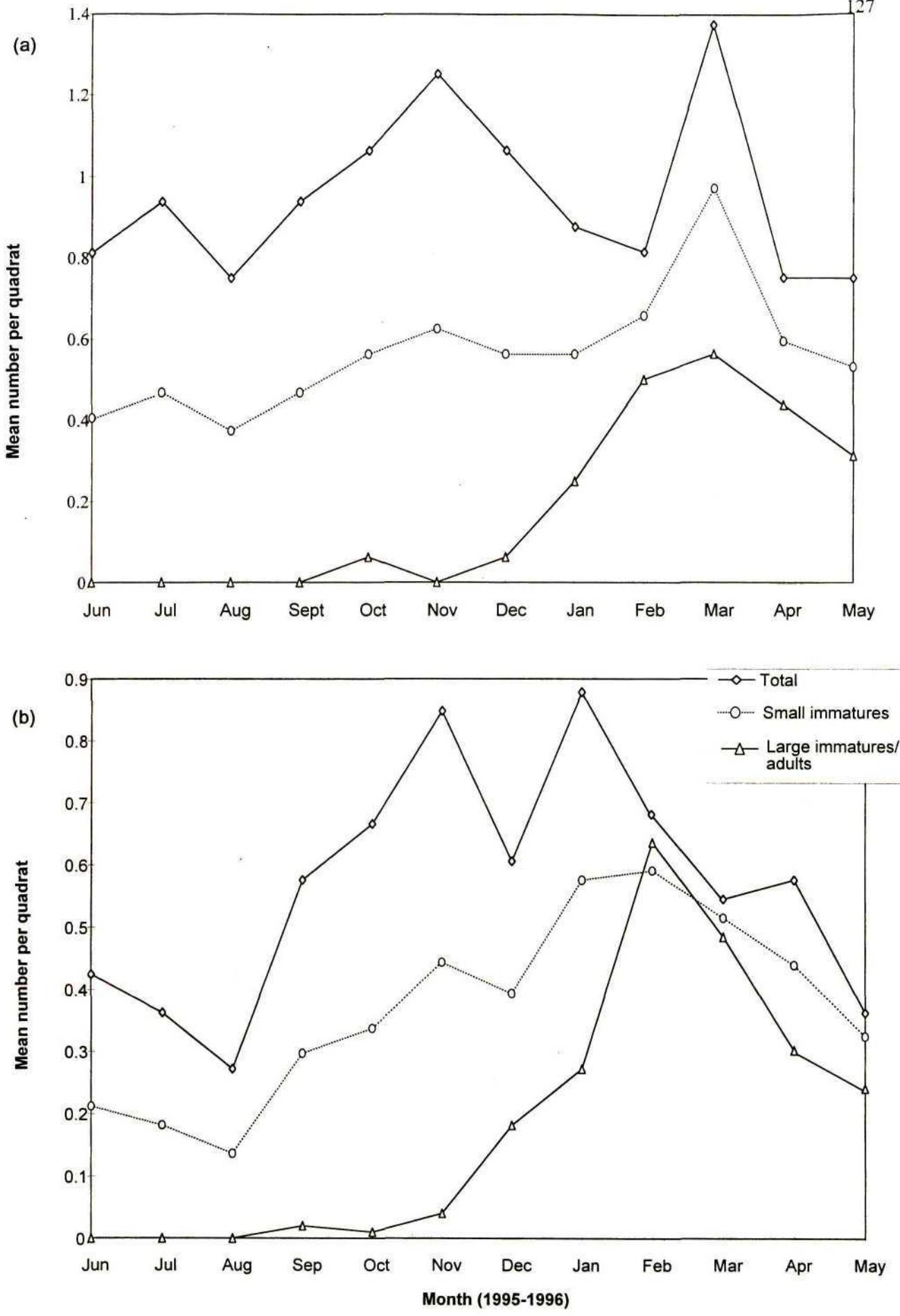


Figure 23. Monthly mean abundances per quadrat of *Lepptyphantès rimicola* adults (arbitrarily assigned to the >2mm long size-class) and immatures(<2mm long) in (a) Bats' cave and (b) Wynberg cave. Visual counts were conducted monthly for one year in 16 and 33 2m²-quadrats in Bats' and Wynberg caves respectively. Total number of individuals counted were 199 and 217 in Wynberg and Bats' caves respectively.

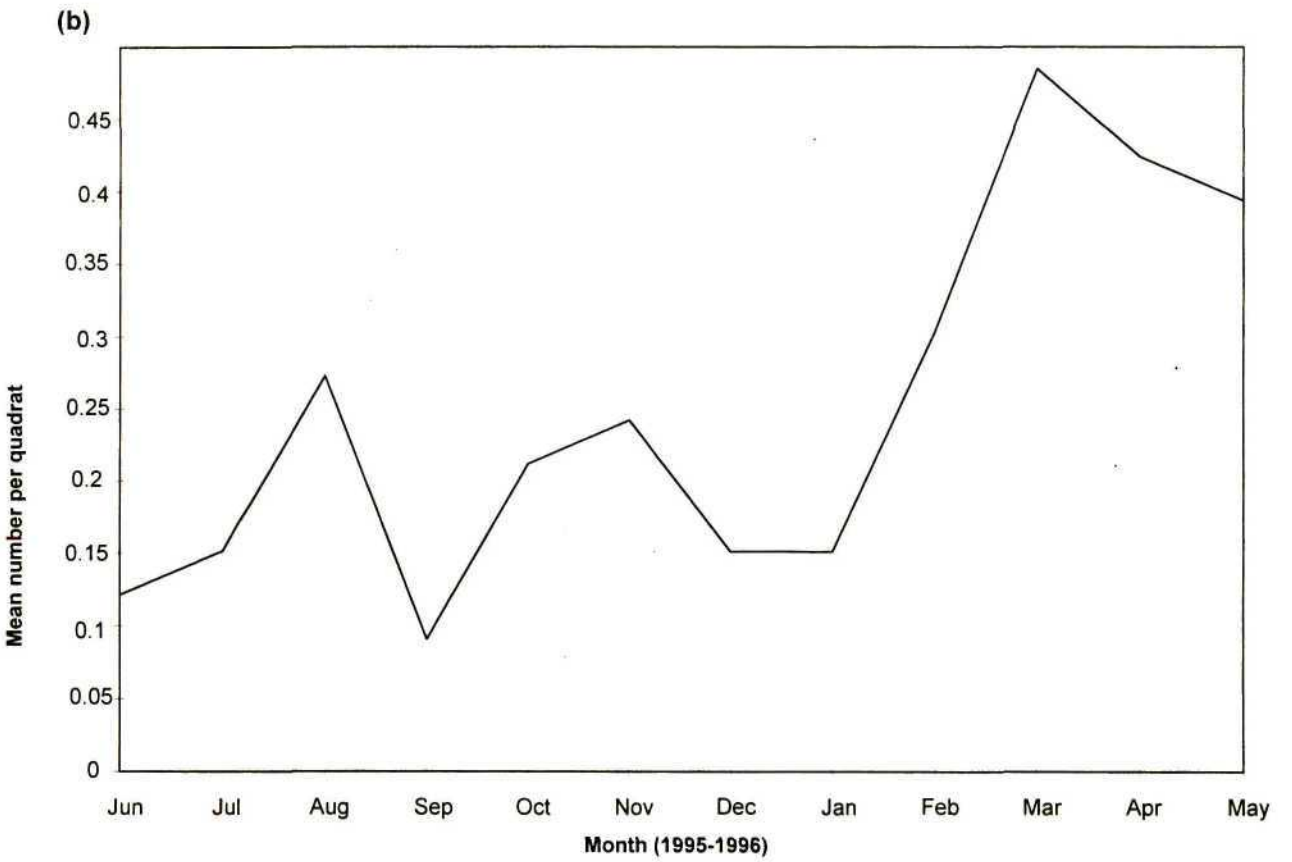
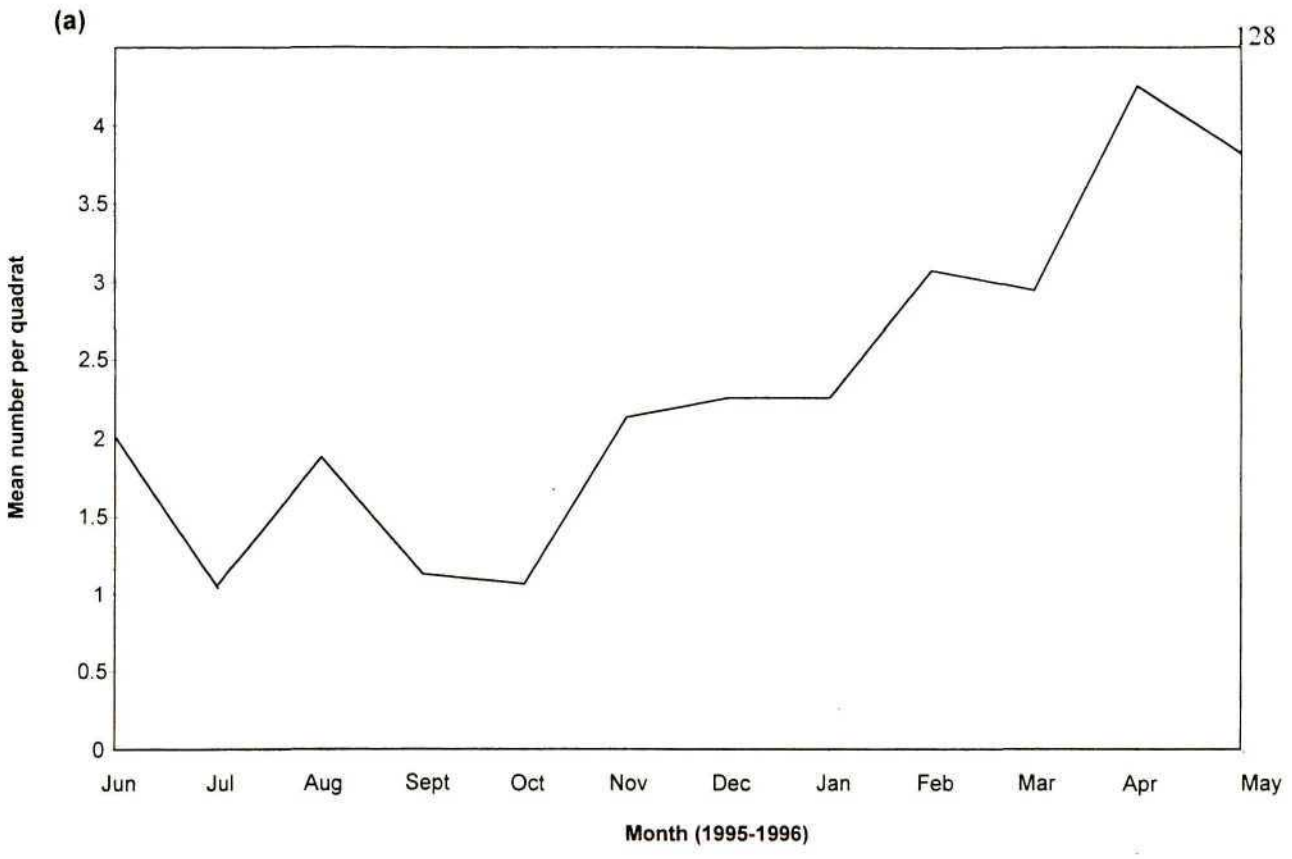


Figure 24. Monthly mean abundances per quadrat of *Crozetulus scutatus* in (a) Bats' cave and (b) Wynberg cave. Visual counts were conducted monthly for one year in 16 and 33 2m²-quadrats in Bats' and Wynberg caves respectively. Total number of individuals counted were 297 and 465 in Wynberg and Bats' caves respectively.

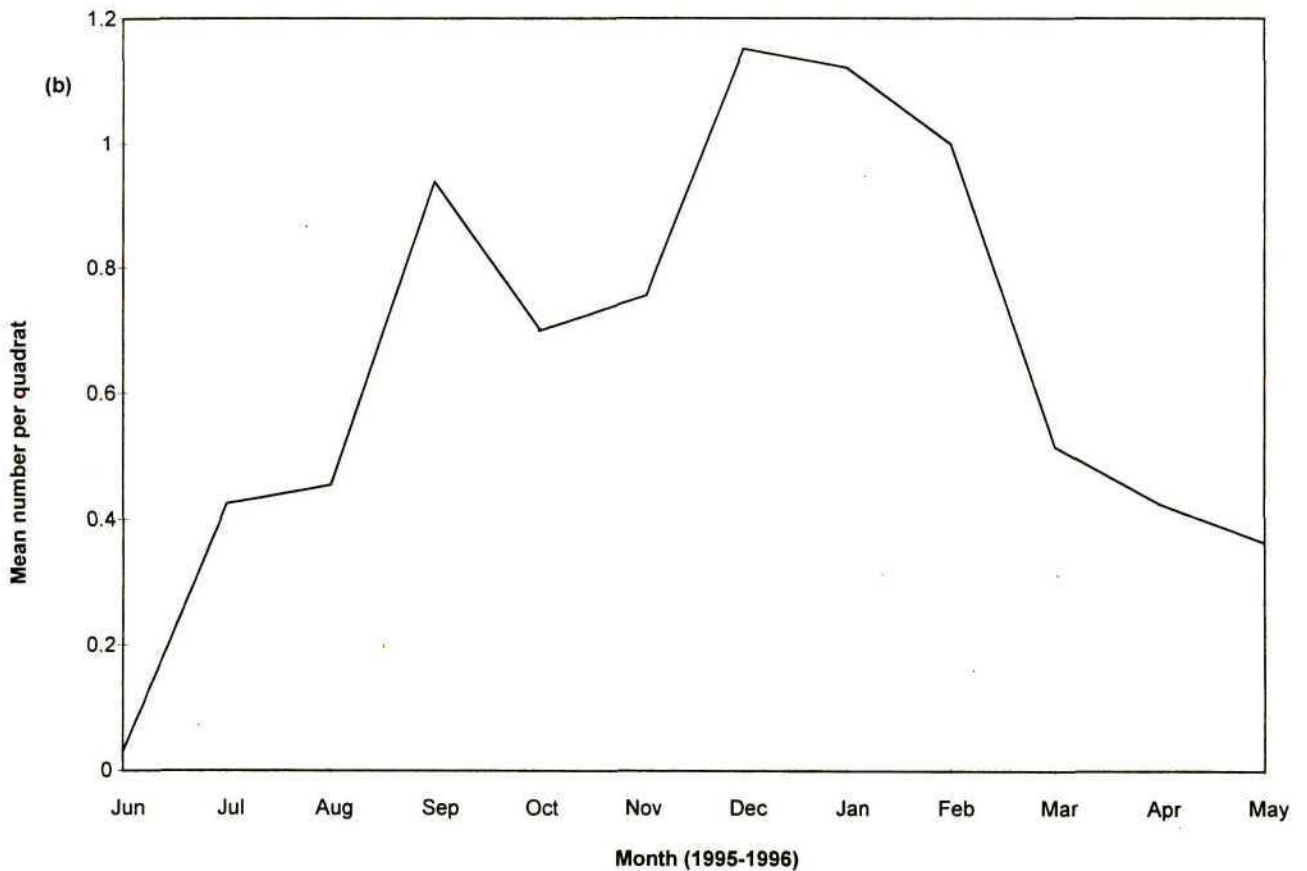
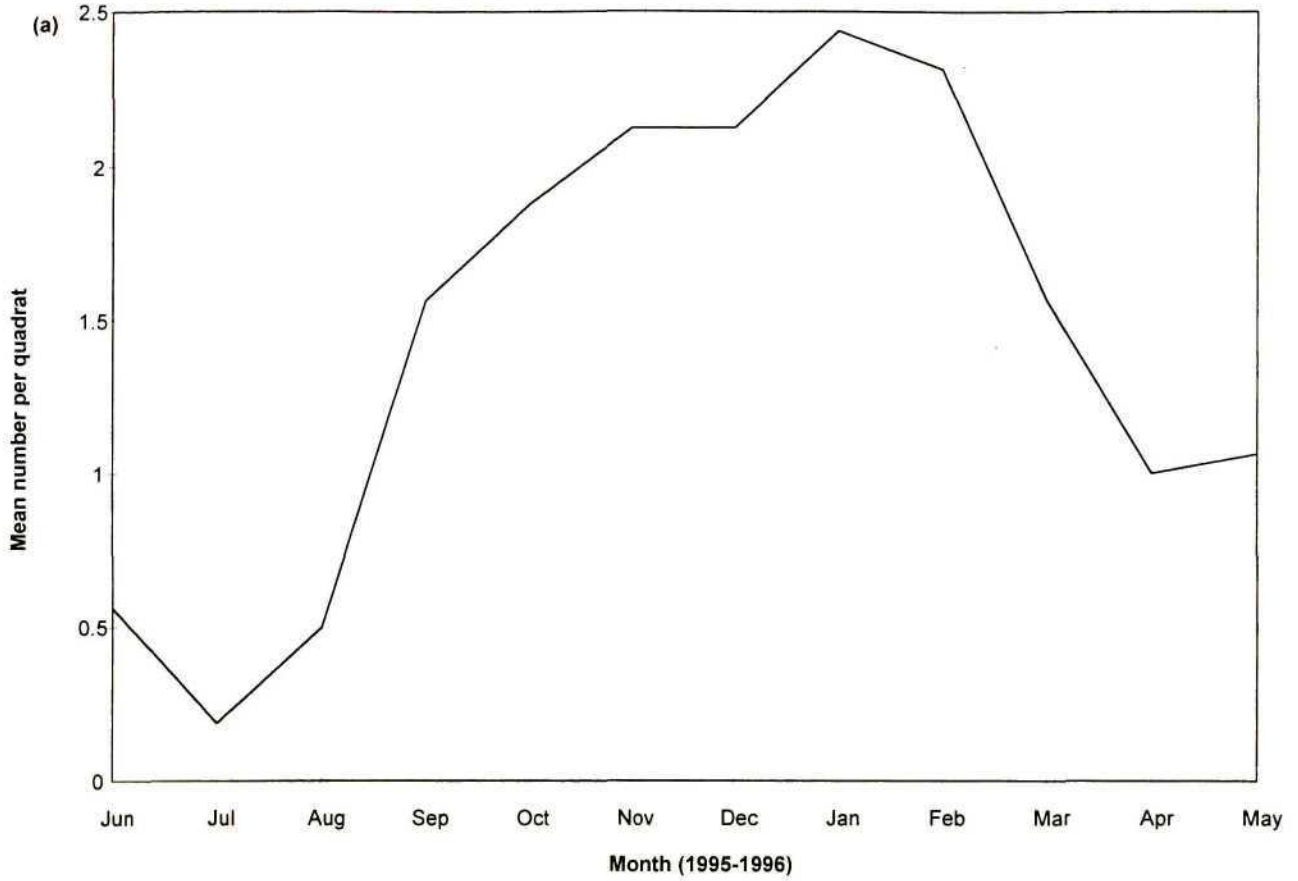


Figure 25. Monthly mean abundances per quadrat of *Speliosiro argasiformes* in (a) Bats' cave and (b) Wynberg cave. Visual counts were conducted monthly for one year in 16 and 33 2m²-quadrats in Bats' and Wynberg cave respectively. Total number of individuals counted were 251 and 277 in Wynberg and Bats' caves respectively.

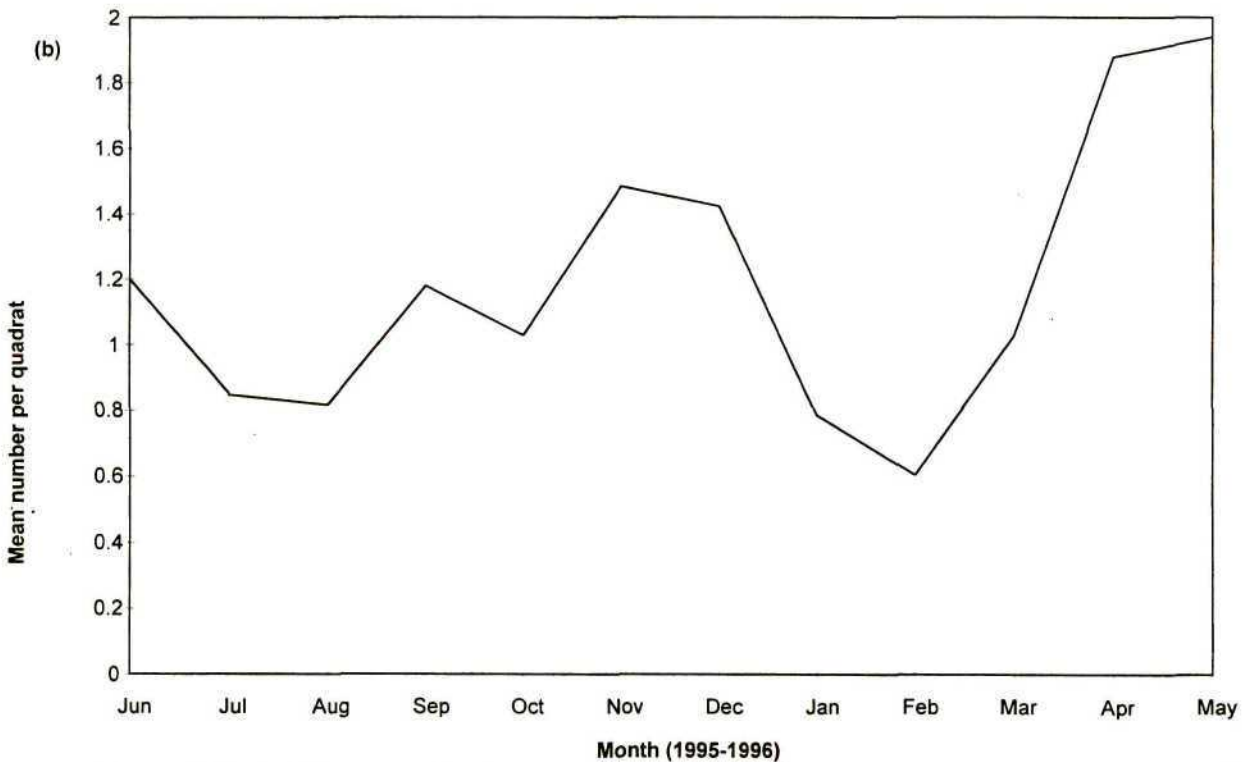
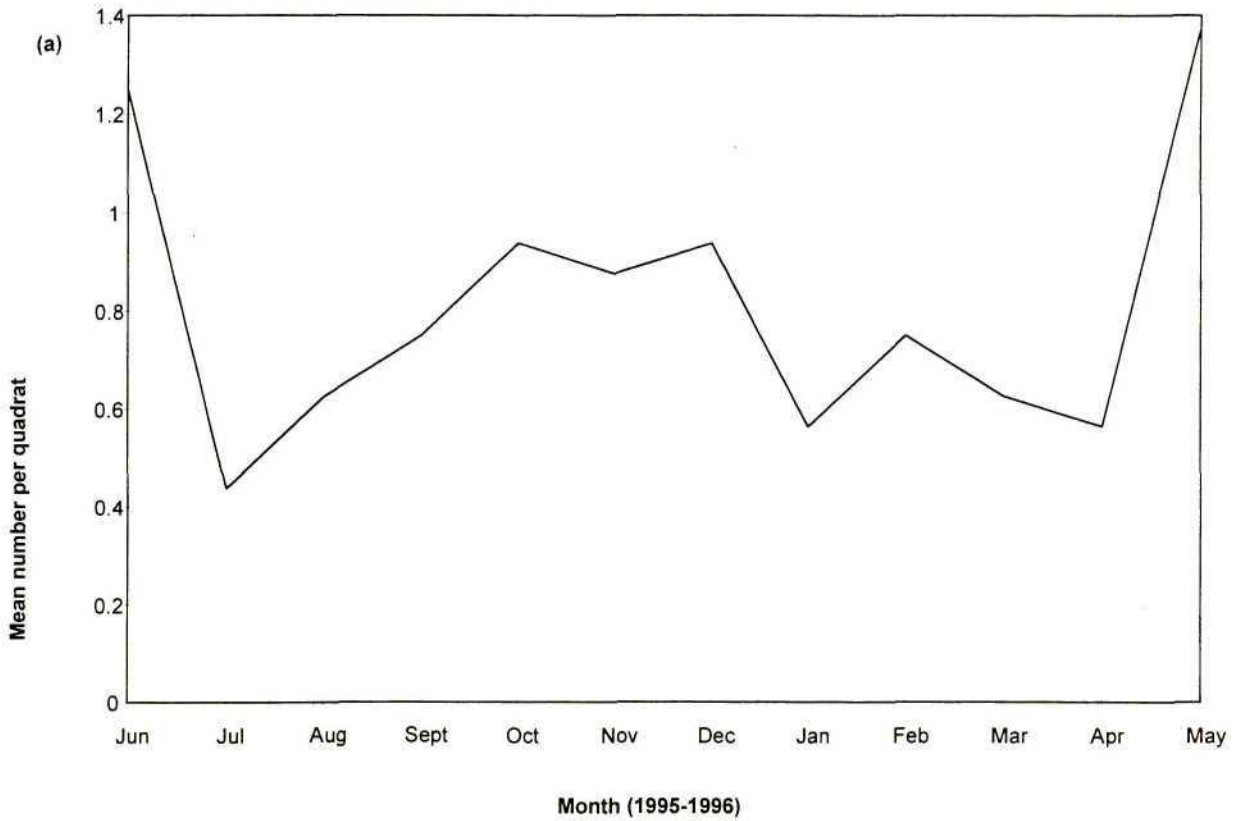


Figure 26. Monthly mean abundances per quadrat of *Speleomontia cavernicola* in (a) Bats' cave and (b) Wynberg cave. Visual counts were conducted monthly for one year in 16 and 33 2m²-quadrats in Bats' and Wynberg caves respectively. Total number of individuals counted were 445 and 155 in Wynberg and Bats' caves respectively.

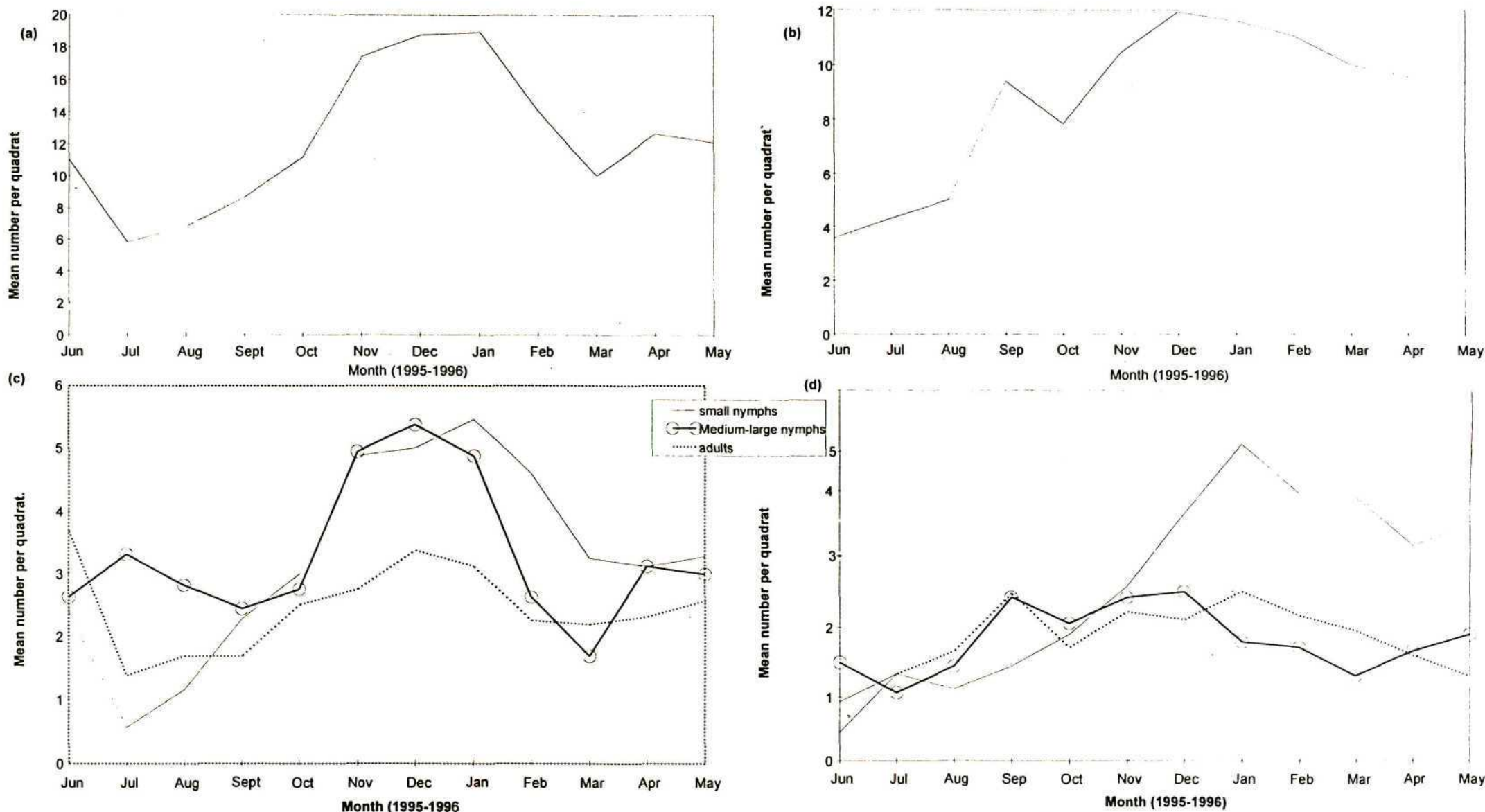


Figure 27. Monthly mean abundances per quadrat of *Speleiacris tabulae* in (a) Bats' cave and (b) Wynberg cave. Mean abundances of small nymphs (subjectively assigned to the 0-0.6mm size class, excluding appendages, and of indeterminate sex), medium to large nymphs (0.61-1.4 mm of recognizable sex) and adults (>1.4mm of recognizable sex) are given for (c) Bats' cave and (d) Wynberg cave. Visual counts were conducted monthly for one year in 16 and 33 2m²-quadrats in Bats' and Wynberg caves respectively. Total number of small nymphs, medium to large nymphs and adults counted were 1137, 775 and 768 in Wynberg cave and 1247, 633 and 472 in Bats' cave respectively.

between the two size classes, as large nymphs and adults were often difficult to distinguish in the field. In Wynberg cave, the number of older nymphs and adults remained relatively constant throughout the year, a slight increase in abundance being evident in the summer months only. In Bats' cave, on the other hand, a pronounced rise and decline in numbers occurred. This was more evident in medium to large nymphs than in adults (Figure 27c and d), indicating that the durations of adult and subadult stages were longer (possibly extending over more than one year).

7.1.1. Discussion

Clearly changes occurred in the abundance patterns of several cavernicoles. However, as this study only extended over one year and considered relatively few individuals, it is not possible to draw any definitive conclusions, particularly about life cycles which may have extended over more than one year.

Seasonal patterns differed between caves, peaks in abundance generally occurring in Wynberg cave one month prior to peaks in Bats' cave. For example, maximum abundance for *Lephtyphantes rimicola* occurred in January in Wynberg cave but in February in Bats' cave. Similarly, *Crozetulus scutatus* showed increased abundance until May in Wynberg cave and until June in Bats' cave. This is probably explained by the fact that environmental changes were evident more-or-less a month earlier in Wynberg cave than in Bats' cave (Figures 21 and 22). A clearly recognizable breeding response to environmental cues is therefore indicated.

Peaks in abundance also differed in time and intensity between species. *Lephtyphantes rimicola*, *Speleosiro argasiformes* and *Speleiacris tabulae* all showed pronounced seasonality, with increased abundances in summer when temperatures and relative humidities were highest, and decreased abundances in the cold, wet winter months. This trend was also observed in coleopteran populations in Mitchell Caverns, California (Aalbu 1989). *Crozetulus scutatus* and *Speleomontia cavernicola* showed less pronounced seasonal changes. *Crozetulus scutatus* was most abundant in autumn and spring, while *Speleomontia cavernicola* populations peaked in spring, early summer and in autumn.

As Deeleman-Reinhold and Deeleman (1980) pointed out, seasonal fluctuations in numbers may be an indication of animals moving further into crack systems when conditions in macrocaverns are unfavourable, rather than reflecting changes in overall abundance. For this reason microhabitat preferences were further investigated. The frequency of occurrence of species within crevices and on exposed surfaces was noted during months of minimum and maximum abundance in all quadrats in Wynberg cave. A t-test on log transformed data revealed *Speleomontia cavernicola* to be the only species to show a significant difference ($P < 0.05$) in habitat selection. Population abundance in crevices was significantly higher than on exposed surfaces in July and August, but not in April and May. This suggests that seasonal changes in abundance recorded for this species (Figure 26) may not reflect a seasonal life cycle as such, but a tendency to be more conspicuous by moving into human-sized passages when environmental conditions are favourable.

Crozetulus scutatus, on the other hand, showed a significant difference ($P < 0.01$) between crevice occupation and occurrence on exposed surfaces during months of both minimum and maximum abundance (September, October, March and April). Similarly, *Speleosiro argasiformes* occurred under rocks more frequently than in crevices ($P < 0.01$) in months of both minimum and maximum abundances (January, February, June and July). This suggests that these species have distinct microhabitat preferences. *Speleiacris tabulae* and *Lephtyphantes rimicola*, on the other hand, showed no statistically significant microhabitat preference. These results were consistent between months of minimum and maximum abundance, and the observed seasonal fluctuations of all four species (Figures 23, 24, 25 and 27) can therefore be regarded as reliable reflections of overall abundance. The pronounced seasonal change shown by *Speleosiro argasiformes* over the 12-month period, suggests that the life cycle extends over a single year. However, the data set was too limited to reach any definitive conclusions on life history strategies and microhabitat preferences.

All life cycle stages of *Speleiacris tabulae* were present throughout the year, indicating continuous breeding and a so-called K-adaptive reproductive strategy (Grindley 1956; Carchini *et al.* 1991a). Continuous reproduction is an adaptation to stable cave habitats and a common characteristic of troglobites (Barr 1968; Culver 1982; Howarth 1983). The troglobite, *Lephtyphantes rimicola*, however, appeared to have a 'breeding season' with

adults being absent in winter. Continuous breeding in crickets is a habit peculiar to tropical species (Masaki and Walker 1987) and cave-adapted species (Alexander 1968; Northup and Crawford 1991; Carchini *et al.* 1991a, 1991b; Carchini *et al.* 1994). In contrast, temperate epigeal crickets are strongly influenced by seasonality (Alexander 1968; Masaki and Walker 1987). Although continuous breeding is clearly indicated for *Speleiacris tabulae*, a distinct egg-laying and egg-hatching period occurred in summer from November onwards (Figure 27). The presence of small nymphs throughout the year may indicate two possible reproductive strategies: continuous breeding and/or diapausing egg or nymphal stages.

Fluctuations in numbers of medium to large nymphs and adults were less pronounced than those of small nymphs. This may partly be because instar times were longer and mortality rates lower. Rhabdophorid life cycles generally last longer than one year (Alexander 1968; Richards 1969; Carchini *et al.* 1991b). For example, the life cycle of *Dolichopoda* in Italian caves extends over approximately two years with a total of nine nymphal stages (Di Russo *et al.* 1987). A long life cycle also appears to occur in *Speleiacris tabulae*. Therefore, overlap between broods of successive years may have obscured abundance patterns of medium to large nymphs. Overlap between consecutive generations would also explain the presence of medium and large nymphs throughout the year. Determination of instar duration times and more accurate allocation of life cycle stages, would undoubtedly further elucidate life history patterns.

Seasonal fluctuations of *Speleiacris tabulae* populations were more pronounced in Bats' cave than in Wynberg cave for all size classes. Differences in seasonal patterns between age classes were also more pronounced in Bats' cave. For example, small nymphs showed a sharper decline in number after January in Bats' cave than was evident in Wynberg cave (Figure 27 c and d). The decline is probably due to mortality and recruitment of individuals into the next age class (Carchini *et al.* 1994) and suggests that mortality was greater, or development faster, in Bats' cave after January. Alternatively, the greater stability of environmental conditions in Wynberg cave (Figures 21 and 22) resulted in a decreased exposure to environmental cues and therefore increased response times. Therefore, the period of oviposition and hatching may have been extended, resulting in a steady recruitment of

small nymphs over a longer period of time. Shorter response times in Bats' cave would also have explained the greater seasonal fluctuations of larger nymphs and adults in this cave.

According to Carchini *et al.* (1983, 1991b, 1994), stability of trophic resources (i.e. constant high guano concentrations) is the main determinant of seasonal strategies in *Dolichopoda* crickets inhabiting natural and artificial caves in Italy. Age heterogeneity was greater in natural caves in Italy, while in artificial caves, different age classes dominated in alternate seasons. Under conditions of stable guano availability, a non-synchronised life cycle would reduce intraspecific competition. Northup and Crawford (1991) further found that the seasonality of raphidophorids in Carlsbad Caverns may have been influenced by the seasonal input of guano from a bat colony. It could be argued, therefore, that the stable guano deposits, together with relatively stable environmental conditions in the dark zone of Wynberg cave, would explain the decreased seasonality of its *Speleiacris tabulae* population. In Bats' cave, on the other hand, the deep zone lacks stable guano deposits, while the guano-rich entrance zone is exposed to seasonal fluctuations in environmental conditions, as well as of bat guano, thus explaining the greater seasonality of its *Speleiacris tabulae* population. Therefore, it appears that stability of guano deposits and of the physical environment are important determinants of seasonal fluctuations of populations in the Table Mountain caves.

Since cave crickets are considered to be relicts of tertiary temperate forest faunas, seasonal age structures would appear to be an ancestral condition (Alexander 1968). The difference in seasonality between the two Table Mountain caves indicates that, while aseasonality has evolved in *Speleiacris tabulae* populations in the Table Mountain caves, the degree of fluctuations varies according to the intensity of environmental cues.

7.2. Diet of cavernicoles

Caves are relatively nutrient-poor, thus supporting few species in relatively uncomplicated food webs (Barr 1968; Howarth 1983). All caves tend to have two or three food input types, each with a group of stenophagic exploiters and their associated predators (Howarth 1973, 1983; Martin 1977; Chapman 1979). Allochthonous food input into the Table Mountain caves includes bat guano, plant debris and dissolved organic matter. Food preferences of selected Table Mountain cavernicoles, based on field observations, are listed in Table 11.

Table 11. Feeding preferences of invertebrates in Bats' and Wynberg caves, based on direct observations of feeding behaviours. Generalist feeders with overlapping trophic categories, are listed under each applicable category. Question marks indicate likely trophic categories in the absence of direct observations. Numbers in brackets indicate the number of observations.

Trophic category	Animal	Food item
Predators	<i>Spermophora peninsulae</i>	lepidopterans (3), tipulids (7), psychodids (4), heliomyzids (3)
	<i>Phyxelida grindleyi</i>	psychodids (2), dipterans (6)
	<i>Loxosceles valida</i>	tipulids (2), lepidopterans (4), cricket nymph(1), cricket remains?
	<i>Lephtyphantes rimicola</i>	psychodids (1)
	Araneae	?
	Opiliones	?
	Carabidae	small insects and eggs?
	Staphylinidae	mites, ptiliids?
	<i>Peripatopsis alba</i>	cricket nymphs?
	Mites	?
Scavengers/ necrophages	<i>Speleosiro argasiformes</i>	cricket and earthworm remains, bat carcasses (2), cricket (?) eggs
	<i>Plocamotrechus longulus</i>	arthropod remains (crickets), bat carcasses?
	<i>Speleiacris tabulae</i>	bat guano (18), bat carcasses (5), arthropod remains (earthworms, diplopods, small cricket nymphs)
	Oniscidae	associated with plant debris
	Talitridae	associated with plant debris
	Staphylinidae	associated with bat carcasses
	Calliphoridae; Sarcophagidae larvae	bat carcasses (2)
Detritivores	<i>Paramelita barnardi</i>	aquatic detritus, bat carcass (1)
	Turbellaria	aquatic detritus, bat carcass (1)
	<i>Spelaeogriphus lepidops</i>	aquatic detritus
	<i>Harpethrix caecae</i>	decaying plant material, lichen (1)
	Collembola	decaying plant material?
	Meinertellidae: <i>Machiloides</i> sp.	lichen, moss (1)
Fungivores	Ptiliidae: <i>Malkinella cavatica</i>	fungus, (guano?)
Coprophages	Sarcophagidae larvae	bat guano
	Muscidae larvae	bat guano
	Sciaridae larvae	bat guano
	Phoridae larvae	bat guano ?
	Tipulidae, Psychodidae larvae	bat guano ?
	Lepidoptera larvae	bat guano ?
	Collembola: <i>Schaefferia</i> sp.nov.	bat guano
	<i>Speleiacris tabulae</i>	bat guano (18), bat carcasses (5), invertebrate remains (earthworms, diplopods, small cricket nymphs)
Mites	bat guano ?	

Predatory species listed in Table 11 showed great variation in prey preferences. *Spermophora peninsulae*, *Malaika longipes* and *Loxosceles valida* were observed to have small lepidopterans, tipulids, psychodids or dipterans in their webs. *Loxosceles valida* webs were also observed to contain cricket remains. Prey availability clearly affected the distribution patterns of these species, as they preferred cave entrances where dipteran and lepidopteran abundances were highest (as discussed in Chapter 5). The predatory carabid, *Plocamotrechus longulus*, was observed to feed on invertebrate remains (dead cricket nymphs). Similarly, the opilionid, *Speleosiro argasiformes*, was observed to feed on earthworms and dead cricket nymphs (Table 11). Therefore, both species appear to supplement their predatory diet with scavenging.

Bat guano is a rich source of food for cavernicoles, although few, if any, troglobites are directly dependent on it (Barr 1968). Bat guano in the Table Mountain caves appeared to be directly utilised by the collembolan, *Schaefferia* sp.nov., various dipterans, lepidopterans and *Speleiacris tabulae* (Table 11). *S. tabulae* individuals were observed on several occasions feeding on or manipulating guano in their mouthparts. Also associated with guano were numerous guanophiles, including ptiliids (probably fungivorous), scavengers and predators (such as araneads, chilopods, staphylinids, carabids and *Speleosiro argasiformes*). No guanophiles are troglobitic (Barr and Reddell 1967; Barr 1968), although troglobitic predators (such as the pseudoscorpion, *Cthoniella cavernicola* and the chilopod, *Cryptops stupendus*) may prey on guanophiles under favourable conditions of temperature and relative humidity.

Bat carcasses were observed to have scavengers, saprophages, detritivores and predators associated with them. *Speleiacris tabulae* (a scavenger), *Speleosiro argasiformes*, *Plocamotrechus longulus*, staphylinids (predators and/or scavengers), paramelitids, flatworms (aquatic detritivores), ptiliids (probably fungivores) and dipteran larvae (saprophages) were all observed in large numbers in association with bat carcasses (Table 11).

Plant debris and detritus were washed in or blown into the caves. Like guano, detritus is utilised by few troglobites (Barr 1968). Troglobitic collembolans, for example, tend to feed on fungal spores and hyphae, rather than the decaying wood itself (Christiansen 1965). In the

Table Mountain caves, polydesmid diplopods (including the troglophile, *Harpethrix caeca*), oniscid isopods, talitrids and mites were commonly associated with plant debris (Table 11). The diplopods fed directly on plant debris, while the isopods and amphipods are probably detritivores or scavengers feeding on decomposers (Barr 1968). Predators and scavengers such as chilopods and carabids, would, in turn, be represented at the top of this food chain.

Like most other raphidophorids, *Speleiacris tabulae* is an omnivorous scavenger (Richards 1962, 1969; Hubbel and Norton 1978; Carchini *et al.* 1991a; Di Russo *et al.* 1991). In the Table Mountain caves it was observed feeding on guano, bat carcasses and invertebrate remains (including an adult feeding on a dead nymph). Carchini *et al.* (1994) similarly noted that *Dolichopoda geniculata* crickets in Valmarino cave, Italy, fed mainly on guano, but also on dead insects and exuvia.

Speleiacris tabulae crickets kept in aquaria in constant environment cells at 94% relative humidity and 10°C, consumed a variety of food items (cheese, oats, lettuce, apples and dead moths), further confirming their omnivorous habit. Fresh vegetable matter was generally consumed first, indicating that their preference for cave environments is not primarily related to food preferences. Carchini *et al.* (1991a) found vegetable matter in *Speleiacris tabulae* faecal pellets and suggested that foraging migrations occurred at night in search of plants outside the cave. This behaviour is well known in other Raphidophoridae (Richards 1962, 1969; Hubbel and Norton 1978; Di Russo *et al.* 1991 and Carchini *et al.* 1994), but was not observed in the Table Mountain caves. Eight pitfall traps (baited with peanut butter) were set outside the entrance of Wynberg cave over four non-consecutive nights. Only four *Speleiacris* nymphs were caught. This suggests that crickets do not make foraging trips out of the cave, but that entrance populations of crickets may wander out of cave entrances at night if relative humidities are high enough and temperatures low enough. This behaviour has been observed in *Pallidotettix nullarborensis* crickets in Nullarbor caves (Richards 1969). This species emerged from caves at night when relative humidities were over 98% and temperatures equalled that of the entrance. Richards (1969) also reported *Pallidotettix* crickets to be more active in twilight zones at night. A similar observation was made in the Table Mountain caves, as *Speleiacris tabulae* crickets tended to be active at night in the cave entrances, but were relatively inactive during daylight hours when they sheltered in cracks

and crevices. Relative humidity, and possibly light, were clearly important factors inhibiting activity in both these species.

7.2.1. Discussion

Most Table Mountain cavernicoles (troglophiles in particular) were omnivorous scavengers or detritivores with broad, overlapping dietary preferences. Troglaxenes and accidentals served as an important food source for these omnivorous scavengers, while most troglobites were predatory. This is consistent with Peck's (1994) findings in Jamaican caves, where 20 out of 26 terrestrial troglobites were predatory.

Euryphagy is an apparent adaptation to limited food resources (Barr 1968; Howarth 1983; Aalbu 1989). In epigeal environments, a prevalence of euryphagy could lead to interspecific competition but, as Barr (1968) points out, the coexistence of many species of detritivores and of predators in the same cave, is an indication of dietary overlap.

Speleiacris tabulae, being the most abundant censused invertebrate that contributed the greatest biomass (Table 2), played a crucial role in the food chain as omnivorous scavenger. Primarily dependent on allochthonous bat guano concentrations, *Speleiacris tabulae* also served as an important prey item for troglophilic and troglobitic scavengers and predators (such as *Loxosceles valida*, *Malaika longipes*, *Paralamyctes spenceri* and, quite likely, rare troglobites such as *Cryptops stupendus* and *Peripatopsis alba*). Disturbance of *Speleiacris tabulae* populations would undoubtedly have serious repercussions throughout the cave communities. Clearly *S. tabulae* should be regarded as a keystone species.

Cricket eggs and guano are, quite possibly, additional important food sources for cavernicolous scavengers. The guano of *Hadenoeus* crickets in central Kentucky is extensively utilised by both troglobites and troglophiles (Barr 1968; Barr and Kuehne 1971; Peck 1978; Poulson and Kane 1981; Howarth 1983). Barr (1968) reported cricket guano utilisation to be more important in areas (or seasons) of low bat guano availability. Predation on cricket eggs occurs in a number of species of Carabidae in North America (Mitchell 1968, 1971; Barr and Kuehne 1971; Norton *et al.* 1975; Poulson 1975). No such behaviours were

observed in the Table Mountain caves. However, it is possible that *Speleosiro argasiformes* feeds on cricket eggs, as it was often observed to burrow into guano-enriched mud where cricket oviposition had previously been observed.

7.3. Conclusion

The biological observations discussed here raise many interesting questions prompting further research. Seasonal changes in abundance were observed in the troglobites,

Lephtyphantes rimicola, *Crozetulus scutatus*, *Speleosiro argasiformes* and *Speleomontia cavernicola*, as well as in the troglophile, *Speleiacris tabulae*. Seasonality was most pronounced in *Speleiacris tabulae*, *Speleosiro argasiformes* and *Lephtyphantes rimicola*.

However, marked differences occurred between caves and seasonality appeared to be affected by the stability of both the environment and the availability of bat guano. This explained the more pronounced seasonal fluctuations of *Speleiacris tabulae* in Bats' cave. However, to what extent seasonal population fluctuations truly reflected life history patterns bares further investigation. Populations need to be monitored over a period of several years, and fecundity, mortality rates and generation times need to be established. e.g. the life cycle of *Speleiacris tabulae* apparently extends over more than one year with possible diapause stages.

Microhabitat preference is an additional factor requiring investigation. *Crozetulus scutatus* and *Speleosiro argasiformes* showed distinct preferences for crevices and occurring under rocks respectively. *Speleomontia cavernicola* showed a preference for crevices only when physical conditions on exposed surfaces were unfavourable. This has important implications for ecological and behavioural studies, and emphasises the importance of mesocaverns and microclimate in troglobite abundance and distribution patterns, both temporally and spatially. The role of the mesokarst environment could be assessed by studying the Milieu Souterraine Superficiel (MSS) using methods suggested by French biospelaologists of the Moulis lab.

Most Table Mountain cavernicoles were omnivorous scavengers, predators or detritivores directly or indirectly dependent on bat guano, the most voluminous, reliable and widely-utilised allochthonous food resource. The predominance of euryphagy is an apparent adaptation to a food-limiting environment. *Speleiacris tabulae*, the most common terrestrial invertebrate contributing the greatest biomass (as discussed in Chapter 4), plays a key role in the food chain as an omnivorous scavenger and prey item for troglobitic and troglophilic

predators and scavengers. These are likely to include rare troglobites such as *Peripatopsis alba* and *Cryptops stupendus*. *Speleiacris tabulae* can therefore be regarded as a keystone species, as disturbance of *S. tabulae* populations would have serious repercussions throughout the cave communities. Cricket guano and eggs are also likely to be of trophic importance and this bears further investigation. Further research, based on feeding trials and gut analyses, would add to the present knowledge of food preferences, while the roles of competition and predation in the Table Mountain cave communities, also need to be addressed.

8. Conservation implications

Conservation of caves is not only important in terms of the preservation of biodiversity, but also because they serve as natural laboratories to study evolutionary processes of adaptation and speciation (Howarth 1983). Cave animals are particularly vulnerable to disturbance because of their rarity in discrete habitats with isolated island-like distributions (Slaney and Weinstein 1997). Disturbances, even local or temporary, may disrupt populations or cause extinctions. Threats of disturbance need to be assessed so that conservation measures can be implemented. The Table Mountain cave invertebrates are particularly vulnerable to disturbance considering their high conservation status. Factors that are usually considered in determining conservation status include number of species, abundance, rarity, taxonomic uniqueness (May 1995), phylogeny (Faith 1995), geographic distribution (Rabinowitz 1981; Rabinowitz *et al.* 1986) and specialised habitat requirements (Magurran 1988). Therefore, conservation of the Table Mountain caves is a clear priority for the following reasons:

- They contain a number of rare species. There is cause for concern for the low numbers of, for example, *Cryptops stupendus*, *Protojanira leleupi* and *Peripatopsis alba*.
- They contain several species with restricted distributions. *Peripatopsis alba* and *Spelaeogriphus lepidops* (and possibly *Hahnia* sp.nov. and *Dermaptera* sp.nov.) are restricted to a few caves on Table Mountain and should therefore be regarded as Critically Endangered according to the *IUCN Red list categories* (1994) (extent of occurrence <100km²). Twenty-one cavernicolous species are endemic to the Cape Peninsula, all of which can be considered Endangered (extent of occurrence <5000km²) (Table 5).
- They contain highly specialised troglobitic species with very specific habitat requirements.
- They contain phylogenetically unique species. All troglobitic species as well as the troglophile, *Speleiacris tabulae*, are descendants of ancient Gondwanan lineages, their closest relatives occurring in South America or Australia. *Spelaeogriphus lepidops* is one of only two species within the order Spelaeogriphacea in the world.

Major threats to cave ecosystems include land use changes (e.g. road or dam construction), alteration of groundwater flow (e.g. abstraction of water for urban use), pollution (e.g. sewage or refuse disposal), introduction of exotic plants or animals (facultative cavernicoles

often being introduced species that may disrupt community processes), removal or loss of bat colonies or other food sources and, finally, disturbance by human visitation (Howarth 1981). The current major threat to the Table Mountain cave fauna, is that of human visitation. Howarth (1981) observed that diversity and population levels in caves are inversely proportional to the frequency of human visitation. Trampling of cave invertebrates (Spate and Hamilton-Smith 1991) and compaction of the cave floor (Middleton 1979) are the two main problems. *Speleiacris tabulae*, being the most active and conspicuous invertebrate species in Peninsula caves, is particularly susceptible to trampling. As a keystone species, this is cause for concern. Spate and Hamilton-Smith (1991) report the loss of an invertebrate community as a result of soil compaction in Mount Widderton cave, South Australia. In addition, walking through cave pools may affect aquatic species by, for example, changing silt levels or turbidity. Cave visitors are also sources of pollution such as tobacco smoke, carbide (calcium carbide is a toxic by-product of acetylene torches) and leachate from discarded batteries.

Visitation by humans can disrupt environmental conditions that are essential for the maintenance of troglobite populations. Table Mountain troglobites occurred mainly in the deep zone which is characterised by an absence of light or air currents, low constant temperatures, near-saturated relative humidities, permanently wet surfaces, and nutrient-poor conditions. Human visitation affects all these conditions, most notably temperature and relative humidity. Smoke from torches and cigarettes, in particular, reduce relative humidity levels (Howarth 1981). Troglobite distribution patterns within the Table Mountain caves were most highly correlated with relative humidity, this therefore representing a crucial limiting factor.

Disturbance of bat colonies is also a serious threat to the Table Mountain cave fauna. This study has shown bat guano to be the most important allochthonous food source, directly or indirectly supporting a wide range of cavernicoles (most notably, *Speleiacris tabulae*). In turn, scavenging and predatory troglobites (e.g. *Speleosiro argasiformes* and, quite possibly, rare species such as *Cryptops stupendus*, and *Peripatopsis alba*) feed on *Speleiacris tabulae* and guanophiles. Therefore, disturbance of Table Mountain bat colonies would undoubtedly have serious repercussions throughout the cave communities. *Rousettus leachii* forages on fruit in and around the suburbs of Cape Town (D. Jacobs pers. comm.). Pesticides used on these fruit

trees may be carried by bats back to the caves, thus being incorporated into the cave food chains with deleterious effects on cavernicole populations. The fruit bats are also regarded as problem animals by many residents because of the damage their faeces cause (by staining and corrosion) to paintwork on outside walls (D. Jacobs, unpublished report 1996). This has prompted various preventative measures (such as removal of trees and application of pesticides) which could negatively impact on bat populations (Jacobs, unpublished report). Bat population sizes have not been monitored in the past and it is not clear whether population numbers are stable or declining (D. Jacobs pers. comm.).

Although human visitation to the Table Mountain caves is still relatively low, the steady rise in tourism levels is cause for concern. Considering that South Africa has few or no other caves with a comparable degree of endemism, diversity and richness, management considerations are a matter of urgency. The formulation of conservation policies is hampered by a lack of taxonomic and ecological data. Further research is therefore a priority. Faunal collections and taxonomic work are necessary in both the Table Mountain and Kalk Bay caves, as the probability of finding additional new (possibly endemic) species is high. Furthermore, population estimates need to be made of apparently endangered species such as *Peripatopsis alba*, *Spelaeogriphus lepidops* and *Cryptops stupendus*, as their low numbers are cause for concern. Furthermore, population sizes of *Protojanira leleupi* and *Paramelita barnardi* in the Kalk Bay caves are not known and are in urgent need of investigation. Monitoring of troglobite populations needs to be conducted over a period of several years to establish whether numbers are declining, to detect disturbances and to assign or reassess *IUCN Red list Categories*. Pitfall trapping should be avoided in future ecological work, as this technique is known to cause community disturbances (Peck 1975, 1976; Howarth 1981). Instead, replacement-trapping techniques (Yang *et al.* 1994; Weinstein and Slaney 1995; Slaney and Weinstein 1996, 1997) should be considered as a means of population monitoring.

Finally, there is a requirement for experimental ecological work to determine a) the duration of life cycles of troglobitic species, and b) the extent and nature of environmental factors that would threaten troglobite populations. Methodologies need to be developed to distinguish between short-term population fluctuations and longer term irreversible changes (Howarth

and Ramsay 1991). The impact of human visitation also needs to be established as well as the level of visitation that can be tolerated. That is, is there a threshold level of visitation beyond which community processes are disrupted? Access should be restricted by, for example, implementing a permit system whereby cavers would be required to obtain special access permission from a local conservation organisation.

The major long-term strategy in the conservation of cave invertebrates is in the protection of suitable habitats (Howarth 1981), as habitat and species conservation are closely linked in invertebrates (Key 1978). Therefore, the conservation of cave fauna would best be achieved by protecting the entire cave ecosystem as well as the surrounding catchment area. The Table Mountain caves are not discrete entities, but are a highly interconnected system of caves joined by mesocaverns (cracks, voids or channels) inhabited by troglobites. The extent to which caves are interconnected is not known but it is imperative that conservation does not focus on individual caves (navigable by humans), but encompass the entire pseudokarst areas (navigable by invertebrates via mesocaverns). In addition to the caves themselves, associated phenomena such as bat roosts and groundwater quality should also be protected. The proximity of the caves to the reservoirs on the Back Table of Table Mountain, is a matter of concern. Contamination or depletion of these water bodies may affect groundwater quality, thus affecting aquatic cavernicoles. Depletion of groundwater, may also affect moisture availability within caves, thus having a general deleterious effect on cave communities.

The existence of rare and specialised species in the Table Mountain caves (e.g. *Peripatopsis alba* and *Spelaeogriphus lepidops*) provides a convincing reason to consider a species approach to conservation. However, this approach has not always been successful. For example, Harrison (1964) established an earwig reserve in Niah Great cave, Sarawak in an attempt to conserve the rare *Arixenia esau* Jordan. However, the 'earwig sanctuary' that was chosen was separated from roosting sites of the naked bat, *Cheiromeles torquatus* Horsfield, with which the earwigs had an obligatory association. The species approach therefore cannot possibly work without sound ecological knowledge of the species concerned. Furthermore, the fact that more than one cavernicolous species is considered Endangered in the Table Mountain caves (Table 5) necessitates conservation of the cave system as a whole. The Peninsula mountains have recently been granted National Park status, thus affording the

caves a higher conservation status. However, restriction of access to the area for caving activity should still be implemented and recreational caving should be considered in the allocation of land use zones.

No conservation strategy is likely to be successful without effective education of the public. A conservation ethic needs to be instilled in recreational cavers. Informative signs placed in carefully selected sites, or motivational articles in caving literature, can partly achieve this. Care should be taken, however, not to advertise cave locations or to popularise caves or cave fauna. An increase in curiosity from the public would inevitably result in an increase in cave visitation (Howarth 1981).

Therefore, the main conservation focus should be to limit the impact of human visitation. Further management-orientated research, conservation of karst areas and environmental education are urgent priorities to achieve a long-term conservation of the cave fauna, thereby contributing substantially to the conservation and biodiversity of the Cape Peninsula as a whole.

9. Summary

1. Eighty-five invertebrate species were recorded from the Cape Peninsula caves. This represents a fairly depauperate cave fauna by world standards, but a particularly rich and diverse one compared to other South African caves. Twenty-one cavernicolous invertebrate species are endemic to the Cape Peninsula, representing 19% of the 111 recorded endemic invertebrate species (Picker and Samways 1996). Thirteen of these species were considered troglobitic and are clearly Gondwanan relicts. Environmental conditions (e.g. low temperatures and high humidities) in Peninsula caves offered favourable refugia for Gondwanan relicts, thus explaining the greater faunal similarities of the Peninsula caves with South American caves, rather than with other African caves. Several troglobites are highly cave-adapted species with very restricted distributions. For example, *Spelaeogriphus lepidops* and *Peripatopsis alba* were restricted to two or three of the larger Table Mountain caves, while *Paramelita barnardi* and *Protojanira leleupi* were restricted to the Kalk Bay caves. Very little is known of their population sizes and fluctuations, particularly within the Kalk Bay caves. Six new species, possibly Peninsula endemics, were recorded in this study. These included highly troglomorphic species of Dermaptera and *Hahnia*. Both are likely to be troglobites and Table Mountain endemics. Troglobitic hahniids have rarely been encountered in caves worldwide.

2. Troglobitism *per se* was, however, relatively rare, most species being troglaphiles, troglonexes, humicoles or guanophiles. Taxa within these groups achieved wider distributions, occurring in all Peninsula caves. However, the degree of genetic and geographical isolation between cave populations in the Table Mountain and Kalk Bay caves is not known. It may be that allopatric speciation has resulted in a number of closely related sibling species. Furthermore, it is possible that speciation may be occurring by 'adaptive shift' (Howarth 1988) in populations of epigean species that opportunistically exploit rich food resources within caves (e.g. guanophilic staphylinids and the carabid, *Plocamotrechus longulus*).

3. Food availability, habitat heterogeneity and environmental stability affected abundance and diversity patterns. Abundance was generally higher in Bats' cave, while diversity and species

richness were greater in Wynberg cave. Rich fruit bat guano deposits in the entrance zone of Bats' cave resulted in higher overall food availability supporting a greater abundance and biomass of invertebrates. In Wynberg cave, on the other hand, the extensive, relatively stable dark zone with its diffuse supply of insectivorous bat guano, resulted in lower abundance but higher diversity.

4. Most species were relatively rare. *Speleiacris tabulae* was the only censused species that was consistently common throughout both caves. *Spermophora peninsulae* was also relatively common in entrance zones. Species were generally commoner in Bats' cave but rarer in Wynberg cave. Rare species were either accidentals or highly cave-adapted troglobites with restricted distributions. There is cause for concern for the very low numbers of several troglobites, most notably *Cryptops stupendus* and *Peripatopsis alba*. *Peripatopsis alba* and *Spelaeogriphus lepidops* should be listed as Critically Endangered according to the *IUCN Red List Categories* (1994) on account of their limited distributions (extent of occurrence $< 100\text{km}^2$) and phylogenetic uniqueness. All endemic troglobites and troglophiles can be considered Endangered on account of their limited distributions (extent of occurrence $< 5000\text{km}^2$). *Hahnia* sp.nov. and *Dermaptera* sp.nov. may well also be Critically Endangered. There is an urgent need for management-orientated research and population monitoring of these species.

5. Table Mountain cavernicoles were spatially distributed primarily according to the zonal physical environment, entrance and deep zone communities being clearly recognizable in both caves. Transitional and twilight zone communities were also evident in Wynberg cave. Communities defined secondarily by food availability (i.e. plant debris or guano communities) and crevice availability were also detected. However, overlap with zonally-defined communities meant that communities were more easily defined in terms of zones. Each community had its own set of indicator species, although considerable overlap occurred between communities. This overlap was greater where suitable environmental conditions disrupted zonally-defined communities (i.e. where food availability allowed entrance species to enter dark zones, or relative humidity allowed dark zone species to enter entrance zones).

The spatial distribution of cavernicoles was also clearly correlated with their degree of cave-adaptedness. Troglobites and troglophiles predominated in the deep zones (e.g. *Lepthyphantes rimicola*, *Crozetulus scutatus*, *Speleosiro argasiformes*, *Speleomontia cavernicola* and *Speleiacris tabulae*), troglophiles and troglonexes in entrance and transitional zones (e.g. *Malaika longipes*, *Loxosceles valida*, *Spermophora peninsulae* and *Harpethrix caeca*) and troglonexes in twilight zones (e.g. *Isicabu capensis* and *Machiloides* sp.). A degree of overlap did occur between zones and several species occurred in all zones (e.g. *Speleiacris tabulae*, *Speleomontia cavernicola* and *Speleosiro argasiformes*).

6. Factors affecting distribution and abundance patterns of cavernicoles in the Table Mountain caves were exceedingly complex. No single environmental variable satisfactorily explained community patterns. Correlations were particularly low in Wynberg cave due to the relative uniformity of environmental conditions. Factors yielding high correlations differed between caves. Soil nutrients (organic, nitrogen and energy content) were of importance only in Bats' cave, undoubtedly because of the zonally-distributed and abundant fruit bat guano in this cave, as well as the higher densities of the guanophage, *Speleiacris tabulae*.

Relative humidity appears to be of considerable importance in determining community distribution patterns, temperature and moisture availability also being of some importance. However, food availability was more strongly correlated with taxon presence or absence data which also considered uncensused humicoles and guanophiles. Relative humidity and crevice availability were more limiting to deep zone and troglobite communities, so that overlap with entrance communities was only possible where these conditions allowed. On the other hand, food availability was more limiting for entrance communities, species only being able to extend their ranges into deep zones where food was available.

The distribution of troglobitic species showed no striking cross-species uniformity in correlations with environmental variables. However, abundance and distribution patterns of troglobitic species were all negatively correlated with temperature and nutrient availability (i.e. soil energy, organic and nitrogen contents), but positively correlated with relative humidity. Considered collectively, variables yielding the highest correlations with troglobitic

fauna were similar to those associated with deep zone communities. Therefore, although variation exists between species, troglobites can be predicted to occur within deep zones where light and air currents are absent, temperatures are low and constant, relative humidities are near saturation and surfaces are permanently moist. Disruptions to troglobite communities are likely to be caused by disturbances of any of these conditions. Microhabitat is clearly a factor of additional importance, most troglobitic species being positively correlated with crevice availability (most notably, *Hahnia* sp.nov., *Crozetulus scutatus* and *Trichoniscus tabulae*). It appears that certain species (e.g. *Speleomontia cavernicola*) only emerge into human-sized passages when conditions are favourable. This strongly suggests that any determination of limiting factors is not complete until microenvironmental conditions have been taken into account.

7. Environmental cues within the Table Mountain caves were great enough to trigger physiological responses in cave populations. Seasonal fluctuations in populations (over one year) were observed in *Lepthyphantes rimicola*, *Crozetulus scutatus*, *Speleosiro argasiformes*, *Speleomontia cavernicola* and *Speleiacris tabulae*. However, over a 12-month period, very few deductions can be made regarding life history patterns. Nevertheless, population fluctuations of *Lepthyphantes rimicola* and *Speleosiro argasiformes* appear to indicate an annual cycle, while that of *Speleiacris tabulae* appears to extend over two or more years. Continuous breeding (i.e. a so-called K-adaptive reproductive strategy) is clearly evident in *S. tabulae*. However, seasonality was more pronounced in Bats' cave. It appears that the greater the stability of the environment and the predictability of the food supply (i.e. bat guano), the less seasonal the life cycle.

8. There is clear evidence of microhabitat preferences in troglobitic species. *Crozetulus scutatus* and *Speleomontia cavernicola* predominated in crevices, while *Speleosiro argasiformes* tended to occur under rocks. In *Speleomontia cavernicola* this appears to be a response to environmental cues in human-sized passages.

9. *Speleiacris tabulae* can be regarded as a keystone species. As the most common invertebrate contributing the greatest biomass, it served as an important food source for several troglobitic and troglophilic scavengers and predators. Most species were either

predators or scavengers, detritivores also being common. Bat guano was the most abundant and widely-utilised food source, directly or indirectly supporting the majority of cavernicolous invertebrates, most notably *Speleiacris tabulae*.

10. Long-term conservation considerations and further management-orientated research are urgent priorities, considering the rarity, restricted distributions, phylogenetic uniqueness and Endangered status of many cavernicoles. Population monitoring is essential for detecting community disturbances. Replacement trapping techniques, such as those proposed by Yang *et al.* (1994) and Weinstein and Slaney (1995), should be considered for future population studies. Exact population sizes and distributions of cavernicolous species regarded as Critically Endangered, Endangered or Data Deficient (Table 5) (*viz. Peripatopsis alba, Spelaeogriphus lepidops, Protojanira leleupi*) should be established. The nature and intensity of environmental perturbations that would threaten troglobite populations also need to be determined so that appropriate conservation measures can be applied. Conservation of Bats and their foraging areas should also be considered important for the health of cave communities. Finally, the addition of several new species to the faunal list suggests that greater collecting effort, particularly in the Kalk Bay caves, may yield additional new species. This would add further to the already rich biodiversity and high levels of endemism of the Cape Peninsula invertebrate fauna.

Finally, this study has raised a number of ecological questions that bare further investigation. Genetic analyses would elucidate evolutionary processes active in Peninsula caves, while population monitoring over several years, together with studies of fecundity and generation times, would provide accurate information on reproductive cycles. Furthermore, note should be taken of highly abundant or inconspicuous taxa which were not the focus of this study, while microhabitat preferences and feeding behaviours of cavernicoles also merit further investigation (most notably with regard to the importance of cricket eggs and guano). The effects of competition and predation on community distribution patterns need to be ascertained. Finally, the effect of the mesocavernous microenvironment on distribution and abundance patterns of troglobites should be investigated.

10. Conclusion

The caves of Table Mountain should be considered conservation hot-spots. They contribute significantly to the number of endemic species and therefore to the conservation status and biodiversity of the Cape Peninsula as a whole. This provides support for the declaration of Table Mountain as a Natural Heritage Site. The high richness, endemism and biodiversity of the Cape Peninsula can largely be attributed to historical factors. The Cape Peninsula Mountain chain became separated from the rest of the continent by the Cape Flats during the Holocene and Pliocene (Macdonald and Cowling 1996). This resulted in an island-like geography, genetic isolation and low immigration rates, thus explaining the pronounced faunal dissimilarities that exist between Peninsula caves and those of the Hottentots-Holland Mountains. The caves themselves can also be seen as habitat islands suitable for cavernicoles, surrounded by unsuitable epigeal habitats. Therefore, faunal dissimilarities that exist between the Kalk Bay and Table Mountain caves (such as the local endemism of *Peripatopsis alba*, *Speleogriphus lepidops*, *Paramelita barnardi* and *Protojanira lepidops*) indicate that the two pseudokarst cave systems (i.e. Table Mountain and Kalk Bay) can each be regarded as an island. Seen in this light, therefore, the Cape Peninsula caves can be regarded as 'islands within islands', speciation of troglobites being influenced by pronounced geographical isolation and negligible migration rates between islands.

The rarity, phylogenetic uniqueness, cave-adaptedness and specialised habitat requirements of Table Mountain troglobites within their island-like habitat further emphasises the urgent necessity for conservation considerations. *Peripatopsis alba* and *Speleogriphus lepidops* should be regarded as Critically Endangered according to the *IUCN Red List Categories* (1994) on account of their limited distributions (extent of occurrence < 100km²), while all endemic troglobites and troglophiles should be regarded as Endangered on account of their restricted distributions (extent of occurrence < 5000km²). The implementation of conservation measures requires knowledge of the ecological requirements of the species concerned. This study has contributed to our understanding of ecological processes within the Table Mountain caves. For example, abundance was correlated with food availability, bat guano being the most widely utilised food resource within the caves. The most notable guanophage and omnivorous scavenger was the raphidophorid, *Speleiacris tabulae*. This

species should be considered a keystone species on account of its abundance, biomass and importance as prey item for several troglophilic and troglobitic predators and scavengers. Therefore, the maintenance of a voluminous and regular bat guano supply is essential for the maintenance of viable populations of, not only *Speleicris tabulae*, but of all cavernicolous invertebrates. Disturbances to bats or their roosting sites could have serious repercussions throughout the cave communities.

Species diversity and richness were correlated with habitat heterogeneity (or area) and stability. Wynberg cave, with its small entrance, more extensive dark zone, stable and regular supply of guano and relative stability of environmental conditions, supported a greater diversity of species and a larger number of rare species. Furthermore, the most important environmental criteria affecting troglobite distribution were stable high relative humidities, low temperatures, crevice availability and moisture availability. The relative size and environmental stability of Wynberg cave's dark zone resulted in greater availability of moist crevices and surfaces, thus offering more microhabitats favourable to troglobites.

It would therefore be tempting to afford Wynberg greater conservation status. However, the findings of this study strongly suggest that, in terms of their invertebrate inhabitants, the Table Mountain caves are not discrete units but are connected by a network of mesocaverns inhabited by troglobites. *Speleomontia cavernicola* and *Crozetulus scutatus*, for example, were shown to favour this microhabitat, the former apparently only emerging into human-size passages where environmental conditions allowed. Relative humidity is clearly the most important limiting factor for troglobites, generally restricting them to dark zones.

Mesocaverns, however, allowed a certain amount of overlap with entrance communities. Troglobitic species (e.g. *Speleosiro argasiformes* and *Speleomontia cavernicola*) were able to extend their ranges into entrance zones where microhabitats with favourable microenvironmental conditions (most notably high relative humidities) were available. Similarly, troglophiles could extend their ranges into epigeal situations where suitable microhabitats were available (e.g. *Speleiacris tabulae*). Therefore, the caves are clearly more extensive than humanly perceived and should be redefined in terms of their invertebrate inhabitants. Many of the ecological answers to troglobite distribution patterns and their ecological requirements undoubtedly lie within these mesocaverns. The mesocavern should

therefore be considered an additional cave biotope with its own set of ecological parameters. The ecological role of this biotope should be investigated further. More importantly, however, there is an urgent need to estimate population sizes of endangered species, to monitor population levels over several years, to assess the impact of human visitation and to determine the nature and extent of perturbations which would cause irrevocable population disturbances.

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