Natural variation in south-eastern South Australian small mammal communities through the Late Quaternary

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For my grandma, Jean Le Cornu, who inspires me to persist against all odds,
and the memory of my late grandpa, Deane Le Cornu,
from whom I draw the strength to do so.

Declaration

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List of publications:

Macken, A.C., McDowell, M.C., Bartholomeusz, D.H. & Reed, E.H. (2013) Chronology and stratigraphy of the Wet Cave vertebrate fossil deposit, Naracoorte, and relationship to paleoclimatic conditions of the Last Glacial Cycle in south-eastern Australia. *Australian Journal of Earth Sciences* **60,** 271–281.

Macken, A.C., Staff, R.A. & Reed, E.H. (2013) Bayesian age-depth modelling of Late Quaternary deposits from Wet and Blanche Caves, Naracoorte, South Australia: a framework for comparative faunal analyses. *Quaternary Geochronology* **17,** 26–43

Macken, A.C & Reed, E.H. (2013) Late Quaternary small mammal faunas of the Naracoorte Caves World Heritage Area. *Transactions of the Royal Society of South Australia* **137,** 53–67.

Signed ....
Amy Macken

Date..

Abstract

Natural variation is characterised as the normal types of change that occurs within ecosystems in response to disturbances at different spatial and temporal scales. Such changes may be expressed across a range of ecological attributes including community structure and composition. Changes in these attributes are often argued to provide the basis of ecosystem resilience to disturbance; that is, the ability of communities to adapt and reorganise whilst retaining their functional and structural traits. Consequently, the maintenance of natural variation within ecological systems has emerged as a primary biodiversity conservation strategy. However, our understanding of what normal patterns of variation may be expected in different ecosystems and the constraints on resilience within them, remains limited.

Palaeoecological deposits have increasingly been used to fill knowledge gaps about the range, type and extent of natural variation and resilience expressed by ecosystems over long time scales in response to disturbances such as climate change. Using two owl-pellet derived fossil assemblages of the Naracoorte Caves in south-eastern South Australia, this thesis examined patterns of natural variation and resilience of a small mammal palaeocommunity in terms of richness, composition, structure and relative abundances through the last glacial cycle (*c*. 51.4 to 10.2 kyr BP). More specifically, this thesis addressed the following questions:

(a) Did the small mammal palaeocommunity reorganise in response to climate change associated with the last glacial cycle?
(b) How did variation in different ecological variables contribute to the persistence or reorganisation of the palaeocommunity, and
(c) How did sampling variation within and between sites, and temporal resolution, impact patterns detected in the fossil assemblages?

To address these questions, the stratigraphic and chronological contexts of the fossil assemblages were defined using sedimentary principles and age-depth modelling of radiocarbon data. Both deposits were found to be composed of five un-reworked sedimentary units which were statistically correlated between the two sites based on modelled ages. These units provided a coarse temporal scale corresponding to the major climatic phases of the last glacial cycle. Sedimentary layers were identified within the stratigraphic units, providing a finer temporal scale for evaluating the faunal assemblage.

Faunal analyses showed that the two small mammal assemblages were statistically similar and exhibited very little compositional or structural change through the early glacial period and last glacial maximum (LGM). However, two episodes of significant palaeocommunity reorganisation were revealed at the finer temporal scale through the deglaciation/late glacial period. These changes were associated with (a) sea-surface temperatures (SSTs) warming past 16°C, post-dating the onset of warming following the LGM by *c.* 1 to 3 kyrs and (b) continued warming of mean SSTs past 18°C.

The relative abundances of individual species were sensitive to sampling effects and were variable through time at both temporal scales. The whole-palaeocommunity metrics were more robust and showed that a palaeocommunity can be stable for thousands of years, despite variable climatic conditions. Palaeocommunity change during the deglaciation shows that it is not disturbance per se that led to shifts between community states, but disturbance beyond palaeoclimatic thresholds within which particular states were able to persist. Further study of environmental thresholds for the palaeocommunity and individual species will be valuable for assessing the variability of species-environmental associations through time and the potential for their adaptation into the future.

Acknowledgements

First and foremost I acknowledge the support, guidance and insight of my principal supervisor, Dr Liz Reed. I thank her for providing access to resources, support with funding and for the opportunity to study the small mammal fossils that she methodically excavated from Blanche Cave. Most importantly, I acknowledge Liz's contribution to the project through the sharing of ideas and critique of my work. I am grateful to Liz for her unwavering confidence in the project and in me, which gave me the space and freedom to grow personally and professionally. I am also grateful for the support of my associate supervisor, Dr Gavin Prideaux. Gavin provided advice and feedback throughout my candidature and was always available at short notice to help with small, day-to-day problems and more complex questions associated with my research.

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Collection managers and curators of mammal collections from museums across Australia were also generous in sharing their data for use in constructing species distribution maps (Appendix F) and for allowing access to specimens for comparison. I especially thank David Stemmer of the South Australian Museum and Sandy Ingleby of the Australian Museum.

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Contents

1. Introduction

Palaeoecology is concerned with the reconstruction and interpretation of past environments and ecological communities across space and time. 'Natural archives' preserved within palaeoecological sites are critical to these reconstructions and include biotic (e.g., bones, pollen, diatoms, charcoal) and abiotic (e.g., speleothem cave formations, stable isotopes) records of past life and climatic conditions (Smol, 2010). When natural archives are chronologically and stratigraphically constrained, they can be used to gain insight into patterns of species diversity, the timing and role of disturbances in ecosystem development and patterns of extinction and diversification over timescales spanning decades to millennia (Brenchly and Harper, 1998; Barnosky *et al.*, 2003; Willis *et al.*, 2005; MacDonald *et al.*, 2008).

In exposing links between ecological diversity and drivers of assemblage patterns in space and time, natural archives may also be used to address questions associated with biodiversity conservation. The contribution of palaeoecology to biodiversity conservation has been extensively reviewed, firmly establishing the benefits of palaeoecology to contemporary biodiversity crises (e.g., Willis *et al.*, 2005; Lyman, 2006; Willis *et al.*, 2007; Rull, 2010; Willis *et al.*, 2010; Vegas-Vilarrbuia *et al.*, 2011; Appendix A). For example, palaeoecological archives have been used to (a) set conservation baselines (e.g., Foster *et al.*, 1996; Davis *et al.*, 2007; Burbidge *et al.*, 2008; Saunders and Taffs, 2009; Bellingham *et al.*, 2010), (b) establish past rates and direction of ecosystem change to inform predictions and models about future effects (Barnosky *et al.*, 2003; Carrasco *et al.*, 2009; Davies *et al.*, 2009; Finney *et al.*, 2010; Willis *et al.*, 2010); (c) determine the extent and rates of contemporary extinctions against historical baselines (Graham and Grimm, 1990; Braithwaite and Muller, 1997; McKinney, 1997; Williams, 1997; Bilney *et al.*, 2010) and (d) isolate climatic from human drivers of change (Barnosky *et al.*, 2004a; Renberg *et al.*, 2009). Appendix A presents a conference review manuscript prepared during the course of the research presented in this thesis, highlighting examples of palaeoecological research applied to biodiversity conservation problems within Australia and New Zealand.

As shown in the examples described in Appendix A, palaeoecological archives commonly used for specific conservation and management problems are those derived from lake and peat cores containing pollen, diatoms, phytoliths and other fine-scale records of past environments. However, vertebrate fossil assemblages, particularly those preserved in caves and rock shelters, have made significant contributions to understanding the nature of faunal responses to Quaternary climate change at the species and community level in Australia (e.g., Prideaux *et al*., 2007; Price and Sobbe, 2005; Price and Webb, 2006; Baynes and McDowell, 2010; McDowell *et al*., 2013; Price, 2012). In some cases, these records have been used to address contemporary biodiversity problems, both directly and indirectly, through the examination of Pleistocene extinctions and long-term community dynamics.

Fossil deposits of the Naracoorte Caves World Heritage Area

The palaeoecological archives of interest to this thesis derive from the vertebrate fossil deposits of the Naracoorte Caves World Heritage Area (NCWHA). The NCWHA in south-eastern South Australia provides extensive records of faunal diversity over the Quaternary period (Fig. 1.1). The World Heritage Area contains 26 known caves with over 100 fossil sites among them (Reed and Bourne, 2000). The oldest vertebrate assemblage from this locality is dated to the Middle Pleistocene (528±41 ka; Prideaux *et al.,* 2007), while the youngest known *in situ* fossil remains have recently been dated to the late Holocene (<1000 yr BP; Macken and Reed, 2013).

Research into fossil assemblages of the Naracoorte Caves has contributed to knowledge of (a) late Quaternary faunal communities of southern Australia (e.g., Reed and Bourne, 2000; 2009), (b) the taxonomy and systematics of extinct and living faunas (e.g., Prideaux and Wells, 1998; Williams, 1999; Prideaux, 2004), (c) vertebrate taphonomy of cave deposits (e.g., Reed, 2006; 2009) and (d) environmental change over the Quaternary (e.g., Forbes and Bestland, 2007, Darrénougué *et al.,* 2009).The scientific and natural history values of the cave deposits are reflected in not only the publications associated with this research but their World Heritage Listing and extensive on-site interpretation materials.

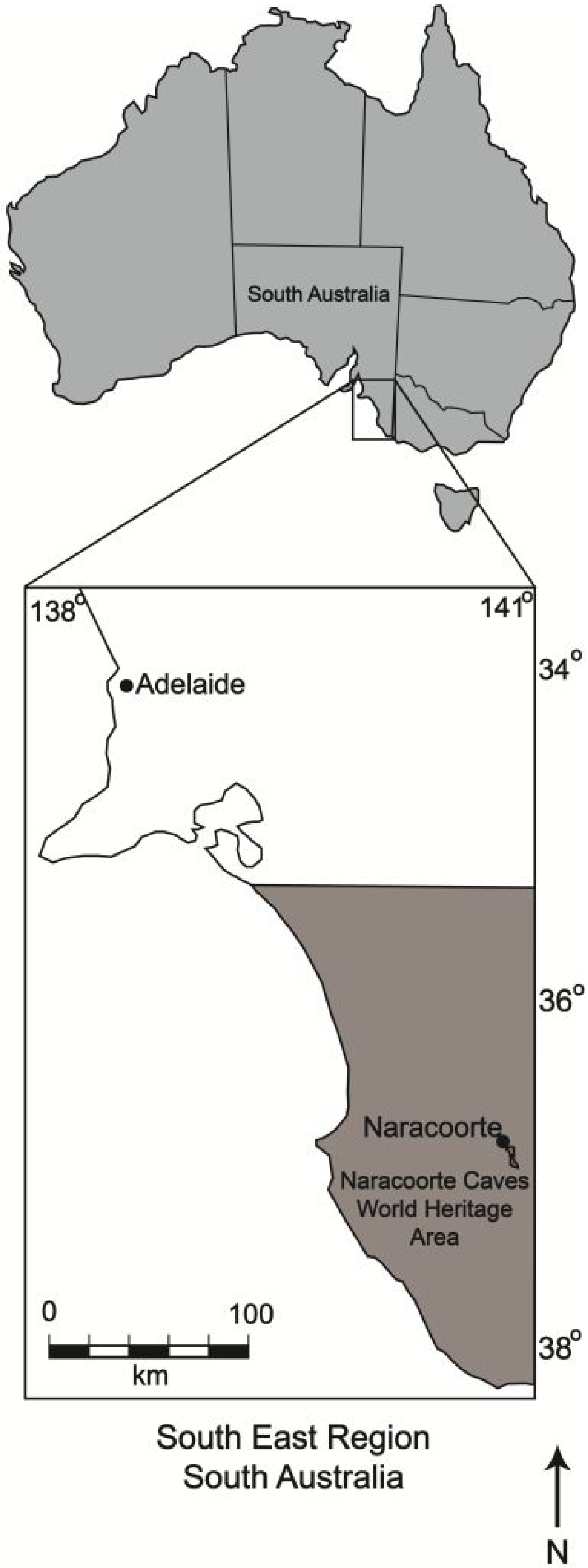


Figure 1.1 Location of the Naracoorte Caves World Heritage Area in south-eastern South Australia, Australia.

Faunal responses to Pleistocene climate change

Despite a general bias in palaeoecological studies in Australia towards the causes of 'megafauna' extinction, research into the faunas of the Naracoorte Caves has included smaller body-sized taxa, particularly in faunal based reconstructions of palaeoenvironmental conditions. For example, the first palaeoenvironmental reconstructions for the NCWHA were based on the habitat characteristics of small vertebrates (Smith, 1971; 1972). More recent studies of last glacial aged deposits (*c.* 50 to 1 kyr BP) used a similar approach, but in a quantified framework based on the ecological characteristics of the faunas preserved in the assemblages (McDowell, 2001; Laslett, 2006).

A significant focus of research at Naracoorte has also been on the effects of Pleistocene climate change on local mammal faunas (e.g., Prideaux *et al.*, 2007; Macken *et al.*, 2012). The first appraisal of faunal responses to Pleistocene climate change was reported by Moriarty *et al.* (2000) and represented an important shift in the type of research question being addressed through analysis of the Naracoorte Caves fossil faunas; that is, rather than reconstructing climatic and environmental conditions based on the fossil assemblages, Moriarty *et al.* (2000) were the first to consider the effects of changing conditions on the fauna themselves.

In their assessment of the composition of six Middle Pleistocene aged assemblages of the NCWHA, Moriarty *et al.* (2000) concluded that there had been "little apparent change in faunal diversity over a period of 300 ka in the Middle Pleistocene, a period spanning at least three glacial-interglacial cycles" (p. 141). The implications of this assessment have been significant in the broader view of not only the Naracoorte Cave deposits, but discussions of faunal dynamics through the Pleistocene. For example, the apparent lack of faunal change recorded in the Naracoorte Caves has been cited as evidence that climate change did not contribute to megafaunal extinction in Australia (Barnosky *et al.*, 2004b), nor that Pleistocene climate changes affected mammalian faunas to the same extent as the Pleistocene–Holocene transition (Koch and Barnosky, 2006).

Sampling limitations in the work by Moriarty *et al.* (2000) are expected to have contributed to the lack of faunal change observed in their study and are explored in the thesis literature review. By comparison, the more rigorous sampling protocol of a Middle Pleistocene aged deposit by Prideaux *et al.* (2007) showed that species relative abundances fluctuated through past glacial-interglacial cycles. Similar, and in some cases divergent patterns in species abundances in response to a later climatic transition were revealed in a Late Pleistocene aged assemblage by Macken *et al.* (2012), suggesting complex, individualistic species responses to climate change at this locality through time. Additionally, changes in species presence/absence revealed in these studies suggest that the ranges of some taxa expanded and contracted from the Naracoorte region through the Pleistocene.

These observations challenge the inference of no faunal change forwarded by Moriarty *et al.* (2000). However, based on the lack of evidence for local faunal extinctions, Prideaux *et al.* (2007) suggested that the mammal faunas of south-eastern South Australia were resilient to Pleistocene climate change. This finding supported arguments for a role of humans in the extinction of the megafauna (Roberts *et al.*, 2001; Prideaux *et al.*, 2007). However, it is also significant from a biodiversity conservation perspective as concepts of resilience are increasingly integrated into conservation management plans (e.g., National Biodiversity Strategy Review Task Group (NBSRTG), 2009).

Application to biodiversity conservation

Research into Pleistocene fossil sites from the Naracoorte Caves has clearly made a significant contribution to understanding local faunas and how they have changed over time. However, as noted by Erwin (2009), understanding the processes that control diversity, rather than simply documenting patterns of change over time is a major challenge for palaeoecologists. He argued that it is only by revealing the processes and drivers that underlie diversity that we can truly understand patterns of change in diversity over time. Erwin (2009) also advocated for greater development and testing of models describing the processes that drive diversity patterns using empirical data derived from natural archives. This argument was supported by Rull (2012) who showed that palaeoecological records can be used to test ecological principles and theories such as equilibrium dynamics, successional processes and community assembly rules. In doing so, the potential reach and impact of palaeoecological studies to biodiversity conservation is deepened by testing those models that directly inform conservation strategies, but which are rarely considered over extended time-frames (Willis *et al.*, 2010; Rull, 2012).

Of interest for this thesis is the observation of faunal resilience and variation across different metric scales (abundance, presence/absence) in the Naracoorte Pleistocene faunal record. More specifically, this thesis is concerned with determining the magnitude and extent of variation exhibited in the composition and structure of a mammal community with time and how such variation reflects processes operating to control local diversity. For example, the resilience of local faunas to extinction through past glacial cycles suggests that the observed variation in occupancy and relative abundances of individual species in the palaeocommunity was constrained within intrinsic (e.g., population size and density, body size, niche breadth, interspecific interactions) and/or extrinsic (e.g., temperature, moisture availability, habitat) limits or thresholds. Had those limits been exceeded, local extinction of some taxa may have occurred through an inability to maintain or recover populations to the Naracoorte region. Further, change in the composition of the palaeocommunity evidenced by variation in species presence/absence suggests that the palaeocommunity itself may not have been resilient to Pleistocene climate change, despite the apparent resilience of the constituent faunas (Prideaux *et al.*, 2007; Macken *et al.*, 2012). These ideas and concepts have not previously been explored in studies of Naracoorte Cave faunas or other Pleistocene aged vertebrate assemblages in Australia, but draw upon the broader conservation-related applications demonstrated for a wide range of palaeoecological sites on other continents (e.g., Bennington and Bambach, 1996; Gorham *et al.*, 2001).

While it is recognised that mammal responses to environmental and climate change are not limited to changes in community composition and structure, but include phenotypic changes such as variation in body-size (Barnosky *et al*., 2003; MacDonald *et al*., 2008; Blois and Hadly, 2009), particular attention is paid to community metrics in this study to (a) develop a greater understanding of the relationship between changes in individual species abundances and community turnover, (b) examine sampling effects on commonly applied measures of climate change response and (c) create a link between community level processes of the past with future climate change responses. Faunal responses across community metrics are also poorly understood for late Pleistocene south-eastern South Australia.

Study Assemblages

The focal assemblages for this thesis were collected from the Late Quaternary aged deposits of Wet and Blanche caves (Figs. 1.2 and 1.3). These caves contain large samples of small mammal fossils, the result of owl pellet accumulation. Previous analysis of the deposits from Wet and Blanche caves provide a foundation for the present study and highlight their value for exploring natural variation and resilience. Of particular significance is that *c*. 55% of the faunas preserved in the two deposits occur in the region today (refer Table 2.1). This means that insights into long-term dynamics of the faunas are directly relevant to the conservation and management of extant species and communities. Further, the deposits span similar temporal periods (Table 1.1), are located with 500 m of each other and have similar accumulation biases (McDowell, 2001; Laslett, 2006). These factors facilitate a statistical test of the similarity of the assemblages to assess sampling effects that may influence observed patterns of community and species level variability and resilience through time. This approach is endorsed by Bennington and Bambach (1996), but is rarely available in the study of vertebrate fossil assemblages where typically, there is only one deposit available for a given time period at a single locality. McDowell (2001) and Laslett (2006) recognised the value of this comparative approach and provided the first comparison of Late Quaternary aged deposits from the Naracoorte Caves. The research presented here aims to develop the qualitative approaches applied in these studies by applying a quantitative analysis based on the example of Bennington and Bambach (1996) and using Bayesian age-depth modelling to statistically correlate the stratigraphic sequences of Wet and Blanche caves. Such an approach has not been previously tested on any Australian vertebrate fossil locality.

Few well dated and stratigraphically constrained analyses of fossil sites of Late Quaternary age are available in Australia. As a consequence, the effects of climate change associated with the last glacial cycle are poorly understood. Former study of the Wet and Blanche cave assemblages revealed a general trend where grassland inhabiting species were more abundant during the last glacial maximum, contrasting with an increase in abundance in woodland species during the Holocene

(McDowell, 2001; Laslett, 2006). However, the limited chronological data and taxonomic uncertainties (M. McDowell pers. comm.) of these studies limits the extent to which the assemblage data, as presently available, may be used to assess patterns of natural variation and resilience of the palaeocommunity and individual species.

Following the studies of McDowell (2001) and Laslett (2006), additional grid-squares were excavated from Blanche Cave by E. Reed. The new excavations followed the stratigraphy exposed by Laslett (2006) and were excavated by sedimentary layer, rather than as arbitrary 5 or 10 cm ‘spits’ (E. Reed, pers. comm.). Given the new sampling procedure for Blanche Cave, there was the potential to examine the faunas from both individual sedimentary layers and stratigraphic units, the latter composed of aggregated layers. This approach enabled an analysis of the fossil faunas at two temporal scales and is significant as it allowed for the effects of time-averaging on the observed patterns of faunal change to be quantified. A similar approach was used by Bobe *et al.* (2002) to examine temporal trends in mammal faunas at two time scales from a Southern Ethiopian hominin site, revealing significant variation at the finer temporal scale not detected from the longer time-averaged units.

Table 1.1 Maximum and minimum ages of the late Quaternary aged deposits of Wet and Blanche caves. Radiocarbon ages calibrated using IntCal09 (Reimer *et al.*, 2009) in OxCal4.1 (Bronk Ramsey, 2009a).

Site	**^{14}C age yr BP (1σ)**	**cal yr BP (2σ)**
Blanche Cave, 3rd Chamber	43,260±1840[1] to 12,470±60[2]	49,986–44,696 to 15,032–14,168
Wet Cave, Entrance Chamber	45,200±1800 to 740±40[3]	45,984–43,334 to 735–569

1 St Pierre *et al.* (2012)
2 Darrénougué *et al.* (2009)
3 Pate *et al.* (2002; 2006)

Aims

The aim of research presented in this thesis was to determine the magnitude and ecological extent of variation (or stability) expressed by the small mammal palaeocommunity of south-eastern South Australia through the last glacial cycle and to examine if such variation occurred within extrinsic and intrinsic thresholds. More specifically, it aimed to:

1. Determine the magnitude of natural variation of the small mammal palaeocommunity and individual species through the last glacial cycle across the following attributes: species richness, evenness, composition, rank-order abundance and the relative abundance of individual species.

2. Identify thresholds of resilience of the small mammal palaeocommunity through the last glacial cycle relating to the following factors:

    a. Intrinsic: palaeocommunity composition, rank-order abundance and species abundances, and
    b. Extrinsic: sea-surface temperature, effective moisture availability and local vegetation types.

3. Examine how sampling variation within and between sites and temporal resolution influenced the patterns of variation and/or stability observed in the small mammal fossil assemblages.

Supporting objectives

A series of supporting aims and objectives associated with establishing the chronological and depositional contexts of the study deposits were critical to achieving the overall aims of the thesis.

The greater chronological control, finer temporal resolution and more adequate and quantitative faunal sampling in the studies of Prideaux *et al.* (2007) and Macken *et al.* (2012) were fundamental in revealing the faunal changes that were previously obscured by poor sampling in studies of the Naracoorte Cave faunas (Moriarty *et* *al*., 2000). The additional objectives listed below reflect the importance of these factors to the aims of this thesis and included:

1. Interpret the stratigraphy of Wet and Blanche caves using sedimentary data.
2. Construct an age-depth model for each of the Wet and Blanche Cave stratigraphic profiles using radiocarbon and sedimentary data.
3. Temporally correlate stratigraphic units and layers between Wet and Blanche caves.
4. Identify new and previously examined fossil assemblages from Wet and Blanche caves.

Research associated with these supporting objectives is presented in chapter three, four and five and provides the background to chapter six in which the primary aims of the thesis were explored.

Figure 1.2 View towards the roof window entrance of Wet Cave (5U10) within the Naracoorte Caves World Heritage Area. The fossil excavation was located on the edge of the sediment cone, located behind the camera in this photograph.

Figure 1.3 View towards the roof window entrance to the Third chamber of Blanche Cave (5U6) within the Naracoorte Caves World Heritage Area. The fossil excavation was located behind the camera. Photograph by Steve Bourne.

Thesis Structure

Introduction to the literature review

In the literature review, I examine the significance of managing for natural variation in biodiversity conservation, particularly in light of climate change effects on species and communities. Given the strong argument presented in ecological and palaeoecological literature for long-term studies of ecosystems, I also explore the methods used to measure and describe faunal change (variability) in long-term data. Of particular relevance to my study of the Naracoorte small mammal faunas was how the techniques used to measure faunal responses and community variability in fossil assemblages, and the biological and metric scale of study, can affect the statistical and inferred ecological significance of observed patterns (e.g., Rahel, 1990; Schopf and Ivany, 1998; Hadly and Barnosky, 2009). Examination of these issues in the review informed the approach I used to measure, define and interpret variability, and hence, resilience of the Late Quaternary small mammal faunas of the NCWHA.

Introduction to the research chapters, style and progression

Research conducted for this thesis is presented in manuscript format, with chapters composed of published papers and submitted manuscripts. As a result, some information is repeated through the thesis, such as descriptions of the study locality, a required element for each individual manuscript.

Where a research chapter has been published, a citation to the paper is provided but the manuscript itself is presented in a format and style consistent with the thesis in order to facilitate ease of reading the thesis as a whole. However, there are some inconsistencies with the use and style of some terminology between chapters. For example, ‘Late Pleistocene’ is interchangeable with both ‘late Pleistocene’ and ‘Upper Pleistocene.’ ‘Middle Pleistocene’ is also referred to as ‘middle Pleistocene’, while ‘Early Pleistocene’ is interchangeable with ‘early Pleistocene’ and ‘Lower Pleistocene’. These terms were used in accordance with directions from the Journal editors associated with each of the published manuscripts. Additionally, the prefix ‘palaeo’ is spelt using American English (‘paleo’) in chapter three, in accordance with the style requested by the editor of The Australian Journal of Earth

Science. All chronological data are presented as calibrated calendar years before present (yr BP), unless otherwise stated.

References for each chapter and appendix are compiled at the end of the thesis to reduce repetition and the size of the thesis. Referencing style varies amongst the sections of the thesis as they were published by, or prepared for, different journals; however, all references are formatted to the same style in the bibliography at the end of the thesis.

As all manuscripts have multiple authors, a summary of the contribution of each author to the work has been provided. All co-authors have given permission for the relevant manuscripts to be included in the thesis as indicated by their signatures on the coversheet for each research chapter. In some cases, co-authors could not provide a signature (due to field work or other travel commitments). In those cases, their names have been typed and a copy of their authorisation by email has been kept for reference.

In Chapter three, I present a review of the stratigraphy and chronology of the Wet Cave deposit. Despite previous sedimentary and faunal analysis of the site, there had been no assessment of the stratigraphic divisions of the excavated section using all the available sedimentary data. In this chapter, sedimentary and chronological data for the site were compiled to identify sedimentary units that could be used to (a) examine the relationship of the sedimentary section of Wet Cave to the contemporaneous deposits of the inner chamber of Robertson Cave and 3rd chamber of Blanche Cave, both located within the NCWHA and, (b) facilitate assessment of the fauna at a coarser temporal resolution than previously available from Wet Cave. The coarser resolution was more consistent with the major climatic phases of the last glacial cycle (e.g., Marine Isotope Stage (MIS) 3, MIS-2 LGM and MIS-2 deglaciation). Chapter three also presents additional radiocarbon ages for the Wet Cave deposit and an extensive review of palaeoclimatic conditions associated with the last glacial cycle in south-eastern South Australia, providing a palaeoclimatic context for the faunal analyses presented in chapter six.

Chapter four presents a Bayesian age-depth model-based analysis of the stratigraphic and chronological contexts of Wet and Blanche Caves. The age models developed for Wet and Blanche caves provided not only a robust assessment of the ages of all stratigraphic layers/units within the sites, but enabled them to be statistically correlated. Using the age-models, we were able to define two temporal scales for analysis of the fossil assemblages (a macroscale and a mesoscale). The coarser macroscale was associated with major climatic phases of the last glacial cycle (e.g., MIS-3, MIS-2 glacial maximum and MIS-2 deglaciation). The mesoscale provided finer time-slices within each of these climatic phases. Without the age models, the temporal correlation of the two sites would have been inferred from the sediments and individually calibrated radiocarbon ages, without estimates of statistical uncertainty which may have biased the comparative faunal analyses and/or been inaccurate.

Chapter five introduces the small mammal taxa identified from the study sites and the methodology used to sample the fossil assemblages. The biogeographic implications of the fossil records of the Naracoorte Caves are also discussed in this chapter, highlighting the need for greater communication of fossil occurrences to enhance knowledge of the past distribution of mammal faunas prior to European arrival in Australia. As 47 species were identified in this project, systematic palaeontology is presented in Appendix D only for species of Dasyuridae previously unrecorded from the NCWHA and/or the Late Pleistocene–Holocene from this locality. Limiting the systematic palaeontology to this selection of the fauna aims to demonstrate how I identified the fauna without eclipsing the thesis with a lengthy descriptive chapter or providing descriptions for taxa that are well described elsewhere. Appendix D also contains a list of references used to aid in the identification of species from other families. In the published manuscript systematic palaeontology was provided for the two unidentified taxa, Dasyuridae sp. 1 and *Sminthopsis* sp. 1 to alert other researchers to the potential of new taxa, or specimens that present morphologically variants of known taxa within the fossil assemblages of the Naracoorte Caves.

In chapter six, a quantitative analysis of the fossil assemblages of Wet and Blanche Cave is presented, directly addressing the aims of the thesis. The analyses in chapter six were used to determine the extent and magnitude of sampling variation within and between the two sites compared against variation that may be considered as temporal change. By combining the numeric and statistical frameworks of Rahel (1990) and Bennington and Bambach (1996), I defined a hierarchy and terminology from which the ecological significance of natural variation in the palaeocommunity could be assessed.

The final chapter presents an overview of the main findings and limitations of the research presented in the thesis and outlines future research questions arising from the current work. The thesis concludes with a synthesis of the research findings within the broader context of the questions which informed the focus for the thesis:

(a) how do ecosystems respond in the short and long-term to disturbance,
(b) what is the natural range of variability expressed by an ecosystem at different spatial, temporal and ecological scales, and
(c) what are the limits of resilience, or thresholds beyond which an ecosystem changes state?

2. Literature Review

Natural variation in (palaeo)ecological assemblages: scale, measurement and interpretation.

"We get closer to understanding the whole by considering its parts at more than one scale." Schopf and Ivany, 1998, p. 187.

Introduction

Climate change: biodiversity adaptation and resilience

The effects of climate change on organisms, communities and ecosystems are of concern to biodiversity managers and are expected to include shifts in the distribution and abundance of species and changes to population, life history and reproductive dynamics (e.g., Williams *et al.*, 2003; Meyeneck, 2004; Preston *et al.*, 2008; Marini *et al.*, 2009). As a result, climate change is expected to increase the extinction risk of vulnerable taxa, facilitate the spread of invasive species and alter the dynamics of ecological processes and interactions (e.g., Green *et al.*, 2008; Brennan *et al.*, 2009; Kannan and James, 2009). Confounding climate change effects are the consequences of human activities on biodiversity. Of concern in Australia is the loss, fragmentation and degradation of habitat, depletion of natural resources, inappropriate fire regimes and changes to aquatic environments and water flows (NBSRTG, 2009).

In order to mediate the combined risks of climate change and anthropogenic landscape disturbance, an emergent goal of biodiversity conservation is to develop the adaptive capacity of ecological communities and populations. In the Australian Biodiversity Conservation Strategy, this goal is defined within the context of building ecosystem resilience (NBSRTG, 2009). At face value, these goals appear to be contradictory; adaptation suggests change while resilience may be equated with stability. However, as defined by Walker *et al.* (2004), ecosystem resilience refers to the "capacity of a system to absorb disturbance and reorganise while undergoing change so as to retain essentially the same function, structure, identity and feedbacks" (p.1). The latter aspect is at the heart of most ecological definitions of resilience, that is, how much pressure or change an ecological system can withstand before it shifts to a new, alternative steady-state (Holling, 1996; Walker *et al.*, 2009). It is perhaps through the recognition that variation in ecosystem components can contribute to overall ecosystem stability that concepts of adaptation and resilience may be integrated (Cumming *et al.*, 2005). However, from a biodiversity conservation perspective, it may not be most critical to quantify resilience per se, but instead to develop a greater understanding of the type, drivers and consequences of variation in ecological systems and communities. For example, it may be more useful to have information about thresholds that operate within systems that when crossed, lead to new ecosystem states, as well as baselines against which such changes may be compared (Hadly and Barnosky, 2009; Dietl and Flessa, 2011).

Although there is an urgency for appropriate biodiversity conservation strategies, addressing questions about variability and resilience is limited by a lack of knowledge about (a) how ecosystems respond in the short and long-term to disturbance (including climate change) (Lepetz *et al.*, 2009), (b) the natural range of variability expressed by an ecosystem at different spatial, temporal and ecological scales (Landres *et al.*, 1999) and (c) the limits of resilience, or thresholds beyond which an ecosystem changes state (Willis *et al.*, 2005; 2007; 2010; NBSRTG, 2009).

To address these questions, long-term studies of ecosystems, in particular, those covering temporal scales sufficient to detect the full extent of ecosystem reorganisation following climatic change and other disturbances, are required. Yet few studies cover temporal scales that are sufficient to detect the full extent of ecosystem reorganisation following disturbance (Van Valkenburgh, 1995; Lepetz *et al.*, 2009). In the absence of long-term data, bioclimatic models have become an important tool in biodiversity management planning. These have been used extensively for predicting the effects of future climate change on species distributions and abundance (e.g., Williams *et al.*, 2003; Shoo *et al.*, 2005); although, there are limitations to the scope, detail and accuracy of modelled responses (Pearson and Dawson, 2003; Willis and Bhagwat, 2009). Extensive habitat fragmentation, species loss and subsequent ecosystem disruption also limits our ability to understand patterns of natural variation and the interaction of ecosystem changes with the long-term persistence or loss of different ecosystem attributes over time (Magurran and Henderson, 2010).

Palaeoecology and biodiversity conservation

Palaeoecological studies are increasingly recognised as a valuable source of empirical data on past ecosystems (e.g., Willis *et al.*, 2005; MacDonald *et al.*, 2008; Hadly and Barnosky, 2009; Willis *et al.*, 2010), with many examples of the use of "natural archives" (Smol, 2010) to contextualise current and future landscape changes (e.g., Barnosky and Shabel, 2005; Saunders and Taffs, 2009; Bellingham *et al.*, 2010; Bilney *et al.*, 2010; Carassco *et al.*, 2010; Finney *et al.*, 2010; Renberg *et al.*, 2010). These natural archives include biotic (e.g., bones, pollen, diatoms) and abiotic (e.g., speleothem cave formations, stable isotopes) records that can be used to reconstruct past environments and empirically test the history of life and models of global change (e.g., Barnosky *et al.*, 2003; Willis *et al.*, 2005; MacDonald *et al.*, 2008).

As shown by Willis *et al.* (2010), the application of palaeoecological archives to modern conservation and management problems are broad in type, scale and value and can include (a) informing predictions about climate change responses and thresholds based on past ecological and climatic variability, (b) identifying the combinations of biotic and abiotic processes that most contributed to past ecological resilience and where these are likely to occur under future climate change scenarios, and (c) providing insights on novel, or non-analogous communities and their management. These applications go some way to addressing the three deficiencies in knowledge identified above: that is, understanding how ecosystems respond to disturbance at different time-scales, the range of variation and types of states that may normally be expressed by different systems under different environmental and climatic scenarios and finally, the thresholds operating within systems that define the limits or boundaries of these states and ultimately, ecosystem resilience.

Of particular interest for this review is not necessarily what palaeoecological records reveal about natural variation and resilience in past ecological systems, but rather how natural variation and resilience are measured and defined. More specifically, the literature review examines how temporal, spatial and taxonomic scales and sampling effects can influence patterns detected in palaeoecological deposits. Ultimately, such issues affect how palaeoecological trends are compared against changes observed in modern systems and the inferred ecological significance of such changes (Bennington *et al.*, 2009).

The literature review is divided into three sections, with the first providing an overview of the geological setting, chronology, faunas, climate and environmental context the vertebrate fossil assemblages of the NCWHA, the study locality. In the second section, particular attention is given to the techniques, results and implications of faunal change observed in the Naracoorte Cave record through time to (a) show how the aims of the thesis have been informed by the findings of past research from this locality, and (b) highlight key sampling issues that can influence patterns of faunal change observed in fossil records and which were considered in the design of the research presented in the thesis.

The final section re-focusses on natural variation and resilience in ecological systems. This section explores how natural variation and resilience have been inferred from faunal changes observed in palaeoecological assemblages, including those of the NCWHA. It also focusses on hierarchical relationships across common metrics used to examine change in fossil assemblages (species richness, composition and abundance) and the biodiversity conservation implications of variation across these metrics. This section of the review aims to complement Hadly and Barnosky (2009) who explored key mechanisms by which vertebrate fossil records contribute knowledge about natural variation in ecosystems.

Fossil deposits of the Naracoorte Caves World Heritage Area

Scientific and natural history values

The fossil deposits of the Naracoorte Caves contain the first dated Middle Pleistocene bone assemblages in Australia (Ayliffe *et al.*, 1998; Prideaux, 2006). They also provide records of the Late Pleistocene and Holocene, a period not well represented in other Australian vertebrate fossil deposits (Prideaux, 2006). In recognition of their natural and scientific value, the Naracoorte Cave fossil deposits were inscribed to the World Heritage List in 1994. Together with Riversleigh in Queensland, they are listed as the Australian Fossil Mammal Sites. There are 26 known caves within the NCWHA, containing nearly 100 fossil sites, each representing a snapshot of past environments and faunas of the region (Reed and Bourne, 2000, 2009). Over their *c.* 500,000 year accumulation history, the caves have acted as pitfall traps and predator dens, preserving a record of faunal diversity and abundance over time.

The potential of the Naracoorte Caves to provide a long-term record of faunal response to climate change was recognised from the earliest scientific exploration of the caves (Wells, 1975; Wells *et al.*, 1984). As research has expanded knowledge of the temporal distribution, diversity and richness of the fossil deposits, three key advantages for researching fauna and climate from the caves have emerged: (a) the ability to track mammal diversity change over multiple climatic cycles at one geographic location (e.g., Prideaux *et al.*, 2007; Macken *et al.*, 2012) (b) the ability to test models of mammal response to climate change across multiple sites of the same age (e.g., McDowell, 2001) and (c) enable the influence of taphonomic and accumulation biases on the fidelity of the palaeontological record to the sampled community to be determined (e.g., Reed, 2003; Fraser and Wells, 2006).

In their recent review of the effects of climate change on biological systems over the Cainozoic, Blois and Hadly (2009) identified that palaeoecological studies integrating climatic, environmental and community patterns are required if such data is to be used to model and predict habitat and species changes in the future. The Naracoorte Caves facilitate such integrated studies as they contain deep sediment deposits, abundant speleothems and other natural archives in addition to bones such as fossil pollen (Darrénougué *et al.*, 2009).

Geological Context

The NCWHA is located in south-eastern South Australia, *c.* 12 km from the township of Naracoorte (37°0'S, 149°48'E; Fig.1.1). The caves lie within an uplifted portion of the Oligocene to Miocene aged Gambier Limestone, a deep fossiliferous limestone of marine sediment origins (Ludbrook, 1961; Li *et al.*, 2000). Overlying this sequence is a series of sub-parallel, stranded Pleistocene beach dune facies that extend from Naracoorte to the coast at Robe (Sprigg, 1952, Murray-Wallace *et al.*, 2001; Fig. 2.1). The oldest and easternmost of these dunes, the Naracoorte East Ridge, was deposited greater than 780 kyr BP and may be as old as 935 kyr BP (Murray-Wallace *et al.*, 2001). These ridges are composed of bioclastic, calcareous carbonates of the Bridgewater formation, intermittently overlain by dune sands and calcrete (Belperio, 1995).

The prevailing model of cave formation that informed the first palaeontological studies of the caves was based on phreatic dissolution of fallen roof blocks of the Gambier Limestone over the late Miocene/early Pliocene (Wells *et al.*, 1984). More recent investigation suggests that movement of the Kanawinka fault uplifted the Gambier Limestone underneath the East Naracoorte Ridge, facilitating cave formation by controlling the development and distribution of joints within the limestone (Lewis *et al.*, 2006).

The development of entrances from the surface into the caves was determined by Reed (2003) based on an extensive survey of caves in the NCWHA and the South East region. Narrow 'solution pipe' openings, up to a maximum of 1.8 m diameter, formed as a result of secondary dissolution of limestone via vadose flow along vertical joints and subsequent lateral enlargement. These entrances contrast with much larger roof 'windows,' which reach up to 13.7 m diameter. Such roof window entrances formed following collapse of thin limestone above domed chambers (Reed, 2003).

Accumulation of vertebrate bone material and clastic sediments in the caves has been constrained by the opening, and in the case of solution pipes, closing of these cave entrances over time (Reed, 2003). Dating of clastic sediments, bone material and speleothem cave formations indicates that the Naracoorte caves first opened to the surface in the Early to Middle Pleistocene (Ayliffe and Veeh, 1988; Ayliffe *et al.*, 1998; Grün *et al.*, 2001; Prideaux *et al.*, 2007). The oldest known sedimentary and bone deposits date to the Middle Pleistocene, 530 kyr BP (Prideaux *et al.*, 2007), while some sites actively accumulate animals and clastic materials today (Reed, 2003).

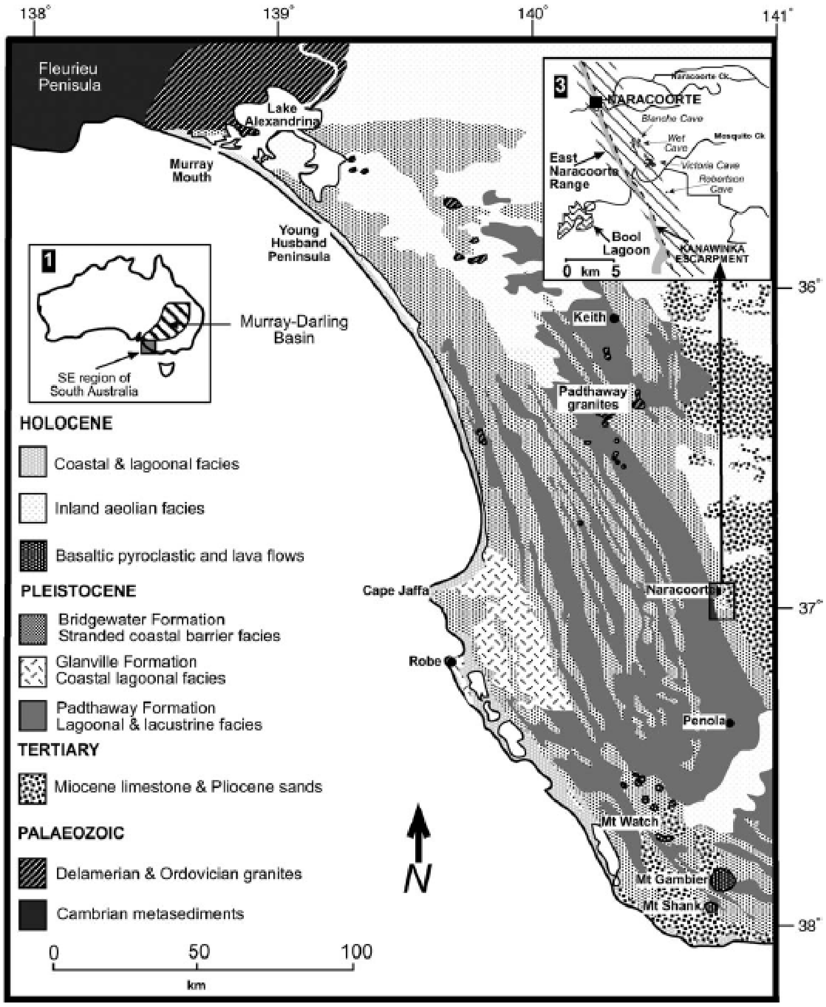


Figure 2.1 Geological map of south-eastern South Australia, indicating position of sub-parallel Pleistocene stranded beach dune facies and location of the Naracoorte Caves in the Upper South East region of South Australia, Australia. Reproduced from Forbes and Bestland (2007) with permission from Dr Matthew Forbes.

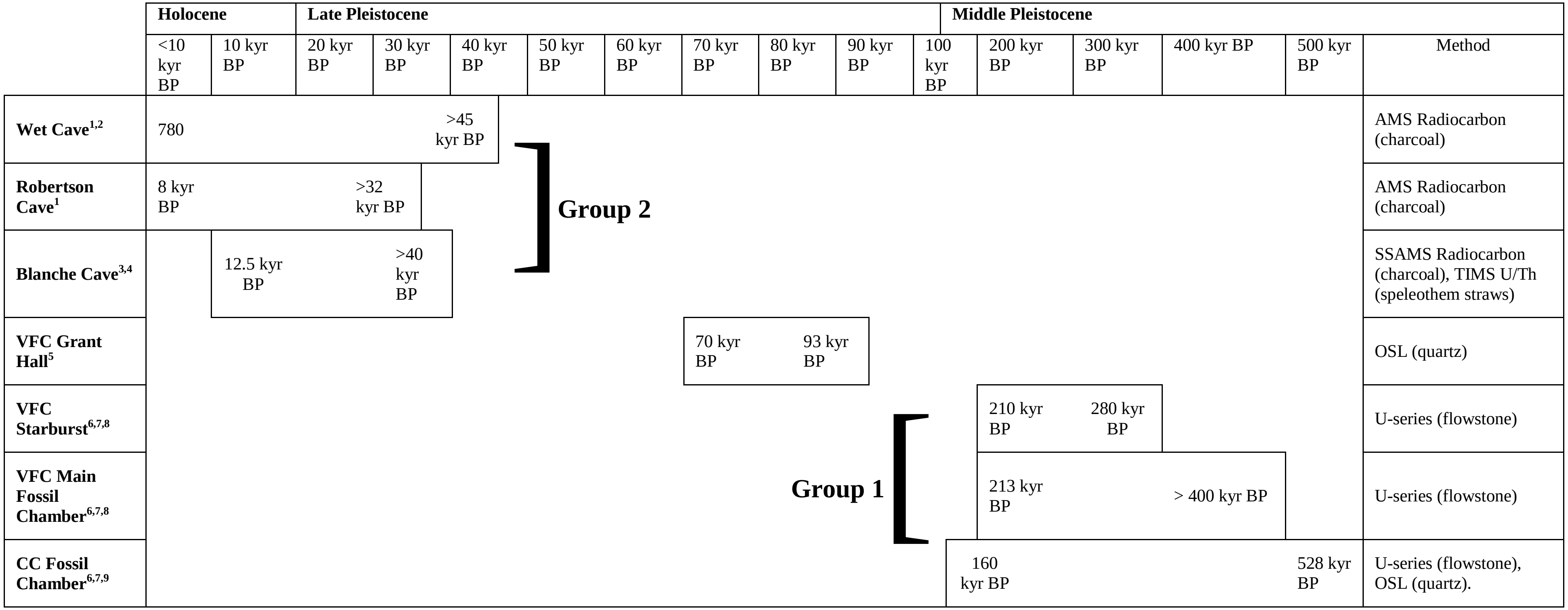
Palaeontological Research

Early exploration and study of the fossil deposits within the NCWHA has been reviewed previously (McDowell, 2001; Reed, 2003). Therefore, this section presents an overview of more recent palaeontological research at the caves since the 1969 discovery of Main Fossil Chamber in Victoria Fossil Cave.

Chronology

Cave deposits such as those of the NCWHA provide the richest source of Pleistocene faunal remains in Australia (Wells, 1978). However, as a result of their complex accumulation histories, cave deposits are considered to be less than ideal for palaeontological studies (Lowe and Walker, 1997; Forbes *et al.*, 2007). Attempts to date the Main Fossil Chamber deposit in Victoria Fossil Cave (VFC) reflect the challenges of dating cave deposits (Wells *et al.*, 1984; Ayliffe and Veeh, 1988; Grün *et al.*, 2001); however, research into other deposits of the NCWHA has yielded valuable palaeontological information within more tightly resolved temporal contexts (Fig. 2.2 and references therein). This has been facilitated by advances in dating techniques and the presence of multiple datable materials in the deposits such as cave speleothems (flowstones, stalagmites, stalactites and straws), quartz-bearing sediments, charcoal, bones and teeth.

The accumulation ages for the deposits listed in Fig. 2.2 indicate that at least three sites accumulated material over the same time intervals of the Middle (Group 1 deposits) and Late Pleistocene (Group 2 deposits) within the NCWHA. Only the Grant Hall deposit represents a time not captured by any other known deposit (Ayliffe and Veeh, 1988; Macken *et al.*, 2011). The age distribution of the NCWHA deposits provides the opportunity to examine faunal change over multiple climatic cycles at one geographic location, test models of mammal response to climate change across multiple sites of the same age and understand how taphonomic and accumulation biases influence the fidelity of the palaeontological record with the sampled community.



	Holocene		Late Pleistocene									Middle Pleistocene				
	<10 kyr BP	10 kyr BP	20 kyr BP	30 kyr BP	40 kyr BP	50 kyr BP	60 kyr BP	70 kyr BP	80 kyr BP	90 kyr BP	100 kyr BP	200 kyr BP	300 kyr BP	400 kyr BP	500 kyr BP	Method
Wet Cave[1,2]	780				>45 kyr BP											AMS Radiocarbon (charcoal)
Robertson Cave[1]	8 kyr BP			>32 kyr BP		**Group 2**										AMS Radiocarbon (charcoal)
Blanche Cave[3,4]		12.5 kyr BP		>40 kyr BP												SSAMS Radiocarbon (charcoal), TIMS U/Th (speleothem straws)
VFC Grant Hall[5]								70 kyr BP		93 kyr BP						OSL (quartz)
VFC Starburst[6,7,8]												210 kyr BP	280 kyr BP			U-series (flowstone)
VFC Main Fossil Chamber[6,7,8]										**Group 1**		213 kyr BP		> 400 kyr BP		U-series (flowstone)
CC Fossil Chamber[6,7,9]											160 kyr BP				528 kyr BP	U-series (flowstone), OSL (quartz).

Figure 2.2 Accumulation ages for dated deposits of the Naracoorte Caves World Heritage Area with details of dating technique(s) applied and datable material. VFC = Victoria Fossil Cave; AMS = Accelerator Mass Spectrometer; SSAMS = single stage accelerator mass spectrometer; OSL = optically stimulated luminescence. AMS radiocarbon ages presented as ^{14}C dates. [1]McDowell (2001); [2]Pate *et al.* (2002; 2006); [3]Darrénogué *et al.* (2009); [4]St Pierre *et al.* (2012); [5]Macken *et al.* (2011); [6]Ayliffe *et al.* (1998); [7]Moriarty *et al.* (2000); [8]Grün *et al.* (2001); [9]Prideaux *et al.* (2007).

Sediments and Stratigraphy

Defining the stratigraphic and sedimentological context of fossil deposits is an important prerequisite to their excavation and interpretation. The first sediment analyses from the NCWHA were of the clastic infills of Main Fossil Chamber, Victoria Fossil Cave (Wells *et al.*, 1984) and analyses have now been conducted on other bone-bearing deposits (e.g., Moriarty *et al.*, 2000; McDowell, 2001; Laslett, 2006; Forbes and Bestland, 2007; Forbes *et al.*, 2007; Prideaux *et al.*, 2007; Darrénougué *et al.*, 2009; Macken *et al.*, 2011). Typical sediment types found in the caves range from homogenous yellow sands (e.g., middle unit of Robertson Cave; Forbes *et al.*, 2007) to organic rich, brown silty sands (e.g., Unit 2 of Blanche Cave; Darrénougué *et al.*, 2009) and reddish silts (e.g., Grant Hall; Macken, 2009; Macken *et al.*, 2011) as originally described by Forbes and Bestland (2007).

Transport and deposition of clastic sediments into the caves has occurred largely via wind and water action, producing sedimentary cones and fans with unique stratigraphic and physical characteristics. The mode and rate of sediment transport and resulting sediment profiles within the caves is influenced by a wide range of factors. These include:

(a) Surface conditions such as vegetation and soil cover which control the rate of water flow and therefore rates of accumulation (Wells *et al.*, 1984).

(b) The presence and size of dolines (shallow depressions) in the limestone bedrock above the cave entrance which may concentrate sediments and organic matter via run-off flows prior to deposition into the chambers below. Moriarty *et al.* (2000) suggested this as the primary mode of accumulation of sediments into the caves at Naracoorte, implying discrete, bulk depositional episodes in the past resulting in aggraded stratigraphic layers in the deposit.

(c) Cave entrance type and size, which influences the nature of the sedimentary cone and rates of accumulation over time. In caves with large roof windows, the sediment cone is typically composed of limestone debris and is built up over time by clastic and organic material inputs (Reed, 2003). In many of these caves, plants, fungi and algae grow within the light zone over the sedimentary cone (Reed, 2003). In contrast, smaller solution pipe entrances may block up over time as the sediment cone fills the pipe. Large water inputs may cause mass slumping events and distal transport of sediments, re-opening the solution pipe.

(d) Within-cave processes such as water transport, slumping, saturated mud flows and animal movements, which can lead to secondary deposition and erosion across sedimentary cones and fans. These processes produce unique stratigraphic features including deep scours, cut and fill structures and flames (e.g., McDowell, 2001).

Fauna

Taphonomy and accumulation

The first extensive taphonomic investigation of fossil deposits of the NCWHA was conducted by Reed (2003). This work focused on the large mammal bone material of the Main Fossil Chamber, Victoria Fossil Cave and included neo-taphonomic observations in caves acting as contemporary pitfall traps. Reed (2003) documented the range of physical and biological factors influencing pitfall entrapment in the Naracoorte Caves, including cave entrance dynamics, animal locomotion and behaviour.

Reed (2003) showed that pitfall entrapment, or ‘pitfall mortality’ produces a near random sample of the mammal community through cumulative accretion over time. By comparison, roof window deposits record a more diverse species assemblage, resulting in higher fidelity to the actual composition of the palaeocommunity that was sampled in the deposit. This occurs largely as a result of taphonomic biases associated with the cave entrance type. Solution pipes bias entrapment of saltatorial species while roof windows captured a more equal representation of faunas with different movement habits (i.e., saltatorial, scansorial and arboreal). This occurs as roof windows facilitate a combination of pitfall entrapment, predator accumulation and within-cave habitation (Reed, 2003).

In the Naracoorte fossil sites, Barn and Masked Owl (*Tyto alba* and *Tyto novaehollandiae*) are the main predatory accumulating agents; although, mammalian carnivores may be responsible for some deposits (Reed and Bourne, 2000). The Late Pleistocene fossil assemblages of the Group 2 deposits are predominantly owl pellet derived (McDowell, 2001; Laslett, 2006). These assemblages are dominated by small mammals with high concentrations of bones. In grid square B2 from Blanche Cave, mammals with a maximum body mass of <100 g composed between 74 and 86% (average 79.6%) of the sample through the depositional sequence, and those of body mass 101–500 g only 3 to 14% (average 6.6%; Laslett 2006). A similar bias is reflected in assemblage from the inner chamber of Robertson Cave and the assemblage from Wet Cave where *c.* 80% of the two assemblages are composed of small mammals of body mass <300 g (NB. No small mammals of body mass 301–500g were identified in the study; McDowell 2001). There is also a bias towards juvenile animals for species in the body mass range 500–3000 g. This is attributed to selective predation of smaller body-sized individuals (usually juveniles) with a higher susceptibility to predation (Andrews, 1990; Laslett, 2006). Poor representation of large mammals in the Group 2 deposits may be due to enhanced visual detection of the larger cave openings (Reed, 2003; Laslett, 2006). By comparison, solution pipe entrances are less likely to be used as roosting sites by owls. All known Late Pleistocene sites of the NCWHA (Group 2) are in caves with large roof windows dominated by owl pellet derived faunas while Middle Pleistocene sites (Group 1) are largely pitfall accumulations.

Diversity

The occurrence of mammal faunas across the most extensively sampled and dated fossil deposits of the NCWHA are presented in Table 2.1. Mammal faunas represented in the fossil deposits of the Naracoorte Caves include extant species such as: Echidna (*Tachyglossus aculeatus*); Dasyuridae (*Antechinus flavipes* and *Sminthopsis crassicaudata)*; Koala (*Phascolarctos cinereus*); Common Wombat (*Vombatus ursinus*); possums and gliders (*Trichosurus vulpecula, Pseudocheirus peregrinus* and *Petaurus breviceps*); kangaroos and wallabies (*Macropus fuliginosus/giganteus, Macropus rufogriseus* and *Wallabia bicolor*); bats (*Miniopterus schreibersii*); and native rats and mice (*Hydromys chrysogaster, Notomys mitchelli, Pseudomys apodemoides* and *Rattus fuscipes*) (Reed and Bourne, 2000, 2009; Foulkes *et al*., 2003a).

There are also extensive records of amphibians, reptiles and birds within the Naracoorte Cave assemblages. However, these faunas have received less attention than the mammal faunas. Species in the fossil record that are still observed in the region today include Australian magpie (*Gymnorhina tibicen*), Emu (*Dromaius* *novaehollandiae*), Malleefowl (*Leipoa ocellata*) and Noisy Miner (*Manorina melanocephala;* Hopton *et al*., 2003). The amphibian record includes Brown Tree frog (*Littoria ewingi*), Common froglet (*Crinia signifera*), Eastern Banjo frog (*Limnodynastes dumerilii*) and Smooth frog (*Geocrinia laevis*). Bougainville's skink (*Lerista bougainville*), Sleepy lizard (*Tiliqua rugosa*), Common Long-necked tortoise (*Chelodina longicollis*), Eastern Bearded dragon (*Pogona barbata*), Eastern Tiger snake (*Notechis scutatus*) and Eastern Brown snake (*Pseudonaja textilis*) are represented in the fossil record (Reed and Bourne, 2000) and are still found in the region today (Foulkes *et al*., 2003b).

The Naracoorte Caves also preserve a record of Australian 'megafauna', a collective term to describe animals of body mass >30 kg that became extinct in the Late Pleistocene, such as *Thylacoleo carnifex*, *Zygomaturus trilobus*, *Diprotodon optatum, Palorchestes azael* and many sthenurine kangaroos including *Procoptodon goliah, 'Procoptodon' gilli*, *Simosthenurus occidentalis* and *Sthenurus andersoni*. The large madtsoiid snake *Wonambi naracoortensis* and the giant Pleistocene dromornithid *Genyornis newtoni* are also represented as fossils from the Naracoorte Caves.

The last recorded occurrence for a number of megafaunal species occurs in the Naracoorte record. For example, the presence of *Simosthenurus maddocki* in the Grant Hall deposit represents the youngest known record for this species, *c.* 74 kyr BP (Macken, 2009). Wet Cave provides the most recent occurrence for *Protemnodon brehus*, *'Procoptodon' browneorum*, *Thylacoleo carnifex* and *Zygomaturus trilobus, c.* 46 kyr BP (Pate *et al.,* 2002).

Late Pleistocene vertebrate deposits indicate that despite loss of the megafauna as indicated by their absence in sediments dating < *c.* 45 kyr BP (Pate *et al*., 2006), faunal diversity remained high well into the Holocene with an estimated 47 mammal species identified from the Group 2 assemblages (McDowell, 2001; Laslett, 2006; Table 2.1). Unfortunately, this diversity has drastically declined in the region, at least since European settlement (Foulkes *et al.*, 2003a). Many species are now extinct (e.g., *Macropus greyi*, *Potorous platyops* and *Thylacinus cynocephalus*), or no longer occur in the region (e.g., *Macropus eugenii*, *Mastacomys fuscus*, *Bettongia penicillata* and *Perameles bougainville*). Extensive habitat clearance, predation and competition from introduced species have contributed to the loss of these species. According to the 2001 Naracoorte Caves National Park Management Plan (SERNPWSA, 2001), 26 native mammal species, 90 native birds and 27 species of reptiles persist in the Naracoorte Caves National Park at the present time. Many of these extant species are considered rare or endangered as a result of human modification to the landscape.

Table 2.1 Mammal species (excluding bats) identified in six well-studied fossil assemblages of the Naracoorte Caves World Heritage Area. 1 indicates present, 0 absent. Species occurrences marked with *cf.* indicate tentative identification of species. Differentiation of Group 1 (Main Fossil Chamber, Victoria Fossil Cave (VFC); Fossil Chamber, Cathedral Cave and Grant Hall, VFC) and Group 2 sites (Inner Chamber, Robertson Cave; 5U10 Entrance Chamber, Wet Cave and 3rd Chamber, Blanche Cave) on basis of age of fossil accumulations (Group 1: Middle to Late Pleistocene, *c.* minimum of 74 kyr BP; Group 2: Late Pleistocene, age maximum *c.* 45 kyr BP) and primary accumulation mode (Group 1: pitfall entrapment; Group 2: owl pellet aggradation). Grant Hall represents a temporal period not captured by any other known Naracoorte Cave deposit. Sourced from Reed and Bourne (2000; 2009); McDowell (2001); Laslett (2006); Prideaux *et al.* (2007a) and Macken *et al.* (2012). Note that species occurrences are plotted for an assemblage as a whole, rather than for individual stratigraphic layers within each deposit. Authorities from Strahan and Conder (2007) and Reed and Bourne (2000).

			Group 1			**Group 2**		
Family	**Species**	**Authority**	**VFC, Main Fossil Chamber**	**Cathedral Cave, Fossil Chamber**	**VFC, Grant Hall**	**Robertson Cave, Inner Chamber**	**Wet Cave**	**Blanche Cave, 3rd Chamber**
TACHYGLOSSIDAE	*Tachyglossus aculeatus*	Shaw, 1792	1	1	1	1	0	0
	Megalibgwilia ramsayi‡	Owen, 1884	1	0	0	0	0	0
THYLACINIDAE	*Thylacinus cynocephalus*†	Harris, 1808	1	1	1	0	1	1
DASYURIDAE	*Antechinus agilis**	Dickman, Parnaby, Crowther and King, 1998	0	1	*cf.*	0	0	0
	Antechinus flavipes	Waterhouse, 1837	1	1	1	1	1	1
	Antechinus minimus	Geoffroy, 1803	0	1	*cf.*	0	0	0
	*Antechinus stuartii**	Macleay, 1841	1	0	*cf.*	0	0	0
	*Antechinus swainsonii**	Waterhouse, 1840	1	1	1	0	0	0
	*Dasyurus maculatus**	Kerr, 1792	1	1	0	0	0	0
	*Dasyurus viverrinus**	Shaw, 1800	1	1	1	1	1	1
	*Ningaui yvonneae**	Kitchener, Stoddart and Henry, 1983	*cf.*	1	0	1	1	1

Family	Species	Authority	Group 1			Group 2		
			VFC, Main Fossil Chamber	Cathedral Cave, Fossil Chamber	VFC, Grant Hall	Robertson Cave, Inner Chamber	Wet Cave	Blanche Cave, 3rd Chamber
	*Phascogale calura**	Gould, 1844	1	1	1	0	0	0
	Phascogale tapoatafa	Meyer, 1893	1	1	1	1	1	1
	Sarcophilus laniarius†	Owen, 1838	1	1	0	0	1	0
	Sminthopsis crassicaudata	Gould, 1844	1	1	1	1	1	1
	Sminthopsis murina	Waterhouse, 1837	1	1	1	1	1	1
PERAMELIDAE	*Isoodon obesulus*	Shaw, 1787	1	1	1	1	0	1
	*Perameles bougainville**	Quoy and Gaimard, 1824	1	1	1	0	0	1
	*Perameles gunnii**	Gray, 1838	1	1	1	1	1	1
PHASCOLARCTIDAE	*Phascolarctos cinereus*	Goldfuss, 1817.	1	0	1	1	1	1
	Phascolarctos stirtoni‡	Bartholomai, 1968	0	1	0	0	0	0
DIPROTODONTIDAE	*Zygomaturus trilobus‡*	Macleay, 1858	1	1	1	0	1	0
PALORCHESTIDAE	*Palorchestes azael‡*	Owen, 1874	1	0	0	0	0	0
VOMBATIDAE	*Lasiorhinus krefftii**	Owen, 1872	1	1	0	0	0	0
	*Lasiorhinus latifrons**	Owen, 1845	1	1	0	0	0	0
	Vombatus ursinus	Shaw, 1800	1	1	1	1	1	0
THYLACOLEONIDAE	*Thylacoleo carnifex‡*	Owen, 1858	1	1	1	1	1	1
PHALANGERIDAE	*Trichosurus vulpecula*	Kerr, 1792	1	1	0	1	1	1
HYPSIPRYMNODONTIDAE	*Propleopus oscillans*	De Vis, 1888	*cf.*	0	0	0	0	0
POTOROIDAE	*Aepyprymnus rufescens*	Gray, 1837	*cf.*	0	0	0	0	0
	Bettongia gaimardi	Desmarest, 1822	1	1	0	0	0	1
	Bettongia lesueur†	Quoy and Gaimard, 1824	*cf.*	0	0	1	1	1

Family	Species	Authority	Group 1			Group 2		
			VFC, Main Fossil Chamber	**Cathedral Cave, Fossil Chamber**	**VFC, Grant Hall**	**Robertson Cave, Inner Chamber**	**Wet Cave**	**Blanche Cave, 3^{rd} Chamber**
MACROPODIDAE	*Bettongia penicillata*	Gray, 1837	1	1	0	0	0	0
	Potorous platyops†	Gould, 1844	1	1	1	1	1	1
	*Potorous tridactylus**	Kerr, 1792	1	1	1	0	0	0
	*Lagorchestes leporides***	Gould, 1840	1	1	0	1	1	1
	*Lagostrophus fasciatus***	Péron and Lesueur, 1807	1	0	0	0	0	0
	Macropus eugenii	Desmarest, 1817	1	0	0	0	0	0
	Macropus fuliginosus/giganteus	Desmarest, 1817 / Shaw, 1789	1	1	1	1	1	1
	Macropus greyi†	Waterhouse, 1846	1	1	1	0	0	0
	Macropus rufogriseus	Desmarest, 1817	1	1	1	1	1	1
	Onychogalea lunata†	Gould, 1840	0	1	0	0	0	1
	Protemnodon brehus‡	Owen, 1874	0	*cf.*	*cf.*	1	1	1
	Protemnodon roechus†	Owen, 1874	1	0	0	0	0	0
	Wallabia bicolor	Desmarest, 1803	1	1	1	1	0	0
	Sthenurus andersoni‡	Marcus, 1962	1	1	1	0	0	*cf.*
	Metasthenurus newtonae‡	Prideaux, 2000	1	1	0	0	1	0
	Procoptodon goliah	Owen, 1846	1	1	0	0	0	0
	'Procoptodon' browneorum‡	Merrilees, 1968	1	1	1	0	1	1
	'Procoptodon' gilli‡	Merrilees, 1965	1	1	1	1	1	1
	Simosthenurus baileyi	Prideaux and Wells, 1998	1	0	0	0	0	0
	Simosthenurus maddocki‡	Wells and Murray, 1979	1	1	1	0	0	0
	Simosthenurus occidentalis‡	Glauert, 1910	1	1	1	1	1	1

Family	Species	Authority	Group 1			Group 2		
			VFC, Main Fossil Chamber	**Cathedral Cave, Fossil Chamber**	**VFC, Grant Hall**	**Robertson Cave, Inner Chamber**	**Wet Cave**	**Blanche Cave, 3rd Chamber**
	'Simosthenurus' pales‡	De Vis, 1895	1	1	0	0	0	0
Burramyidae	*Cercartetus concinnus*	Gould, 1845	0	0	0	0	1	0
	Cercartetus lepidus	Thomas, 1888	1	1	0	1	1	1
	Cercartetus nanus	Desmarest, 1818	1	1	1	1	1	1
Pseudocheiridae	*Petauroides volans*	Kerr, 1792	0	0	0	1	0	0
	Pseudocheirus peregrinus	Boddaert, 1785	1	1	1	1	1	1
Petauridae	*Petaurus breviceps*	Waterhouse, 1838	1	1	1	1	1	1
	Petaurus norfolcensis	Kerr, 1792	0	0	0	1	0	0
Acrobatidae	*Acrobates pygmaeus**	Shaw, 1793	*cf.*	1	0	0	0	1
Muridae	*Conilurus albipes†*	Lichtenstein, 1829	1	1	0	1	1	1
	Hydromys chrysogaster	Geoffroy, 1804	1	1	1	1	0	0
	*Mastacomys fuscus**	Thomas, 1882	1	1	1	1	1	1
	*Notomys mitchellii**	Ogilby, 1841	*cf.*	1	0	1	1	1
	Pseudomys apodemoides	Finlayson, 1932	1	1	1	1	1	1
	Pseudomys auritus†	Thomas, 1910	0	1	1	1	1	1
	*Pseudomys australis**	Gray, 1832	1	1	1	1	1	1
	*Pseudomys fumeus**	Brazenor, 1936	*cf.*	1	1	1	1	0
	Pseudomys gouldii†	Waterhouse, 1839	*cf.*	1	1	1	*cf.*	*cf.*
	Pseudomys shortridgei	Thomas, 1906	1	1	1	1	1	1
	*Rattus fuscipes **	Waterhouse, 1839	1	1	1	1	1	1
	Rattus lutreolus	Gray, 1841	0	1	1	1	1	1

			Group 1			Group 2		
Family	**Species**	**Authority**	**VFC, Main Fossil Chamber**	**Cathedral Cave, Fossil Chamber**	**VFC, Grant Hall**	**Robertson Cave, Inner Chamber**	**Wet Cave**	**Blanche Cave, 3rd Chamber**
	*Rattus tunneyi**	Thomas, 1904	1	1	1	1	1	0
	Total No. Species		**64**	**61**	**45**	**41**	**41**	**40**

* species regionally extinct; † species extinct in late Holocene; ‡ species extinct during Pleistocene.

Climate

An advantage of the Naracoorte Caves for palaeontological study is that they contain abundant speleothem material which can provide information about local climate conditions using carbon and oxygen stable isotopes. These can be linked to a high resolution chronology (U-series dating) and related to regional and global climatic data (Ayliffe *et al.*, 1998). Speleothems are common secondary calcium carbonate structures of limestone caves and include stalagmites, stalactites, flowstones and calcite straws. They form from the precipitation of calcium carbonate from seepage water that has flowed through the overlying limestone and surface soil horizons into the cave. Growth and formation of speleothems is controlled by the interaction of a range of factors including regional temperatures, the amount of water infiltrating from the surface and the partial pressure of Ca and CO_2 in seepage water (Ayliffe *et al.*, 1998).

It was originally assumed that speleothem growth coincided with interglacial periods in the past due to higher rainfall when compared with more arid, glacial times (Ayliffe and Veeh, 1988). However, this was not supported by analysis of a number of speleothems of differing age from a range of cave sites within the NCWHA (Ayliffe *et al.*, 1998). In contrast to expectations, speleothem growth coincided with stadial and cool interstadials (periods of lesser glacial and interglacial extremes) of the Middle to Late Pleistocene (Ayliffe *et al.*, 1998; Demarshelier *et al.*, 2000; Bestland and Rennie, 2006; Fig. 2.3).

Ayliffe *et al.* (1998) hypothesised that the lack of speleothem growth in the Naracoorte Caves over the penultimate interglacial, Marine Isotope Stage (MIS) 5e, reflected conditions of high evaporation and reduced effective moisture availability as a result of elevated temperatures. Conversely, temperature declines during glacials and cool interstadials may have ‘depressed’ evapotranspiration, increasing effective moisture availability and infiltration through the surface soil horizons and limestone bedrock. Further, speleothem growth appears to have coincided with average ocean temperatures at least 3°C lower than present (Ayliffe *et al.*, 1998). This is supported by pollen deposits in western Tasmania which indicate temperature reductions of greater than 3.5°C when compared with modern times (Colhoun, 2000), coincident with speleothem growth in south-eastern South Australia during the cool interstadial phase, *c.* 85 kyr BP, at the end of MIS-5.

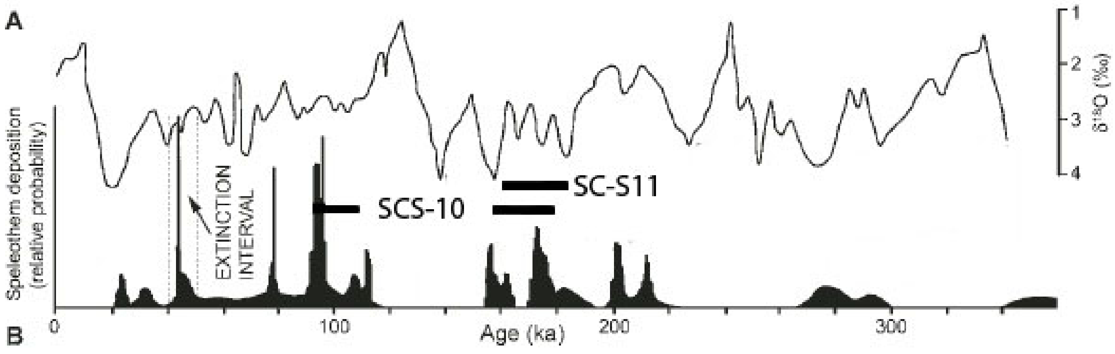


Fig. 2.3 Composite Naracoorte Cave speleothem and global climate record modified from Prideaux *et al.* (2007). (A) δ^{18}O record of deep sea core MD97–2120, southwest Pacific (Pahnke *et al.*, 2003), (B) Histogram of ^{230}Th/^{234}U ages of Naracoorte Cave speleothems with composite Gaussian probability curves for each date, normalised to unit area. Height of peaks indicates probability of accuracy (Ayliffe *et al.*, 1998). Horizontal lines indicate depositional ages of Naracoorte Cave speleothems determined by ^{230}Th/^{234}U dating (SC-10: Bestland and Rennie, 2006; SC-S11: Demarshelier *et al.*, 2000). Megafaunal extinction interval from Roberts *et al.* (2001).

Vegetation

Interpretation of vegetation communities surrounding the Naracoorte Caves at the time of faunal accumulation has traditionally relied upon palaeoenvironmental reconstructions based on faunal diversity, as well as extrapolation from regional palynological records. This is due to a long held perception that the caves do not contain micro or macro plant fossils (E. Reed, pers. comm.). However, pollen records reported by Darrénougué *et al.* (2009) provide the first challenge to this assumption. The record retrieved from Blanche Cave shows fluctuations in the abundance of woody and herbaceous vegetation groupings through the last glacial cycle at this locality (Darrénougué *et al.*, 2009). A more detailed and extensive evaluation of the pollen record from this site is in preparation by E. Reed and S. van der Kaars (pers. comm.).

Regional vegetation records reveal changes to the composition of vegetation communities over the Late Pleistocene. These records include Lake Leake and Wyrie

Swamp near Millicent in South Australia (Dodson, 1975, 1977) and Lakes Wangoom (Harle *et al.*, 2002), Bolac and Turangmoroke (Cook, 2009) in south-western Victoria. Palynological records from marine core E55-6, collected offshore from the southern tip of south-eastern South Australia, shows that during the cool phase of MIS-2, heath and grass communities characterised the region (Harle, 1997). In contrast, the records from Wyrie Swamp and Lake Leake indicate that a mosaic of vegetation types was maintained on the landscape through the last glacial cycle. This mosaic was characterised by *Eucalyptus* woodland with heath understorey and more open woodlands and grasslands dominated by Asteraceae and Poaceae (Dodson, 1975, 1977).

From the start of the Holocene, regional records document the appearance of more seasonally adapted species in the vegetation communities (Dodson, 1975; Cook, 2009). The influence of seasonal water availability across the landscape was a feature recognised in early historical records from the region (Croft, 2003). As a result of this seasonality and the variation in landscape features, the pre-European South East vegetation comprised a “complex mosaic of plant communities” (Croft, 2003, p. 43), reflecting the early Holocene pollen records from the lower South East and Blanche Cave (Dodson, 1975, 1977; Darrénougué *et al.*, 2009). The composition of these communities has been extensively interpreted and described elsewhere from historical records (Croft, 2003).

The present composition and distribution of vegetation within the Naracoorte Coastal Plains bioregion reflects the extensive modification and clearance that has occurred in historical times. Land uses including irrigated agriculture and pasture, forestry and the expansion of human settlement have reduced native vegetation in the region to only 13% of original coverage (Foulkes and Heard, 2003). Within the NCWHA, very little remnant vegetation remains, reflecting the impact of historical clearance and the introduction of non-indigenous native plants and introduced species, including herbs, annual grasses, broadleaved trees and palms (South East Region National Parks and Wildlife South Australia (SENPWSA), 2001).

Palaeoecology of the NCWHA

Against the backdrop of research into the geological setting, diversity and palaeoenvironmental context of the Naracoorte Caves has been research into the palaeoecology of the assemblages themselves. Palaeoecological analyses of the fossil assemblages have focussed on two general aims: (1) to reconstruct past environmental and climatic conditions from fossil faunas to understand the timing and nature of local and regional climate change (e.g., McDowell, 2001; Laslett, 2006), and/or (2) to understand how past climate change affected local faunas (e.g., Moriarty *et al.*, 2000).

Palaeoenvironmental reconstructions

Palaeoenvironmental reconstructions are a common technique in palaeoecological analyses and use a wide range of natural archives including pollen, diatoms, ostracods and vertebrate faunas to interpret the past environmental and climatic conditions of different localities. Reconstructions are typically based on the known phenotypic (e.g., body size, locomotion, taxonomy) and adaptive (e.g., geographic distribution, habitat and diet) responses that define the contemporary environmental tolerance ranges of a species or assemblage (Lundelius, 1964; Andrews and Lord, 1979; Reed, 1998). Variation in the composition of a fossil assemblage is then assumed to indicate when and how environmental and/or climatic conditions have changed through time. This is based on the concept of ‘ecological replacement’ where faunal succession reflects environmental change (Brenchly and Harper, 1998).

Increasingly, palaeoenvironmental reconstructions have adopted a bioclimatic modelling approach. Similar to those used in the projection of species distributions under future climate change scenarios, these models have been developed to reconstruct past climates using the modern distributions of mammal faunas (e.g., Hernández Fernández and Peláez-Campomanes, 2005). However, as recognised by Shabel *et al*. (2004), climatic tolerance limits are only one part of an organisms niche; other factors such as food and habitat availability and interspecific interactions also control a species geographic distribution and, hence, tolerance limits.

The earliest temporal analyses of fossil faunas of the NCWHA involved palaeoenvironmental reconstructions based on the small vertebrate remains from Main Fossil Chamber, VFC. In these reconstructions, the modern distribution and habitat preferences of extant taxa identified in the deposit were used to infer the dominant vegetation types surrounding the cave at the time of accumulation (Smith, 1971; 1972; Wells *et al.*, 1984). Later, more sophisticated palaeoenvironmental reconstructions were conducted using the Late Quaternary aged fossil faunas of Wet, Robertson and Blanche Cave (McDowell, 2001; Laslett, 2006). In these studies, ecological characteristics such as habitat preferences, diet, activity and body size were weighted by the relative abundance of species within each excavation layer to reconstruct Late Quaternary climate and habitats around the caves, as well as to examine change in these conditions through the last glacial cycle. In defining the broad ecological niches of the faunas, McDowell (2001) and Laslett (2006) also considered the functional diversity of the palaeocommunities.

Smith (1972) suggested that the local vegetation at the time of accumulation of the assemblage from Main Fossil Chamber, VFC was dry sclerophyllous forest; however, later reconstructions based on the faunas of other sites have been more specific and consistently found that a “mosaic” of vegetation types was likely present at various times throughout the Pleistocene (e.g., McDowell, 2001; Laslett, 2006; Fraser and Wells, 2008), consistent with the immediately pre-European vegetation communities of the region as described by Croft (2003). Descriptions of this mosaic have typically included grasslands and woodlands. Swamps and forests appear to have been persistent habitat types, but are not as well-represented due to either their rarity in the palaeoenvironment (e.g., covered smaller areas when compared with grasslands and woodlands) or poor representation by associated faunas as a result of biases in the fossil record.

Climate change is presumed to have driven variation in the relative proportion of these vegetation types through the Pleistocene (Laslett, 2006). For example, the assemblages from Wet, Robertson and Blanche caves revealed a relatively higher percentage of grassland-inhabiting faunas in the sand-rich layers associated with MIS-2 (last glacial) when compared with the younger, organic-rich Holocene aged sediments which contained a higher percentage of woodland species (McDowell, 2001; Laslett, 2006).

Assumptions and inference in palaeoenvironmental reconstructions

While palaeoenvironmental reconstructions are used extensively in palaeoecological studies, they are also criticised for their reliance on a number of assumptions (e.g., Belyea, 2007) and on higher-order extrapolations that may not be accurate (Caran, 1998). Examples of the former include the following assumptions: (a) the environmental and climatic tolerances of species have not changed over time, (b) the present-day distribution and ecological preferences (ecological niches) of a species represent the full limits for that species and (c) present-day habitat types existed in the past. An example of a higher-order extrapolation, as described by Caran (1998) may include inferring reduced effective moisture at a given locality based on the last appearance of a wetland inhabiting species (e.g., lemmings) through the following sequence of inference: last appearance of remains of lemmings in a fossil sequence = local extirpation of lemmings = loss of lemming habitat (wetlands) = reduced stream flow = increased aridity (reduced effective moisture). Clearly, a range of alternative explanations may account for the absence of lemming remains in a fossil assemblage from a particular stratigraphic level and need to be considered as alternative explanations. These include taphonomic or sampling bias, post-depositional loss of bone bearing sediments, community-level processes such as competition, as well as factors other than aridity that may reduce the extent of wetland habitats such as increased rates of water flow and storm events.

Niche preservation through time

It is generally assumed that ecological niches function at the generic level in mammals and are also conserved at this taxonomic level over time (Hadly *et al.*, 2009). However, the generality of this assumption has been challenged (e.g., DeSantis *et al.*, 2009) and may not be valid for all species. For example, using a comparative based analysis of the pre-European and contemporary small mammal diet of sooty owls (*Tyto tenebricosa tenebricosa*), Bilney *et al.* (2010) demonstrated that the ecological niches of small mammals in south-eastern Australian forests have been severely underestimated; niche contraction and denial as a result of restricted distribution and abundance suggests that the difference between a species' fundamental and realised niche is significant (Bilney *et al.*, 2010).

Geographic range contraction as a result of historic and contemporary landscape change is also likely to result in under- or misrepresentation of the climatic range of many species. An example stemming from the Naracoorte Caves is the Pleistocene occurrence of Plains Mouse (*Pseudomys australis*), showing that the species was formerly present within the vicinity of the caves. However, the species is today restricted to cracking clays in central Australia and is considered an arid-land species (Van Dyck and Strahan, 2008). The extent to which the presence of *P. australis* at Naracoorte represents more arid climatic conditions in the past, the presence of cracking clays (or similar substrate), or niche contraction is unknown. It is also possible that the specimens identified as *P. australis* represent a cryptic, new species as suggested for fossil specimens from a fossil locality on Yorke Peninsula (McDowell *et al.*, 2012), limiting the usefulness of reconstructions based on the observed ecology of the species today.

There are also problems associated with the definition of the ecological traits of different species, especially generalist taxa that may use a wide range of habitat types or dietary items. For example, in the palaeoenvironmental reconstructions based on the assemblages from Wet and Robertson caves, individual species were, in some cases, allocated to more than one habitat category (McDowell, 2001). For example, *Rattus fuscipes* was counted as a forest, scrub and woodland species. In addition, where the ecological characteristics of a species were unknown (e.g., for extinct taxa) or where specimens were identified to genus or family level only, the data were not adjusted to account for the absence of these taxa in the cumulative per cent data. The effect of these methods was that the total abundance of faunas in any layer of the assemblage was either greater than or less than 100%. These challenges make it difficult to assess the overall robustness of the palaeoenvironmental reconstructions and functional diversity of Late Pleistocene Naracoorte based on the fossil faunas of Wet and Robertson Caves.

As a result of these challenges it is generally accepted that reconstructions based on whole assemblages provide a more accurate reflection of palaeoenvironmental conditions than those based on a single species (Lowe and Walker, 1997). Further, Lundelius (1964) argued that multi-taxon based interpretations are required to reduce the effect of species' evolutionary adaptation over time. Despite these recommendations, divergence in the abundance trends of taxa that are considered to have similar ecological niches observed in Naracoorte fossil records shows that species' responses to climatic change may not necessary reflect (a) linear relationships between niches and climate change responses, nor (b) that species with overlapping niches today had so in the past (Macken *et al.*, 2012). As a consequence, palaeoecological techniques that focus on functional diversity should attempt, where possible, to measure functional traits from the fossils rather than through inference based on modern niches. Functional traits are not considered in this thesis where attention is given to measures of diversity (e.g., species richness, relative abundance) but could include body size and diet. Palaeoecological techniques that may be used to study diet from fossil specimens include microwear (e.g., Rivals and Deniaux, 2003) and stable carbon isotopes (DeSantis *et al.*, 2009).

No-analogue assemblages

An outcome of historic contraction in the geographic, and hence climatic and habitat ranges of many species, is the occurrence of no-analogue assemblages in Quaternary fossil deposits. 'No-analogue assemblage' is used to describe the co-occurrence of species in fossil deposits that have allopatric distributions today (Lundelius, 1989). No-analogue assemblages are common in Pleistocene fossil deposits and typically result in greater estimates of species diversity in Pleistocene communities than those of the Holocene and present. This is commonly attributed to more equable climates with less seasonal extremes and greater habitat diversity during the Pleistocene when compared with today (e.g., Graham, 1985; Lundelius, 1989; Carrasco *et al.*, 2009; Ceballos *et al.*, 2010). Evidence that is commonly used to support this assumption is the severity of global climate change at the Pleistocene–Holocene transition (Graham, 1985); however, this perspective contrasts with the more general view of Swetnam *et al.* (1999) who suggested that no-analogue assemblages represent changed physical and biological recording processes and their interaction with the environment through time.

In order to avoid the issues associated with no-analogous assemblages, Carrasco *et al.* (2009) assessed change through time in North America faunas from 30 million to 500 years ago. In reconstructing the pre-European baseline of biodiversity, they were able to maintain the same sampling and analytical techniques for all temporal periods, rather than comparing the fossil samples against the highly modified faunal diversity of modern times. McDowell (2001) used a similar approach in his analysis of the Late Quaternary aged deposits from Wet Cave where he aimed to reconstruct the immediately pre-European mammal community of the Naracoorte region. The purpose was to provide a pre-impact baseline from which to compare Pleistocene palaeocommunity diversity. Unfortunately, the immediately pre-European fossil assemblage from Wet Cave contained older, re-worked Pleistocene aged fossil material, limiting its usefulness for such a comparison (McDowell, 2001).

Climate change effects on local faunas

In comparison to these examples of palaeoenvironmental reconstructions, Moriarty *et al.* (2000) presented the first appraisal of faunal responses to climate change from the Naracoorte Caves. Their study represented an important shift in the focus or type of research question being addressed through analysis of the Naracoorte Caves fossil faunas; that is, rather than reconstructing conditions based on the fossil assemblages, Moriarty *et al.* (2000) were the first to explicitly consider what effect climate change had on the fauna themselves.

As argued by Moriarty *et al.* (2000), changes in faunal diversity are expected to have occurred during periods of “climate stress” (p. 140). However, in their assessment of the composition of six Middle Pleistocene aged assemblages of the NCWHA, Moriarty *et al.* (2000) concluded that there had been “little apparent change in faunal diversity over a period of 300 kyr BP in the Middle Pleistocene, a period spanning at least three glacial-interglacial cycles” (p. 141).

Subsequent analyses of faunal responses to climate change from assemblages of the Naracoorte Caves have shown that this model of limited faunal change is simplistic and, in light of more rigorous sampling in other deposits, unsupported. For example, in their study of the mammal assemblage of Main Fossil Chamber, Cathedral Cave (one of the sites examined by Moriarty *et al.*, 2000), Prideaux *et al.* (2007) found evidence for change in the relative abundance of individual species between sedimentary units associated with wetter and drier climatic phases of the Middle Pleistocene (Fig. 2.4a). The site also showed that there was a local decline in the density of larger mammals, including megafauna, as the climate became more arid over the transition from MIS-9 to MIS-8, likely reflecting a reduction in the number of individuals within populations living around the caves (Prideaux *et al.*, 2007; Fig. 2.4b).

Another site examined by Moriarty *et al.* (2000), the Late Pleistocene aged deposit of Grant Hall, VFC also revealed community-level change in the local mammal fauna between MIS-5 and -4, *c.* 95 to 70 kyr BP. (Fraser and Wells, 2008; Macken *et al.*, 2012). A stand out feature of this deposit is the rarity of *Macropus fuliginosus/giganteus*, which is represented by only three individuals. In older deposits this species it is the most abundant of the larger-body sized grazing macropodines (Reed, 2003; Prideaux *et al.*, 2007; Macken *et al.*, 2012). This pattern suggests that there was a significant change in species abundances within the palaeocommunity associated either directly with climate change, or indirectly through climate change effects on community-level processes. Macken *et al.* (2012) also found evidence for a decline in small mammal species richness and variation in the relative abundances of smaller body sized taxa through the Grant Hall deposit (Fig. 2.4c and d).

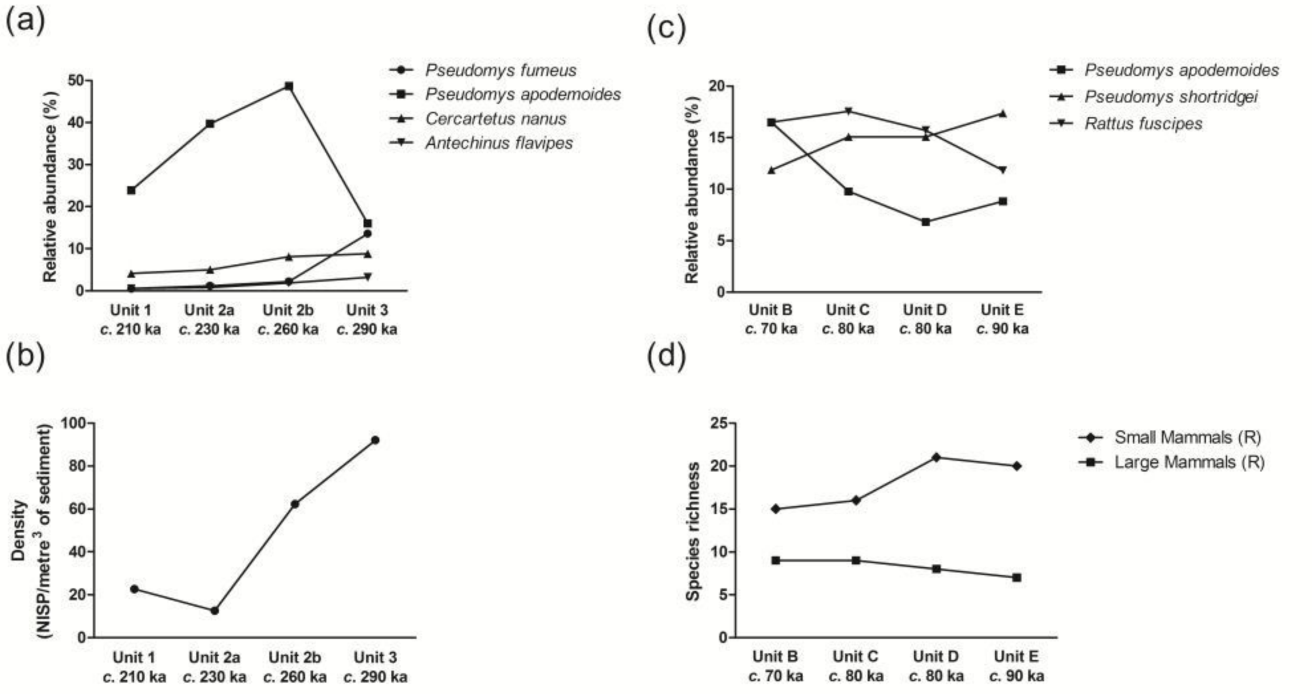


Figure 2.4 Faunal responses to Pleistocene climate change recorded in the Cathedral Cave and Grant Hall fossil assemblages. (a) Relative abundance trends of small mammal species (<5 kg) and (b) fluctuation in the density of large mammals (>5 kg) through the Cathedral Cave sequence (Prideaux *et al*., 2007). (c) Relative abundance trends of small mammal species and (d) rarefied small (<2 kg) and large (>2 kg) mammal richness through the Grant Hall sequence (Macken *et al*., 2012).

Species-area effects on the detection of faunal responses to climate change

The contrast between Moriarty *et al.*'s (2000) observation of limited faunal change against the evidence for variation in species richness, density and abundances from other studies raises questions about how and why such different conclusions may be drawn from the same fossil sites. While the reasons are more obvious when comparing the sampling designs of these studies, different observations from the same sites suggests that sampling and analytical methods exert a strong influence on observed ecological patterns and can influence the inferred significance of those patterns (Rahel, 1990; DiMichele *et al.*, 2004).

The particular sampling concerns of the study by Moriarty *et al.* (2000) relate to time-averaging (temporal scale) and inadequate and highly variable sample sizes between samples (sampling effects). These are commonly cited issues associated with the analysis of palaeoecological assemblages, including those designed as palaeoenvironmental reconstructions and are related to the mathematical relationship between sampling area and species richness (the species-area curve; Lomolino, 2000). That is, the greater the geographic area sampled by a deposit (and hence range of environments and climatic zones) the higher its species diversity (e.g., Barnosky *et al.*, 2005).

Time-averaging and sampling-effort demonstrate a similar relationship with species richness as geographic sampling area and are related to sampling issues associated with the fidelity of a fossil assemblage to the living palaeocommunity from which it was sampled. This is an important consideration in palaeoecology as it affects the accuracy of data derived from natural archives to the true ecological patterns exhibited in the past. Sampling biases associated with this relationship typically concern taphonomic factors (e.g., accumulation mode, agent and depositional history) in addition to temporal and spatial scale, and sampling biases. As these issues have been extensively examined for a wide range of sites and types of palaeoecological archives (e.g., Kidwell and Flessa, 1996, Terry 2010a; b), particular attention is given here to the influence of sampling effects on observed patterns, not necessarily the relationship between the observed patterns and the sampled palaeocommunity.

Time-averaging

Time averaging is defined by Hadly and Barnosky (2009) as the number of years over which a community sample accumulated, with examples of time-averaging scales for different palaeoecological settings provided in Roy *et al.* (1996). Greater time averaging, either through post-depositional or analytical mixing of faunas of different ages, or through slow accumulation and burial, is expected to inflate species richness by (a) increasing the likelihood of sampling rare fauna and (b) sampling successive faunal communities from a single locality. These processes can result in the consolidation of fauna from different environmental ‘regimes’ into one assemblage (Graham, 1985). The effect of time-averaging across multiple climatic phases has been termed ‘climate-mixing’ by Hopely and Maslin (2010) and results in a weakened signal of climate effects on faunas (Stenseth and Mysterus, 2005). From a more general perspective, it also means that the term ‘palaeocommunity’ is not comparable to ‘community’ as used in neontolgoical studies. ‘Community’ is used to describe an interacting assemblage of species at a particular time and place. The term ‘palaeocommunity’ is used throughout the thesis, following the definition of Bennington and Bambach (1996; Table 2.3) and with acknowledgement of its limitations given time-averaging within fossil assemblages.

In the analysis by Moriarty *et al.* (2000), faunal change was assessed through a comparison of the richness and composition of mammal faunas among six assemblages of Middle Pleistocene age (Table 2.2). However, there were no stratigraphic and chronological controls assigned to the faunas within those sites and as acknowledged by Moriarty *et al.* (2000), this sampling effect introduced gross time-averaging to the fossil data presented.

As shown in the analysis of the Cathedral Cave and Grant Hall deposits by Prideaux *et al.* (2007) and Macken *et al.* (2012), time-averaging by Moriarty *et al.* (2000) mixed faunas of at least two climatic phases in both sites (MIS-9 to MIS-8 and MIS-5a to MIS-4, respectively). Although the poor chronological resolution and few data for Main Fossil Chamber of VFC makes it difficult to assess the extent of time-averaging of the faunas in this deposit when it is considered as a whole, the presence of sedimentary layers and structures clearly reflects separate stages of deposition (Wells *et al.*, 1984; Reed, 2003). As a consequence, any differences in faunal composition associated with separate climatic regimes preserved by the Naracoorte Cave deposits studied by Moriarty *et al.* (2000) were obscured by considering the assemblages as single depositional units.

Table 2.2 Total species richness (number of species), fossil sample size, volume of sediment excavated to obtain fossil sample and age of fossil faunas of six Middle to Late Pleistocene deposits of the NCWHA as reported by Moriarty *et al.* (2000). NISP = number of identified specimens. NB. The ages of Grant Hall and Cathedral Cave Fossil Chamber were refined by Macken *et al.* (2011) and Prideaux *et al.* (2007), respectively.

	Victoria Fossil Cave					**Cathedral Cave**
	Main Fossil Chamber	Starburst Chamber Pit A (Lower fan)	Starburst Chamber Pit A (Upper fan)	Starburst Chamber Pit B (Cone)	Grant Hall	Fossil Chamber
Total Species Richness	108	1	8	5	24	24
NISP	5200	Unknown	unknown	unknown	unknown	unknown
Volume (approx.)	$138 m^3$	$2 m^3$	$0.40 m^3$	$0.6 m^3$	unknown	$0.75 m^3$
Age (approx.)	>213 kyr BP	350–327 and 280–190 kyr BP			130–120 kyr BP	279–159 kyr BP

In a recent review, Bennington *et al.* (2009) noted that a critical issue of concern for palaeoecologists is how multi-scaled ecological data provided by natural archives can be integrated to improve knowledge of past ecological change and better contribute to the prediction of future ecosystem changes. The review posed a range of questions and issues for palaeoecologists to consider when designing and undertaking research, including the following: (1) how are ecological patterns dependent upon the temporal scales of palaeoecological assemblages, and (2) at what temporal scales can individual fossils be considered to have been members of the same palaeocommunity and to have inhabited the same habitats?

To address these questions, Bennington *et al.* (2009) recommended that palaeoecologists report the stratigraphy of deposits to clearly show how temporally independent samples were identified. They also recommended that chronological data be collected and presented to show the age and temporal resolution of the individual samples, the position of potential gaps in the record and the overall temporal range of the sequence.

As noted earlier, cave deposits are considered to be less than ideal for palaeoecological studies. This is because of the general difficulties associated with dating depositional sequences and the long-time averaging of these deposits when compared with other palaeoecological sites such as lake beds or marine sediments (Lowe and Walker, 1997; Forbes *et al.*, 2007). Cave deposits and other vertebrate fossil assemblages also generally provide unevenly sampled faunas through time, such that time-averaging varies between units or layers within an assemblage, as well as between sites (Roy *et al.*, 1996). Despite these limitations, the majority of research into the fossil deposits of the NCWHA has involved extensive sedimentary, stratigraphic and chronological analyses. While the scale of time-averaging cannot be standardised across or within a deposit, the use of these techniques fulfils many of the recommendations by Bennington *et al.* (2009) and have been critical in enabling more robust analysis of faunal change with time (e.g., Forbes and Bestland, 2007; Prideaux *et al.*, 2007; Darrénougué *et al.*, 2009; Macken *et al.*, 2011).

Sample-size

Differences in sampling effort also strongly influenced the comparative data presented by Moriarty *et al.* (2000), challenging both the technique used to assess faunal change with time and the robustness of their conclusions based on the available data. Of particular concern are the different species richness values presented by Moriarty *et al.* (2000) which ranged from 108 species for Main Fossil Chamber, VFC, to only one for the lower fan of Spring Chamber, VFC (Table 2.2). The second highest species richness value was 24, reported for Fossil Chamber, Cathedral Cave and Grant Hall, VFC (Moriarty *et al.*, 2000). The magnitude of difference between these species richness values questions the validity of their conclusion that faunal composition did not differ significantly between these deposits, for how can composition be judged to be the same when comparing 108 species against 24 or one?

The difference in species richness values of these assemblages clearly reflects variation in sampling effort at the time of the original study (Table 2.2). Moriarty *et al.* (2000) acknowledged this limitation, stating that the small sample sizes from each site except Main Fossil Chamber, VFC “preclude any statistical analysis of faunas” (p. 140). Although sample size was only reported for one assemblage, the difference in excavation volume for each deposit suggests that the fossil samples were of vastly different sizes (Table 2.2). A similar issue was identified in the analysis of Graham *et al.* (1996), where sampling variation was suggested to have biased the raw presence/absence data used to assess change in the geographic distribution of North American vertebrates over the Quaternary (Alroy, 1999).

Analytical standardisation techniques are commonly applied to fossil occurrence data to account for variation in sample size between deposits and depositional units within single sites. Techniques include analytic rarefaction, where the richness of different depositional units is estimated based on a standard sample size, usually the smallest sample size of the units within a deposit (e.g., Prideaux *et al.*, 2007). Hammer and Harper (2006) provide a brief discussion of other mathematical richness estimation techniques including first and second order jack-knife and bootstrapping.

Bootstrapping has been used on small mammal assemblages for comparing species richness through time and between different types of samples (e.g., Blois *et al.*, 2010; Terry, 2010a; b). The technique involves re-sampling with replacement from an assemblage until a pre-determined number of sub-samples have been generated, often 1000 (Chernick, 2008). Using bootstrapping, confidence limits on statistics (e.g., species richness) measured from an assemblage may be generated (e.g., Blois *et al*., 2010). Bootstrapping may re-sample an assemblage to either the original sample size or a predetermined sample size, often corresponding to the smallest sample size measured from each layer within a stratigraphic sequence.

Sample size can also influence the representativeness of a fossil sample in relation to the full range of species preserved in a depositional setting. The representativeness of a fossil sample is also commonly assessed using analytic rarefaction. In this procedure, it is assumed that as the slope of the cumulative species curve approaches zero, the probability of additional specimens representing new species declines to a point where further excavation effort is unlikely to dramatically increase species richness. For example, Laslett (2006) reported specimen counts ranging from a minimum of 58 to a maximum of 1777 from the five units analysed from Blanche Cave. A rarefaction curve constructed by Laslett (2006) for the whole deposit suggested that a minimum sample of 1200 specimens adequately sampled the true richness of species preserved in the deposit. When this figure was applied to the individual units, only two were expected to have adequate specimens to accurately represent species richness (Laslett, 2006).

Defining natural variation and resilience in palaeoecological systems

Resilience of Naracoorte mammal faunas to past climate change

As shown in the faunal analyses of Prideaux *et al.* (2007) and Macken *et al.* (2012), the Moriarty *et al.* (2000) model of 'no faunal change' for the Naracoorte Cave faunas was strongly influenced by sampling effects. However, based on the lack of evidence for local faunal extinctions, Prideaux *et al.* (2007) argued that the Middle Pleistocene mammal faunas of south-eastern South Australia were resilient to Pleistocene climate change. While this conclusion has implications for understanding the drivers of megafaunal extinction in Australia, it is also significant from a broader ecological perspective.

Of particular interest is the observation that the abundances and/or presence/absence of individual mammal species did in fact fluctuate in response to Pleistocene climate change, but that this did not result in their extinction. This suggests that, despite climatic and environmental disturbances, faunal changes occurred within thresholds relating to the survival, reproduction, interspecific interactions and dispersal of populations.

As defined by Groffman *et al.* (2006), an ecological threshold represents either a point of abrupt change in an ecosystem "quality, property or phenomenon", or where small environmental changes cumulatively lead to large ecosystem responses (p. 1). In the case of the Naracoorte mammal faunas, the ecosystem property considered by Prideaux *et al.* (2007) was individual species persistence and/or survival through the Pleistocene. However, despite the long-term survival of individual species evident in the Naracoorte Cave assemblages, there is also evidence for palaeocommunity change. Of note is the decline in richness of small mammals in the palaeocommunity over the accumulation of Grant Hall and the lower overall richness of small mammals in this deposit when compared with both older and younger assemblages (Macken *et al.*, 2012; Table 2.1; Fig. 2.4c). These patterns suggest that the composition of the small mammal palaeocommunity was not stable throughout the Pleistocene and that the palaeocommunity as a whole may not have been resilient to climate change.

Natural variation/resilience framework

Increasingly, theoretical concepts of natural variation have been identified as a useful framework for evaluating change in palaeoecological assemblages (Hadly and Barnosky, 2009). Natural variation is defined as the normal range of fluctuations and trends in ecosystem attributes, condition and/or processes within an ecological system across space and time (Landres *et al.*, 1999). Biodiversity conservation and management strategies increasingly aim to manage for natural variation in ecosystems given the advantages of this approach when compared with more traditional management strategies that focus on a single steady-state. These advantages include greater cost-effectiveness and lack of reliance on a single pre-impact state that may or may not be well defined or relevant in the context of modern and future societal, ecological and climatic parameters (Landres *et al.*, 1999; Swetnam *et al.*, 1999).

Even more significant than these factors in explaining the increased attention on natural variation in ecological management is the relationship between natural variation and resilience. Natural variation provides an ecological ‘buffer,’ allowing ecosystems to undergo turnover and reorganise in response to external pressures, whilst maintaining ecological functions, structure, ecological connections and general character or type (Holling and Meffe, 1996; Folke *et al.*, 2004; Walker *et al.*, 2004).

As noted in the introduction, ‘resilience’ generally describes how much pressure or change an ecological system can withstand before it shifts to a new, alternative steady-state (Holling, 1996; Walker *et al.*, 2009). This definition contrasts with the concept of ‘engineering resilience’ which describes how quickly a system recovers following a disturbance event (Holling, 1996). This latter definition is based on an assumption that ecosystem equilibrium occurs through the persistence of a single steady-state; that is, a system returns to its pre-disturbance condition following a period of change.

While the former definition is generally considered most suitable for describing resilience in ecological systems, resilience is very difficult to quantify (North and Stein, 2012). This difficulty arises in part because more complex definitions of resilience incorporate aspects of both ecological and engineering resilience; that is, change and reorganisation coupled with maintenance of “essentially the same ecosystem function, structure, identity and feedbacks” (Walker *et al.*, 2004; p1).

Inherent within any concept of resilience are thresholds which represent the limits of change that an ecological system can undergo before its fundamental properties are shifted to a new state or regime. Thus, critical questions that emerge for quantifying the resilience of a system include: (a) how much change can an ecological system absorb or experience before ecosystem functions, structure, identity and feedbacks are no longer maintained? (b) If these properties do change, how are they judged to be either “essentially the same” (Walker *et al.*, 2004, p.1), or significantly different, and (c) can a system be considered resilient if only its identity changes, but function and structure are maintained?

While these questions are generally posed in relation to the management of contemporary ecosystems, they are relevant to the study of faunal and other ecological and environmental changes observed in palaeoecological assemblages. DiMichele *et al.* (2004) noted there are no clear guidelines from which to assess if changes observed in palaeoecological assemblages represent significant palaeocommunity change. In other words, how is significant palaeocommunity change or reorganisation defined and when do such changes represent a breach of resilience thresholds?

Numeric and ecological hierarchy of natural variation

The ecological and numeric hierarchies of Rahel (1990) and Bennington and Bambach (1996) may provide a useful framework for the assessment of natural variation and resilience across different scales in palaeoecological archives. They are based on common metrics used to define the character and condition of ecological and palaeoecological systems (e.g., species richness, composition and relative abundance).

As noted by Hadly and Barnosky (2009), species richness is correlated with the productivity, disturbance regime and heterogeneity of an ecological community, with fluctuations in the number of species within an assemblage reflecting change in ecological niches and their connections. The composition of a community reflects the character of those niches, while species abundances are a function of life history traits, interspecific interactions and the relationship of individual species and individuals to local abiotic conditions (Hadly and Barnosky, 2009).

Variation in these metrics operates across an ecological hierarchy and can be used to contextualise changes in the relative abundances of individual species against whole community level variation (Rahel, 1990; Fig. 2.5). For example, presence/absence data (species composition) provides the lowest resolution of long-term community persistence: communities are least stable (highly variable) when the presence/absence of species is unpredictable over time (Fig. 2.5d). By comparison, a community may be considered more stable if only the abundances of species vary with time but the overall composition remains the same (Fig. 2.5c), with the greatest stability occurring when species abundances do not change at all (Fig. 2.5a). Interestingly, Magurran and Henderson (2010) suggested that variation in the abundances of individual species may in fact contribute to the overall stability of the palaeocommunity, highlighting a complex interplay between variation and persistence across scales.

The use of species abundance data in palaeoecological analyses is advocated by Vermeji and Herbert (2004) for their ability to provide information about the ecological ‘success’ of a species and as a means of linking species traits to environmental and evolutional processes. They also argue that abundance data can reveal palaeocommunity change that may not be revealed at other numeric scales (such as composition), as is evident in the fossil assemblages of the NCWHA. Species level changes in palaeoecological records also indicate those species that have been most sensitive to past climate change (Dietl and Flessa, 2010).

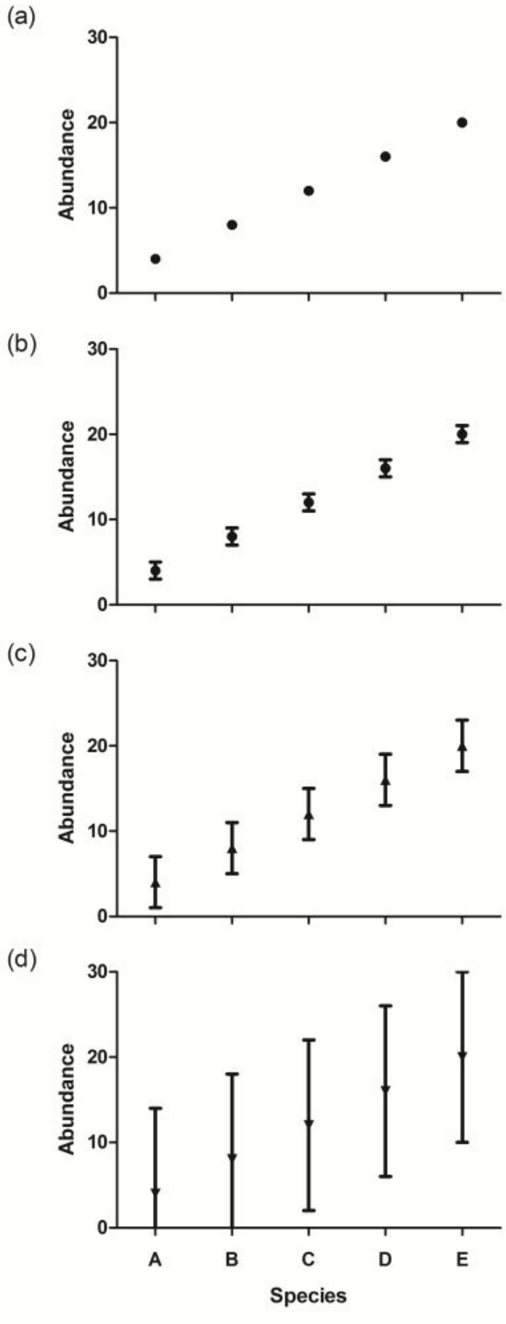


Figure 2.5 Numeric hierarchy of stability demonstrated in a hypothetical assemblage of five species (A–E). (a) Species' abundances are highly stable (no variation). (b) There is variation in species abundances, but their rank-order stays the same. (c) Variation in species' abundances leads to variation in the rank-order of the species. (d) Species' abundances are so variable that even the presence/absence of species' is unpredictable. Modified from Rahel (1990).

Based on their review of vertebrate responses to climate change from a range of fossil localities, Hadly and Barnosky (2009) suggested that changes in the relative abundances of species are the “early warning signal” of environmental effects on species (p. 47). However, they also argued that changes in species relative abundance alone do not constitute significant change from a normal baseline of variation operating at the species level within a palaeocommunity (Hadly and Barnosky, 2009). Rather, based on evidence from fossil and modern assemblages, they suggested that variation in the relative abundances of species is the normal type of response to climate change and other disturbances across different temporal scales.

When then, if ever, are changes in species abundances in fossil assemblages ecologically significant in terms of assessing faunal change through time? The first step to addressing this question may be to assess the statistical significance of change in these ecological variables, as according to Bennington and Bambach (1996), after site-effects are accounted for, if two samples have statistically different species abundance distributions then they may be assumed to have come from different palaeocommunity types (Table 2.3). In this context, palaeocommunity types are separated on the basis of having similar, but not statistically identical species abundance distributions (Bennington and Bambach, 1996). Within these definitions, it is acknowledged that given the extent of time-averaging, biasing and information loss through taphonomic processes in fossil assemblages, a local palaeocommunity is not equivalent to a local community observed in neontolgoical studies where contemporaneity can be established.

However, the numeric hierarchy of Rahel (1990) and discussions of Hadly and Barnosky (2009) caution that the relative abundances of species can be highly variable with time and may not necessary reflect ecologically significant change between local palaeocommunities. An intermediate level within Rahel’s (1990) numeric hierarchy is rank-order abundance. A commonly used measure of abundance ranks is Spearman’s Rho. This metric has been used in the analysis of fossil assemblages, particularly to assess the fidelity of live-dead assemblages (e.g., Kidwell 2001; Terry 2010a; b). It is also used in a wide range of ecological studies (e.g., Rabonsky *et al.*, 2011) and has been suggested as a useful measure for detecting early signs of change in ecological assemblages (Magurran and Henderson 2010).

Of particular interest then for the fossil assemblages of the Naracoorte Caves is whether the relative abundance of species varied sufficiently to lead to a new rank-order abundance structure. An ecological driver of stability in abundance ranks may be synchrony of changes in the relative abundance of species within a community in response to disturbance, reflecting similar responses of individual species to environmental or climatic changes (Rahel, 1990). However, based on the observed fluctuations in the relative abundances of species in assemblages of the Naracoorte Caves (e.g., Macken *et al*., 2012), synchronous responses are very rare. For example, while some species demonstrated similar patterns of change in response to transitions from relatively dry to relatively wet conditions and visa-versa between the Cathedral Cave and Grant Hall assemblages (Macken *et al.,* 2012), not all species with similar ecological characteristics (e.g., dietary and habitat preferences) had the same pattern of response within the two sites. Further, some species demonstrated different responses to the climate changes between the two sites (Prideaux *et al.,* 2007; Macken *et al.,* 2012). These divergent patterns in species abundance are consistent with evidence elsewhere for individualistic species responses to climate change (Stewart, 2008). They also likely reflect the influence of other factors on species responses, including a combination of environmental and climatic thresholds and community and population dynamics associated with intrinsic responses described by Williams *et al.* (2011).

Intrinsic responses are those changes associated with non-linear ecological processes, thresholds and tipping points and are characterised by variable timings and rates of change among species and localities. Extrinsic ecological changes are driven by external, abrupt climate changes and are characterised by synchronous biotic responses within and between localities (Williams *et al.*, 2011). While extrinsic responses are clearly important in revealing the drivers and general responses to change operating at large temporal and spatial scales, intrinsic responses are expected to reveal more about the past resilience of ecosystems and the range of variation exhibited by different ecosystem components in response to disturbances operating across spatial and temporal scales.

Intrinsic responses are expected to vary amongst sites not only in timing and rate but also in the extent and magnitude of change across ecosystem components (Williams *et al*., 2011). Within the resilience framework established by Cumming *et al.* (2005), ecosystem components are defined as the functional traits or identity of species within an ecosystem or community and the relationships between them (e.g., predator-prey interactions). Thus, patterns of change, and the inferred ecological significance of such change is highly dependent upon what components of an ecosystem are measured in palaeoecological analyses. As noted earlier, the focus for this thesis is the identity of the palaeocommunity defined by a hierarchy of taxonomy based diversity measures, rather than functional diversity.

Table 2.3 Palaeocommunity definitions described by Bennington and Bambach (1996).

Term	Definition
Local palaeocommunity	Fossil assemblage associated with samples from a single stratigraphic unit or phase.
Palaeocommunity	Statistically indistinguishable local palaeocommunities.
Palaeocommunity type	Similar but not statistically identical local palaeocommunities.

Forward projection of trends: challenges and potential

Palaeoecological study of faunal changes in assemblages from the Naracoorte Caves shows that not only does temporal scale and sample size strongly influence observed trends, but that numerical scales influence the extent and inferred ecological significance of variation detected with time. These sampling effects in turn influence our ability to predict (and test) the mechanisms underlying such variation.

Fluctuation in the relative abundances of individual species indicates that variation in individual survival, range contraction/expansion and local extinction/recolonisation patterns affected local populations and species, without broad scale community turnover (Prideaux *et al*., 2007; Macken 2009). These patterns reinforce the recommendation of Rahel (1990) that community patterns be analysed at more than one scale to enable the detection of different factors that structure communities.

Insights into the range, scale and types of ecological responses to past climate change gained from fossil assemblages may be used to address the questions identified at the start of this review. These were (a) how do ecosystems respond in the short and long-term to disturbance (including climate change), (b) what is the natural range of variability expressed by an ecosystem at different spatial, temporal and ecological scales and (c) what are the limits of resilience, or thresholds beyond which an ecosystem changes state? Biodiversity conservation strategies that develop the adaptive and resilience capacity of communities and species to future climate change may be enhanced by knowledge that addresses these questions.

As recognised by Lyman (2006), collaborations between ecology, palaeontology and conservation biology are imperative for biodiversity conservation in light of the threats posed by future climate change on species, communities and ecosystems. By focussing on the data needs of resource managers and using relatively simple, easily interpreted metrics, palaeontological studies may overcome some of the challenges associated with the application of past histories to biodiversity conservation today. However, Swetnam *et al.* (1999) warn that past trends cannot be directly extrapolated to present or future conditions. Rather, they argue that long-term perspectives can guide the development and testing of predictive models and generate hypotheses that can be tested. Further, they can inform biodiversity managers about the limits or thresholds inherent in an ecological and environmental setting, and may provide a context for current landscape conditions. According to Swetnam *et al.* (1999), we must “decide if past mechanisms of change and the dynamical processes involved are desirable for today’s landscapes” (p. 1202). This requires an acknowledgement of the limitations of ecosystems; we can’t exceed these without causing system collapse (Swetnam *et al.*, 1999). Patterns of natural variation in small mammal palaeocommunity composition and structure through the last glacial cycle provide a unique opportunity to examine and identify these limits or constraints across time scales far exceeding those available to traditional ecological studies.

3. Chronology and stratigraphy of the Wet Cave vertebrate fossil deposit, Naracoorte, and relationship to paleoclimatic conditions of the Last Glacial Cycle in south-eastern Australia

Citation

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Contribution of Authors

Amy Macken:

- Devised and planned the project.
- Compiled and assessed the data on the Wet Cave stratigraphy and sediments presented in the paper and identified stratigraphic units for the deposit based on these data.
- Sourced grant of $1000.00 from the Linnean Society of New South Wales to support costs associated with additional radiocarbon dating for the site.
- Selected and prepared additional charcoal samples for radiocarbon dating.
- Reviewed the palaeoclimatic literature presented in the manuscript.
- Prepared the manuscript for publication.

Matthew McDowell:

- Provided the original descriptions of the Wet Cave sediments and the stratigraphic diagram of sedimentary layers in his Masters thesis.
- Provided comments on the manuscript.

David Bartholomeusz:

- Led the excavation of the Wet Cave site in 1997 and 1998 and provided sedimentary descriptions and photographs of the exposed profile in his field note books.
- Provided comments on the manuscript.

Elizabeth Reed:

- Provided funding for the additional radiocarbon dating.
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Abstract

The Wet Cave vertebrate fossil deposit of the Naracoorte Caves in south-eastern South Australia contains a rich and diverse assemblage of small mammal fauna known to span the Upper Pleistocene–Holocene. Here, we describe five previously unidentified *in situ* units (A, B, C, E and F) and one likely reworked unit (D) in the Wet Cave sedimentary profile, which are correlated with paleoclimatic conditions associated with the Last Glacial Cycle. Additional radiocarbon dates presented here provide a finer temporal resolution for the upper sections of the sequence than previously available and reveal rapid deposition of polished quartz sands laminated with brown silts during the last glacial maximum (LGM). Change in sediment type and depositional processes are dated from 16.8–16.4 k cal y BP and are associated with the onset of deglaciation. The characteristics of the five *in situ* depositional units are similar to those identified from the contemporaneous fossil and sedimentary sequence of Blanche Cave 3rd Chamber, located approximately 400 m away, reflecting interactions between paleoclimate, sediment mobility and deposition at this locality. Greater variation is evident between the Wet Cave sedimentary profile and the inner chamber of Robertson Cave, located approximately 6 km away and shows that local processes and cave structure exerted some control on sediment accumulation. Paleoclimatic inferences from the depositional sequence of Wet Cave are broadly consistent with those inferred from regional landforms for south-eastern Australia but provide a local signal more suitable for cross-correlation of the fossil faunas. In particular, the Wet Cave sequence suggests that local conditions were relatively stable in the lead up to the LGM despite fluctuation in both local and regional effective precipitation. Sedimentary units associated with the post LGM deglaciation are characterised by alternating sand and sandy-silt layers, assumed to reflect the impact of enhanced seasonality and/or climatic fluctuation leading towards the Holocene.

Keywords cave sediments, Last Glacial Cycle, Naracoorte Caves, paleoclimate, radiocarbon dating, stratigraphy

Introduction

The Upper Pleistocene–Holocene sedimentary and fossil sequences of Wet Cave (5U10, 11) were first studied by McDowell (2001), following excavation of the site in 1997 and 1998. Re-evaluation of the Wet Cave small mammal fauna (body mass ≤2 kg) and comparison with more recently excavated, contemporaneous deposits of the Naracoorte Caves World Heritage Area (NCWHA), aims to elucidate patterns of natural variability in small mammal communities through the Upper Pleistocene–Holocene. However, the capacity for such comparison is limited by the lack of identified and described stratigraphic division of the Wet Cave sequence and by temporal gaps in the current chronology, which restricts the resolution at which the fossil faunas may be evaluated.

Following severe storms and high rainfalls in December, 2010, the excavated section of the Wet Cave deposit was completely buried by flood sediments. As a result, no further sedimentary sampling from the section has been possible. Analysis of sediments from the Wet Cave excavation site by McDowell (2001) and Forbes and Bestland (2006, 2007) provides the only available data on the sedimentary sequence for the site. By collating these data, we provide a refined stratigraphic framework for the Wet Cave fossil assemblage. Backup charcoal samples collected at the time of original sampling were available for radiocarbon dating, enabling the chronology of the sequence to be more finely resolved.

Here, we review the stratigraphy and chronology of the Wet Cave deposit to identify depositional units, which may be used in future examination of the faunal assemblage at a resolution that is consistent with major depositional episodes and for comparison of the paleoenvironmental history represented in Wet Cave with other Naracoorte Cave deposits of similar age. Presentation of additional radiocarbon ages for the Wet Cave sequence provides a finer chronology than previously available and improves the resolution at which (a) the depositional history of the site can be assessed and (b) other caves deposits of similar age may be compared. Detailed evaluation of Upper Pleistocene–Holocene climates and the paleoenvironmental signals interpreted from Wet Cave also enhances our understanding of the Last Glacial Cycle by identifying local variation in the timing, character and environmental impacts of changes in available moisture, temperature and vegetation across south-eastern Australia.

Site Description, Excavation and Original Sedimentary Analysis

Geological Setting

Wet Cave, also referred to as Tomato-Stick Cave, is one of 26 known caves in the NCWHA, located 12 km southeast of Naracoorte in south-eastern South Australia (Figure 3.1a). These caves are located in an uplifted section of the Naracoorte member of the Gambier Limestone, a fossiliferous marine carbonate formation of Oligocene–Miocene age (Ludbrook, 1961). Uplift of this plateau is associated with movement of the Kanawinka Fault, which controlled the direction and distribution of joints in the caves (Sprigg, 1952). The caves were formed largely by phreatic dissolution of the Gambier Limestone and structural processes (Wells *et al.,* 1984; White, 2005). Overlying the Gambier Limestone is a sequence of Pleistocene-aged dune facies known as the Bridgewater Formation. The oldest of these facies, the East Naracoorte Ridge, overlies the phreatic caves system of the NCWHA and is dated to 935 ± 178 ka (Murray-Wallace *et al.,* 2001). Dating of clastic sediments, bone material and speleothems indicates that the Naracoorte caves first opened to the surface during the Middle Pleistocene, *ca* 528 ka (Ayliffe and Veeh, 1988; Ayliffe *et al.,* 1998; Grün *et al.,* 2001; Prideaux *et al.,* 2007).

Excavation

Two roof collapse window entrances (5U10 and 5U11) of approximately 8 m diameter provide access to Wet Cave from the surface. The fossil excavation was located on the south-eastern edge of the sediment cone in the chamber associated with entrance 5U10 (140°47’50.59”E, –37°02’11.634”S; Figure 3.1b).

The sedimentary sequence was excavated across two separate pits, measuring 1 m^2, identified as Pit 1 (lower) and Pit 2 (upper) (McDowell, 2001). A steel peg positioned in a corner of Pit 2 at the top of the section was allocated as the primary datum. Each 1 m^2 pit was divided into four quadrants (A–D) measuring 0.25 m^2.

Pit 2 was excavated from 0 to –110 cm and Pit 1 from –110 to –350 cm relative to the primary datum (Figure 3.2). The sequence was excavated as quadrants within individual sedimentary layers identified by visual observations of the sediments. These were labelled with the cave number (5U10), pit number (1 or 2), quadrant (A–D), layer number (Pit 2: 1–6; Pit 1: 5–7) and excavation interval (minimum 1 to maximum 12), e.g., U10 1A:6/8 = Wet cave, pit 1, quadrant A, layer 6, interval 8 (Figure 3.2; McDowell, 2001). The depth of each interval was measured during excavation using a steel rule aligned to a line level and plumb bob running from the datum down the centre of each pit.

Excavation was largely conducted using trowels and brushes, with all material removed from the site in labelled bags and subsequently wet screened. Larger fossil specimens were excavated *in situ*. Some sections were excavated as blocks of 2.5 cm^3 due to high clay content. During excavation, a 2 kg bulk sample of sediment from each excavated interval was collected. Unfortunately, these bags cannot be located for further sedimentary analysis. However, McDowell (2001) and notes recorded on data sheets during excavation provide detailed descriptions of the sediments, which are compiled here.

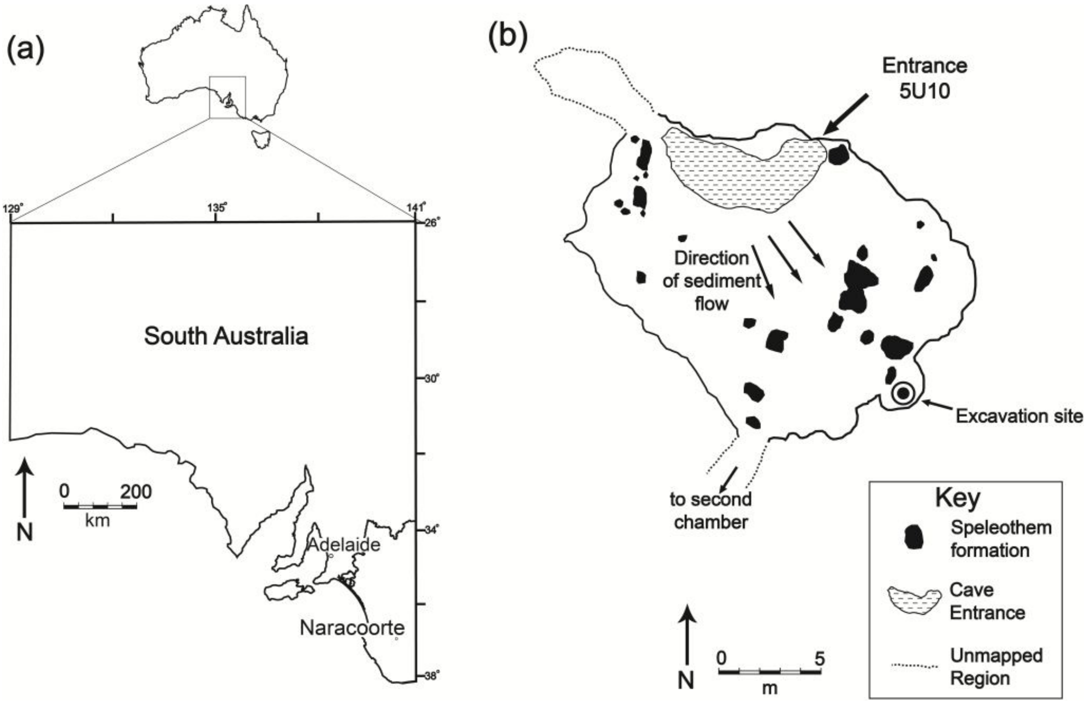

Figure 3.1 (a) Location of Naracoorte in south-eastern South Australia. The Naracoorte Caves World Heritage Area is situated 12 km south east of Naracoorte. (b) Map of Wet Cave (5U10 entrance chamber), modified from Cave Exploration Group of South Australia map CEG 394 and McDowell (2001).

Sedimentary Analysis

Sedimentary characteristics measured by McDowell (2001) included grain size, sorting and shape using a standard sand gauge. Sediment colour was determined from undried sediment samples using a Munsell soil colour chart (McDowell, 2001). These characteristics were measured from each excavation layer of the exposed section and from 50 mm diameter sediment cores taken at 1 m intervals along the sediment cone and fan. The samples were used to construct a generalised diagram of the sub-surface stratigraphy of the entrance chamber, presented in McDowell (2001). Forbes and Bestland (2006, 2007) measured grain size distribution, strontium and stable nitrogen isotopes, sediment mineralogy and major and trace elemental geochemistry for seven sedimentary samples collected from the Wet Cave profile (Table B.1 Appendix B).

The Wet Cave sediments were described as brown organic-rich silty sands and reddish silts by Forbes and Bestland (2007); although, homogenous sand horizons were present (McDowell, 2001; Forbes and Bestland, 2007). The Wet Cave sequence was characterised by well layered bands of these sediment types, which ranged from a few centimetres to greater than 40 cm thick (Figure 3.2; McDowell, 2001). The presence of herringbone-like bedding planes, channel-fill and slump structures indicates that some layers of sediment were transported by water into the deposit from the sediment cone (McDowell, 2001).

Methods

Stratigraphic sequence

The sedimentary profile and sediment descriptions for Wet Cave from McDowell (2001) and Forbes and Bestland (2006, 2007) were evaluated to identify sections of the profile that represented discrete depositional units. This was based on the general principles of sedimentary geology such that, (1) changes in sediment colour through the sequence may correspond to different sediment types, and thus, sedimentary input sources, accumulation mode, depositional processes and/or fluctuation of the water table, and (2) the location of bedding planes in the stratigraphic profile likely represent breaks in deposition or boundaries between units.

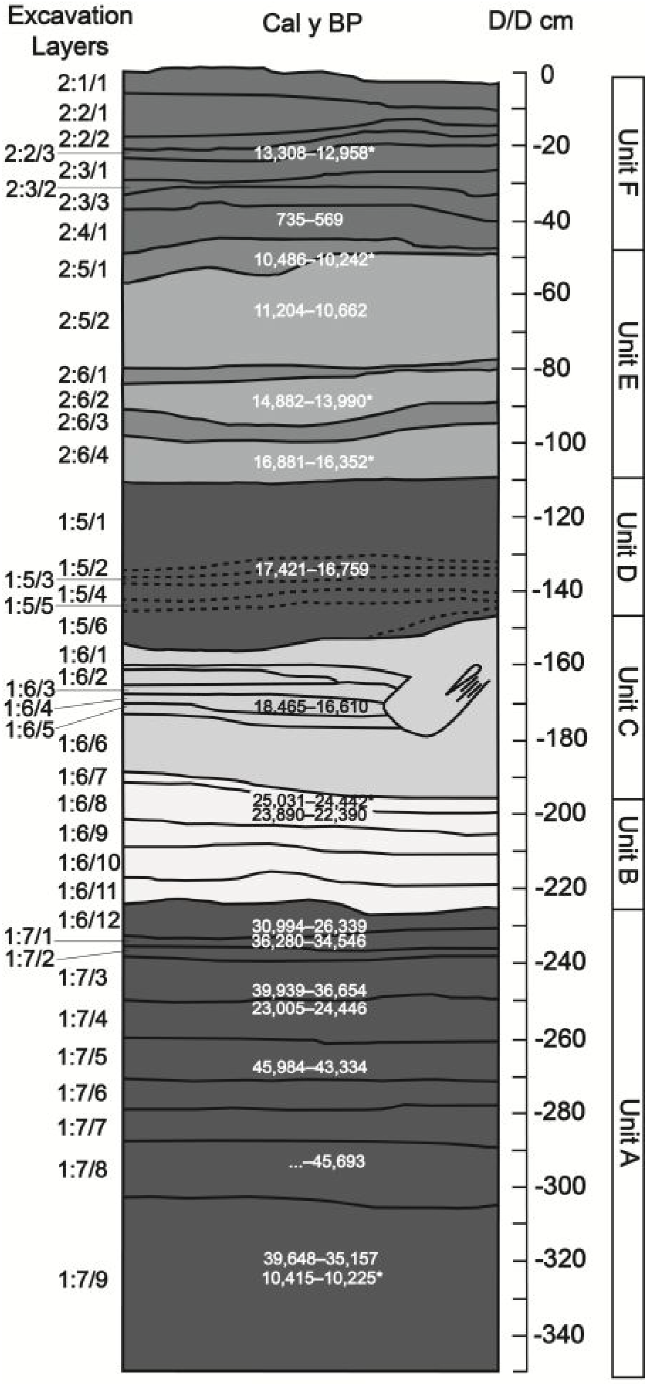

Figure 3.2 Stratigraphic section for Wet Cave, indicating sedimentary and excavation layers identified by author DNB and described by McDowell (2001). Calibrated radiocarbon dates based on the INTCAL09 database (Reimer *et al.,* 2009). Ages marked with an asterisk are new dates acquired in the current study; other ages are calibrated radiocarbon dates from Pate *et al.,* (2002, 2006). Sedimentary units defined in text. Profile modified from stratigraphic section produced by McDowell (2001).

Radiocarbon Dating

In addition to the 14 radiocarbon ages obtained and reported by Pate *et al.*, (2002, 2006; Table 3.1), six additional charcoal samples were selected for further dating of the site. The additional samples were picked from backup samples sorted from bulk material excavated during the original work on the deposit. These samples had been stored since their collection in labelled vials in the Flinders University Palaeontology Laboratory at the Naracoorte Caves National Park. Samples for analysis in the current study were selected from excavation intervals for which there were no existing dates and which would enable greater refinement of the depositional chronology.

Samples were analysed using AMS radiocarbon dating by Beta Analytic, Florida, USA, using standard acid/alkali/acid pre-treatment. The conventional radiocarbon ages of these samples, and the original AMS radiocarbon dates measured for the site, were calibrated to calendar years BP in OxCal 4.1 (Bronk Ramsey, 2009a) using the INTCAL09 database (Reimer *et al.*, 2009).

Table 3.1 Radiocarbon chronology for the Wet Cave stratigraphic sequence. Calibrated ages represent calendar years BP, based on the INTCAL09 database (Reimer *et al.* 2009) and calibrated in OxCal4.1 (Bronk Ramsey 2009a). 5U10- sample codes correspond to dates acquired in the current study. WeC samples are from Pate *et al.* (2002, 2006).

Sample ID	AMS laboratory ID	Depth (cm)	Unit	C mass (µg)	^{14}C age	1σ	Cal y BP (95.4%)
5U10-6	BETA-298177	-21.5 to -24 cm	F	4600	11,260	60	13,308 – 12,958
WeC36	OZE 539	-41		2570	740	40	735 – 569
5U10-5	BETA-298176	-52 to -60	E	2000	9,180	40	10,486 – 10,242
WeC1	OZD 284	-64		1770	9,590	100	11,204 – 10,662
5U10-4	BETA-298175	-87 to -94		4000	12,310	50	14,882 – 13,990
5U10-3	BETA-298174	-100 to -110		2200	13,470	50	16,881 – 16,352
WeC4	OZD 504	-134	D	1320	13,920	130	17,421 – 16,759
WeC33*	OZE 541	-170	C	12	14,150	350	18,465 – 16,610
5U10-2	BETA-298173	-187 to -192	B	2000	20,750	90	25,031 – 24,442
WeC32	OZE 536	-199		120	19,400	300	23,890 – 22,390
WeC10	OZD 292	-223	A	100	23,850	1020	30,944 – 26,339
WeC25	OZD 714	-234		1380	30,500	400	36,280 – 34,546
WeC21	OZD 715	-249		350	33,400	650	39,939 – 36,654
WeC23[*]	OZD 721	-252		20	23,400	1600	23,005 – 24,446
WeC27	OZD 717	-269		1950	40,900	850	45,984 – 43,334
WeC12[*]	OZD 291[^]	-275		70	>29,000		
WeC35	OZE 538	-276		1360	45,200	1800	... – 45,693
5U10-1	BETA-298172	-305 to -350		2200	9,140	40	10,415 – 10,225
WeC30	OZD 724	-320		200	32,600	900	39,648 – 35,157
WeC16	OZD 506	-358		1640	>45,000[!]		

[*] low extracted carbon values based on <100 µg threshold.

[^] AMS laboratory code reported by Pate *et al*. (2006) as OZE. ANSTO reports indicate that code was OZD (Q. Hua, pers. comm.)

[!] not distinguishable from background.

Results

Sedimentary Sequence and Chronology

Sedimentary characteristics through the Wet Cave sequence indicate that it was composed of a minimum of six sedimentary units (A to F) that are expected to represent separate episodes of sediment and bone input to the cave (Figure 3.2). Table B.1 (Appendix B) presents the collated data associated with the sediments and chronology of the sequence and are summarised in the descriptions below. In these following descriptions, the depths of each unit within the stratigraphic profile are reported as depths below the primary datum. The individual layers, which together compose each sedimentary unit, are also provided. Radiocarbon and calibrated ages for the Wet Cave sequence are presented in Table 3.1.

Unit A (–350 to –220 cm; Layers 1: 7/9 to 1: 6/12; >45 ka to 30.9–26.3 k Cal y BP)

Unit A is characterised by dark red, well sorted, sandy clays. The bottom 60 cm of the unit has a lower sand content than the upper section (McDowell, 2001); although, SiO_2 content is similar for the two sedimentary samples positioned at the top and bottom of the Unit (sediment samples W10 = 86 wt% and W15 = 91 wt%; Forbes and Bestland, 2007). By comparison, sample W10 has the highest Al_2O_3 and Fe_2O_3 contents of all samples (6.6 and 2.5 wt%), contrasting with W15, which contains only 2.6 and 1.3 wt% Al_2O_3 and Fe_2O_3, respectively. W15 is distinguished by a P_2O_5 content of 0.8 wt%, more than four times higher than any other sample. A CaO content for W15 of 1.4 wt% contrasts with W10 of only 0.1 wt% (Forbes and Bestland, 2007) and supports the observations of McDowell (2001) who noted that limestone fragments were common in the silt and clay layers at the bottom of the Wet Cave sequence, likely the result of roof-fall and fretting from the cave walls. This suggests that deposition of the lower unit was relatively slow and is supported by the radiocarbon chronology for this unit, which spans at least 15,000 years (Table 3.1).

Despite the geochemical differences between the samples from Unit A, the grain size distributions are similar (Forbes and Bestland, 2007) and reflect a higher coarse to fine silt fraction when compared with samples from higher in the sequence, with the exception of Wp1d (depth –40 cm). However, this sample has a higher medium to fine sand fraction than the samples from Unit A, differentiating it from the lower sediments.

The mineralogical composition of sedimentary sample W15 (depth –335 cm) shows that sediments at the bottom of Unit A are composed of 65 vol% clay minerals and 27 vol% quartz, contrasting with samples W2 and Wp1d from Units C and F which contain 99 and 75 vol% quartz, respectively (Forbes and Bestland, 2007).

One of the additional radiocarbon ages obtained in this study suggests that Layer 1:7/9 (depth –305 to –350 cm) may be of Holocene age (Table 3.1). However, eight ages reported in Pate *et al.,* (2002, 2006) show that Unit A accumulated in the Upper Pleistocene. The anomalous age is probably the result of young charcoal being transported down slope during the paleontological excavation and is not considered to represent a significant reworking of younger material to the bottom layer of the sequence. The lack of physical structures in the profile such as cut and fills, and the consistency of the sedimentary character through Unit A, supports this assumption.

Unit B (–187 to –220 cm; Layers 1: 6/7 to 1: 6/11; *ca* 26.3 to 25.0–24.4 k Cal y BP)

Unit B is characterised by yellow, moderately sorted, polished quartz sands (McDowell, 2001), bounded by bands of brown clayey sands. Samples W4 and W8 have similar grain size distributions, which vary from other samples being composed of ~ 56 and 53 vol% very fine sand to coarse silts, respectively (Forbes and Bestland, 2007). SiO_2, Al_2O_3 and Fe_2O_3 contents are similar in these samples, while the concentrations of Zr and Y are identical (Forbes and Bestland, 2007), supporting the interpretation that they are associated with a single depositional unit.

Unit C (–150 to –187 cm; Layers 1: 6/1 to 1: 6/6; *ca* 24.4 to *ca* 18.5–16.6 K Cal y BP)

Overlying Unit B, from depth –150 cm, is a thick layer of yellow, well sorted, rounded quartz sand, interspersed with dark brown silty lamina. The grain size distribution of sample W2 is unique from all other samples, containing ~ 53 vol% coarse to medium sands with a very low % of silt-sized fractions (Forbes and

Bestland, 2007). This sample is composed of 99 vol% quartz (Forbes and Bestland, 2007) and has the lowest Al_2O_3 and Fe_2O_3 contents of all samples (1.2 and 0.2 wt%, respectively). Strontium concentration is also lower in sample W2 than measured in samples from Units A and B, consistent with the positive correlation between Sr concentration and silt content observed through the Wet Cave profile (Forbes and Bestland, 2007).

Unit D (–110 to –150 cm; Layers 1: 5/1 to 1: 5/6)

Overlying Unit C are brown, poorly sorted and sub-rounded clayey sands. Due to the presence of megafauna fossil remains and similarity in sediment characteristics with the uppermost and lowermost sections of the profile, McDowell (2001) suggested that this section of the Wet Cave profile may have been be reworked. The calibrated age of 17.4–16.8 k cal y BP for charcoal from within this unit (at depth –134 cm) is broadly consistent with the chronology across the entire sequence but overlaps the age from Unit C, suggesting a more complex depositional history at this section of the profile.

Forbes and Bestland (2006) did not investigate the poorly sorted and sub-rounded clayey sands at the top of Pit 1 and instead described only the homogeneous sands identified here as Unit C as the “top 60 cm of the Lower Pit” (p. 136). However, the sedimentary descriptions and profile for Wet Cave provided by McDowell (2001; Figure 3.2; Table B.1 Appendix B) show that the homogeneous sands extended for a maximum of 45 cm through the sedimentary profile and clearly indicate the presence of sediments that are here labelled as Unit D.

Although the discrepancy between the two available descriptions of the Wet Cave sequence further challenges interpretation of the depositional history of Pit 1, a photograph of the sequence reported in McDowell (2001) clearly shows the dark sediments on top of the sands of Unit C. Descriptions of the profile prior to excavation also note the presence of this layer. It is possible that Forbes and Bestland (2006) ignored these sediments in their description of the Wet Cave sequence as they considered it to be a reworked layer as a result of slumping down the edge of the sedimentary cone. While this interpretation is considered here to be the most likely explanation for the presence and character of the sediments in Unit

D, we have classified and labelled them as a unit to enable a more comprehensive assessment of the depositional history of the site.

Unit E (–52 to –110 cm; layers 2: 5/1 to 2: 6/4; 16.9–16.3 to 10.5–10.2 k Cal y BP)

Unit E is characterised by alternating bands of light yellow brown and dark grey, moderately sorted, sub-rounded clayey and silty sands. The grain size distribution of sample Wp1h (depth –85 cm) indicates that the dark grey bands are composed of ~ 66 vol% very fine sands to coarse silts, contrasting with all other samples. The uppermost band of Unit E contains limestone gravel suggesting a depositional hiatus occurred from *ca* 10.5–10.2 k cal y BP.

Unit F (0 to –52 cm; Layers 2: 1/1 to 2: 4/1; Holocene age; containing some reworked material from Unit E)

The uppermost unit of the deposit was characterised by very dark grey to very dark brown, moderately sorted, sub-rounded silty sands, interposed with clean sandy lamina (McDowell, 2001). The boundary between Units E and F was indicated by the presence of flowstone at depth –39 to –52 cm (McDowell, 2001); although it is unknown if the flowstone was attached to the cave wall or free floating. The grain size distribution and geochemistry of sample Wp1d (depth –40 cm) contrasts with all other samples, indicating the unique composition of sediments at this part of the profile.

As noted by Forbes and Bestland (2006), the sample incorporated a milky white non-clastic material not observed elsewhere in the profile. Wp1d is characterised by very low SiO_2 content; although, this does not correlate with high Al_2O_3 and Fe_2O_3 contents as would be expected based on the strong linear correlation of these oxides with SiO_2 in the other samples. As noted by Forbes and Bestland (2006), high LOI (5.8 wt%) and CaO (11.9 wt%) contents in combination with a SO_3 content of 15.3 wt% suggests bat guano contributions to these sediments. The presence of bat guano at this section of the profile in addition to the flowstone indicates minimal allogenic inputs for a period of time prior to the deposition of the largely Holocene-aged dark brown silts and sub-rounded quartz laminations.

The calibrated radiocarbon age of a charcoal sample from layer 2:2/3 (depth –21.5 to –24 cm; 13.3–13.0 k cal y BP) suggests possible reworking of Pleistocene material from Unit E, likely via natural post-depositional processes and anthropogenic disturbance as evidenced by the presence of European artifacts (e.g., ceramic and glass shards) recovered from sediments in Pit 2.

Discussion

Relationship to other Upper Pleistocene sequences of the NCWHA

The Wet Cave sedimentary and fossil sequence spans *ca* 45,000 years, providing a record of the latter part of Last Glacial Cycle and Holocene for the NCWHA. While the deposit is broadly contemporaneous with the inner chamber deposit of Robertson Cave 5U17 (RCIC), located approximately 6 km south of Wet Cave, the Wet Cave sequence is more continuous and contains sediments dated to the last glacial maximum (LGM; *ca*, 20–17 ka; Barrows *et al.*, 2002) which are absent from RCIC (Forbes *et al.*, 2007). Radiocarbon ages for the 3rd chamber deposit in Blanche Cave 5U6 (BC3C), located within 400 m of Wet Cave, show that it also contains an LGM sequence, but does not contain *in situ* Holocene aged material (St Pierre *et al.*, 2012). Hence, Wet Cave is an important sequence for the NCWHA, providing a record of temporal periods not represented elsewhere and a sequence against which environmental and paleoclimatic signals interpreted from other Upper Pleistocene deposits may be compared.

The identification of six sedimentary units, including the reworked Unit D, within the Wet Cave sequence compares well with BC3C where five units, plus a reworked layer, were identified from a stratigraphic core (Darrénougué *et al.*, 2009). Available chronological data (Darrénougué *et al.*, 2009; St Pierre *et al.*, 2012) suggest that the analogous units identified in the two caves are broadly contemporaneous and may be used to assess local paleoenvironmental interpretations for the Upper Pleistocene based on the sediments from a single deposit (e.g., Darrénougué *et al.*, 2009).

Despite similarities in the character of the sedimentary units between the Wet Cave and BC3C deposits, the depth profiles of the sequences are quite different. This variation is expected to reflect local accumulation and post-depositional processes associated with the shape and structure of the cave chambers, entrances and surface topography. Such processes are expected to also account for the differences in the composition and temporal span of the sedimentary sequences of Wet Cave and RCIC, which is composed of only three units; Lower, Middle and Upper (Forbes *et al.,* 2007). These units share similar characteristics respectively with Units A, B and E of the Wet Cave sequence and their analogues in BC3C.

The sources of sediments that fill Wet Cave were first inferred by McDowell (2001) and later expanded by Forbes and Bestland (2007) using geochemical assessment of surficial and NCWHA sediments. Correlations identified by Forbes and Bestland (2007) generally supported the interpretations of McDowell (2001) and previous researchers (e.g., Wells *et al.,* 1984; Moriarty *et al.,* 2000). The proximal sources of clays and silts to the NCWHA deposits were found to be the medium–silt sized fractions of local Terra Rossa Soils, while sands were largely derived from the sandy A horizon of Coonawarra Terra Rossa Soils, and the medium-grained sands of the coastal barrier dunes, the Bridgewater Formation (Forbes and Bestland, 2007). It is interesting to note that there was poor geochemical correlation with the coarser-grained, calcite-rich component of the Bridgewater Formation. This suggests that carbonate grains and cement of the Bridgewater Formation had been dissolved leaving the medium-grained quartz component free to be transported around the landscape. Finally, the organic-rich sediments from Wet Cave Unit F were correlated with local Holocene podsols and/or anthropogenically disturbed soils (McDowell, 2001; Forbes and Bestland, 2007).

Paleoclimatic Context

McDowell (2001) summarised a depositional and environmental history for the NCWHA from the Wet and RCIC sequences. In light of the refined chronology and sedimentary sequence for Wet Cave, the paleoclimatic context of the deposit is re-examined here. This assessment also utilises more recent literature and proxy data for Upper Pleistocene climates in south-eastern Australia. The chronology for marine isotope stages follows Martinson *et al.,* (1987) with age refinements for MIS-2 and MIS-3 sub-stages from Thompson and Goldstein (2006).

Unit A: MIS-3

The calibrated radiocarbon chronology for Wet Cave indicates that the red-brown sandy clays of Unit A accumulated during MIS-3. On the basis of apparent full lake levels in the Willandra region of the south-eastern Australian Mallee, Darrénougué *et al.,* (2009) suggested that the MIS-3 aged unit of BC3C accumulated during a very wet climatic phase. However, a broader review of paleoclimatic data for this period suggests more temporally and spatially variable climatic conditions during the deposition of the red-brown clays in BC3C, and hence Wet Cave at this time.

Cool conditions relative to today during MIS-3 are evident in the global oxygen isotope SPECMAP curve which indicates a gradual decline in global temperatures prior to the LGM depression (Martinson *et al.*, 1987). Regional sea surface temperatures reconstructed using alketones in Murray Canyons core MD03-2607 also show cooler temperatures than today, and reveal frequent fluctuations within the range of *ca*. 12–17°C during MIS-3 (Lopes dos Santos *et al.,* 2012). Episodic high fluvial activity through the rivers of the Riverine Plain suggests pluvial conditions during MIS-3 in south-eastern Australia is consistent with this fluctuation, with two primary phases identified at *ca* 55–35 ka (Kerabury Phase) and *ca* 35–25 ka (Gum Creek Phase) (Page *et al.,* 1996, 2001). These phases of high episodic flows have been linked with periods of glaciation and periglacial conditions in the Snowy Mountains that feed the Riverine Plain; a lower snowline is expected to have increased the volume of winter snowpack and hence, snowmelt during spring (Barrows *et al.,* 2001). The episodic/seasonal nature of large flows of the Riverine Plain is evidenced by the near synchronous ages of source-bordering dunes, indicating deflation from the paleochannels during periods of low flow and higher evaporation (Page *et al.,* 2001; Kemp and Spooner, 2007).

A fine scale review of the water level record for the Willandra system shows that MIS-3 was characterised by fluctuation between phases of higher and lower lacustral activity (lake levels), correlated with lesser and greater pelletal clay dune building indicative of drier periods (Bowler, 1998; Bowler *et al.,* 2007, 2012). The early phase of sedimentation of Unit A into Wet Cave coincides with a pre-LGM glacial advance in Tasmania at *ca* 45–40 ka (Barrows *et al.,* 2002; Mackintosh *et al.,* 2006), coincident with transition from a phase of high water level at *ca* 44–42 ka to a dune building phase at 42–41 ka at Willandra (Bowler *et al.,* 2012). Fluctuation between lacustral and dune phases at Willandra is expected to have been controlled by a range of factors including regional hydrology (e.g., runoff and fluvial inputs; Page *et al.,* 2009; Bowler *et al.,* 2012) and local water budget (precipitation and evaporation; e.g., Kemp and Spooner, 2007). The Naracoorte Caves speleothem growth record, which provides a proxy for local effective precipitation, shows a hiatus in deposition at *ca* 40–35 ka, reflecting conditions of low effective moisture (Ayliffe *et al.,* 1998). These combined paleoclimatic indicators suggest that the early phase of deposition of Unit A into Wet Cave was coincident with regionally cool conditions and a relative decline in effective moisture at least when compared with the preceding pluvial phases of south-eastern Australia at *ca* 45–55 ka (Page *et al.,* 1996, 2001; Bowler *et al.,* 2012) and the relatively wet local conditions during MIS-5b–a (Ayliffe *et al.,* 1998).

Deposition of the upper sections of Unit A coincide with a phase of speleothem growth in the Naracoorte Caves from *ca* 35–20 ka (Ayliffe *et al.,* 1998), indicating increased effective moisture availability, consistent with both the pollen record from BC3C, which is composed of predominantly woody taxa for the period from *ca* 35–32 ka, and the continued pluvial conditions noted for south-eastern Australia (Page *et al.,* 1996, 2001; Darrénougué *et al.,* 2009). Despite glacial advance in the Snowy Mountains at *ca* 32 ka (Barrows *et al.,* 2001) and expansion of Antarctic sea ice at 32–25 ka (Williams *et al.,* 2009), more humid conditions in the later stages of MIS-3 are indicated for subtropical eastern Australia (Petherick *et al.,* 2008). In contrast, aeolian dune building in the Strzelecki and Tirari deserts at *ca* 35–32 ka and in the western Murray Basin at *ca* 38–18 ka suggests drier surface conditions further inland at this time (Fitzimmons *et al.,* 2007; Lomax *et al.,* 2011). Although the Willandra Lakes record remains highly variable through the later stages of MIS-3, a significant and sustained period of high lake level from *ca* 30–25 ka and 23–19 ka suggests high effective moisture towards the end of MIS-3 and early MIS-2 in south-eastern Australia. Synchronous thermo-luminescence ages for the Lachlan paleochannel (Ulgutherie system) and an adjacent source-bordering dune of 32 ka suggest that seasonal or episodic snowmelts and deflation from the paleochannels remained a feature of the Riverine fluvial system through the later stages of MIS-3 (Kemp and Spooner, 2007). However, Nanson *et al.,* (2003) suggested that peak flows in the Riverine were reduced in MIS-3 from MIS-5 levels. This suggests that lower evaporation, as a result of lower temperatures approaching the LGM, was the primary driver of sustained high lake levels at Willandra, although Chappell (1991) suggests increased runoff and precipitation remained important paleoclimatic features of this time.

Despite the apparent fluctuations in relative moisture availability and temperature during MIS-3 across south-eastern Australia, the sedimentary character of Unit A suggests relative stability in prevailing climatic conditions of the Naracoorte region from *ca* 45–25 ka. Local changes in hydrology reflected in the speleothem record do not appear to have significantly impacted the primary mode and source of the red-brown sandy clays into Wet Cave. Sandy laminations described by McDowell (2001) suggest short-term changes in the source and likely accumulation mode of sediments into Wet Cave during the accumulation of Unit A, although it is not expected that this reflects significant and sustained changes in the local climate.

Darrénougué *et al.,* (2009) suggested that the lower unit of red-brown sandy clays in BC3C were a mixture of aeolian and water transported material. In contrast, accumulation of the RCIC Lower Unit, which shares similar sedimentary characteristics with Unit A and BC3C Unit 1, has been attributed to airborne dust fluxes through the cave and from animal inhabitants (Forbes *et al.,* 2007). Water is not expected to have played a significant role in the deposition of the Lower Unit in RCIC, as indicated by the high concentration of water soluble minerals (Forbes *et al.,* 2007). In comparison to the thin laminations present in the BC3C profile, the thicker layers in Wet Cave Unit A suggests water was not a significant agent of sediment transport from the depositional cone to the excavation site during MIS-3. However, no confident assessment of the relative contribution of water *vs*. aeolian or dust deposition to Unit A can be made as the site is no longer available for further sedimentary analysis.

Unit B: MIS-2 and LGM

The well sorted and polished quartz sands of Unit B are temporally associated with the end of MIS-3 and at least the early stages of MIS-2. Dates for the LGM in Australia typically range from 22–17 ka, inferred from glacial advance in Tasmania at *ca,* 20–17 ka (Barrows *et al.,* 2002), minimum sea surface temperatures dated to, 20.5 ka (Barrows and Juggins, 2005) and a phase of dune building in the Tirari and Strzelecki deserts from *ca* 22–18 ka (Fitzimmons *et al.,* 2007). In contrast, Petherick *et al.,* (2008) suggest that the LGM in eastern Australia spanned *ca* 10,000 years, temporally constrained by cold events at 31 and 21 ka. The calibrated radiocarbon age for Unit B at depth -199 cm of 23.9–22.4 k cal y BP suggests that Wet Cave contains sedimentary material associated with the second cold stage at *ca* 21 ka, more traditionally associated as the LGM; however the extent of glacial maximum representation in the deposit is more difficult to ascertain from the current chronology. An age of 18.5–16.6 k cal y BP at depth -170cm suggests that the mottled sands and clay laminations of Unit C accumulated over the first phase of rapid deglaciation following the LGM and provide an estimate for the temporal representation of the LGM in Wet Cave, assuming constant deposition through this phase. As the dated sample (WeC33) had a low extracted carbon value of 12 µg, well below the threshold identified by Pate *et al.,* (2006) of 100 µg, it may not provide a reliable estimate for the accumulation of Unit C; however, the calibrated age for sample WeC33 is consistent with the calibrated ages for the underlying Unit B and overlying Unit E.

The sedimentary character of Unit B is similar to the homogeneous sands of the Middle Unit in RCIC, thought to be aeolian-derived sands which accumulated rapidly into Robertson Cave (Forbes and Bestland, 2007). The age inversion evident in the radiocarbon ages for Unit B may be the result of rapid accumulation of this unit and slumping through the cave as noted for Robertson Cave (Forbes and Bestland, 2007). Rounded, polished quartz grains in Unit 3 of BC3C are also aeolian derived and are expected to have undergone a high degree of transportation and reworking through their geological history (Darrénougué *et al.,* 2009). As already noted, sandy deposits in the caves have been associated with the A horizon of local Terra Rossa Soils and the medium grained sands of the Bridgewater Formation (Forbes *et al.,* 2007). Strong winds, dry conditions and minimal vegetation cover are expected to have facilitated movement of these materials in the landscape, contributing to their accumulation in the caves during MIS-2 and the LGM (Forbes and Bestland, 2007; Darrénougué *et al.,* 2009).

Climatic cooling through MIS-3 and into MIS-2 is correlated with sea level decline to -107 m at *ca* 24 ka and a minimum of -120m at *ca* 21 ka (Cutler *et al.,* 2003; Williams *et al.,* 2009). Consequently, over the accumulation of the sandy Unit B in Wet Cave and similar units in RCIC and BC3C, the Naracoorte Caves were more continental than both the present day and during MIS-3. This is expected to have resulted in more arid and variable local climatic conditions. As discussed by Petherick *et al.,* (2011), pollen records from temperate south-eastern Australia reflect cool, dry conditions through the LGM, consistent with paleoclimatic inferences from the deposits of the Naracoorte Caves and McEachern's Deathtrap cave in south west Victoria (Kos, 2001). Speleothem growth in the Naracoorte Caves is dated to 20 ka (Ayliffe *et al.*, 1998) and dune development at Willandra from *ca* 19 ka (Bowler *et al.,* 2012), providing further evidence of locally dry conditions during the LGM and accumulation of Units B and C in Wet Cave. Regional aridity is also indicated by the lack of fluvial activity in the Riverine Plain at *ca* 25–20 ka (Page *et al.,* 1996).

Units C and E: Deglaciation

Unit C shares similar sedimentary characteristics to those observed in the Upper Unit of RCIC which are attributed to cyclic rainwash deposition into Robertson Cave following the LGM (Forbes *et al.,* 2007). It is expected that the silty laminations of Unit C represent similar rainwash events; although, the sandy horizons of Units C and E suggest that cool, dry conditions favouring aeolian sedimentation continued through MIS-2 following the LGM, despite increased seasonal runoff. A calibrated age of 16.9–16.4 k yr at depth -100 to -110 cm, the bottom of Unit E, provides a minimum age for Unit C and, in combination with the slump structure evident in the stratigraphic profile, indicates rapid accumulation of sediments at the edge of the sediment cone at this time. This is also evidenced by the position of a likely re-worked layer of sediment, Unit D, at the top of Pit 1. It is expected that Unit D represents older material re-transported and slumped onto the edge of the sediment cone following initial deposition into the cave at an earlier time, likely during MIS-3 (McDowell, 2001). We also consider that the older sediments may have been reworked onto the cone by cavers when they investigated the site to find cave extensions.

The thicker and more defined alternating sand-clay laminations of Unit E may correspond to greater fluctuation in paleoenvironmental or climatic conditions locally and more regionally during the LGM deglaciation. Initial assessment of the ages of the yellow-brown sandy clays suggests *ca* 2,000 year intervals between deposition of these layers. These laminations are similar to the sequence described in Unit 4 of BC3C; however, the internal chronology for Unit 4 reflects post depositional disturbance and mixing of the sedimentary layers in this section of the BC3C deposit (St Pierre *et al.*, 2012), whereas there is no evidence for disturbance in Unit E of Wet Cave.

Warming following the cold-dry glacial conditions of the LGM across south-eastern Australia is variable: an initial phase of deglaciation is evidenced in rapid sea level rise over a few hundred years from 19 ka (Yokoyama *et al.*, 2000) and warming of oceans off the South Australian coast at *ca* 19–15.5 ka (Calvo *et al.*, 2007). However, regional variation in prevailing conditions is apparent with short term glacial advances in the Snowy Mountains at *ca* 19 ka and 17 ka (Barrows *et al.*, 2002). In south-eastern South Australia, dry conditions prevailed to the Holocene as indicated in the pollen and sedimentation records of Lake Leake and Wyrie Swamp (Dodson, 1975, 1977), the persistence of steppe-grasslands with low tree cover from *ca* 18 ka to the Holocene (*ca* 11.5 ka) in western Victoria (Kershaw *et al.*, 2004) and erosional deflation of Lakes Bolac and Turangmoroke, also in western Victoria between 18 and 11 ka (Cook, 2009). Pollen sequences from the Basalt Plains of western Victoria also suggests that lowest rainfall in the region was experienced at *ca* 14–12 ka rather than at the LGM (D’Costa *et al.*, 1989; Kershaw *et al.*, 2004), but is expected to be a function of increased evaporation with rising temperatures. This phase of maximum aridity is coincident with a post LGM phase of dune building in the Strzelecki and Tirari deserts from 14–10 ka (Fitzimmons *et al.*, 2007) and the Antarctic cold reversal at *ca* 14.5–13 ka (Jouzel *et al.*, 1995). The evolution of modern flow regimes associated with reduced flows and greater suspended loads on the Riverine Plain is dated from *ca* 12 ka, coinciding with reduction in the periglacial zone and elevation of the treeline which reduced the amount of debris and melt flows from the Snowy Mountains (Page *et al.*, 2009) and a second phase of post LGM warming dated from *ca* 13.3–11 ka (Calvo *et al.*, 2007).

Relatively dry conditions at the Naracoorte Caves during the LGM deglaciation are indicated by lack of speleothem growth from 20 ka (Ayliffe *et al.*, 1998). A Local increase in effective moisture is not indicated until *ca* 10 ka, as reflected in the pollen records of Lake Leake and Wyrie Swamp (Dodson, 1975, 1977). In contrast, high fluvial activity on the Riverine Plain from 20–13 ka suggests the maintenance of a seasonal positive water budget through the LGM deglaciation, likely associated with increased effective moisture and runoff from snowpack and glaciers associated with the late glacial advances at *ca* 19 and 17 ka in the Snowy Mountains (Page *et al.*, 2009).

Unit F: Holocene

Unit F contains Holocene aged material (dated to 0.7–0.6 k cal y BP) that is expected to have accumulated following a depositional hiatus of unknown duration, evidenced by the presence of a flowstone and layer of bat guano at depth -52 cm (McDowell, 2001; Forbes and Bestland, 2007). The high concentration of SO_3 in sediment sample Wp1d (Forbes and Bestland, 2006) suggests that the top of the profile remained relatively dry through the last *ca* 750 years, consistent with observed dry conditions in the late Holocene as reflected in regional pollen records (e.g., D’Costa *et al.*, 1989; Kershaw *et al.*, 2004; Cook, 2009). However, Dodson and Mooney’s (2002) review of changes in Holocene temperatures and effective moisture, and a recent study of the Willandra Lakes (Kemp *et al.*, 2012), suggest greater temporal and spatial variation in these parameters than noted here. It is not possible to temporally constrain the growth period associated with the flowstone noted from the Wet Cave sequence; however, it is expected that it is older than the Holocene aged sediments of Unit F and represents climatic conditions or a phase of higher effective moisture than represented by sediment sample Wp1d.

Human disturbance to the upper layers of the BC3C deposit is evident in the poor chronological consistency noted by Darrénougué *et al.*, (2009) and St Pierre *et al.*, (2012). McDowell (2001) suggested that Wet Cave contains a pre-European record of the local fauna but identified the very top layer of sediment as reworked based on the presence of orange clays and European artifacts. Further radiocarbon dating suggests that the sediments of Unit F may contain material of a mixture of

Pleistocene and Holocene ages, cautioning paleoecological interpretation of the faunas from Unit F (Table 3.1).

Environmental changes associated with European arrival, measured in sedimentary and pollen deposits of eastern Australia, commonly show increased sedimentation and vegetation change at rates higher than recorded from pre-European sequences (Dodson and Mooney, 2002). Darrénougué *et al.,* (2009) found no correlation between the thin layer of dark, organic matter-rich sediment at the top of the BC3C sediment core (Unit 5) and regional/local surface deposits and suggested that it represents a unique depositional episode, likely associated with human activity. In contrast, McDowell (2001) and Forbes and Bestland (2007) suggested that the dark, organic matter-rich Holocene aged silty sands within the Naracoorte Caves were derived from local podsols. Forbes *et al.,* (2007) suggested that the high organic matter and charcoal content of the early Holocene aged material in RCIC reflects climatic warming and wetting following the LGM, an inference supported by $\delta^{13}C$ isotopic data from charcoal and soil organic matter measured from RCIC. As the upper unit in Wet Cave is younger than the Upper Unit of RCIC, it is expected that Wet Cave provides a record of changed conditions from the early, warm and wet phase of the Holocene to drier conditions associated with higher temperatures and increased impacts of human activity on the surrounding landscape.

Conclusions

Collation of stratigraphic and sedimentary data collected during past studies of Wet Cave has enabled a review of the stratigraphy and paleoclimatic and environmental signals for the Upper Pleistocene–Holocene from this deposit. Five *in situ* and one reworked sedimentary unit have been identified in the Wet Cave sequence, each representing depositional episodes correlated with changes in paleoclimatic conditions of the Last Glacial Cycle in south-eastern Australia, spanning from mid MIS-3 to the Holocene. Additional radiocarbon ages have provided further constraints on the age of some units and have revealed possible re-worked areas in the sequence. This review of the Wet Cave sequence and its paleoclimatic context provides a basis for future investigation of the Wet Cave fossil assemblage and environmental record. It was also critical for enabling the Wet Cave assemblage to be correlated with contemporaneous records from other caves within the NCWHA in order to test the paleoecological signals interpreted from a single deposit.

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4. Bayesian age-depth modelling of Late Quaternary deposits from Wet and Blanche Caves, Naracoorte, South Australia: a framework for comparative faunal analyses

Citation

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Contribution of Authors

Amy Macken:

- Devised and planned the project.
- Compiled stratigraphic and chronological data that were integrated into the models.
- Worked closely with RS to develop the models.
- Prepared the manuscript for publication with the support of RS.

Richard Staff:

- Developed the models in OxCal.
- Supported AM with preparation of the manuscript.

Elizabeth Reed:

- Provided stratigraphic data for Blanche Cave.
- Assisted with the stratigraphic interpretation of the Blanche Cave sequence for the purpose of age modelling.
- Provided comments on the manuscript.

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Abstract

Bayesian age-depth models were constructed for two Late Quaternary aged fossil-bearing sedimentary sequences from caves in south eastern South Australia. The deposits in Wet and Blanche Caves contain dense assemblages of vertebrate fossils, largely the result of owl pellet accumulation. While individually calibrated radiocarbon determinations from the fossil sequences have provided a chronology for their accumulation, there was limited capacity available with such data to (a) temporally constrain assemblages associated with different depositional units and layers within the two sites, (b) interpret the chronological relationships among successive units and layers and (c) correlate sedimentary units and layers of similar age between the two deposits. Here, Bayesian age-depth models were constructed in OxCal for the Wet and Blanche Cave sequences, incorporating the available radiocarbon data and stratigraphic information collected during their excavation. Despite the low precision of the age-depth models for Wet and Blanche Caves which results in part from there being only single radiocarbon determinations available for a number of units and layers, the models enabled the relationships within and between the two sites to be established. Of particular utility for future faunal analyses is quantification of the temporal relationship between strata from the two sites, where groups of individual layers from Blanche Cave were found to be temporally equivalent with the longer-duration units in Wet Cave. We suggest that the use of `Phase` modelling, as performed here, is useful for cave deposits that have complex depositional histories and even in such instances where, as is common for palaeontological sites, few radiocarbon data are collected relative to the time-spans of tens of millennia that are often represented by them.

Keywords ^{14}C dating, age-depth modelling, Bayesian statistics, cave sequence, last glacial cycle, Naracoorte Caves

Introduction

The utility of radiocarbon (^{14}C) dating to provide chronologies for late Quaternary aged archaeological and palaeontological sites is well demonstrated (e.g., Gillespie, 2002; Vasil’ev *et al.*, 2002; Crowley, 2010). However, sparse radiocarbon data and statistical uncertainty often restrict the resolution and accuracy of site chronologies based on individually calibrated ^{14}C determinations (Parnell *et al.*, 2011). Bayesian chronological methods can overcome these limitations and have increasingly been used to develop chronologies for palaeontological and archaeological sites where a high level of dating precision is required (e.g., Petrie and Torrence, 2008; Beramendi-Orosco *et al.*, 2009; Calcagnile *et al.*, 2010; Higham *et al.*, 2010; Zhu *et al.*, 2010). By integrating ^{14}C data (*likelihoods*) and stratigraphic information (*priors*), Bayesian age-depth models produce *posterior* (modelled) site chronologies that not only refine the chronological information available for a given sequence, but also provide quantified uncertainties for such profiles, given the model prior applied (Bronk Ramsey, 2008; Parnell *et al.*, 2011). As demonstrated by Blaauw *et al.* (2007), Bayesian age-depth models can also be used to temporally correlate the proxy records from contemporaneous sequences. While correlation of depositional sequences commonly utilises stratigraphic, sedimentary and chronological data (e.g., Birkland *et al.*, 1971; Magee *et al.*, 1995; Frumkin *et al.*, 2001), these past approaches have rarely taken account of the underlying chronological uncertainties both within and between records.

Cave sites are particularly important in Quaternary palaeontological studies as they contain deep, well stratified sedimentary sequences often spanning multiple millennia (e.g., Cuenca-Bescos *et al.*, 2009). Caves also provide stable conditions for the long term preservation of skeletal remains of a diverse range of vertebrates, which may have been collected through pitfall entrapment, cave inhabitant death and/or carnivore accumulation (Nielsen-Marsh, 2000). In some cases, vertebrate deposits in caves are associated with a range of other palaeoecological materials such as charcoal, calcium carbonate cave formations (speleothems) and pollen, which may be correlated with fossil faunal assemblages to provide a more accurate interpretation of past environmental conditions (e.g., Burney *et al.*, 2001; Carrión *et al.*, 2003; Auler *et al.*, 2006). The application of Bayesian age-depth models to cave sequences has been valuable where the complex and sometimes random nature of accumulation processes in caves can limit the resolution and accuracy of chronologies for these sites (e.g., Jacobi and Higham, 2009; Blockey and Pinhasi, 2011; Pinhasi *et al.*, 2011).

In south eastern South Australia, 26 caves within the Naracoorte Caves complex contain 100 known vertebrate fossil deposits ranging from early Pleistocene to

Holocene age (Reed and Bourne, 2000; Prideaux *et al.*, 2007; Macken *et al.*, 2013a; Fig. 4.1). Within this cave complex, deposits in two of these caves, Wet and Blanche, are broadly contemporaneous, spanning the late Pleistocene from *ca.* 45 ka, to the Holocene period (Darrénougué *et al.*, 2009; St. Pierre *et al.*, 2012; Macken *et al.*, 2013a). Fine stratigraphic laminations contained within broader sedimentary units in these cave sequences, in combination with the high density of bone material identified from these deposits (McDowell, 2001; Laslett, 2006; Macken and Reed, 2013) makes them suitable for the analysis of faunal patterns through the last glacial cycle at a range of temporal scales, incorporating both long and short term phases of accumulation. As these sites are of similar age, they also provide an opportunity to quantify inter-site variability within the palaeocommunity through similarity tests of contemporaneous, replicate fossil samples from the one locality, an approach endorsed by Bennington and Bambach (1996).

Data on the calibrated age, duration and temporal continuity of depositional units and layers of the fossil bearing sedimentary profiles of Wet and Blanche Caves are required to temporally constrain the faunal assemblages and to enable an evaluation of faunal change through time, both within and between the two sites. To facilitate such analyses, greater chronological resolution is required than has been previously published. In the case of Wet Cave, only a small number of ^{14}C determinations are available (Macken *et al.*, 2013a; Table 4.1). In Blanche Cave, although more ^{14}C determinations are available for the sequence (St Pierre *et al.*, 2012; Table 4.2), overlap in the calibrated radiocarbon ages of successive layers limits the resolution at which faunal analyses may be conducted.

Here, we use Bayesian age-depth models to assess the chronological histories of Wet and Blanche Cave and the temporal relationships between strata from the two sites. As fossil-bearing deposits, understanding these relationships is critical for robust and informed comparative faunal analyses. More specifically we use Bayesian age-depth modelling to (a) construct probabilistic site chronologies that provide modelled ages for the lower and upper boundaries (reflecting the start and end) of depositional episodes (stratigraphic units and finer sedimentary layers) within the two sequences, (b) determine the temporal duration (resolution) of these depositional episodes and potential hiatuses between them, and (c) identify contemporaneous depositional episodes between the two sites. We discuss the challenges and opportunities presented by such models for the study of complex cave sequences and explore the implications of these models for future study of the fossil assemblages specifically associated with Wet and Blanche Caves.

Regional Setting and Study Sites

Geological setting of the Naracoorte Caves

Wet and Blanche Caves are located within the Naracoorte Caves World Heritage Area, 12 km south-east of Naracoorte in south eastern South Australia (Fig. 4.1). The caves lie in an uplifted portion of the Oligocene to Miocene aged Gambier Limestone, which originated from fossiliferous marine sediments. Phreatic dissolution of this limestone and structural processes along joints contributed to cave formation (Wells *et al.*, 1984; White, 2005). The oldest sedimentary deposits in the Naracoorte Caves have been dated to 528±41 ka using optically stimulated luminescence dating (Prideaux *et al.* 2007), suggesting that the caves first opened to the surface during the early to middle Pleistocene. Overlying the Gambier Limestone is a series of stranded Pleistocene beach dune facies known as the Bridgewater Formation. The oldest of these is the East Naracoorte Ridge, dated by whole-rock amino acid racemisation to 935±178 ka (Murray-Wallace *et al.* 2001) and overlies the Naracoorte Caves. All known caves in the region are registered with the Australian Karst Index (Matthews, 1985) and are identified by unique cave numbers (e.g., 5U10, 11). Here, the ‘5’ refers to the state of South Australia, ‘U’ to the Upper south east, and ‘10’ and ‘11’ are the numbers allocated to the entrances associated with Wet Cave.

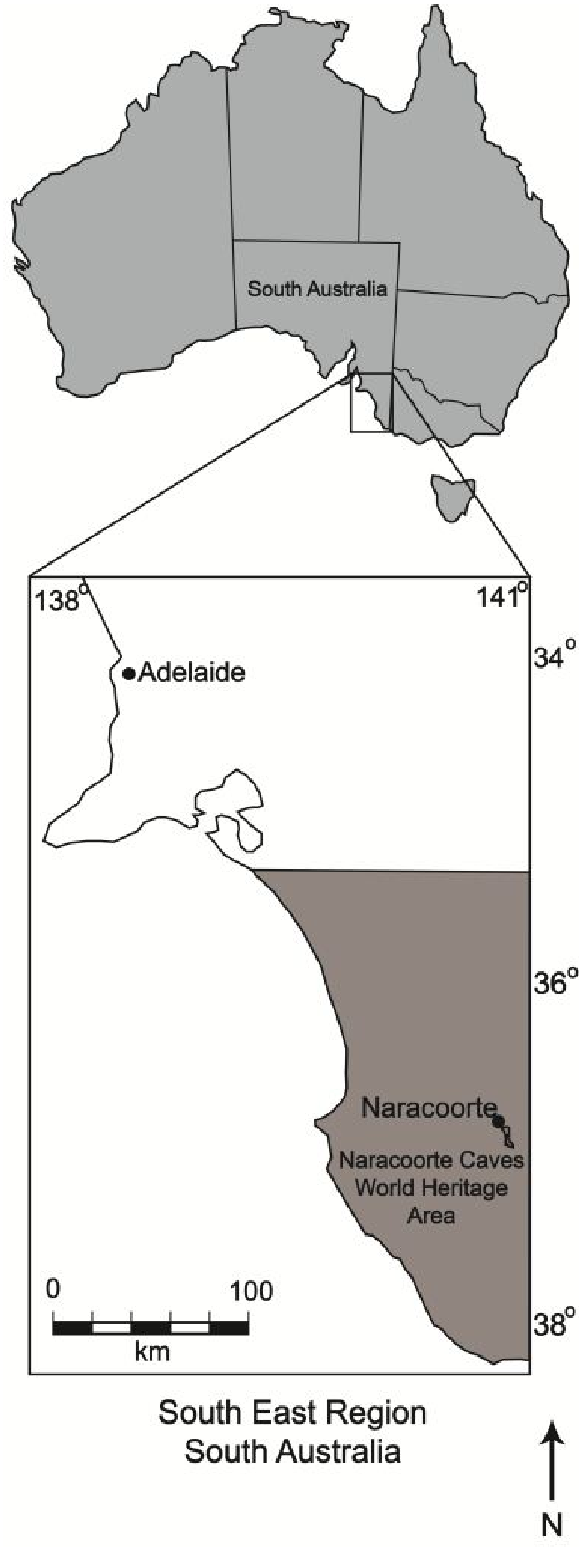

Figure 4.1 Location of the Naracoorte Caves World Heritage Area in south eastern South Australia, Australia.

Wet Cave (5U10, 11)

Wet Cave is composed of three chambers. An upper and lower chamber are accessed via entrance 5U10, located on the southern edge of the main road into the Naracoorte Caves National Park. A third chamber is open to the surface through entrance 5U11, approximately 130 m south of entrance 5U10. The excavated sedimentary sequence was located on the south eastern edge of the sediment cone in the upper chamber associated with entrance 5U10. The sequence was excavated across two 1 m^2 pits (1, lower and 2, upper) in 1998 and 1999 to a total depth of 350 cm. Sedimentary layers through the sequence were excavated separately and their depths measured from a datum established at the top of Pit 2 (*Macken et al., 2013a*; NB. The Wet Cave stratigraphy is represented in Fig. 4.5 with the results).

Following severe storms in December 2010, the excavated section of Wet Cave was filled with flood sediments, limiting further assessment of the site. Prior to this event, the excavated section of Wet Cave was composed of six depositional units; Units A (lower) to F (upper; Macken *et al.*, 2013a). While stratigraphic and sedimentary observation of the units suggests that the majority were deposited in chronological order, Unit D appears to have incorporated reworked sediments from an older depositional episode (Macken *et al.*, 2013a). These stratigraphic relationships were formalised into the Bayesian model framework for Wet Cave, as detailed in the methods.

Dating of charcoal samples from Wet Cave occurred in two stages. Initial AMS ^{14}C determinations were made on charcoal collected from the exposed stratigraphic profile in the late 1990s with 14 ages published by Pate *et al.* (2002; 2006). An additional six AMS ^{14}C determinations have since been reported by Macken *et al.* (2013a), measured from charcoal samples sorted from wet-screened material during the original excavation and stored in vials in the fossil laboratory since 1998. The specific depths of these samples are unknown as they were labelled only with the source layer code (Table 4.1).

Table 4.1 ^{14}C determinations for the Wet Cave stratigraphic sequence. 'WeC' samples are from Pate *et al.* (2002, 2006); '5U10' samples are from Macken *et al.* (2013a). Reporting of ^{14}C data follows standard protocol outlined in Stuiver and Polach (1977). All samples were charred material.

Sample ID	AMS laboratory ID	C mass (µg)	C yield (%)	δ^{13}C (%o)	Conventional ^{14}C age BP	1σ	Unit	Unit depth (cm)
5U10-6	BETA-298177	4600	66	-24.9	11,260	60	F	0 to -52
WeC36	OZE 539	2570	62.7	-24.2	740	40		
5U10-5	BETA-298176	2000	51	-24.6	9,180	40	E	-52 to -110
WeC1	OZD 284	1770	63.2	-23.7	9,590	100		
5U10-4	BETA-298175	4000	59	-25.3	12,310	50		
5U10-3	BETA-298174	2200	67	-25.6	13,470	50		
WeC4	OZD 504	1320	47.1	-28.7	13,920	130	D	-110 to -150
WeC33[1,2]	OZE 541	12	1.8	-25	14,150	350	C	-150 to -187
5U10-2	BETA-298173	2000	70	-24.6	20,750	90	B	-187 to -220
WeC32[2]	OZE 536	122	0.2	-26.4	19,400	300		
WeC10[1]	OZD 292	100	50	-25	23,850	1020	A	-220 to -350
WeC25	OZD 714	1380	43.1	-24.2	30,500	400		
WeC21[1]	OZD 715	350	58.3	-25	33,400	650		
WeC23[1,2]	OZD 721	290	1.8	-25	23,400	1600		
WeC27	OZD 717	1950	54.2	-25.9	40,900	850		
WeC12[1,3,4]	OZD 291	70	17.5	-25	>29,000			
WeC35	OZE 538	1360	35.8	-24.8	45,200	1800		
5U10-1	BETA-298172	2200	76	-24.2	9,140	40		
WeC30[1,2]	OZD 724	200	0.7	-25	32,600	900		
WeC16[5]	OZD 506	1640	54.7	-26.4	>45,000			

[1] Assumed δ^{13}C value of -25o was used as no measured δ^{13}C was available due to small sample size.

[2] Pretreated sample contained some sand/sediment. Estimated C yield may not be reliable.

[3] AMS laboratory code reported by Pate *et al.* (2006) as OZE. ANSTO reports indicate that code was OZD (Q. Hua, pers. comm.)

[4] F^{14}C measurement 0.0098±0.0099 (D. Pate, pers. comm.)

[5] F^{14}C measurement 0.0031±0.001 (D. Pate, pers. comm.)

Blanche Cave (5U4, 5, 6)

The structure of Blanche Cave and the sedimentary character, stratigraphic division and chronology of a sediment core from the excavation site has been described by Darrénougué *et al.* (2009). The Blanche Cave fossil excavation is located in the 3rd chamber associated with entrance 5U6, approximately 400 m north west of Wet Cave entrance 5U10. Fossil excavation in the 3rd chamber occurred between 2006 and 2007. The first excavation was conducted by Laslett (2006) who excavated four 1 m^2 grid squares (A1, B1, A2 and B2) in 5 cm layers to a maximum depth of 1.1 m; however, three of the grid squares were obstructed by the presence of a large limestone boulder. A second excavation was conducted by EHR in 2006/2007 from two grid squares (A3 and B3), both excavated to a depth of 1 m. Excavation of these grid squares followed the stratigraphy such that 27 individual sedimentary layers were excavated as discrete bands, ranging from 1 to 6 cm thick (the Blanche Cave stratigraphy is represented in Fig. 4.5, Results). The Bayesian model developed here integrates the stratigraphic information associated with the 27 sedimentary layers described from grid squares A3 and B3, rather than the earlier, depth-standardised spit data from Laslett (2006).

Five units (1, lower to 5, upper) have been described from the top 100 cm of the Blanche Cave stratigraphic sequence (Darrénougué *et al.*, 2009), corresponding to the 27 individual sedimentary layers; however, precise depth information relating to the units is not integrated into the Blanche age-depth model. This is because the ^{14}C determinations are stratigraphically constrained at a finer resolution by the 27 layers noted from grid squares A3 and B3. A total of 40 AMS ^{14}C determinations are available from across the 27 layers (Darrénougué *et al.*, 2009; St Pierre *et al.*, 2012; Table 4.2).

Table 4.2 ^{14}C determinations for Blanche Cave 3rd chamber stratigraphic sequence, from Darrénougué *et al.* (2009) and St Pierre *et al.* (2012), the former marked with an asterisk. A3 and B3 in the sample code refer to the grid square from which the sample was sourced and 'L' refers to the depositional layer. Samples with BW in the code were exposed to bore water to isolate charcoal from sediment matrix. Layer depths measured as depth from sediment surface at boundary of grid squares A3 and B3 (refer Figure 4.4). NB. No samples for radiocarbon analysis were collected from Layers 9 and 12. Reporting of ^{14}C data follows standard protocol outlined in Stuiver and Polach (1977). All samples were charred material.

Sample ID	**AMS laboratory ID (SSAMS ANU #)**	**C mass (µg)**	**C yield (%)**	**δ^{13}C (‰)**	**±1σ**	**Conventional ^{14}C age BP**	**1σ**	**Layer**	**Layer depth (cm)**
5U6A3-L1*	2805	1230	59	-20.8	1.9	12470	60	1	-5.5 to -11.5
5U6A3-L2BW*	3137	860	54	-30.2	5.8	12700	80	2	-11.5 to -14.5
5U6B3-L3*	2806	1110	61	-24.9	4.8	13200	80	3	-14.5 to -18.5
5U6B3-L4*	2807	950	56	-30.8	3.5	13230	70	4	-18.5 to -23
5U6B3-L4 repeat*	3323	920	59	-10.2	2.1	13410	100		
5U6B3-L4BW	2809	1040	59	-22.1	4.5	1310	45		
5U6B3-L4BW repeat	3324	900	55	-23.4	3.4	1370	50		
5U6B3-L5BW*	2810	1060	63	-29.4	1.3	13300	70	5	-23 to -25
5U6B3-L6*	2811	900	61	-33.2	3.9	13420	80	6	-25 to -29

Sample ID	AMS laboratory ID (SSAMS ANU #)	C mass (µg)	C yield (%)	$\delta^{13}C$ (‰)	±1σ	Conventional ^{14}C age BP	1σ	Layer	Layer depth (cm)
5U6A3-L7BW	2812	1080	62	-28.2	3.5	9550	60	7	-29 to -31.5
5U6A3-L7BW repeat	3325	970	58	-23.6	2.6	9420	60		
5U6B3-L8	2813	900	60	-28.8	1.7	14160	70	8	-31.5 to -34
5U6B3-L8 repeat	3326	1110	53	-11.7	3.8	14270	90		
5U6B3-L8BW	2814	1360	63	-26.0	2.1	3895	35		
5U6B3-L8BW repeat	3327	930	54	-13.6	5.9	4060	70		
5U6A3-L10*	2816	1050	68	-33.0	3.8	13890	80	10	-35.5 to -40
5U6A3-L10BW	3135	860	59	-22.7	9.0	14630	110		
5U6A3-L11	2817	1030	59	-29.3	2.8	13840	70	11	-40 to -42.5
5U6B3-L13BW*	2818	1080	59	-35.3	5.3	14180	90	13	-42.5 to -46.5
5U6A3-L14*	3136	750	48	-31.0	2.2	20010	110	14	-46.5 to -49
5U6A3-L15*	2819	960	51	-34.6	6.9	15860	100	15	-49 to -51
5U6A3-L15BW	2820	1000	63	-25.8	3.5	16760	100		
5U6A3-L16*	2821	1030	48	-32.7	2.5	16430	90	16	-51 to -54
5U6B3-L16BW	2823	1050	56	-25.5	2.7	17160	100		
5U6B3-L17*	3328	930	52	-21.5	1.7	15390	90	17	-54 to -58.5
5U6B3-L18BW*	2825	990	58	-23.8	5.5	15200	90	18	-58.5 to -63
5U6B3-L18BW repeat*	3329	990	56	-14.2	5.8	14330	100		

Sample ID	AMS laboratory ID (SSAMS ANU #)	C mass (µg)	C yield (%)	$\delta^{13}C$ (‰)	±1σ	Conventional ^{14}C age BP	1σ	Layer	Layer depth (cm)
5U6B3-L19*	2826	950	57	-32.9	4.1	18550	110	19	-63 to -69
5U6B3-L19BW*	2827	810	57	-24.3	2.6	20000	120		
5U6A3-L20BW*	2829	1100	53	-23.3	2.1	20590	130	20	-69 to -70
5U6A3-L21BW*	2830	790	61	-25.2	3.5	20710	130	21	-70 to -73.5
5U6B3-L22*	2831	830	57	-31.7	2.9	20670	130	22	-73.5 to -77
5U6B3-L22BW	2832	980	59	-21.7	1.5	27680	280		
5U6B3-L22BW repeat	3330	900	58	-28.5	7.8	27570	300		
5U6B3-L23BW*	2833	900	60	-14.8	5.3	25120	220	23	-77 to -80
5U6B3-L24BW*	3138	940	52	-29.3	2.2	28070	230	24	-80 to -84.5
5U6B3-L24BW repeat*	3139	910	51	-32.0	3.6	27820	240		
5U6A3-L25BW	2835	840	57	-27.6	1.6	30060	380	25	-84.5 to -89
5U6B3-L26BW*	2836	950	58	-21.2	3.6	36290	790	26	-89 to -95
5U6A3-L27BW	2837	880	58	-21.2	1.2	43260	1840	27	-95 to -99.5

Materials and Methods

Bayesian age-depth models

Bayesian age-depth models were developed in OxCal ver. 4.1 (Bronk Ramsey, 2008; 2009a), applying the IntCal09 calibration curve (Reimer *et al.*, 2009), but allowing for an offset from this for calibration in the Southern Hemisphere (SH) of 56±24 years. This offset is the same as that applied to the earliest 500 years of the SHCal04 calibration curve (McCormac *et al.*, 2004). Although the SH calibration curve is only recommended back to 11,000 cal yr BP, we applied the average offset value for the earliest 500 years of the modelled SH dataset across the entire time period sampled in Wet and Blanche Caves. We acknowledge that the accuracy of this offset may decline through the pre-Holocene period (ca. 11,000 to 50,000 cal yr BP) due to a potentially more variable inter-hemispheric offset resulting from changes in ocean circulation and carbon cycling processes under full Glacial conditions. However, no current calibration curve is available for the SH into the Pleistocene, necessitating the compromise approach adopted here. Leaving the oldest ages uncalibrated, as was the approach used by Crowly (2010) would limit the reliability with which the two sites could be correlated. Alternatively, calibrating the pre-Holocene ages to IntCal09 (without an allowance for an inter-hemispheric offset) would affect the reliability of any future comparison of the Wet and Blanche Cave sequences with Northern Hemisphere data. As we apply the same calibration offset to both sites here, the choice of calibration curve (or offset) does not affect the correlation of the two cave sequences. Furthermore, given the resolution of the chronological data, the offset applied does not strongly alter the modelled chronologies for the sequences when compared with models calibrated without an offset.

Both sites were constructed as `Phases` within a `Sequence` deposition model (Bronk Ramsey, 2008), incorporating prior information about the order of events, as determined from the stratigraphy. `Sequence` and `Phase` models are suitable for sites such as caves where the rate or continuity of deposition is unknown, contrasting with lacustrine or marine sediment profiles that might exhibit more regular depositional phases (Bronk Ramsey, 1995; 2008). In both the Wet and Blanche Cave sequences, few assumptions about deposition could be made from the available stratigraphic data. For example, a possible depositional hiatus during accumulation of the Wet Cave sequence is indicated by the presence of bat guano derived materials at depth below datum (D/D) -39 to -52 cm, representing the bottom 13 cm of Unit F; however, the duration of this event is unknown (Macken *et al.*, 2013a).

`Boundaries` were applied to the top and bottom of each sequence constraining the maximum age of the models to 60,000 cal yr BP (conservatively earlier than the 50,000 cal yr BP limit of the IntCal09 calibration curve; Reimer *et al.*, 2009) and the minimum age to -50 cal yr BP (i.e., AD 2000). All modelled data are reported at the 68.2 and 95.4% highest probability density (hpd) ranges (approximately equivalent to 1 and 2σ uncertainty, respectively).

Wet Cave

A schematic of the OxCal model for the Wet Cave sequence is presented in Fig. 4.2a. Separate `Phases` were assigned to each depositional unit identified in the Wet Cave sequence (Macken *et al.*, 2013a). These were constrained to be in chronological order (from Unit A, oldest, to Unit F, youngest), except for the potentially re-worked Unit D. In order to utilise the extra chronological data nevertheless available from Unit D (i.e., adding extra potential *terminus post quem* data for the commencement of the overlying Unit E), this `Phase` was constrained to lie anywhere between the start of the deposition sequence (i.e., the 'Wet Cave bottom' `Boundary`) and the bottom of Unit E (Fig. 4.2a). In OxCal, this was achieved by nesting the `Sequence` of Units A, B and C, and the independent `Phase` of Unit D, within a broader `Phase` for Units A, B, C and D.

From stratigraphic observation it was deemed that each of the depositional units (except Unit E) were internally heterogeneous such that no assumption of relative chronological ordering could be made of the sediment within each of these units. Unit E, however, demonstrated reliable sub-structure, and therefore additional sub-`Phases`, themselves constrained to lie in stratigraphic order, were nested within Unit E, representing six lenses (2:6/4, oldest, 2:6/3, 2:6/2, 2:6/1, 2:5/2, and 2:5/1, youngest).

All of the ^{14}C data for the Wet Cave samples were inserted within this model framework as `R_Dates`, except WeC12 and WeC16, which were inserted with the `R_F14C` function. `R_F14C` uses the raw F^{14}C measurement, rather than the calculated conventional radiocarbon age, to account for the fact that these samples provided ‘infinite’ (‘greater than’) radiocarbon dates (Table 4.1). Outlier analysis was applied using the ‘general’ `Outlier_Model` described by Bronk Ramsey (2009b). An equal prior `Outlier` probability of 5% was applied to the majority of ^{14}C determinations (`R_Dates` and `R_F14C`). However, based on the threshold identified by Pate *et al.* (2006), ^{14}C determinations from samples with extracted carbon values of ≤100 μg C were deemed more likely to be questionable and were given an increased prior `Outlier` probability of 10% (i.e., samples WeC33, WeC23, WeC12). While Pate *et al.* (2006) argued that sample WeC30 had a low extracted carbon value when compared with the other samples, its mass of 200 μg exceeds the threshold criterion originally identified by the same authors and was assigned a prior probability of 5% here.

Blanche Cave

A schematic of the Blanche Cave OxCal model is presented in Fig. 4.2b. The model was constructed in a similar manner to that for Wet Cave, with separate `Phases` assigned to each sedimentary layer. However, stratigraphic observations and sedimentary data could not reliably differentiate whether Layers 23–21, 18–15, 13–10 and 9–4 represented single, sequential depositional phases, or sediments of mixed age within broader depositional episodes. For these sections, overlapping sub-`Phases` (representing each individual layer) were nested within broader `Phases` for the combined layer sections (Layers 23, 22 and 21; Layers 18, 17, 16 and 15; Layers 13, 12, 11 and 10; and Layers 09, 08, 07, 06, 05 and 04) such that no relative ordering of the sub-`Phases` was presumed, *a priori*, within these four broader `Phases` (Fig. 4.2b). The remaining layers, as well as the four broad `Phases`, were then constrained to be in stratigraphic order in the overall model `Sequence` (from Layer 27, oldest, to Layer 1, youngest), except for the potentially re-worked Layer 14 (‘special event layer’ identified by Darrénougué *et al.*, 2009). As with Unit D in Wet Cave, the `Phase` for Layer 14 was constrained to lie anywhere between the start of the deposition sequence (i.e., the ‘Blanche Cave bottom' `Boundary`) and the bottom of the overlying `Phase` (Layer 13), thus providing additional potential *terminus post quem* data for the overlying strata.

The ^{14}C data were inserted within this model framework. `Outlier` analysis was again applied using the 'general' `Outlier_Model` (Bronk Ramsey, 2009b), with a prior `Outlier` probability of 5% applied to all of the ^{14}C determinations. For this site, there was no *a priori* reason to believe that any of the samples were more likely to be erroneous than others. However, six samples, 5U6B3-L8BW, 5U6B3-L8BW repeat, 5U6A3-L7BW, 5U6A3-L7BW repeat, 5U6B3-L4BW and 5U6B3-L4BW repeat, were so outlying that their inclusion prevented the model from running. The prior `Outlier` probabilities of these samples were necessarily increased to 100% to allow the model to run.

Temporal Duration of Phases and Potential Hiatuses between Phases

The modelled duration of `Phases` representing depositional units in Wet Cave and layers or groups of layers in Blanche Cave were obtained using the `Difference` query function in OxCal. Assessment of the presence and duration of potential temporal hiatuses between successive `Phases` within each sequence were also modelled using the `Difference` function. `Difference` provides the range in calendar years between two events and can be used to test a null hypothesis (H_0) that the two events are contiguous (i.e., that, given the dating evidence available, there is no temporal hiatus/missing sediment between the end of the first event and the start of the next). If the calculated hpd range (for the `Difference` query) does not contain 0 at a given confidence level (typically the 95.4% confidence), H_0 is rejected and there is some evidence to suggest that, at the dating resolution available, there is missing material or a temporal gap detected between the two events. If the null is not rejected, it is possible that the ages of the two events could overlap. Specific cases where sedimentary observations suggest that such overlap is possible (as a result of depositional or post-depositional mixing of materials of different age) have been incorporated into the model priors (Wet Cave Unit D; Blanche Cave Layer 14). All other `Phases` have been assumed, based on sedimentary observations, to be successive and in stratigraphic superposition based on age (with the exception of the individual layers within Blanche Cave Layers 9–4, 10–13, 15–18 and 23–21), and the model priors constructed accordingly.

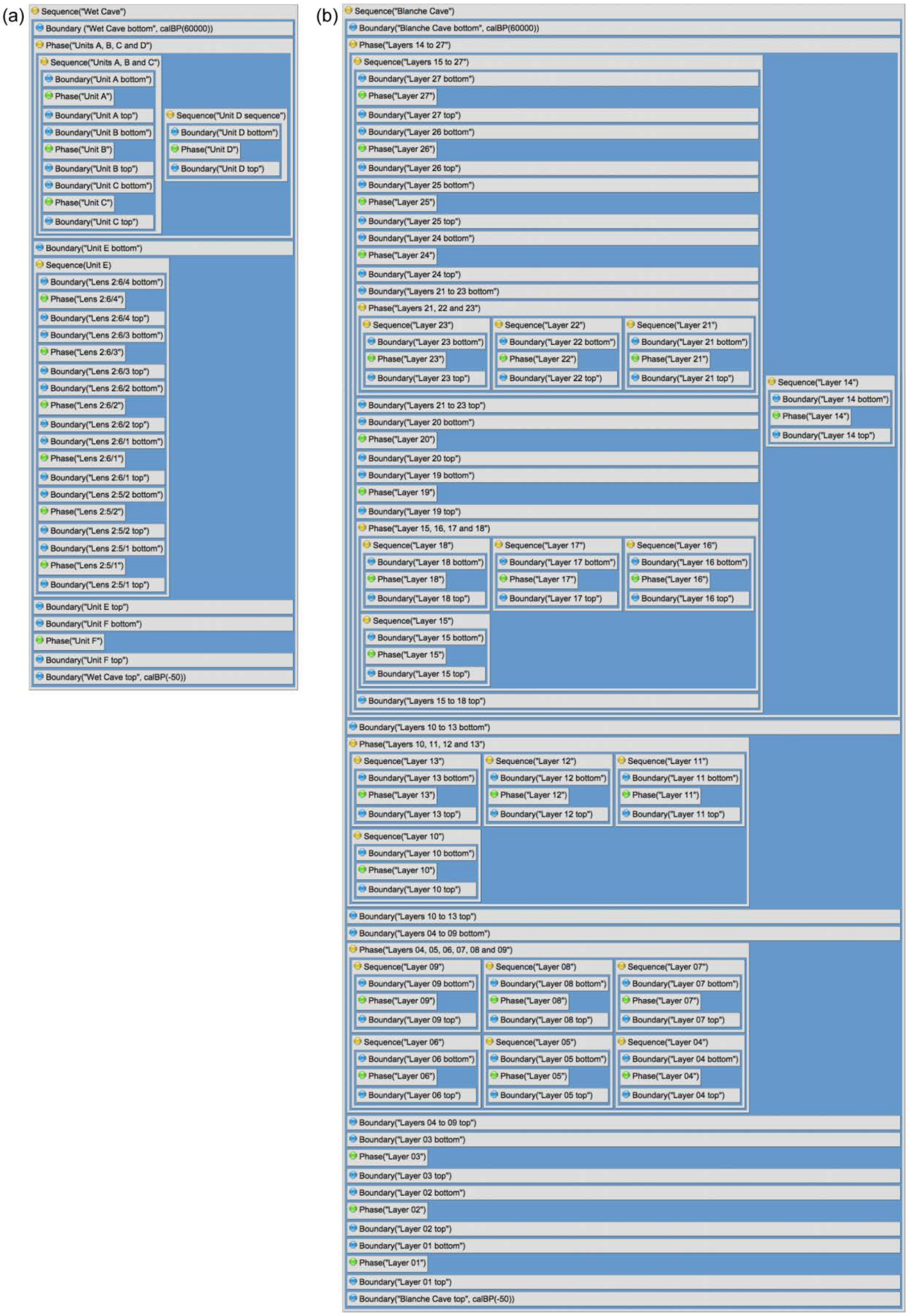

Figure 4.2 Bayesian model frameworks run in OxCal for (a) Wet Cave and (b) Blanche Cave. `Phases` and nested sub-`Phases` were constructed within `Sequence` models, based upon stratigraphic and sedimentary observations of the two sites.

Correlation of Wet and Blanche Cave Phases

The OxCal queries `Order` and `Difference` were used to examine the temporal relationship between the Wet Cave depositional units and Blanche Cave layers. These functions were queried for all pairwise comparisons of the posterior probability distributions for the Wet and Blanche Cave `Boundaries`, which had been saved as `Priors` from the output data from the two individual site models.

`Order` finds the probability that one event (i.e., t_1) is older than another (t_2). Therefore, the function simply provides the 'most likely' relative ordering of events between the two `Sequences` (i.e., providing a probability threshold of 50%). Application of the `Difference` function provides a more rigorous, quantified probability distribution of these relationships. As with the intra-site queries described above, a `Difference` function with a 95.4% hpd range including 0 prevents rejection of the null hypothesis and implies that, given the available data, synchrony of the two events cannot be excluded.

Results

Wet and Blanche Cave Bayesian Models

Modelled ages for the upper and lower `Boundaries` of Wet Cave `Phases` are presented in Table 4.3 and Fig. 4.3. Modelled ages for the `R_Dates/R_F14Cs` and associated posterior outlier probabilities for these data are also presented in Table 4.3. Samples 5U6-6 and 5U6-1 were both found to be 100% outliers by the model; all other `R_Dates/R_F14Cs` had posterior outlier probabilities of ≤11%. The modelled ages for the lower and upper `Boundaries` of Units A and F, respectively, constrain the age of the Wet Cave sequence from 56,032–46,523 to 680– -43 cal yr BP (95.4% hpd range), ostensibly influenced by the prior maximum and minimum age constraints applied to the model.

Modelled ages for the upper and lower `Boundaries` of `Phases`, `R_Dates` and associated posterior outlier probabilities for the Blanche Cave sequence are presented in Table 4.4. Hpd ranges of the modelled `Boundaries` are presented in Fig. 4.4. While the majority of `R_Dates` fitted the applied model construction well (i.e., posterior outlier probability ≤ the prior of 5%), `R_Dates` 5U6B3-22 and 5U6A3-L21BW returned posterior outlier probabilities of 95 and 92%, respectively.

Nine samples, representing `R_Dates` from Layers 23, 19, 18, 16, 10, 8 and 1, had posterior outlier probability values >5%, ranging between 8 and 38%.

The modelled ages for the upper and lower-most `Boundaries` of the Blanche Cave sequence (Layer 27 bottom and Layer 1 top) place the modelled `Sequence` between a maximum of 59,997–46,259 cal yr BP and 14814– -50 cal yr BP, again heavily constrained by the maximum and minimum prior ages assigned to the model.

Phase Durations and Potential Hiatuses

68.2% and 95.4% hpd confidence ranges for the `Phase` durations of units and potential hiatuses between Wet Cave units and Unit E lenses are presented in Table 4.5. Table 4.6 presents these data for the Blanche Cave layers. The duration ranges for Wet Cave Units C, D and F and all Unit E lenses contain 0. In contrast, the duration of Unit A ranges from 18,343 to 30,429 years. The 95.4% hpd ranges for Units B and E also point to rejection of the null hypothesis, with upper values of 7,492, and 7,712 years respectively. All `Difference` functions between successive units and Unit E lenses contain 0 at the 95.4% confidence level. As a result, there is insufficient evidence to reject H_0 (for contiguous deposition) given the radiocarbon data available. The model prior for Unit D was such that it could overlap in age with units A, B or C. The single ^{14}C measurement from Unit D is insufficient to provide refined information (compared to the unmodelled data) to constrain this unit more precisely. For the same reason, there is insufficient information to reject the null hypothesis that Units C and D are contiguous.

Only the duration of the `Phase` for Layers 18–15 of Blanche Cave does not contain 0 at the 95.4% confidence level, suggesting that, at the dating resolution available, instantaneous deposition of each of the remaining `Phases` cannot be excluded. Similarly, the null hypothesis of contiguous deposition of successive layers was not rejected at the 95.4% confidence level for all successive layer `Boundaries`.

Table 4.3 Modelled ages of unit `Boundaries` and radiocarbon determinations (`R_Dates` and `R_F14C` functions) for the Wet Cave stratigraphic sequence. All data are given as both the 68.2 and 95.4% highest probability density ranges. Modelled ages calibrated using the IntCal09 calibration curve (Reimer *et al.*, 2009) with a Southern Hemisphere offset of 56±24 years applied (McCormac *et al.*, 2004).

`Boundary`	**`R_Date/R_F14C`**	**Modelled calibrated age (cal yr BP)**				**`R_Date/R_F14C` posterior `Outlier` probability**
		68.2%		**95.4%**		
		from	**to**	**from**	**to**	
Wet Cave top		-49	-50	-49	-50	
Unit F top		677	190	680	-43	
	5U10-6	9,519	294	9,729	227	100
	WeC36	722	662	744	565	2
Unit F bottom		10,287	664	10,313	662	
Unit E top		10,403	10,016	10,491	9,204	
	5U10-5	10,390	10,253	10,488	10,240	2
Lens 2:5/1 bottom		10,583	10,291	10,870	10,252	
Lens 2:5/2 top		11,004	10,594	11,151	10,410	
	WeC1	11,142	10,824	11,217	10,677	2
Lens 2:5/2 bottom		11,471	10,806	12,416	10,671	
Lens 2:6/1 top		12,697	11,210	13,604	10,948	
Lens 2:6/1 bottom		13,974	12,441	14,291	11,536	
Lens 2:6/2 top		14,441	13,629	14,810	12,646	
	5U10-4	14,473	14,041	14,879	13,966	3
Lens 2:6/2 bottom		14,779	14,113	15,520	14,019	
Lens 2:6/3 top		15,586	14,489	16,183	14,202	
Lens 2:6/3 bottom		16,381	15,271	16,611	14,624	
Lens 2:6/4 top		16,720	16,096	16,816	15,213	
	5U10-3	16,757	16,420	16,879	15,516	8
Unit E bottom		16,868	16,469	17,130	15,601	
Unit D top		17,132	16,632	18,659	15,680	
	WeC4	17,386	16,846	19,751	16,690	11
Unit D bottom		31,921	16,785	59,998	16,775	
Unit C top		17,502	16,698	18,406	16,197	
	WeC33	17,851	17,049	18,601	16,712	9

Boundary	**R_Date /R_F14C**	**Modelled calibrated age (cal yr BP)**				**R_Date/R_F14C posterior Outlier probability**
		68.2%		**95.4%**		
		from	**to**	**from**	**to**	
Unit C bottom		19,360	17,078	21,928	16,885	
Unit B top		23,577	21,111	24,138	18,599	
	5U10-2	24,884	24,521	25,170	23,293	6
	WeC32	23,727	22,706	24,294	22,371	5
Unit B bottom		26,091	24,591	28,383	24,348	
Unit A top		28,596	25,952	29,889	24,954	
	WeC10	30,237	28,092	31,506	26,671	10
	WeC25	36,124	34,640	36,413	34,476	5
	WeC21	38,874	37,126	40,157	36,593	5
	WeC23	30,833	27,719	33,549	26,074	10
	WeC27	45,367	44,047	46,172	43,193	5
	WeC12	47,259	37,550	50,002	34,457	10
	WeC35	48,919	46,311	50,002	45,669	5
	5U10-1	37,060	26,716	47,698	25,982	100
	WeC30	38,586	36,441	39,946	35,137	5
	WeC16	49,243	46,498	50,003	45,659	5
Unit A bottom		51,815	47,780	56,032	46,523	
Wet Cave bottom		60,001	60,000	60,001	60,000	

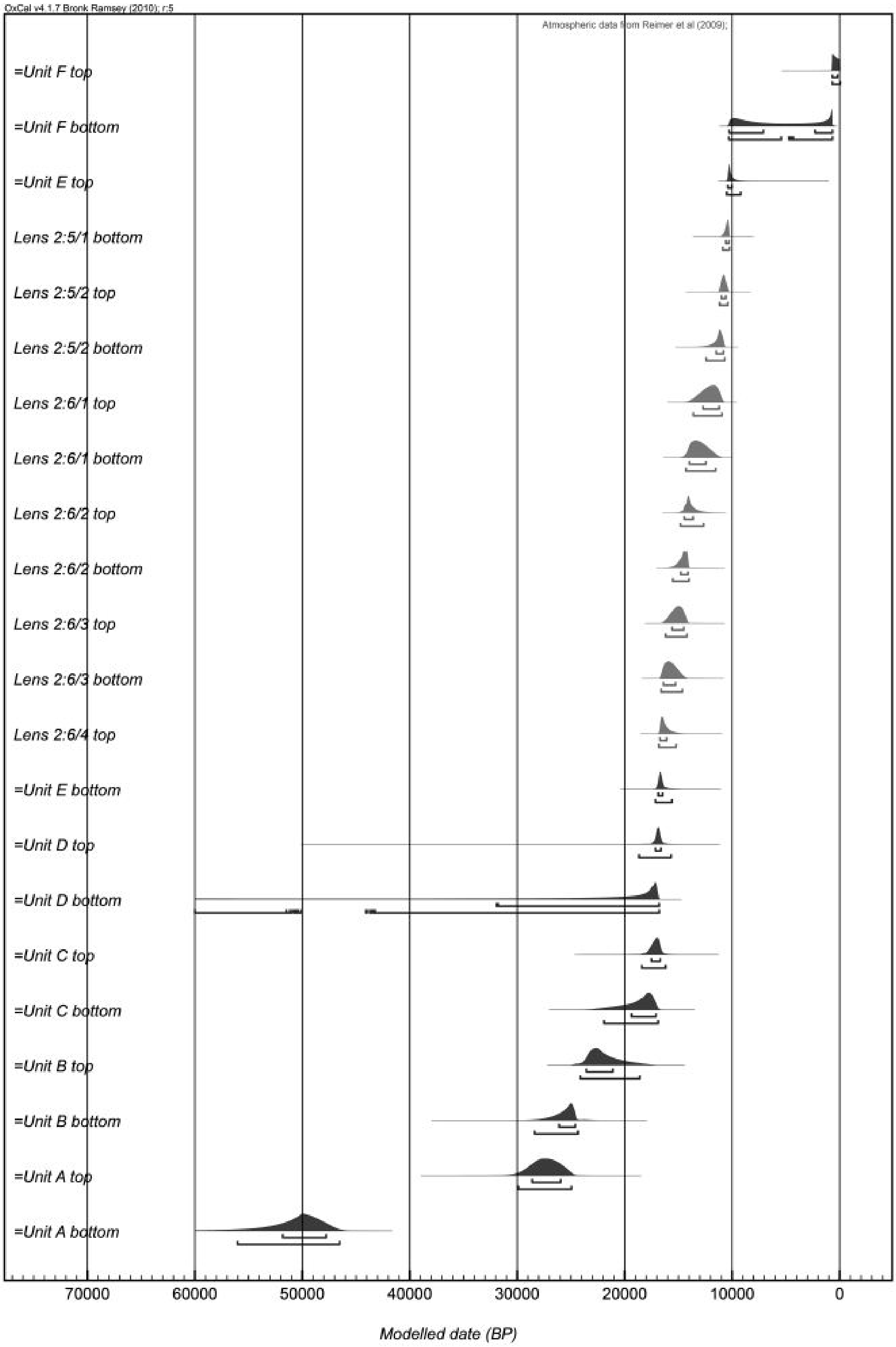

Figure 4.3 Modelled ages for unit `Boundaries` of the Wet Cave stratigraphic sequence. `Boundaries` for lenses of Unit E also indicated. Horizontal bars underneath each function represent the posterior 68.2% and 95.4% highest probability density ranges. Model generated using OxCal 4.1 (Bronk Ramsey *et al*., 2010), calibrated with IntCal09 and Southern Hemisphere offset of 56±24 years (McCormac *et al.*, 2004; Reimer *et al.*, 2009).

Table 4.4 Modelled ages of layer `Boundaries` and `R_Dates` for the Blanche Cave stratigraphic sequence. All data are given as both 68.2% and 95.4% highest probability density ranges. Modelled ages calibrated using the IntCal09 calibration curve (Reimer *et al.*, 2009) with a Southern Hemisphere offset of 56±24 years applied (McCormac *et al.*, 2004). Samples 5U6B3-L8BW, 5U6B3-L8BW repeat, 5U6A3-L7BW, 5U6A3-L7BW repeat, 5U6B3-L4BW and 5U6B3-L4BW repeat were excluded from the model as they were so outlying that their inclusion prevented the model from running.

`Boundary`	**`R_Date`**	**Modelled calibrated age (cal yr BP)**				**`R_Date` Posterior `Outlier` probability**
		68.2%		**95.4%**		
		from	**to**	**from**	**to**	
Blanche Cave top		-49	-50	-49	-50	
Layer 01 top		14,791	-51	14,814	-51	
	5U6A3-L1	14,701	14,156	15,076	7,481	21
Layer 01 bottom		14,978	14,308	15,450	9,858	
Layer 02 top		15,172	14,647	15,594	13,401	
	5U6A3-L2BW	15,227	14,887	15,530	14,639	1
Layer 02 bottom		15,526	14,986	15,919	14,736	
Layer 03 top		16,066	15,405	16,318	15,118	
	5U6B3-L3	16,204	15,648	16,421	15,391	1
Layer 03 bottom		16,405	15,872	16,540	15,544	
Layers 04 to 09 top		16,576	16,246	16,667	15,926	
Layer 04 top		16,628	16,379	16,732	16,148	
	5U6B3-L4	16,660	16,436	16,781	16,264	1
	5U6B3-L4 repeat	16,681	16,452	16,804	16,300	1
Layer 04 bottom		16,765	16,466	17,018	16,331	
Layer 05 top		16,645	16,374	16,769	16,134	
	5U6B3-L5BW	16,684	16,441	16,817	16,273	1
Layer 05 bottom		16,811	16,461	17,080	16,320	
Layer 06 top		16,675	16,403	16,803	16,188	
	5U6B3-L6	16,735	16,487	16,848	16,352	1
Layer 06 bottom		16,859	16,498	17,091	16,370	
Layer 07 top		16,721	16,351	16,980	16,112	
Layer 07 bottom		16,978	16,486	17,174	16,332	
Layer 08 top		17,068	16,445	17,165	16,311	
	5U6B3-L8	17,111	16,492	17,226	16,341	35
	5U6B3-L8 repeat	17,112	16,488	17,238	16,339	38
Layer 08 bottom		17,148	16,503	17,284	16,372	
Layer 09 top		16,721	16,351	16,978	16,112	
Layer 09 bottom		16,979	16,487	17,175	16,332	
Layers 04 to 09		17,186	16,535	17,342	16,439	

Boundary	R_Date	Modelled calibrated age (cal yr BP)				R_Date Posterior Outlier probability
		68.2%		95.4%		
		from	to	from	to	
bottom						
Layers 10 to 13 top		17,336	16,865	17,419	16,657	
Layer 10 top		17,353	16,919	17,447	16,811	
	5U6A3-L10	17,227	16,948	17,449	16,885	3
	5U6A3-L10BW	17,375	16,975	17,533	16,846	33
Layer 10 bottom		17,399	16,995	17,617	16,868	
Layer 11 top		17,209	16,898	17,441	16,787	
	5U6A3-L11	17,211	16,933	17,449	16,851	5
Layer 11 bottom		17,387	16,965	17,491	16,881	
Layer 12 top		17,362	16,932	17,467	16,790	
Layer 12 bottom		17,398	16,991	17,586	16,862	
Layer 13 top		17,352	16,942	17,451	16,849	
	5U6B3-L13BW	17,375	16,982	17,465	16,915	1
Layer 13 bottom		17,396	17,003	17,539	16,905	
Layers 10 to 13 bottom		17,426	17,036	17,802	16,908	
Layer 14 top		23,963	19,917	24,036	17,576	
	5U6A3-L14	24,151	23,726	24,338	23,470	2
Layer 14 bottom		37,098	23,623	55,164	23,528	
Layers 15 to 18 top,		17,751	17,147	18,381	17,075	
Layer 15 top		19,249	18,394	19,369	17,588	
	5U6A3-L15	19,375	18,911	19,413	18,806	3
	5U6A3-L15BW	20,015	19,570	20,241	19,477	4
Layer 15 bottom		20,386	19,662	21,156	19,543	
Layer 16 top		19,800	18,842	19,994	17,734	
	5U6A3-L16	19,815	19,440	20,036	19,404	2
	5U6B3-L16BW	20,455	20,127	20,814	19,382	9
Layer 16 bottom		20,772	20,160	21,165	19,520	
Layer 17 top		18,696	18,077	18,781	17,491	
	5U6B3-L17	18,716	18,559	18,863	18,496	1
Layer 17 bottom		19,560	18,572	20,767	18,526	
Layer 18 top		18,554	17,312	18,595	17,235	
	5U6B3-L18BW	18,618	18,114	18,681	18,014	2
	5U6B3-L18BW repeat	18,645	17,440	19,151	17,289	37
Layer 18 bottom		19,252	18,149	20,535	18,053	
Layers 15 to 18 bottom		21,237	20,337	21,894	19,935	

Boundary	R_Date	**Modelled calibrated age (cal yr BP)**				R_Date **Posterior** Outlier **probability**
		68.2%		**95.4%**		
		from	**to**	**from**	**to**	
Layer 19 top		22,252	21,299	23,855	20,405	
	5U6B3-L19	22,388	22,051	24,001	21,533	8
	5U6B3-L19BW	24,046	23,473	24,303	21,664	18
Layer 19 bottom		24,431	23,676	24,768	22,052	
Layer 20 top		24,753	24,113	25,016	23,009	
	5U6A3-L20BW	24,878	24,441	25,094	24,098	4
Layer 20 bottom		26,105	24,326	28,838	24,114	
Layers 21 to 23 top		30,168	24,440	31,742	24,249	
Layer 21 top		31,617	24,696	31,925	24,406	
	5U6A3-L21BW	31,706	24,838	32,042	24,538	92
Layer 21 bottom		31,954	30,063	32,348	24,744	
Layer 22 top		31,771	31,013	32,059	24,345	
	5U6B3-L22	31,840	31,275	32,191	24,537	95
	5U6B3-L22BW	31,727	31,401	32,020	31,262	3
	5U6B3-L22BW repeat	31,716	31,381	32,000	31,236	3
Layer 22 bottom		31,889	31,485	32,231	31,356	
Layer 23 top		30,309	29,090	31,913	27,098	
	5U6B3-L23BW	30,305	29,705	31,803	29,449	10
Layer 23 bottom		31,644	29,868	31,931	29,663	
Layers 21 to 23 bottom		32,151	31,624	32,502	31,456	
Layer 24 top		32,488	31,900	32,751	31,660	
	5U6B3-L24BW	32,703	32,108	32,941	31,824	1
	5U6B3-L24BW repeat	32,675	32,085	32,899	31,801	2
Layer 24 bottom		32,982	32,187	33,656	31,843	
Layer 25 top		34,797	33,354	35,130	32,402	
	5U6A3-L25BW	35,087	34,491	36,167	33,625	3
Layer 25 bottom		37,165	34,511	40,131	33,988	
Layer 26 top		41,741	38,632	42,244	35,836	
	5U6B3-L26BW	42,021	40,661	42,700	39,507	3
Layer 26 bottom		43,696	40,898	46,473	39,896	
Layer 27 top		47,523	43,331	49,295	41,700	
	5U6A3-L27BW	49,089	45,832	50,003	44,803	4
Layer 27 bottom		59,997	46,406	59,997	46,259	
Blanche Cave bottom		60,001	60,000	60,001	60,000	

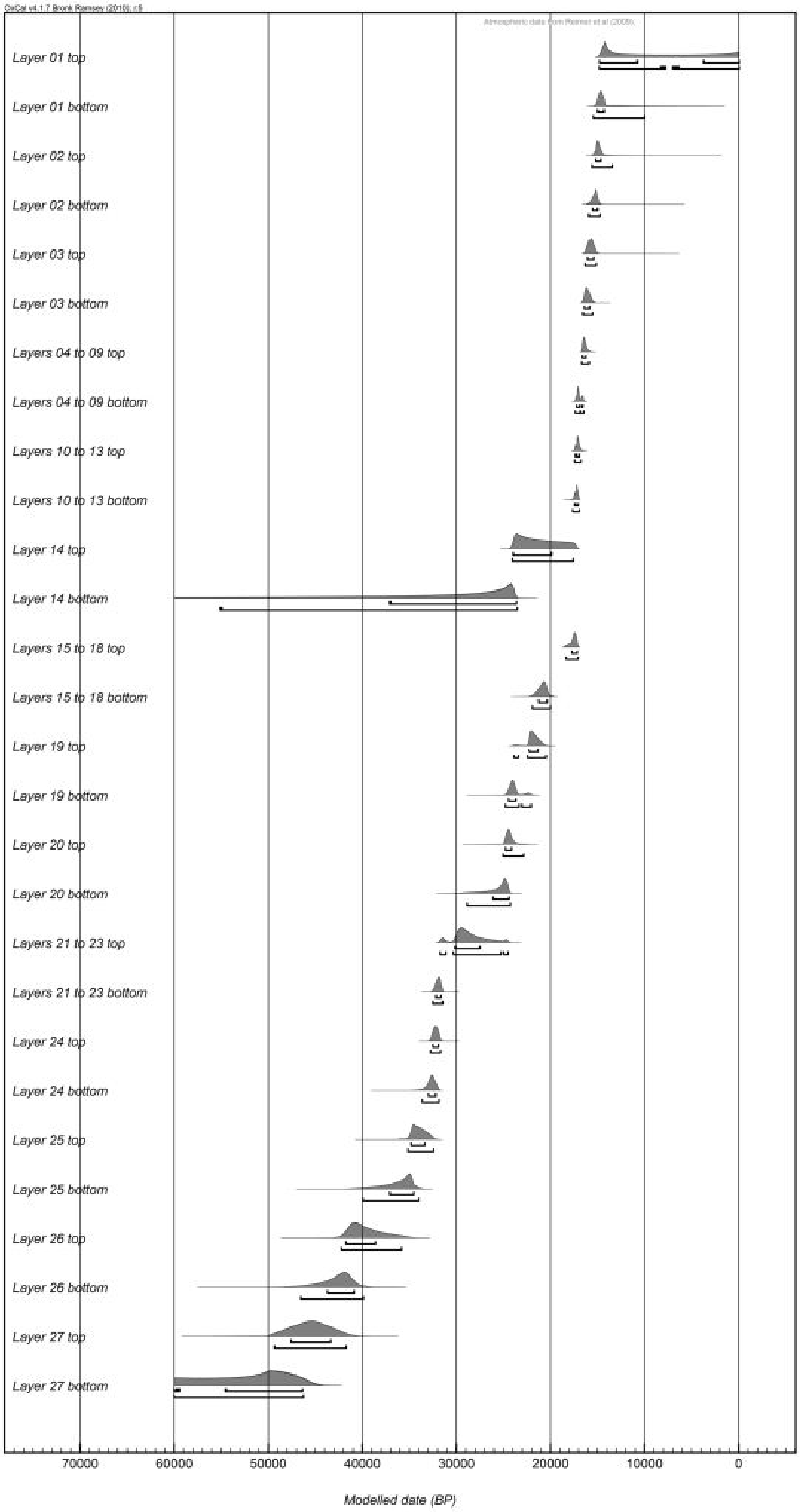

Figure 4.4 Modelled ages for layer `Boundaries` of the Blanche Cave stratigraphic sequence. Horizontal bars underneath each function represent the posterior 68.2% and 95.4% highest probability density ranges. Model generated using OxCal 4.1 (Bronk Ramsey, 2010), calibrated with IntCal09 and Southern Hemisphere offset of 56±24 years (McCormac *et al.*, 2004; Reimer *et al.*, 2009).

Table 4.5 Modelled, posterior duration of `Phases` (sedimentary units and lenses from Unit E) and suggested hiatuses between them for the Wet Cave stratigraphic sequence. All data are given as both the 68.2% and 95.4% highest probability density ranges. Modelled ages calibrated using the IntCal09 calibration curve (Reimer *et al.*, 2009) with a Southern Hemisphere offset of 56±24 years applied (McCormac *et al.*, 2004).

Unit /Lens `Phase`	**Modelled posterior `Phase` duration (cal yr)**				**Modelled posterior hiatus (cal yr)**				**Modelled posterior hiatus (cal yr)**			
	68.2%		**95.4%**		**68.2%**		**95.4%**		**68.2%**		**95.4%**	
	from	**to**	**from**	**to**	**from**	**to**	**from**	**to**	**from**	**to**	**from**	**to**
F	0	9,916	0	9,956					Units C–E			
					0	9,644	-1	9,655				
E	6,046	6,871	4,896	7,712								
					0	446	-4	2,213				
D	-4	15,470	-4	42,829					1	17, 681	0	17,743
					-16,424	1,001	-42,428	1,083				
C	0	1,859	-2	4,456								
					1,485	5,269	2	5,775				
B	1,434	4,944	365	7,492								
					1	2,127	-1	4,042				
A	20,448	25,781	18,343	30,429								
2:5/1	-4	4	-4	188								
					-4	4	-4	187				

Unit /Lens Phase	**Modelled posterior Phase duration (cal yr)**				**Modelled posterior hiatus (cal yr)**				**Modelled posterior hiatus (cal yr)**			
	68.2%		**95.4%**		**68.2%**		**95.4%**		**68.2%**		**95.4%**	
	from	**to**	**from**	**to**	**from**	**to**	**from**	**to**	**from**	**to**	**from**	**to**
2:5/2	-4	4	-4	219								
					-4	4	-4	289				
2:6/1	-4	4	-4	369								
					-4	4	-4	453				
2:6/2	-4	4	-4	263								
					-4	5	-4	184				
2:6/3	-4	5	-4	236								
					-4	5	-4	291				
2:6/4	-4	6	-4	180								

Table 4.6 Modelled, posterior duration of `Phases` (sedimentary layers) and suggested hiatuses between them for the Blanche Cave stratigraphic sequence. All data are given as both the 68.2% and 95.4% highest probability density ranges. Modelled ages calibrated using the IntCal09 calibration curve (Reimer *et al.*, 2009) with a Southern Hemisphere offset of 56±24 years applied (McCormac *et al.*, 2004). The duration of Layer 14 and potential hiatuses between Layer 15 and 14, and Layer 14 and 13 were not modelled as Layer 14 is reworked (see Section 3.1.2 for details).

Layer / Phase	**Modelled posterior Phase duration (cal yr)**				**Modelled posterior hiatus duration (cal yr)**			
	68.2%		**95.4%**		**68.2%**		**95.4%**	
	from	**to**	**from**	**to**	**from**	**to**	**from**	**to**
1	-2	14,720	-2	14,776				
					-1	488	-4	3,808
2	0	526	-4	1,726				
					1	565	-1	1,076
3	0	442	-2	931				
					0	381	-2	797
4–9	1	956	-1	1,220				
					-1	207	-4	461
10–13	-1	196	-4	699				
					0	389	-4	988
15–18	2,759	3,954	2,064	4,589				
					3	1,150	-1	1,899
19	3	3,108	0	3,425				

Layer / Phase	Modelled posterior Phase duration (cal yr)				Modelled posterior hiatus duration (cal yr)			
	68.2%		95.4%		68.2%		95.4%	
	from	to	from	to	from	to	from	to
					0	559	-4	1,746
20	-1	1,535	-4	4,425				
					-4	1,463	-4	4,703
21–23	1,689	7,670	0	8,080				
					-4	341	-4	7,289
24	0	536	-4	1,401				
					379	2,013	0	2,571
25	1	2,899	-2	6,006				
					3	5,352	1	6,426
26	1	4,014	-2	7,820				
					1	3,529	-1	6,431
27	1	8,745	-1	14,800				

Correlation of Wet and Blanche Cave Phases

Table C.1 (Appendix C) presents the likely chronological order of Wet and Blanche Cave `Boundaries` based on a 50% probability threshold. Ranges for the difference in ages between Wet and Blanche Cave `Boundaries` for which the null hypothesis is not rejected are presented in Table C.2 (Appendix C). Figure 4.5 presents the most likely relationships between the Wet and Blanche Cave units and layers.

Wet Cave Units A, B and C demonstrate a statistically significant relationship with groups of layers from Blanche Cave: Layers 27–21 together are temporally equivalent to Unit A; Layers 19 and 20 with Unit B; Layers 18–15 and 13–10 with Unit C (Fig. 4.5; Tables B.1 and B.2). The relationship of Layers 9 to 4 with Wet Cave units/lenses is less clear. The bottom `Boundary` of Layer 8 has a similar modelled age range (at 95.4% probability) to the bottom `Boundary` of Unit C while the lowest `Boundary` that Layers 9, 7, 6, 5 and 4 overlap with is the top of Unit C. Layers 1, 2 and 3 correspond to Unit E, but cannot be constrained to specific lenses from Unit E because there are only single ^{14}C determinations available for each `Phase`, limiting the model resolution.

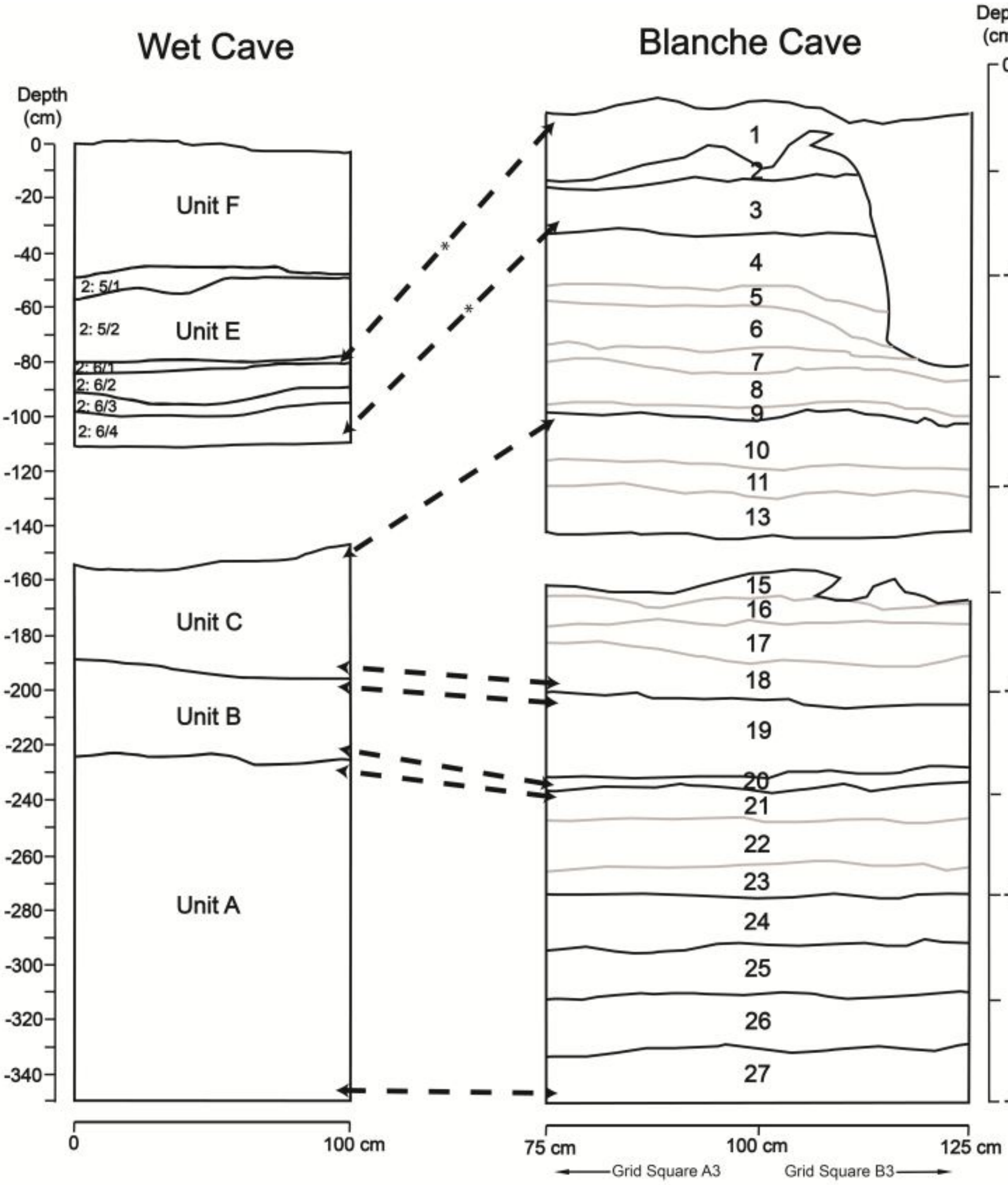

Figure 4.5 Correlation of Wet Cave units and Blanche Cave layers based on 50% probability threshold for relative order of `Boundaries` and null `Difference` distributions (i.e., where there is no difference in the modelled age of `Boundaries` between the two sites). Black dotted lines indicate relationship between Wet Cave units with groups of Blanche Cave layers. * represents an inferred correlation between Layers 1, 2 and 3 with Wet Cave lenses, based on the balance of probabilities, stratigraphic information and un-modelled ^{14}C determinations. Gaps in the stratigraphic sequences indicate position of Unit D (Wet Cave) and Layer 14 (Blanche Cave), both of which contain material of mixed age and origin. Groups of layers in Blanche Cave that were modelled as single `Phases` are indicated by the grey lines between stratigraphic layers.

Discussion

Wet and Blanche Cave Bayesian age-depth model priors

The aggraded sedimentary sequences in Wet and Blanche Caves reflect multiple modes of accumulation and source materials through the late Pleistocene to Holocene period, incorporating the last glacial cycle. Sedimentary characteristics range from aeolian and water transported red-brown sandy clays in Units A and Layers 27 to 21, to aeolian derived pale brown to yellow sands, intersected by likely water transported narrow lenses of darker, silty sands through Units B to E and Layers 20 to 2 (Macken *et al.*, 2013a). While the sequence of sediment types in Wet and Blanche Caves is similar, the depth profiles of analogous layers between the sites vary. The thicker depositional strata of Wet Cave contrast with the narrower and more discrete layers of Blanche Cave. As discussed in Macken *et al.* (2013a) these differences in the depth profiles of the two deposits likely result from local accumulation and post-depositional processes associated with each cave and depositional site, despite their geographic proximity (ca. 400 m).

As discussed by Bronk Ramsey (2008), depositional processes that should be considered when developing priors for Bayesian age models include (i) the mechanisms underlying deposition, (ii) random events and (iii) abrupt changes in deposition mode. Deposition of sediments into caves is controlled by a range of interacting factors including cave entrance type, prevailing climatic conditions, proximal vegetation cover and local sediments and their transport (e.g., Farrand, 2001; Hearty *et al.*, 2004; White, 2007). These factors are expected to have affected the mechanisms of sediment deposition into Wet and Blanche Caves, primarily aeolian (dust) and water transportation (Darrénougué *et al.* 2009; *Macken et al., 2013a*). Random events such as sedimentary slumping and transport of flood-sediments also shape stratigraphic sequences in caves (e.g., Kos, 2001) and have been observed in the Naracoorte Caves in modern times (e.g., filling of Wet Cave with flood sediments and surficial sediment washes and pooling water in Blanche Cave, following severe storms in December 2010). Stratigraphic features such as cut and fills, lenses and flame structures indicate that these random processes have influenced the two cave sequences during their accumulation through the last ca. 60,000 cal yrs. Abrupt changes in deposition are reflected by well-defined sedimentary transitions in both cave sequences (e.g., Unit A to B in Wet Cave), contrasting with other interfaces that are less clear and may reflect more gradual changes in sediment source and/or depositional mode (e.g., Layers 9 to 4 in Blanche Cave).

We suggest that the `Sequence` depositional model in OxCal, incorporating `Phases` of uniform prior duration is of particular utility when working with complex depositional environments, such as caves, as they are based on fewer assumptions about the rate and process of deposition when compared with other OxCal deposition models (e.g., `P_Sequence`) and that they are also suitable when modelling sequences for which there are few radiocarbon determinations relative to the timespan covered by the study site. By constructing the Wet and Blanche Cave Bayesian age-depth models within a `Sequence` framework, the order of the ^{14}C data within depositional units/layers could be integrated *a priori* based on an inference of stratigraphic superposition, such that deeper sediments were deposited earlier than those higher in the profile. The finest stratigraphic resolution that could be applied to the Wet Cave model was the depositional units, with the exception of Unit E for which the six lenses were well defined (Fig. 4.5). In contrast, the potential temporal resolution available in Blanche Cave was much finer, with 27 individual sedimentary layers that could be integrated as prior stratigraphic divisions within the model.

In two cases (Wet Cave Unit D and Blanche Cave Layer 14) the assumption of stratigraphic superposition was challenged by sedimentary data and/or observations, resulting in more complex model constructions but, nonetheless, could be accounted for using a series of nested `Phases`. The OxCal `Phase` function also allowed us to differentiate prior information for which we had varying levels of certainty, as was the case for the depositional and temporal relationships of groups of individual layers in Blanche Cave (e.g., Layers 9 to 4), particularly where sedimentary transitions were less clear. We note that these layer groupings in the Blanche Cave model contrast with the depositional units defined for Blanche Cave by Darrénougué *et al.* (2009). These differences arise because the priors for the Blanche Cave model were informed by observations directly from the exposed, excavated section from which the radiocarbon samples were collected. In addition, not all layers were evident in the stratigraphic core from which the units were defined (St Pierre *et al.*, 2012).

Outliers

Wet Cave `R_Dates` 5U10-1 and 5U10-6 were identified as 100% outliers and were thus excluded by OxCal in the model output. As noted by Bronk Ramsey *et al.* (2010), there are four main circumstances under which ^{14}C data may conflict with each other or with model priors. These are: (i) uncertainty in the reservoir ^{14}C concentration, (ii) sample contamination, (iii) incorrect ^{14}C measurement and (iv) uncertainties in the chronological models applied. In applying an offset to the calibration for the SH, we have tried to account for systematic uncertainties associated with scenario (i). While the offset we have applied might not be wholly accurate for the entire calibration range, at the chronological resolution available for Wet and Blanche Caves, the impact of this is expected to be negligible. Scenarios (ii) and (iii) may be sample-specific and result in individual or consistent offsets and biases among the ^{14}C measurements. These scenarios would be indistinguishable from each other based on the ^{14}C data alone. Scenario (iv) accounts for circumstances where sample(s) may be residual (older than context) or intrusive (younger than context) (Bronk Ramsey *et al.*, 2010). Uncertainties may also arise when parameters of a deposition model are not clearly defined (e.g., k, the number of accumulation events per unit depth for use in `P_Sequence` models). Such a scenario is not expected to apply to the less rigid `Sequence` models applied to Wet and Blanche Caves, unless the assignment of sequential `Phases` or overlapping sub-`Phases` is incorrect.

Sample 5U10-1 may be an outlier because of measurement issues (scenario iii); however, it is not possible to confirm which of the circumstances identified above most likely accounts for its far outlying ^{14}C determination in comparison to the other samples from Unit A. Sample 5U10-1 was previously noted as being wrongly associated with Unit A (Macken *et al.*, 2013a), consistent with scenario (iv) above. However, rather than representing re-worked material as a result of post-depositional mixing of younger sediments with the Pleistocene sediments of Unit A, it was hypothesised that the charcoal sample was disturbed by human activity, most likely during excavation when the deeper sections of the profile were exposed. The consistent character of the sediments from Unit A and Pleistocene ages for all other samples supports this hypothesis and argues against contamination of this section of the sequence with younger material, an important consideration for subsequence analysis of the fauna preserved in Unit A.

The rejection of sample 5U10-6 points to OxCal accepting the young Holocene age for Unit F given the model prior. The age constraint for the Wet Cave upper `Boundary` of AD 2000 strongly influences the modelled age for the upper `Boundary` of Unit F and likely contributes to the rejection of 5U10-6 which does not conform to this `Boundary` and is older than some samples from Unit E. In contrast to Unit A, for which little contamination is evident, it is more difficult to determine the extent of potential mixing of Pleistocene aged material into Unit F. The presence of European artifacts (glass and ceramic shards) in Unit F informed the assumption that materials, including charcoal, may have been deposited into Wet Cave in more modern times and also suggests that anthropogenic disturbance of the upper sections of the Wet Cave profile may have occurred (Macken *et al.*, 2013a). Based on these assumptions, sample 5U10-6 is expected to reflect contamination of Unit F with Pleistocene aged sediments, possibly by transport and mixing of sediments of different ages at the top of the sequence by human activity. In this case, rejection of sample 5U10-6 by OxCal is assumed to be consistent with scenario (iv) and points to post-depositional mixing of material of different ages in Unit F.

Blanche Cave samples 5U6A3-L21BW and 5U6B3-L22 were identified as outliers by OxCal and were heavily down-weighted in the model. The identification of these samples as outliers seemed somewhat unexpected compared to our prior expectation of the data (based upon casual ‘eyeballing’). As a sensitivity test of the whole model, an alternative Blanche Cave model was run with `R_Dates` from Layers 23 to 21 grouped together into a single `Phase` but without allocating them to individual sub-`Phases`. In this latter case, samples 5U6A3-L21BW and 5U6B3-L22 were no longer identified as outliers.

Unless otherwise specified in the model prior, a uniform `Phase` prior is assumed in OxCal. Within this prior, there is no bias towards longer or shorter `Phases` and it is assumed that all of the events within the group are equally likely to occur anywhere between the start and end of the `Phase`; that is, there is no internal sorting (Bronk Ramsey, 2009a). Of the three `R_Dates` from Layer 22, the unmodelled, calibrated age of sample 5U6B3-L22 is ca. 7,000 cal yr younger than the other two samples. Under the uniform `Phase` prior, if the true duration of the Layer 22 sub-`Phase` was represented by the `R_Dates`, then the ^{14}C determinations would be expected to be more evenly spread out (i.e., it would be extremely unlikely, though not impossible, to have two closely temporally spaced dates, with a third dating so much younger). On this basis the model found 5U6B3-L22 to be an outlier. Of the scenarios previously discussed, the reason for such an outlier could be because of either (ii), (iii) or (iv). As noted, in the alternative model in which all of the ^{14}C determinations from Layers 23 to 21 are assessed together under a uniform `Phase` prior (rather than constrained within individual sub-`Phases`), sample 5U6B3-L22 is not found to be an outlier because it is supported by the similarity in age with sample 5U6A3-L21. Despite this, we did not use the alternative model as it provided no capacity to gain additional precision or resolution available from the individual layers within the broader `Phases`, if they were found to be chronologically independent within the model. However, as samples 5U6A3-L21BW and 5U6B3-L22 were found to be outliers within the more complex final model adopted, no greater resolution was gained by assessing these layers individually. We suggest that the most likely reason for this is that the samples are intrusive (i.e., younger than the context), limiting the resolution at which the layers within the broader `Phase` of Layer 23–21 can be evaluated.

Posterior outlier probabilities of 18 to 38% for samples from Layers 8, 10, 18 and 19 suggests that the likelihoods do not fit the model prior particularly well. That said, despite the elevated outlier probabilities of these samples compared to the initial 5% prior probabilities applied, there is still a greater probability of the samples not being, rather than of their being, outliers as all posterior probabilities are < 50%. Using the `Outlier_Model`, OxCal downweights the impact of these samples on the model output.

In contrast, ^{14}C determinations for samples 5U6B3-L17 and 5U6B3-L18BW were discarded by Darrénougué *et al.* (2009) who considered that they had infiltrated the stratigraphic section, presumably during sample collection. However, the posterior outlier probabilities for these samples in the model do not support this assertion. If the model prior for Blanche Cave had been set such that Layer 19 is older than (>) Layer 18 > Layer 17 > Layer 16, then it is highly likely that samples 5U6B3-L17 and 5U6B3-L18BW would have been identified as outliers. However, the model prior grouped Layers 18 to 15 within a single `Phase` highlighting that whether or not samples are identified as outliers clearly depends on the specifics of the model prior applied.

Holocene ^{14}C determinations from Blanche Cave Layers 4, 7 and 8 were excluded from the model as, even with the `Outlier_Model` applied, the model would not run with these samples included. Despite their exclusion from the model, the Holocene aged samples are expected to represent post-depositional reworking of younger material through the sedimentary section (St Pierre *et al.*, 2012). This inference is supported by a U-series age of 4.72±0.21 ka from a soda straw stalactite collected from nearby grid square A1 at a depth of 20–25 cm, corresponding to Layers 3 and 4 in grid squares A3 and B3 (St Pierre *et al.*, 2012; Fig. 4.5). Further, it is less likely that the Holocene ^{14}C determinations are incorrect due to measurement error or disturbance during collection as in each of Layers 4, 7 and 8, two samples provide very similar ages that are younger than the ^{14}C determinations of adjacent samples.

Additional Holocene aged soda straw stalactites were measured from depths 0–5 cm, 5–10 cm and 55–60 cm from grid squares A1 and B2, corresponding to Layers 1, and 17 and 18 in grid squares A3 and B3 respectively (St Pierre *et al.*, 2012). As noted by St Pierre *et al.* (2012), reworking may have occurred during or following deposition as a result of material worked down through cracks in the sediment during dry `Phases` or worked down as a result of trampling by animals or humans. However, it is more difficult to explain why many of the ^{14}C and soda straw U-series ages are relatively well ordered such that age increases with depth (St Pierre *et al.*, 2012). The sedimentary layers described from grid squares A3 and B3 are moderately intact; flame structures present in Layers 4 and 8 and a laterally constrained channel fill from Layer 1 through to Layer 7 in grid square B3 provide some evidence of physical disturbance (Fig. 4.5). However, given the limited lateral extent of these structures, it is unlikely that these features represent significant, broad scale turnover or reworking of sedimentary material through the profile. Despite this, as multiple and varied chronological samples returned Holocene ages for the upper section of the deposit through Layer 8, we caution interpretations of the vertebrate fossil material from these sections which, being small, may have moved through the sedimentary layers in a similar way to the charcoal and soda straws. In contrast, we suggest that the Holocene-aged straw measured from grid square A1 at 55–60 cm depth may not reflect contamination of Layers 17 and 18 in grid squares A3 and B3; the ^{14}C data from these layers accord well with the adjacent samples within the combined `Phase` of Layers 18–15 with none rejected as outliers.

Phase durations, hiatuses and chronological interpretation

As a result of the relatively small number of ^{14}C data available relative to the long temporal coverage of the two sites, the precision of the unit and layer `Boundaries` is on the order of 100s to 1000s of years. If there were more radiocarbon data, the modelled `Boundaries` would be expected to be more precise and, in turn, allow for more precise estimates of the durations of individual units and layers and potential hiatuses between them. This would also allow for a more robust comparison of the temporal correlation of the two sites. However, despite the overall low precision of the modelled `Boundary` ages, statistical estimates of the minimum and maximum age of individual depositional `Phases` would otherwise have been unavailable from the unmodelled ^{14}C determinations.

The modelled `Phase` durations for Wet Cave reveal slow and rapid phases of accumulation through the depositional sequence. Unit A represents the longest phase between both Wet and Blanche Caves, followed by Units E and B. In the case of Units C, D and F, the null hypothesis of instantaneous accumulation (or, at least, deposition from <1 calendar year) cannot be rejected on the basis of the dating evidence available. For Unit C, this results from having only a single radiocarbon measurement from this Unit. The same is true for Unit F, where the identification of sample 5U10-6 as an outlier (100% posterior `Outlier` probability) gave only a single 'reliable' radiocarbon determination. It is expected that, were additional radiocarbon (or other chronological) data available, these units would not, in reality, represent instantaneous deposition. The presence of silty laminations through the sands of Unit C supports this assumption, as such banding or horizonation is rarely associated with sediments that have slumped or been deposited during a single event, as observed in the homogenous sands of nearby Robertson Cave (Forbes *et al.*, 2007). Sandy laminations observed in Unit F also argue against instantaneous deposition for the upper-most section of Wet Cave.

Having only a single radiocarbon measurement for Unit D accounts for the inability of the model to discount the null hypothesis of instantaneous deposition for this `Phase`, as noted for Units C and F. However, the mottled orange and brown, poorly sorted sandy clays of Unit D do not contain internal structuring as observed in the former two units. The sedimentary character of Unit D and presence of megafaunal bone material suggests that it contains sediments of similar type, origin and age as Unit A (Macken *et al.*, 2013a). An hypothesis for the presence of Unit D at the top of Pit 1, stratigraphically above Unit C, is that it represents late Pleistocene aged materials from another part of the cave, transported and slumped down the sedimentary cone during accumulation of the Wet Cave sequence. If this were the case, then it may represent an anomalous, single 'instantaneous' event that re-worked sedimentary and fossil material of mixed origin and age.

In Blanche Cave, only a single `Phase` (Layers 18–15) returned a modelled duration statistically indistinguishable from 0 years at the 95.4% confidence level. Limited rejection of the null hypothesis for the majority of Blanche Cave `Phases` again results from the small number of radiocarbon measurements for many layers. However, the sedimentary and stratigraphic character of some layers suggests that they may represent single, 'instantaneous' depositional episodes associated with surficial water movement of sediments during single flood events (e.g., Layers 7, 9 and 20). For these layers, rejection of the null is in accord with the inference of rapid deposition based on sedimentary observations.

The coarse resolution of the modelled `Boundaries` for both the Wet and Blanche Cave sequences similarly limits the capacity of the model to detect temporal gaps in accumulation between successive `Phases` and/or where there may be missing material between the end of one `Phase` and the start of the next. In all cases, the null hypothesis for contiguous deposition was not able to be rejected at the 95.4% confidence level. A hiatus of 1,485 to 5,269 cal yrs between Units B and C and of 379 to 2,013 cal years between layers 25 and 24 was measured at the 68.2% confidence level. As these hiatuses are not supported at the higher confidence level, there is little that can be concluded from these values; however, as both Wet and Blanche Caves have large open-roof window entrances, it is unlikely that prolonged hiatuses in deposition into the caves occurred due to the constant movement and flux of dust across the landscape. The potential for post-depositional erosion of sediments from these sites is more difficult to ascertain.

In contrast, breaks in deposition have been argued for two late Pleistocene cave sequences from south eastern Australia; the inner chamber of Robertson Cave located ca. 6 km south of Wet Cave and McEachern's Deathtrap Cave, ca. 100 km south of the Naracoorte Caves World Heritage Area. The sedimentary sequences from both of these caves reflect hiatuses in deposition over the peak of the last glacial cycle, the Last Glacial Maximum (LGM; Kos, 2001; Forbes *et al.*, 2007). McEachern's Deathtrap Cave has a narrow-pipe entrance that became blocked with sands during the LGM, contrasting with the larger roof-window entrances of Wet and Blanche Caves that are not expected to become blocked in this way. Although Robertson Cave has a roof-window style entrance, the inner chamber is expected to have blocked as a result of high sediment loads in the entrance chamber, which restricted movement through narrower caverns in the cave system connecting the two chambers. In McEachern's Deathtrap Cave there is also evidence for the post-depositional erosion of sediments as a result of groundwater fluctuations, resulting in a gap in the record.

A potential hiatus in deposition between Units E and F of Wet Cave was indicated by the presence of bat guano derived materials at the transition between these units, reflecting minimal sediment input prior to the deposition of the dark brown silty sands of Unit F (Forbes and Bestland, 2006; Macken *et al.*, 2013a). The presence of a flowstone at the transitional boundary of Units E and F was also noted in the original excavation notes for Wet Cave; however, it is unknown if the flowstone was attached to the cave wall or free floating, limiting the extent to which it confirms a hiatus in sediment deposition at the end of the Pleistocene in Wet Cave. There is no other sedimentary or stratigraphic evidence to indicate temporal breaks and/or the loss of sediments through erosion in Wet Cave, nor in Blanche Cave. However, we suggest that the lack of statistically significant evidence for depositional breaks detected through the sequences is more likely a consequence of the dating resolution, rather than implicit evidence for continuous deposition into Wet and Blanche Caves during the last glacial cycle. Ultimately, more ^{14}C determinations or other dating evidence is required to improve the resolution of the modelled `Boundaries` and hence, detection of potential hiatuses that may be of shorter duration than the resolution of the current chronology.

Correlation of Wet and Blanche Cave Phases

As discussed by Blaauw *et al.* (2007), demonstrating synchronicity of events is dependent upon the assumed duration of the events of interest. In the case of Wet and Blanche Caves, the events are depositional episodes that are expected to represent, through sedimentary and stratigraphic characteristics, prevailing climatic conditions. Thus, transitions between events represented by stratigraphic boundaries are assumed to ultimately reflect changes in a range of interacting and complex climatic and depositional parameters operating at both a local and regional scale (Forbes and Bestland, 2007; Forbes *et al.*, 2007; Macken *et al.*, 2013a). In most cases, the Blanche Cave layers were expected to be of shorter duration than the Wet Cave units as the latter represent individual phases that together may be consolidated into longer depositional periods (units) characterised by (a) similar sediment type and depositional mode and (2) relatively constant prevailing climatic conditions during their deposition. Relationships between the Wet and Blanche Cave `Phases` support this assumption as each Wet Cave unit is temporally equivalent to multiple Blanche Cave layers (Fig. 4.5).

On the balance of probabilities, Blanche Cave Layers 27 to 21 together overlap in age with Wet Cave Unit A as reflected in the order of the associated `Boundaries` and the statistically indistinguishable posterior calibrated hpd ranges of Unit A top and Layer 21 bottom. Layers 27 to 21 in Blanche Cave therefore represent sub-divisions of the pre-LGM period which may be used to assess the fossil assemblage at a finer resolution, contrasting with the longer time-averaged fauna (i.e., the number of years an assemblage took to accumulate; Hadly, 1999) represented in Unit A as a whole and combined Layers 27 to 21.

Blanche Cave Layers 19 and 20, 18–15 and 13–10 similarly provide a reliable, finer resolution for the LGM period represented in Wet Cave Units B and C, respectively. Modelled ages for the start and end of deposition of Layers 19 and 20 are both statistically indistinguishable from the start and end of the deposition of Unit B; however, given the relative stratigraphic positions of Layers 19 and 20, they are expected to provide successive sub-divisions of the first LGM period. A similar pattern is noted for the modelled ages of the start and end of the deposition of combined Layers 18–15 and 13–10 with Unit C but nonetheless, provide two sub-divisions of the second LGM period represented in the deposits. The statistical correlation of multiple `Boundaries` between Wet and Blanche Cave arises as a result of the resolution of the model, limiting its ability to temporally differentiate the upper and lower `Boundaries` of `Phases`, similar to the impacts noted for the durations and hiatuses.

For Layers 9–4, there is insufficient information to reject the possibility that they temporally overlap both Units B and/or C of Wet Cave. As these layers contain Holocene aged material, the temporal relationship of Layers 9–4 with Wet Cave is not meaningful. In addition, these layers are considered to be unsuitable for inclusion in the analyses of the small mammal faunas unless it can be shown that no fossil material has intruded into this section of the Blanche Cave stratigraphy.

The relationships between Blanche Cave Layers 1 to 3 with Wet Cave are not well differentiated at the available resolution of the modelled `Sequences`. `Order` suggests that Layer 3 is temporally constrained between the bottom `Boundary` of Unit E and the bottom `Boundary` of Lens 2:5/2. The upper `Boundary` of Layer 1 is statistically indistinguishable from all Wet Cave `Boundaries` from 2:6/3 top to Unit F top, a consequence of the insufficient resolution of the modelled data to identify a more precise relationship. As noted in the results, the modelled age for the upper `Boundary` of Layer 1 is strongly influenced by the prior applied for the top of the Blanche Cave sequence of AD 2000. While this model prior was appropriate for constraining the minimum age of the sequence (based on disturbance through human access to the site in modern times and the presence of *Pinus* pollen indicating European settlement; Darrénougué *et al.*, 2009), it is unlikely to be the true minimum age for fossil material contained within Layer 1. As there was only one radiocarbon determination available for Layer 1, the true age of this `Phase` is not well represented by the model. While the correlation is consistent with the output of the model, knowledge of the two sites suggests that Layer 1 is more likely to be temporally equivalent to Lenses 2:6/4 to 2:6/2 and cautions inferences that may be drawn from the fossil material of Layer 1 when compared with Wet Cave.

Conclusion

Bayesian age-depth models were developed for the fossil-bearing sedimentary sequences of Wet and Blanche Caves in south eastern South Australia, utilising available ^{14}C determinations and stratigraphic information. At the dating resolution available from these data, the modelled ages for the start and end of successive units and layers within the two sites show that deposition was contiguous and characterised by phases of slower and more rapid accumulation, as is common for many cave deposits. Statistically supported temporal correlation of depositional phases between Wet and Blanche Caves provides a robust basis for comparative analysis of the fossil assemblages contained within them, and builds upon previous stratigraphic correlations that were based only on sparse, individually calibrated radiocarbon data and sedimentary descriptions.

In contrast to other age-depth models available in OxCal, `Sequence` was applied for modelling Wet and Blanche Caves where only the relative order of events within the two sites could be incorporated as a model prior. By incorporating the depositional events as `Phases` within the model, we were also able to incorporate uncertainties associated with the internal continuity of individual layers and units. `Phases` also offered flexibility in the model where there was more uncertainty associated with both (a) the stratigraphic relationships of individual layers in Blanche Cave and (b) known reworked layers which nevertheless provided extra *terminus post quem data* for overlying layers.

Despite the rigour applied to the chronologies of Wet and Blanche Caves, the resolution of the models is limited by the few ^{14}C determinations relative to the late Pleistocene to Holocene time-span covered by the sites. However, while we acknowledge that the resolution of the model would be improved if more ^{14}C determination were available, we also recognise the practical limitations in obtaining large numbers of radiocarbon data in palaeontological studies. These include the availability of research funds and samples suitable for dating, as well as limitations presented by the time resolution captured in study sites. In light of these challenges, we recommend that, where possible more than one sample is obtained from each stratigraphic layer. Nonetheless, analysis of radiocarbon data within a Bayesian framework provides a means of critically evaluating site chronologies, regardless of the number of ^{14}C determinations available, and provides a means of quantifying the uncertainties associated with the start and end of different accumulation phases.

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5. Late Quaternary small mammal faunas of the Naracoorte Caves World Heritage Area

Citation

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Contribution of Authors

Amy Macken:

- Devised and planned the project.
- Identified and registered the specimens from Wet, Robertson and Blanche Cave used for the research presented in the manuscript.
- Prepared manuscript for publication.

Elizabeth Reed:

- Excavated fossil material from Robertson Cave Entrance Chamber and Blanche Cave used in the research.
- Provided funding for the project.
- Provided comments on the manuscript and advice on revisions.

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Signed ....Date ....

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Abstract

The vertebrate fossil deposits of the Naracoorte Caves in south eastern South Australia preserve a long-term record of local faunas. We provide here an updated list of small mammal faunas of late Quaternary (*c.* <50 ka) aged fossil assemblages from Wet, Robertson and Blanche Caves as a basis for understanding past and future patterns in species occurrence. The updated list includes seven species previously unrecorded from the <50 ka period from this region. Of these, two species (*Dasycercus* sp. indet. and *Pseudomys novaehollandiae*) are new to the Naracoorte fossil record and have no known regional historical (European colonisation to 1950) or contemporary (post 1950) distribution. Review of fossil collections such as these is crucial for providing up-to-date species occurrence data which can be used to establish baselines of past species diversity and information about the past geographic ranges of individual taxa through time.

Introduction

The vertebrate fossil deposits of the Naracoorte Caves World Heritage Area (NCWHA) contain a record of faunal diversity for the south east region of South Australia spanning the Middle Pleistocene to Holocene (Reed and Bourne, 2000, 2009). Research into the Naracoorte Cave fossil assemblages has made significant contributions to knowledge of (i) Middle to Late Pleistocene faunal communities of southern Australia (e.g., Prideaux *et al*., 2007; Macken *et al*., 2012), (ii) taxonomy and systematics of extinct and living faunas (e.g., Prideaux and Wells, 1998; Williams, 1999; Prideaux, 2004), (iii) vertebrate taphonomy of cave deposits (e.g., Reed, 2006, 2009) and (iv) environmental change over the Pleistocene (e.g., Forbes and Bestland, 2007, Darrénougué *et al*., 2009, Macken *et al.* 2013a). As the Naracoorte Caves contain 'megafauna' species such as *Thylacoleo carnifex, Zygomaturus trilobus, 'Procoptodon' gilli* and *Wonambi naracoortensis,* research into the cave assemblages has provided insights into the diversity, distribution and extinction dynamics of this group of large body-sized faunas at the end of the Pleistocene (e.g., Pate *et al*., 2006; Prideaux *et al*., 2007).

The Naracoorte Caves also contain extensive assemblages of smaller body-sized taxa, providing a reference for the diversity, distribution and historical extinction dynamics of these often understudied faunas through the late Quaternary (e.g., Macken *et al*., 2012). Three caves (Wet, Robertson and Blanche Cave) within the NCWHA contain well dated small mammal-dominated assemblages which together span the late Quaternary from *c*. 50 ka to 1 ka (Forbes *et al*., 2007; Darrénougué *et al*., 2009; St Pierre *et al*., 2009; St Pierre *et al*., 2012; Macken *et al.* 2013). As largely owl pellet derived faunas, the fossil collections from these caves are bone rich and have yielded valuable information about the composition and structure of the local small mammal community through the last glacial cycle and pre-European times (McDowell, 2001; Laslett, 2006).

In this study, collections of small mammal fossils from previously studied and new assemblages were examined with the aim of providing an up-to-date list of small mammal faunas for the late Quaternary period. Of particular interest were observed patterns in species occurrence in the late Quaternary period when compared with older Naracoorte Cave deposits as revealed by previous faunal lists for the NCWHA. Six species of small body-sized Dasyuridae (*Antechinus agilis, Antechinus minimus, Antechinus stuartii, Antechinus swainsonii*, *Dasyurus maculatus* and *Phascogale calura*) and two Potoroidae (B*ettongia penicillata* and *Potorous tridactylus*) are not known from the <50 ka aged assemblages of Wet, Robertson and Blanche Caves, but are identified from one or more older assemblages within nearby Victoria Fossil and Cathedral Caves (*c*. 530 ka to 70 ka; Prideaux *et al*., 2007; Reed and Bourne, 2000, 2009; Macken *et al*., 2012). By comparison, three species of small possum, *Cercartetus concinnus*, *Petauroides volans* and *Petaurus norfolcensis* are listed from the late Quaternary (<50 ka) assemblages but have no known older fossil distribution (Reed and Bourne, 2000, 2009).

The updated species list for the late Quaternary aged assemblages presented here provides a basis for exploring the accuracy and significance of these observed patterns in species occurrence, as well as patterns in species local and regional biogeography from historical to present times. As continued research into late Quaternary aged fossil assemblages of the NCWHA aims to increase our knowledge of local faunas (Reed, 2012), ongoing review of small mammal assemblages provides a valuable foundation by ensuring that species occurrence data is widely available and up-to-date.

Methods

Study site

The NCWHA is located in south eastern South Australia, 12 km from the township of Naracoorte (Fig. 5.1). The geological and palaeontological setting of the Naracoorte Caves has been well documented (Wells *et al*., 1984; Reed and Bourne, 2000; Forbes and Bestland, 2007; Macken *et al*., 2011). Three caves contain late Quaternary aged fossil assemblages dating from *c*. 50 ka to the Holocene (Wet, Robertson and Blanche Cave). As the stratigraphic and geochronological context of assemblages from these caves have been described elsewhere (Pate *et al*., 2002; Pate *et al*., 2006; Forbes and Bestland, 2007; Forbes *et al*., 2007; Darrénougué *et al*., 2009; St Pierre *et al*., 2009; St Pierre *et al*., 2012; Macken *et al.* 2013), only the minimum and maximum ages of the deposits are summarised here (Table 5.1).

Table 5.1 Maximum and minimum ages of the late Quaternary aged deposits of the Naracoorte Caves World Heritage Area. Radiocarbon ages calibrated using INTCAL09 (Reimer *et al.* 2009) in OxCal4.1 (Bronk Ramsey 2009).

Site	**^{14}C age yr BP (1σ)**	**cal yr BP (2σ)**
Blanche Cave, 3rd Chamber	43,260±1840[1] to 12,470±60[2]	49,986–44,696 to 15,032–14,168
Robertson Cave, Inner Chamber	31,450±250 to 8,080±100[3]	36,584–35,092 to 9,290.5–8,637.5
Robertson Cave, Entrance Chamber	20,070±70 to 1,085±30[4]	24,343–23,681 to 1,056–935[3]
Wet Cave, Entrance Chamber	45,200±1800 to 740±40[5]	45,984–43,334 to 735–569

4 St Pierre *et al.* (2012)

5 Darrénougué *et al.* (2009)

6 Forbes *et al.* (2007)

7 Radiocarbon determinations for RCEC performed at ANU Radiocarbon Dating Centre, Canberra by Dr. S. Fallon. ANU sample numbers S-ANU27630 and S-ANU27618 (see Fallon *et al.* 2010 for technical details of technique).

8 Pate *et al.* (2002; 2006)

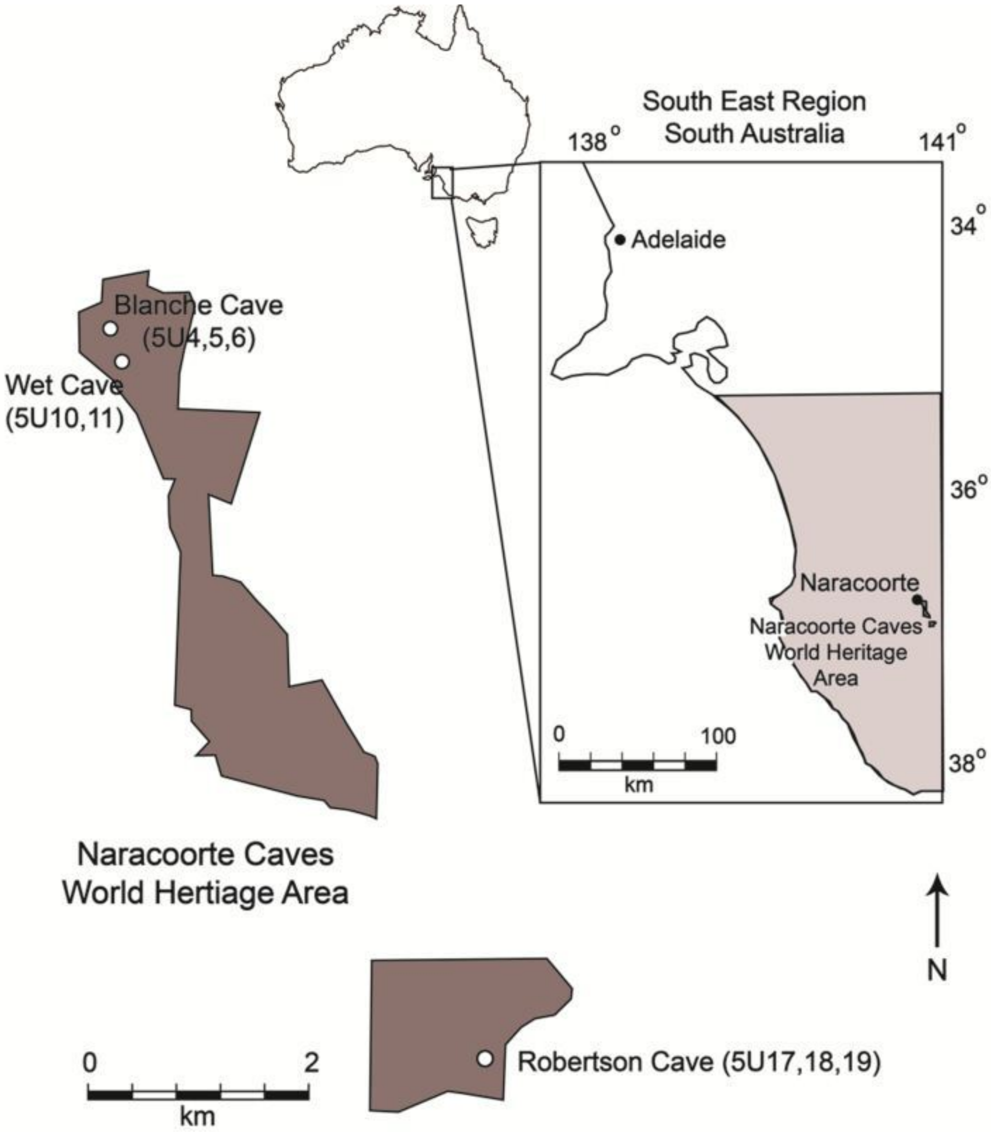

Figure 5.1 Location of the Naracoorte Caves World Heritage Area in south east South Australia. Relative locations of Wet, Blanche and Robertson Caves indicated in map of the Naracoorte Caves World Heritage Area.

Fossil assemblages

Wet Cave (5U10, 11)

A late Quaternary aged sedimentary and fossil sequence within the entrance chamber (5U10) of Wet Cave was first studied by McDowell (2001), following excavation of the site in 1997 and 1998. The sequence was excavated according to sedimentary layers across two separate 1 m^2 pits, identified as Pit 1 (lower) and Pit 2 (upper) to a combined depth of 3.5 m. Each pit was divided into four 0.5 m^2 quadrants (A–D), which were excavated separately (McDowell, 2001). A review of the stratigraphy and chronology for the Wet Cave deposit is compiled in Macken *et al.* (2013a).

McDowell (2001) analysed a total of 17,214 cranial specimens from Wet Cave, the largest single fossil sample identified and analysed from the NCWHA. Marsupial specimens from all four quadrants were re-examined in the current study. Muridae specimens composed 81% of the assemblage analysed by McDowell (2001). Due to this volume of material, only a sub-sample of Muridae specimens from the assemblage was re-examined in the present study. In layers where the total murid number of identified specimens (NISP) was <300 as documented in McDowell (2001), material from all quadrants (A–D) was re-examined. For layers where the total NISP was >300, only specimens from a single quadrant were assessed. In most cases, sub-samples were examined from quadrant A with the exception of layer 1:7/3 where the sub-sample was derived from quadrant C. Previously unsorted and unidentified specimens from this collection were also identified.

Only those specimens re-examined from the Wet Cave assemblage are discussed here. The studied specimens were registered to the Flinders University Palaeontology Register (FU20000–20997) and are stored in the Palaeontology Laboratory on site in the NCWHA.

Robertson Cave (5U17, 18, 19)

Two sites within Robertson Cave contain late Quaternary aged faunal assemblages. The Robertson Cave Inner Chamber (RCIC) fossil assemblage was excavated and analysed by McDowell (2001). Due to the similar taxonomic composition of the

RCIC to other late Quaternary aged assemblages of the NCWHA, only specimens of species unique to this deposit were re-examined.

Fossil material was excavated by EHR from the entrance chamber of Robertson Cave (RCEC) in a pilot study of the site consisting of a 0.5 m^3 pit excavated across five layers of varying depth. The main excavation, also conducted by EHR, was composed of two 1 m^2 grid squares (1 and 2) which were excavated by strata in layers of approximately 5 cm to a total depth of 1 m. Sedimentary analysis and further dating of this deposit is currently under investigation by one of us (EHR).

Small mammal specimens from the RCEC excavations (pilot and grid-square 1) were examined and identified in the current study. Specimens from the pilot excavation were registered to the Flinders University Palaeontology Register (FU9000–9062 and 9142–9151) and are stored in the Palaeontology Laboratory on site in the NCWHA. Specimens from grid square 1 were registered to the Palaeontology collection of the South Australia Museum (SAM P47215–47682).

Blanche Cave (5U4, 5, 6)

Small mammal specimens from Blanche Cave were identified from collections excavated by EHR from a 1 m^3 grid square (A3) in the 3rd Chamber deposit (see Laslett (2006) and Darrénougué *et al*. (2009) for site details and chronology). Specimens from two layers (4 and 14) were identified from samples excavated from the neighbouring grid square B3. Grid squares A3 and B3 were excavated according to 27 discrete sedimentary layers ranging from 1 cm to 6 cm thick to a total depth of 1 m.

As observed in the Wet Cave assemblage, murids were the most abundant taxonomic group within the Blanche Cave A3 and B3 fossil collections. Of a total NISP of 22,678 from grid square A3, 80% of the assemblage were murids. As a result of the large volume of specimens, murids were sub-sampled from the deposit as completed for Wet Cave. For excavation layers where the murid NISP was <300, all specimens were identified. In cases where the layer NISP was >300, a quarter of the layer sample was examined. Sub-samples were determined using a random sample of one quarter of the volume of material excavated from each layer of the grid square. During excavation, the volume of each bag of sediment and bone was controlled to 24 litres. As the number of bags per layer was recorded, a quarter of the sample by volume could be calculated by dividing the number of bags excavated for a given layer by four. Bags were randomly assigned numbers during the original processing of the material and for the sub-sampling, bags were selected in order from bag 1 to bag 2 etc. In order to randomly select a fraction of the specimens from a bag where necessary (e.g., when half the volume of material from a bag was required), all craniodental specimens from the bag were laid out on a numbered grid square. A random number generator in Excel was then used to select the required fraction of specimens for the sub-sample.

All Blanche Cave specimens were registered to the Flinders University Palaeontology Register (FU14100–14685) and are stored in the Palaeontology Laboratory on site in the NCWHA.

Accumulation mode

The density and quantity of specimens from Wet Cave, Robertson Cave Inner Chamber and Blanche Cave 3rd Chamber is primarily the result of accumulation of bone in pellets regurgitated by owls. These caves have large, roof collapse window entrances, facilitating owl habitation. Evidence for owl collection is reflected in the proportion of small mammal remains when compared with larger animals in these deposits. In grid square B2 from Blanche Cave, mammals with a maximum body mass of <100 g composed between 74 and 86% (average 79.6%) of the sample through the depositional sequence, and those of body mass 101–500g only 3 to 14% (average 6.6%; Laslett, 2006). A similar bias is reflected in RCIC and Wet Cave where *c*. 80% of the two assemblages are composed of small mammals of body mass <300 g (NB. No small mammals of body mass 301–500g were identified in the study; McDowell, 2001). Age class analysis showed that specimens from species of intermediate body mass in all three sites were overrepresented by juveniles, a common feature of owl pellet derived assemblages (Andrews, 1990; McDowell, 2001; Laslett, 2006). The presence of digestive corrosion on small mammal bones further supports this mode of accumulation (Laslett, 2006; Reed, 2012). *Tyto alba* (Barn Owl) has been identified as the primary collecting agent of the RCIC and Wet Cave assemblages (McDowell, 2001); although, *Tyto* *novaehollandiae* (Masked Owl) is expected to have contributed some small mammal material to Blanche Cave as well (EHR, pers. obs.)

The taphonomic history of the RCEC is currently being investigated by EHR. Preliminary analysis suggests that a range of collecting modes may have resulted in the bone assemblage. Owl pellet deposition is expected to be the primary accumulating mode with some input via pitfall entrapment, death of within cave inhabitants and carnivore accumulation (EHR, pers. obs.).

Species identification

Here, small mammals are defined as those species of body mass ≤2.5 kg. Although of greater body mass, *Trichosurus vulpecula* and *Dasyurus maculatus* were included in the list as they are commonly represented by juvenile animals that are within the size range for owl predation. *T. vulpecula* is also expected to have been a cave inhabitant over the late Quaternary as observed with this species in the NCWHA today.

For all assemblages, bulk sediment and bone removed from the caves during excavation were wet-screened in sieves of 1 to 2 mm^2. Once dry, all sieved material was sorted for diagnostic elements (maxillae, dentaries and teeth). For identification, cranio-dental specimens were compared with modern specimens from the South Australian Museum (SAM) and the Australian Museum (AM). Comparative material was also sourced from the SAM sub-fossil and the Naracoorte Caves fossil collections. Published descriptions of species maxillary, mandibular and dental morphology were also used to aid species identification where available.

As taxonomic descriptions for the majority of the taxa identified from the Naracoorte Caves are published elsewhere, we provide descriptions and diagnoses only for two unknown species of Dasyuridae identified from the studied assemblages (refer Appendix D).

Results

Diversity

A total of 41 species were identified from the fossil assemblages of Wet, Robertson and Blanche Caves (Table 5.2), representing an addition of seven species to the known diversity of the late Quaternary period from *c.* <50 ka for the Naracoorte Caves. Of these, five are known from older Naracoorte Cave deposits (*Antechinus* sp. cf. *A. agilis, Dasyurus maculatus, Phascogale calura, Bettongia penicillata* and *Potorous tridactylus*), accounting for just over half of the taxa previously thought to have been absent from the late Quaternary period (six Dasyuridae and two Potoroidae as listed in the Introduction).

By comparison, two of the seven newly identified species for this time period (*Dasycercus* sp. indet. and *Pseudomys novaehollandiae*) have no previous record from the NCWHA (Reed and Bourne, 2000, 2009; Macken *et al*., 2012). An additional two unknown taxa (Dasyuridae sp. 1 and *Sminthopsis* sp. 1; Appendix D) were common in the late Quaternary aged assemblages examined here but have not been noted in older fossil assemblages (Reed and Bourne, 2000; Prideaux *et al*., 2007; Macken *et al*., 2012).

Two species previously listed for Wet Cave and RCIC respectively, *Cercartetus concinnus* and *Petauroides volans*, were not identified in the current re-examination of these fossil collections. *P. volans* had been recorded from a single specimen from RCIC but this specimen was re-identified here as *Pseudocheirus peregrinus*. *Cercartetus concinnus* was previously only known from Wet Cave, but of the 108 specimens originally assigned to this taxon (McDowell, 2001), none were found to be comparable with *C. concinnus* and were commonly found to be *C. lepidus, C. nanus* and *Acrobates pygmaeus*.

Some revisions to the occurrences of small mammals within the individual cave sites were also made and have increased the known diversity across the late Quaternary aged deposits for this locality. For example, *Isoodon obesulus* was previously only known from Robertson and Blanche Caves but has now been identified in the Wet Cave assemblage. *Perameles bougainville*, only known from Blanche Cave, has been identified from fossil material in both Wet Cave and RCEC while *Petaurus norfolcensis*, known from only two specimens in RCIC was identified in all three of the assemblages examined. *Acrobates pygmaeus*, previously known only from Blanche Cave has now been identified in Wet and Robertson Caves and finally, *Hydromys chrysogaster* was identified from Blanche Cave, previously only recorded in Wet Cave and RCIC.

Table 5.2 Occurrence of small mammals within (a) pooled Middle–Late Pleistocene (M–LP) fossil assemblages of Main Fossil Chamber and Grant Hall, Victoria Fossil Cave and Fossil Chamber, Cathedral Cave (Reed and Bourne 2000; Prideaux *et al.* 2007; Reed and Bourne 2009; Macken *et al.* 2012) and (b) three Late Pleistocene–Holocene (<50 ka) deposits of the Naracoorte Caves (Wet Cave, Robertson Cave Entrance Chamber and Blanche Cave 3rd Chamber). Current species distribution in south east region of South Australia (SE SA) from Van Dyck and Strahan (2008).

Family	**Species**	**M–LP**	**Wet Cave**	**Robertson Cave Entrance Chamber**	**Blanche Cave 3rd Chamber**	**Present Day Distribution In SE SA**
Dasyuridae	Dasyuridae sp. 1		X	X	X	
	*Antechinus (*sp. cf.)$^{!}$ *A. agilis*	X	X	X	X	Coastal Lower SE
	Antechinus flavipes	X	X	X	X	Widespread
	Antechinus minimus	X				Coastal-inland fringe
	*Antechinus stuartii^*	X				
	*Antechinus swainsonii^*	X				
	Dasycercus sp. indet.^		X			
	*Dasyurus maculatus**	X		X	X	
	*Dasyurus viverrinus**	X	X	X	X	
	*Ningaui yvonneae^*	X	X	X	X	
	(Gen. et sp. cf.)$^{!}$ *Phascogale calura^*	X	X	X		
	Phascogale tapoatafa	X	X	X	X	Inland Lower SE
	Sminthopsis crassicaudata	X	X	X	X	Widespread
	Sminthopsis murina	X	X	X	X	Widespread
	Sminthopsis sp. 1		X	X	X	
Peramelidae	*Isoodon obesulus*	X	X	X	X	Lower SE
	*Perameles bougainville^*	X	X	X	X	
	*Perameles gunnii**	X	X	X	X	
Phalangeridae	*Trichosurus vulpecula*	X	X	X	X	Widespread
Potoroidae	*Bettongia* (sp. cf.)$^{!}$ *B. gaimardi**	X	X	X		
	Bettongia (sp. cf.)$^{!!}$ *B. lesueur^*	X	X	X	X	

Family	**Species**	**M–LP**	**Wet Cave**	**Robertson Cave Entrance Chamber**	**Blanche Cave 3rd Chamber**	**Present Day Distribution In SE SA**
	Bettongia penicillata^	X			X	
	Potorous platyops††	X	X	X	X	
	Potorous tridactylus^	X	X	X	X	
Burramyidae	*Cercartetus lepidus*	X	X	X	X	Upper SE
	Cercartetus nanus	X	X	X	X	Coastal Lower SE
Pseudocheiridae	*Pseudocheirus peregrinus*	X	X	X	X	Widespread
Petauridae	*Petaurus breviceps*	X	X	X	X	Widespread
	Petaurus norfolcensis		X	X	X	Inland patch of Upper SE
Acrobatidae	*Acrobates pygmaeus*	X	X	X	X	Widespread but rare
Muridae	*Conilurus albipes*†	X	X	X	X	
	Hydromys chrysogaster	X	X		X	Widespread
	Mastacomys fuscus^	X	X	X	X	
	Notomys mitchellii^	X	X	X	X	
	Pseudomys apodemoides	X	X	X	X	Widespread
	Pseudomys auritus†	X	X	X	X	
	Pseudomys australis^	X	X	X	X	
	Pseudomys fumeus^	X	X	X	X	
	Pseudomys gouldii††	X	X	X	X	
	Pseudomys novaehollandiae^		X	X		
	Pseudomys shortridgei	X	X	X	X	Inland, formerly coastal
	Rattus fuscipes	X	X		X	Widespread
	Rattus lutreolus	X	X	X	X	Widespread
	Rattus tunneyi^	X	X	X	X	

* species regionally extinct. † species extinct since European settlement. †† species extinct since European settlement and no former SE distribution recorded in Van Dyck and Strahan. ^species extant but no present or former SE distribution recorded in Van Dyck and Strahan (2008). ! uncertainty in identification in post-50 ka assemblages assessed here. !! uncertainty in M–LP identification.

Discussion

Late Quaternary small mammal diversity

Despite the limitations presented by examining small mammal diversity across the entire temporal span of the fossil assemblages, examination of existing and new fossil assemblages from Wet, Roberson and Blanche Caves has resulted in significant revision of the diversity of small mammals within the NCWHA for the late Quaternary period from *c*. 50 ka. This revision provides a more accurate baseline from which long-term patterns of species occurrence from the Middle Pleistocene to the present can be examined. Of the eight species previously un-recorded from the assemblages of Wet, Robertson and Blanche Caves, five were identified in this study (*Antechinus* sp. cf. *A. agilis*, *Dasyurus maculatus*, *Phascogale calura*, *Bettongia penicillata* and *Potorous tridactylus*), confirming their persistence, albeit rarity in some cases, into the Late Pleistocene period to at least *c*. 50 ka.

Three species (*Antechinus minimus*, *A. stuartii* and *A. swainsonii*) were not identified in the studied assemblages but are present in assemblages of the NCWHA dated older than *c*. 70 ka (Smith, 1972; Reed and Bourne, 2000; Prideaux *et al*., 2007; Macken *et al*., 2012). Reed and Bourne (, 2000) suggested that identification of *Antechinus* species from NCWHA deposits may require revision, particularly as *A. minimus*, *A. stuartii* and *A. swainsonii* were only known from single deposits at the time of their publication. Subsequent analysis of additional NCWHA deposits has resulted in identification of these taxa from other assemblages (Prideaux *et al*., 2007; Macken *et al*., 2012). However, as a result of the challenges associated with differentiating *A. stuartii* and *A. agilis* in fossil material (Reed and Bourne, 2000; Macken, 2009), the true diversity of this genus in the NCWHA fossil record remains uncertain and warrants further investigation. The isolation of two unknown dasyurid taxa, Dasyuridae sp. 1 and *Sminthopsis* sp. 1 highlights challenges associated with differentiating fossil material at both a generic and species level. Specimens assigned to these categories may represent new, undescribed taxa or morphological variants of known taxa.

If the identification of *A. minimus*, *A. stuartii* and *A. swainsonii* in the older Middle to Late Pleistocene assemblages of Victoria Fossil and Cathedral Caves is correct, their absence in Wet, Robertson and Blanche Caves suggests local decline in Dasyuridae diversity from at least *c*. 50 ka. However, it is not expected that their absence represents severe or unusual palaeocommunity change when examined within the context of both present and past patterns of occurrence. For example, all three of these species occur intermittently through the Middle to Late Pleistocene aged deposits of Cathedral Cave and Grant Hall, suggesting range contraction and dispersal from the Naracoorte region was common throughout the Pleistocene (Prideaux *et al*., 2007; Macken *et al*., 2012). These species are also rare when compared with the number of specimens of other small Dasyuridae in these older deposits, likely reflecting their rarity in the palaeocommunities sampled rather than taphonomic/accumulation biases (Prideaux *et al*., 2007; Macken *et al*., 2012). The present distribution of *A. minimus* does not include the Naracoorte region and instead extends along the coastal-inland fringe of south eastern South Australia (Van Dyck and Strahan, 2008) while *A. stuartii* and *A. swainsonii* do not occur in the region at all. In light of the fossil occurrence of these species, their present distribution suggests that range contraction at least in historic times, has occurred.

Faunal turnover and biogeographic implications

The first occurrence of five species (Dasyuridae sp. 1, *Dasycercus* sp. indet., *Sminthopsis* sp. 1, *Petaurus norfolcensis* and *Pseudomys novaehollandiae*) in deposits of the NCWHA is recorded in the late Quaternary aged assemblages *c*. <50 ka examined here; however, only one of these may be truly representative of range expansion from at least the end of the Late Pleistocene into the Naracoorte region (*P. norfolcensis*). *P. norfolcensis,* although rare in the studied assemblages, was identified from all three examined deposits and persists today in the upper south east region (Van Dyck and Strahan, 2008; Department for Environment and Heritage and South East Natural Resources Management Board, no date). While the absence of *P. norfolcensis* from Middle to Late Pleistocene aged assemblages may be a false absence such that the species is present but has not yet been detected, it is also possible that range expansion through population dispersal did occur into the Naracoorte region at a similar time as northward expansion from Victorian and New South Wales populations in the Late Pleistocene, as reflected in the species' phylogeography (Pavlova *et al*., 2010). Genetic analysis of *P. norfolcensis* across its distribution from south eastern South Australia, along the east coast of Australia to the Wet Tropics bioregion in Queensland, showed that populations south and inland of the Great Dividing Range have been undergoing decline since the northward expansion of the species in the Middle to Late Pleistocene, prior to the LGM (Pavlova *et al*., 2010). Unfortunately, there were only two samples from South Australia used in the genetic analyses which makes it unclear the extent to which patterns of historical population dynamics and occupancy apply in this region; however, it appears unusual that the species is apparently absent from >70 ka aged deposits of the NCWHA when divergence of the most recent common ancestor of the species has been dated from the Early to Middle Pleistocene (Pavlova *et al*., 2010).

Of the other four species that are new records for the NCWHA, it is more difficult to ascertain the extent to which they represent range expansions and hence, community turnover in the Naracoorte region. *Dasycercus* sp. indet. is rare in the examined assemblages, identified from only two specimens in Wet Cave. The contemporary range of *Dasycercus* spp. extends across the north and central-west arid regions of South Australia and eastern Western Australia, representing different environmental, ecological and climatic conditions than are expected to have characterised the south east region of South Australia during the Pleistocene (e.g., Prideaux *et al*., 2007; Macken *et al*., 2012, Macken *et al.* 2013). Consequently, it is expected that the occurrence of *Dasycercus* in Wet Cave represents an usual or stochastic ‘event’ in the distribution or dispersal of individuals of the species during the late Quaternary. Greater temporal resolution for the Wet Cave assemblage may enable its occurrence to be correlated with palaeoclimatic and environmental conditions and is under current investigation by ACM. Interestingly, *Dasycercus cristicauda* was previously included in the taxonomic list for Main Fossil Chamber, Victoria Fossil Cave (Moriarty *et al*., 2000); however, this identification has not been verified as the original specimen could not be located (Reed and Bourne, 2000). If the original identification was correct, the re-occurrence of the species in the late Quaternary may be significant in signalling conditions under which the species expanded or shifted its range more than once in the past.

The two unique Dasyuridae taxa described here (Dasyuridae sp. 1 and *Sminthopsis* sp. 1) are not reported from Middle to Late Pleistocene assemblages of *c*. >70 ka. However, as a result of the limited taxonomic resolution for these specimens, no examination of their temporal occurrence is possible. While further research is recommended to verify the taxonomic identity of the two unnamed taxa, re-examination of older assemblages may also be required to determine their presence or absence through the Pleistocene. A similar recommendation is made to verify the temporal pattern of occurrence through the NCWHA deposits of *Pseudomys novaehollandiae*. In the current re-examination, *P. novaehollandiae* was distinguished from *P. apodemoides* only where whole dentaries were preserved. No dental or maxillary characters were recognised to distinguish modern specimens of these species; however, the shape of the ascending ramus, condyle and angular process was found to be unique for each of the taxa. As a result of the difficulty in distinguishing *P. novaehollandiae* and *P. apodemoides* from fragmentary fossil material it is expected that *P. novaehollandiae* may be underrepresented in the <50 ka aged assemblages studied here, as well as in older deposits. Although the contemporary distribution of *P. novaehollandiae* is restricted to eastern Australia (Tasmania, Victoria and New South Wales), allopatric with *P. apodemoides* which is found south eastern South Australia and the mallee heathlands of Western Victoria (Van Dyck and Strahan, 2008), these species may have been sympatric in south eastern South Australia during at least some stages of the Pleistocene.

In comparison to these ‘first occurrences’, the previous taxonomic list for Wet Cave suggested that *Cercartetus concinnus* also first occurred in the NCWHA in the late Quaternary (Reed and Bourne, 2000). However, the presence of this species was not confirmed in the current study. The absence of *C. concinnus* from the NCWHA record is striking as this species is the most widespread and common of the small possum species in the region today (Foulkes *et al*., 2003). The occurrence of *C. concinnus* in south east South Australia may represent recent dispersal, at least since the middle Holocene into this region. A parallel pattern has been noted for the Eyre Peninsula where the species is widespread today, but has only one known occurrence in the Holocene subfossil record (McDowell and Medlin, 2010).

Fossil records as biodiversity baselines for conservation

Assessment of late Quaternary aged small mammal fossil assemblages of the NCWHA indicates richer long-term regional species diversity in the past than is generally recognised for the south east of South Australia. For example, fifteen species identified in the current study are not recognised as having past distributions in this region (Van Dyck and Strahan, 2008; Table 5.2).

Factors expected to contribute to the lack of knowledge about species past distributions include (a) poor preservation of species remains across their Pleistocene, historical and present ranges and (b) limited communication of palaeontological data between palaeoecologists and other researchers. This latter issue is often perpetuated by a lack of understanding by palaeoecologists of the data needs of resource managers, publication in palaeoecology specific journals and use of confusing terminology and data presentation (Lockley, 1977; Swetnam *et al*., 1999; Willis *et al*., 2005; Jackson and Sax, 2010). Despite these challenges, there is increasing recognition of the importance of fossil data for providing information about species and communities that can be used to enhance, inform and direct conservation and management programs (e.g., Hadly and Barnosky, 2009; McDowell and Medlin, 2010; Willis *et al*., 2010).

In a review of biodiversity conservation strategies for climate change adaptation, Heller *et al*. (2009) identify (a) greater coordination of institutions at a regional scale and (b) broader spatial and temporal perspectives, as two of four commonly cited recommendations for conservation action. These strategies share a commonality with the challenges associated with communicating the fossil record, stressing the need for continued updating and publishing of fossil data for the conservation research community and in turn, greater integration of long-term perspectives of species occurrences and community dynamics in conservation planning.

Conclusion

The temporal range, diversity and high degree of preservation of fossil material in the caves of the NCWHA provide a reference to past species distributions in the south east region of South Australia. Small mammal composition of assemblages from Wet, Robertson and Blanche Caves show that diversity in this group was broadly maintained into the late Quaternary period. When these records are compared with the known historical and current species distributions, severe decline in regional small mammal diversity is apparent through range contraction or historical extinction. Geo-chronological analysis of the fossil assemblages is required to enable patterns of species extinction, dispersal and turnover at a scale more consistent with palaeoclimatic and environmental change to be examined. However, the species identification and registration data reported here provides a valuable basis for these future analyses and a reference for ecologists, conservation managers and others on the past distribution of small mammal taxa in south eastern South Australia.

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6. Late glacial reorganisation of a small mammal palaeocommunity in southern Australia reveals thresholds of change

Citation

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Contribution of Authors

Amy Macken:

- Devised and planned the project.
- Identified and registered the specimens from Wet and Blanche Caves used in the research presented in the manuscript.
- Conducted all faunal analyses.
- Prepared the manuscript for publication.

Elizabeth Reed:

- Discussed research with AM and assisted with planning.
- Provided comments on the manuscript.
- Supplied pollen data from Blanche Cave as published in Darrénougué *et al.* (2009), for presentation in Fig. 6.12.

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Abstract

Natural variation in ecological systems is often argued as the mechanism by which ecosystems adapt and reorganise in response to disturbance, whilst maintaining overall identity and functional capacity. Here, we studied the statistical and ecological significance of natural variation in species richness, composition, structure and relative abundance of species in two contemporaneous small mammal fossil assemblages of late Quaternary age (*c.* 51.4 to 10.2 kyr BP) in south-eastern South Australia. We asked: Did the palaeocommunity reorganise in response to climate change associated with the last glacial cycle? How did variation in different ecological variables contribute to the persistence or reorganisation of the palaeocommunity, and, how did sampling variation within and between sites, and temporal resolution, impact patterns detected in the fossil assemblages? Our results show that the characteristics of the small mammal palaeocommunity were similar between the two sites and that they were generally stable through the early glacial period and last glacial maximum at the temporal scales at which the assemblages were preserved. Thereafter, the assemblages showed evidence of change in the rank-order abundance of constituent taxa from *c.* 17.1 to 10.2 kyr BP (95% CI: 17.4 to 9.2 kyr BP). At a finer temporal scale, palaeocommunity reorganisation was revealed for the first time through the late glacial period based on significant change in species richness. A nearby marine-core record suggests that this shift (dated from *c.* 17.1 to 16.7 kyr BP; 95% CI: 17.4 to 16.2 kyr BP) was associated with sea-surface temperatures (SSTs) warming past 16°C, post-dating the onset of warming following the LGM by *c.* 1 to 3 kyrs. A second likely palaeocommunity shift is reflected in the low rank-order abundance correlation of local palaeocommunity samples from *c.* 10.8 to 10.5 kyr BP (95% CI: 11.2 to 10.9 kyr BP). This shift was associated with continued warming of mean SSTs past 18°C. While the onset of rapid warming was not directly correlated with palaeocommunity change, the fauna appear to have been sensitive to specific temperature thresholds and prolonged relative aridity. These extrinsic factors were important in initiating structural changes that scaled through from individual species to the whole palaeocommunity.

Keywords climate change, mammals, palaeocommunity, persistence, Quaternary, resilience, scale, similarity, variability

Introduction

Concern about the impacts of climate change on biodiversity has led to an increased need for long-term perspectives of ecosystems and their variability through time (Froyd and Willis 2008). Natural variation in ecological systems is characterised by fluctuations and/or trends in community and system attributes, condition and/or processes (Landres *et al*. 1999). Such change is argued to provide an ecological ‘buffer’ that allows ecosystems to undergo turnover and reorganise in response to external pressures, whilst maintaining ecological functions, structure, connections and identity (Holling and Meffe 1996; Folke *et al*. 2004; Walker *et al*. 2004). The latter aspect is at the heart of most ecological definitions of resilience, that is, how much pressure or change an ecological system can withstand before it shifts to a new, alternative steady-state (Holling 1996; Walker *et al*. 2009). Consequently, understanding and managing natural variation in ecological systems at different scales is increasingly being integrated into biodiversity conservation strategies. However, despite an increased focus on natural variation in biodiversity management and ecological literature (Landres *et al*. 1999; Micheli *et al*. 1999; Lundberg *et al*. 2000; Roche *et al*. 2011; Walker *et al*. 2004), our ability to understand patterns of natural variation is limited by the short duration of many ecological studies, extensive habitat fragmentation, species loss and subsequent ecosystem disruption (Swetnam *et al*. 1999). These factors also restrict our knowledge of the interaction of ecosystem changes with the long-term persistence or loss of different ecosystem attributes over time (Magurran and Henderson 2010).

The challenges associated with measuring natural variation in ecosystems can be addressed using empirical data on environmental, climatic and ecological change preserved in palaeoecological assemblages. Such sources are commonly used as a reference to the normal, pre-human extent of natural variation expressed in marine, aquatic and terrestrial ecosystems (e.g., Di Michelle *et al*. 2004; Hadly and Barnosky 2009; Willis *et al*. 2010; Rull 2012). Baseline data from past ecosystems provided by palaeoecological records have been used to (a) inform predictions about climate change responses and thresholds based on ecological and climatic variability, (b) identify the combinations of biotic and abiotic processes that most contributed to ecological resilience in the past and where these are likely to occur under future climate change scenarios, and (c) provide insights on novel, or non-analogous communities and their management (Willis *et al*. 2010).

Fossil assemblages in the World Heritage listed Naracoorte Caves in south-eastern South Australia are widely recognised for their scientific and natural history values, preserving a diverse vertebrate fauna and palaeoclimatic history spanning the last *c*. 500 kyrs (Wells *et al*. 1984; Ayliffe *et al*. 1998; Reed and Bourne 2000; Prideaux *et al*. 2007; Macken *et al*. 2012; Fig. 6.1). Recent study of deposits of Late Pleistocene (<50 kyrs) age show that some sites also preserve a record of local vegetation (Darrénougué *et al*. 2009), which combined with the faunal record, presents an opportunity to examine the responses, thresholds and persistence of different ecosystem variables with time for this locality.

A striking feature of the described Naracoorte mammal faunas is the general consistency of community composition through the Pleistocene, particularly when compared with mammal faunas from other localities such as Middle Pleistocene north-eastern Queensland (Hocknull *et al*. 2007). The limited evidence presented for faunal change in the Naracoorte fossil record has been significant in discussions of faunal dynamics through the Pleistocene. For example, the apparent lack of faunal change recorded in the Naracoorte Caves reported by Moriarty *et al*. (2000) has been used as evidence that interglacial-glacial transitions did not contribute to megafaunal extinction in Australia (Barnosky *et al.* 2004) and that Pleistocene climate changes did not impact mammalian faunas to the same extent as the Late Pleistocene–Holocene transition (Koch and Barnosky 2006).

The assumption of long-term stability of the mammal community through the Pleistocene was first challenged by Prideaux *et al*. (2007) and later Macken *et al.* (2012) who showed that the relative abundance of species within assemblages of the Naracoorte Caves varied through glacial-interglacial cycles of the Middle and Late Pleistocene. Additionally, changes in specimen density and species presence/absence demonstrated in these studies showed that the ranges of some species alternately expanded and contracted from the Naracoorte region through the Pleistocene.

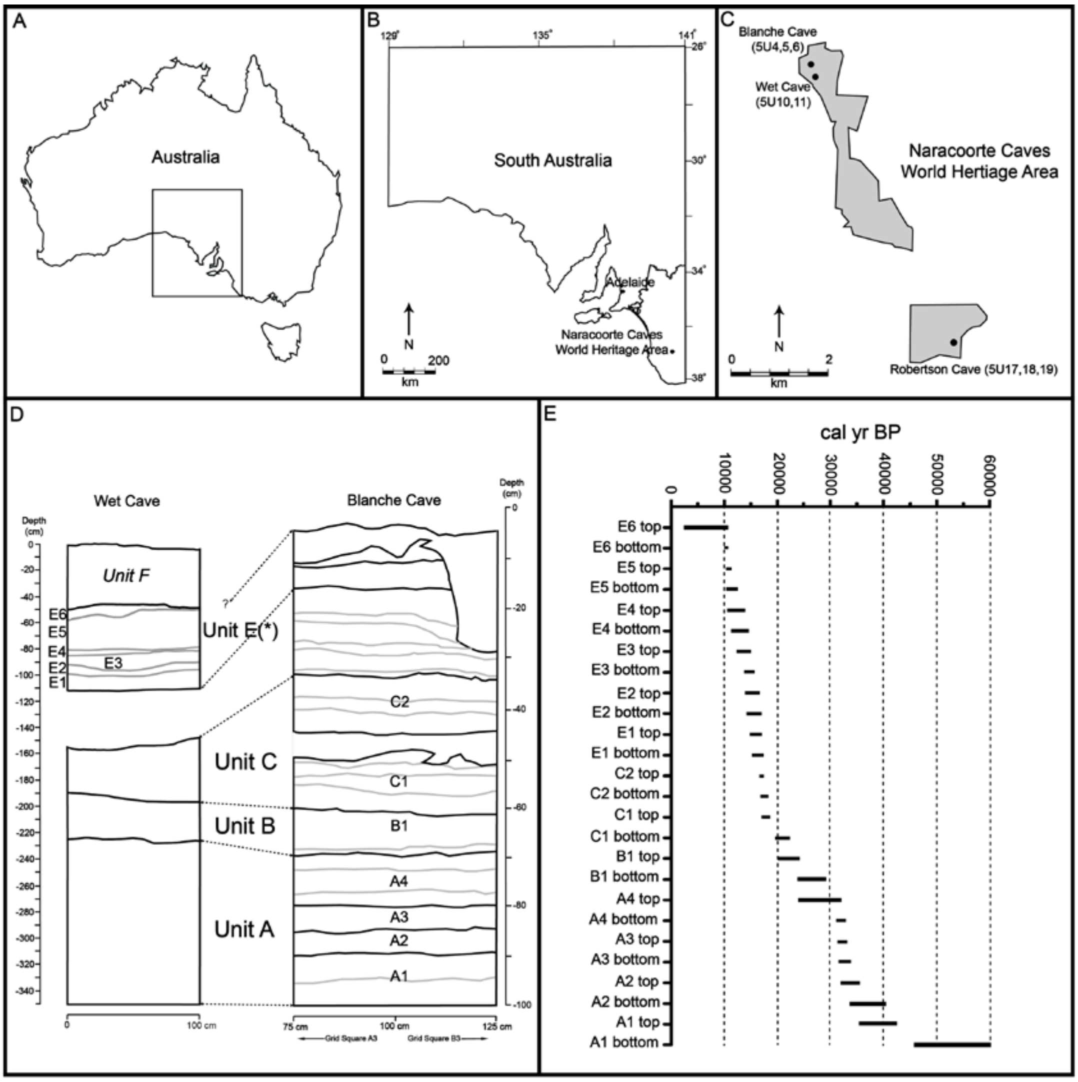

Figure 6.1 Locality, stratigraphy and chronology of the Wet and Blanche Cave fossil assemblages. (A) South Australia, (B) location of the Naracoorte Caves World Heritage Area (NCWHA) in south-eastern South Australia and (C) proximity of Wet and Blanche caves, and Robertson Cave within the NCWHA. (D) Stratigraphic sections of the Wet and Blanche Cave sequences showing the temporal correlation of phases A1 to C2 to units A, B and C of Wet and Blanche caves. Phases E1 to E6 in Wet Cave provide a finer resolution for unit E. The correlation of the upper layers of the Blanche Cave excavation to unit E is uncertain. All temporal relationships follow Macken *et al*. (2013b). Gaps in the sequences correspond to re-worked unit D in Wet Cave and layer 14 in Blanche Cave (Macken *et al*. 2013a, b). Unit F in Wet Cave was not included in the current faunal analysis as it contains Pleistocene and Holocene aged materials (Macken *et al*. 2013a). (E) Modelled 95% highest probability density ranges in calibrated years BP of the top and bottom boundaries of phases A1 to E6 in Wet and Blanche caves (Macken *et al*. 2013b). Modelled ages calibrated using the IntCal09 calibration curve (Reimer *et al*. 2009) with a Southern Hemisphere offset of 56±24 years applied (McCormac *et al*. 2004).

The greater chronological control, finer temporal resolution and more adequate and quantitative faunal sampling in these studies facilitated rigorous analysis of faunal trends with time and were fundamental in revealing the faunal changes that were previously obscured. Further, the patterns of change observed in the Naracoorte mammal record were consistent with observations elsewhere that natural variability, and hence, our perception of stability in ecological systems, is dependent upon not only the scales (temporal, spatial and ecological) at which they are observed (Rahel 1990; Di Michele *et al*. 2004; Devictor and Robert 2009), but also sampling variance which can obscure or enhance temporal signals of variability or persistence (Bennington and Bambach 1996).

Scale and sampling variance are critical to not only the nature of the relationship between natural variation and persistence of faunal communities with time, but how they may be detected and interpreted from long-term ecological records. For example, as demonstrated by Rahel (1990), community composition and structure (rank-order abundance) may be highly persistent, but the abundances of constituent taxa may vary significantly with space and time. Further, Magurran and Henderson (2010) suggested that variation in the abundances of individual species may contribute to the overall stability of the community, highlighting a complex interplay between variation and persistence across scales. Changes in the relative abundance of species may also be considered “early warning signs” of environmental impacts on ecosystems (Hadly and Barnosky 2009; p. 47), highlighting the significance of such responses when monitoring climate change impacts on biodiversity.

From a conservation perspective, these observations raise important questions about the relationship between natural variation and persistence of faunal communities: when does variability at different ecological scales represent, or lead to, a shift to a new community type, and hence the crossing of resilience thresholds? What has been the capacity of faunal communities and populations to resist, recover, adapt or transform in response to past climate changes or other disturbances? Despite the urgent need for appropriate biodiversity conservation strategies, our capacity to address these questions is limited by a lack of knowledge about (a) how faunal communities change over different time scales in response to disturbance (including climate change), (b) the natural range of variability expressed by an ecosystem at different spatial, temporal and ecological scales, (c) the ecological, environmental and climatic thresholds beyond which ecosystems change state and (d) how sampling variance ('noise') is differentiated from true variation ('signal') in community dynamics from long-term ecological records (Willis *et al.* 2005; 2007; NBSRTG 2009).

Here, we examine natural variation in a small mammal palaeocommunity preserved in two proximal, contemporaneous small mammal fossil assemblages of the Naracoorte Caves (Fig. 6.1; Table 6.1). These sites preserve bone-rich, well stratified and chronologically constrained fossil assemblages of late Quaternary age, providing an opportunity to examine natural variation of many extant taxa which today persist in communities non-analogous to those of Pleistocene Naracoorte (Macken *et al*. 2012; Macken and Reed 2013).

The aims of this research were to (a) examine how sampling variation within and between sites, and temporal resolution affect perceived patterns of variation and/or stability in the fossil assemblages, (b) determine if and how the palaeocommunity reorganised in response to climate change associated with the last glacial cycle, and (c) identify how variation in different ecological variables contributed to the persistence or reorganisation of the palaeocommunity at different scales (temporal and ecological). Using local and regional palaeoclimatic and environmental indicators (e.g., estimated sea-surface temperatures from offshore south-eastern South Australia and a vegetation record preserved in Blanche Cave), we also identify climatic and environmental changes associated with significant episodes of faunal turnover recorded in the fossil assemblages.

We use the terminology of Bennington and Bambach (1996) in describing the assemblages sampled from single stratigraphic units or layers as a 'local palaeocommunity'. We also use the terms 'palaeocommunity' and 'palaeocommunity type' to describe groups of samples that are statistically indistinguishable and groups of samples that are similar but are statistically distinguishable, respectively (Bennington and Bambach 1996). These and other palaeoecology-specific and numeric terms used throughout the text are described in

Table 6.2. We recognise that given the extent of time-averaging, biasing and information loss through taphonomic processes in fossil assemblages, a local palaeocommunity is not equivalent to a local community observed in neontolgoical studies where contemporaneity can be established. However, this terminology provides a useful basis for describing the different types of samples examined from the fossil assemblages and an ecological hierarchy from which to describe the biological significance of natural variation observed with time.

Study region

The South East region of South Australia is today characterised climatically by cool, wet winters and long, mild, dry summers, placing it in the temperate climate zone (Hopton 2003). Annual rainfall and mean maximum temperatures range from *c.* 775 mm and 19^{o}C in Mount Gambier to *c.* 470 mm and *c.* 22^{o}C in Keith, located in the southern and northern ends of the region respectably. Naracoorte is located in the centre of south-eastern South Australia and has an annual rainfall of *c.* 580 mm and mean maximum temperature of *c.* 21^{o}C (Hopton 2003). Mean sea-surface temperature along the western coastal edge of the region is in the range of 16 to 18^{o}C (Bureau of Meteorology, 2013). Across the region, effective precipitation (rainfall > evaporation rate) occurs only during the winter.

The region is geomorphically complex, with a range of landforms that historically (immediately pre-European colonisation) supported a diverse range of vegetation communities (Croft 2003). The variety of landforms and vegetation communities supported a diverse mammal fauna through the Pleistocene and into historical times. Forty-one small mammal species (excluding bats) have been identified from Naracoorte fossil sites dated from *c.* 50 to 1 kyr BP (Macken and Reed 2013). Biological surveys in 1997 and museum records indicate that 26 small mammal taxa were known from the region at the time of European arrival and through to more recent times (Robinson *et al.* 2000; Foulkes *et al.* 2003). South-eastern South Australia represents the western-limit of the mainland distribution of many extant south-eastern Australian small mammal species, while others are more widespread across the continent (Van Dyck and Strahan 2008).

Table 6.1 Upper and lower 95% highest probability density ranges and median modelled ages for the top and bottom boundaries of the Wet and Blanche Cave units and phases, from Macken *et al.* (2013b). Modelled ages calibrated using the IntCal09 calibration curve (Reimer *et al.* 2009) with a Southern Hemisphere offset of 56±24 years applied (McCormac *et al.* 2004).

Wet Cave				**Blanche Cave**			
	Modelled calibrated age (cal yr BP)				**Modelled calibrated age (cal yr BP)**		
	95%				**95%**		
Unit/ Phase Boundaries	**from**	**to**	**median**	**Unit/ Phase Boundaries**	**from**	**to**	**median**
Unit F top	680	-43	364				
Unit F bottom	10,313	662	6,374				
Unit E top	10,491	9,204	10,194				
E6 bottom	10,870	10,252	10,470				
E5 top	11,151	10,410	10,789				
E5 bottom	12,416	10,671	11,206				
E4 top	13,604	10,948	12,099				
E4 bottom	14,291	11,536	13,085				
E3 top	14,810	12,646	13,986				
E3 bottom	15,520	14,019	14,512				
E2 top	16,183	14,202	15,094				
E2 bottom	16,611	14,624	15,729				
E1 top	16,816	15,213	16,358	*E* top*	*15,450*	*9,858*	*14,589*
Unit E bottom	17,130	15,601	16,649	*E* bottom*	16,540	15,544	16,098
Unit C top	18,406	16,197	17,120	C2 top	17,419	16,657	17,065
				C2 bottom	17,802	16,908	17,227
				C1 top	18,381	17,075	17,510
Unit C bottom	21,928	16,885	18,425	C1 bottom	21,894	19,935	20,804
Unit B top	24,138	18,599	22,205	B1 top	23,855	20,405	21,756
Unit B bottom	28,383	24,348	25,423	B1 bottom	28,838	24,114	25,251
Unit A top	29,889	24,954	27,361	A4 top	31,742	24,249	28,906
				A4 bottom	32,502	31,456	31,911
				A3 top	32,751	31,660	32,199
				A3 bottom	33,656	31,843	32,632
				A2 top	35,130	32,402	34,009
				A2 bottom	40,131	33,988	35,845
				A1 top	42,244	35,836	39,971
Unit A bottom	56,032	46,523	50,114	A1 bottom	59,997	46,259	51,360

Table 6.2 Palaeoecological and numeric terms used throughout the text.

Term	**Definition**
Local palaeocommunity	Fossil assemblage associated with samples from a single stratigraphic unit or phase (*sensu* Bennington and Bambach 1996). Defined by values for ecological variables, as described below.
Palaeocommunity	Statistically indistinguishable local palaeocommunities based on ecological variables (*sensu* Bennington and Bambach 1996).
Palaeocommunity type	Similar but not statistically identical local palaeocommunities based on ecological variables (*sensu* Bennington and Bambach 1996).
Time-averaging	The amount of time represented in a single stratigraphic unit or phase.
Chronological resolution	The precision of median modelled calibrated ages for the upper and lower boundaries of units and phases, as measured by 95% highest probability density ranges (equivalent to 95% confidence interval; Table 6.1 and Fig. 6.1).
Macroscale	Temporal scale of stratigraphic units A, B, C and E(*) in Wet and Blanche caves (Table 6.1).
Mesoscale	Temporal scale of stratigraphic phases A1, A2, A3, A4, B1, C1, C2 (Blanche Cave) and E1, E2, E3, E4, E5 and E6 (Wet Cave; Table 6.1).
Ecological variables	• Whole-palaeocommunity attributes: species richness, composition, rank-order abundance (structure), relative abundance of species. • Relative abundance of individual species.
Site-effects	Difference in mean values of an ecological variable between replicate samples of the local palaeocommunity from Wet and Blanche Cave. Significant when 95% CI does not include the value 0.
Time-effects	Difference in mean values of an ecological variable between consecutive local palaeocommunity samples at either the macro- or mesoscale. Significant when 95% CI does not include the value 0.
Natural variation	Statistically significant variation (time-effects) in ecological variables at either the macro- or mesoscale.
Temporal stability in ecological variable	Period of time over which an ecological variable does not demonstrate statistically significant variation.

Geological setting of the Naracoorte Caves

The Naracoorte Caves are a complex of 26 caves distributed within an uplifted portion of the Oligocene to Miocene aged Gambier Limestone and are located south-east of Naracoorte (Fig. 6.1). The uplifted section of the Gambier Limestone is overlain by the East Naracoorte Ridge, the oldest of the Pleistocene beach dune facies which transect the South East region (Murray-Wallace *et al*. 2001). The caves formed through phreatic dissolution and structural processes along joints in the Gambier Limestone (Wells *et al*. 1984; Lewis *et al*. 2006), first opening to the surface from at least the Middle Pleistocene (*c.* 530 ka) as indicated by optically stimulated luminescence dating of bone-bearing clastic sediments from an assemblage in Cathedral Cave (5U12 13; Prideaux *et al*. 2007).

There are 100 known fossil vertebrate fossil deposits ranging in age from the Middle Pleistocene to the Holocene within the Naracoorte Caves (Macken *et al*. 2013a; Macken and Reed 2013). The two deposits examined here (Wet Cave Entrance Chamber: 5U10 and Blanche Cave 3rd Chamber: 5U6) are largely contemporaneous, together spanning the last glacial cycle from *c.* 51.4 to 10.2 kyr BP (Darrénougué *et al*. 2009; St. Pierre *et al*. 2012; Macken *et al*. 2013a, b).

The Naracoorte Caves are registered with the Australian Karst Index (Matthews 1985) and are identified by unique cave numbers (e.g., 5U10 11), referred to in text. ‘5’ identifies the state of South Australia, ‘U’ the Upper South East and the numbers (e.g. 10 11) indicate entrances associated with each registered cave.

Chronology and stratigraphy of Wet and Blanche caves

The stratigraphic and geochronological contexts of the fossil deposits of Wet and Blanche caves are described in Darrénougué *et al*. (2009), St Pierre *et al*. (2009), St Pierre *et al*. (2012) and Macken *et al*. (2013a). Bayesian age-depth models for the two deposits were developed by Macken *et al*. (2013b) and were used as the chronological and stratigraphic framework for the faunal analyses presented here (Fig. 6.1; Table 6.1). The Bayesian age-depth models integrated stratigraphic information for the two sites and ^{14}C determinations from charcoal collected across the sequences. A total of 20 ^{14}C determinations were used to build the Wet Cave model and 40 for the Blanche Cave model (Macken *et al*. 2013b). We discuss U/Th dates from speleothem straws (St Pierre *et al*. 2009, 2012) in conjunction with the age-models and ^{14}C determinations in terms of potential reworking of sediments and bone material in the later sections of the paper. Here we provide a general description of the depositional sequences and the age-models as a context for the temporal division and relationships of the fossil assemblages within and between the two sites.

The Wet Cave fossil deposit is composed of four un-reworked depositional units (A, B, C and E; Fig. 6.1; Table 6.1). Unit D and the uppermost unit F contain reworked sedimentary and bone material older than the depositional context and were consequently excluded from the faunal analysis. Units A, B and C lack internal laminations and provide macroscale, time-averaged samples of the fossil assemblage through the period from *c.* 50.1 to 17.1 kyr BP, with maximum modelled durations for the units ranging from *c.* 30.5 to 4.5 kyrs at the 95% highest probability density (hpd) range (Macken *et al*. 2013b; Table 6.1). These depositional units correspond to broad climatic phases of the last glacial cycle (marine isotope stage 3 (MIS-3) and last glacial maximum (LGM) in MIS-2; Macken *et al*. 2013a, b). Unit E is dated to the MIS-2 deglaciation and is composed of six layers (phases E1, oldest to E6, youngest), identified by sedimentary characteristics and representing discrete phases of sediment and bone accumulation (Macken *et al*. 2013a, b). The maximum modelled temporal durations of these phases range from 180 to 370 years at the 95% hpd, providing a finer, mesoscale resolution for the MIS-2 deglaciation period of *c.* 16.7 to 10.2 kyr BP represented by Wet Cave unit E (Macken *et al*. 2013a; Fig. 6.1; Table 6.1).

The deposit in Blanche Cave closely resembles that of Wet Cave in terms of the general sequence of sediment types through the sequence and depositional age, but differs in the depth profile and by the number of sedimentary layers present (Macken *et al*. 2013a, b). Twenty-seven sedimentary layers were originally identified in the Blanche Cave section based on visual observation during excavation. Following analysis of the sediments and further examination of the stratigraphy, these layers were subsequently aggregated into seven separate phases (A1 to C2; Table E.1 Appendix E).

Statistical correlation of the Wet and Blanche Cave sequences showed that phases A1 to C2 from Blanche Cave grouped into units temporally equivalent with those of Wet Cave units A, B and C (Macken *et al*. 2013b; Table 6.1; Fig. 6.1). Together, phases A1 to A4 were temporally correlated with unit A in Wet Cave, phase B1 with unit B, and phases C1 to C2 with unit C (Table E.1 Appendix E). These multiple phases provide a finer, mesoscale resolution for units A, B and C. The use of units and phases as coarse and fine samples of the palaeocommunity, respectively, mirrors the approach used by Bobe *et al*. (2002), who examined temporal trends in mammal faunas at two time scales from a Southern Ethiopian hominin site. Unfortunately, there were no phases in Blanche Cave which were temporally equivalent to Wet Cave unit E. Consequently, the upper section of the Blanche Cave sequence is referred to in text as unit E* (Table 6.1; Macken *et al*. 2013b).

Methods

Sample collection and fossil identification

The fossil assemblage from Wet Cave was collected in 1998 and 1999 by David Bartholomeusz from two 1x1 m pits established down the edge of the sediment cone filling the 5U10 entrance chamber. Excavation of the pits followed natural stratigraphic layers ranging from 1.5 to 10 cm thick, to a total depth of 3.5 m (Fig. 6.1). Each layer was divided into four 0.5 m^2 quadrants (A to D) which were excavated separately (Macken *et al*. 2013a).

The fossil assemblage from Blanche Cave came from a single 1x1 m grid square (A3) excavated in the 3^{rd} chamber of the cave (5U6) in 2006/7 by EHR. The pit was excavated to a depth of 1 m, following the 27 laminations and layers observed in the stratigraphy which had been exposed by a previous excavation adjacent to the grid square used for this study (Laslett 2006).

Cranio-dental specimens of all small mammals (body mass ≤2.5 kg; excluding bats), including the larger *Trichosurus vulpecula* and *Dasyurus maculatus*, were sorted from bulk material excavated from the two sites following wet-screening through sieves of 1 to 2 mm^2. The assemblages are biased towards small mammals as they are largely owl-pellet derived. Barn owl (*Tyto alba*) and Masked owl (*Tyto* *novaehollandiae*) are the most likely predatory agents responsible for the deposits as evidenced by the presence of these species within the fossil assemblages, the prevalence of complete skeletal elements and presence of digestive corrosion consistent with tytonid owls (McDowell 2001; Laslett 2006). Although of greater body mass, *T. vulpecula* and *D. maculatus* were included in the faunal analysis as they are represented by juvenile specimens and hence, may be a component of the largely owl-pellet derived assemblages.

For identification, cranio-dental specimens were compared with modern and sub-fossil specimens in the South Australian Museum and modern specimens held by the Australian Museum as described in Macken and Reed (2013). Published descriptions of species cranio-dental morphology were also used to aid species identification where available. Two un-diagnosed taxa were identified in the fossil assemblages (Dasyuridae sp. 1 and *Sminthopsis* sp. 1) and are discussed by Macken and Reed (2013).

Previous analysis of the Wet Cave assemblage by McDowell (2001) showed that murids composed 81% of the fauna (*c.* 14,000 cranio-dental specimens). Due to this abundance of material, murids were sub-sampled from the Wet Cave collection. For layers where the total Number of Identified Specimens (NISP) of murids was >300 (as indicated in the data tables presented in McDowell 2001), only specimens from quadrant A were examined, approximating 25% of the bulk material for the layer (Macken and Reed 2013). For layers where the NISP of murids was <300, specimens from all quadrants were identified. Marsupial NISP was determined from the sum of specimens identified from all quadrants.

As in Wet Cave, murid cranio-dental specimens from Blanche Cave composed 80% of the fauna (*c.* 18,000 cranio-dental specimens, counted during analysis) and were sub-sampled. For layers where the number of murid specimens counted was >300, only specimens from a random sample of 25% of the volume of bulk material for the layer were identified (see Macken and Reed, 2013), approximating the quadrant method used in Wet Cave. All marsupial specimens from grid square A3 were identified.

All specimens identified from Wet and Blanche caves were registered to the Flinders University fossil collection (Wet Cave: FU20000 to 20997; Blanche Cave: FU14100 to 14685).

Faunal analysis: data standardisation

The total NISP for each murid taxon in the sub-sampled layers was estimated by multiplying the proportion of each taxon by the total murid NISP for the layer (e.g., Blanche Cave Layer 3 had a total counted murid NISP = 782. The sub-sampled murid NISP for Layer 3 = 147. The proportion of *Pseudomys apodemoides* in the sub-sample for Layer 3 = 0.17, based on 25 specimens identified to this taxon. Therefore, the estimated total NISP for *P. apodemoides* in Layer 3 was 0.17 x 782 = 133).

We recognise that our sub-sampling strategy may have resulted in some murid taxa not being identified from the sub-sampled layers, particularly if they were very rare in the assemblage. We tested for such an effect by constructing rarefaction curves for the sub-sampled layers and those where all specimens were identified. Rarefaction curves show that for most samples, the number of species in both the sub-sampled and completely sampled layers approaches asymptote, suggesting negligible sampling effects (Figs. E.1 and E.2 Appendix E). We also note that the minimum sub-sampled murid NISP from a single layer from Wet and Blanche caves was 65, greater than the minimum NISP of any marsupial species (Wet Cave phase E1=36). Rarefaction analysis was conducted in the palaeontological software package PAST (Hammer *et al*. 2001).

NISP values of the small mammal faunas were used to calculate the local palaeocommunity metrics detailed below and were quantified at the two time scales (macro- and meso-) available in the deposits. For analysis, the NISP of *Pseudomys novaehollandiae* was incorporated into the NISP of *P. apodemoides* due to the difficulties in separating these taxa from cranio-dental specimens (Macken and Reed 2013).

To allow for comparison of the local palaeocommunity sampled between and within the two sites at both the macro- and meso- time scales, all samples were standardised to the lowest NISP from a unit or phase (Wet Cave phase E1 = 303) using bootstrapping, following the methods of Blois *et al*. (2010) and Chernick (2008). One-thousand bootstrap samples for each unit and phase were generated by resampling with replacement, using the proportion of each species in the original samples as weights. Resampling was conducted in R version 2.15.1 (R Core Team, 2012).

Faunal analysis: whole-palaeocommunity and individual species variables

Species richness (number of species) and evenness (probability of interspecific encounter; PIE) were calculated using the bootstrapped, sample-size standardised data. Richness and evenness together reflect diversity and are commonly calculated for fossil assemblages (e.g., Blois *et al*. 2010; Terry 2010a, b) and modern ecological communities (e.g., Kelly *et al*. 2010). Richness is generally considered to reflect ecosystem productivity and habitat heterogeneity (Hadly and Barnosky 2009; Bateman *et al*. 2010) while evenness reflects the distribution of relative abundance of species within faunal assemblages.

We also calculated the following beta diversity measures:

- Composition (species presence/absence; Jaccard similarity index),
- Species rank-order abundance (abundance rankings; Spearman's Rho, ρ) and
- Relative abundance of species (Bray-Curtis similarity index), following Rahel (1990).

These metrics are commonly calculated for fossil assemblages (e.g., Terry 2010b) and provide a nested hierarchy for evaluating the ecological extent of variation and stability within the palaeocommunity (Belmaker and Hovers, 2011). The Jaccard and Bray-Curtis similarity indices were calculated from the bootstrapped sample-size standardised data using R, and Spearman's rank-order abundance correlations from the original, un-bootstrapped data in SPSS version 19 (IBM Corp 2010). The 95% confidence intervals of the bootstrapped sample means were calculated using the upper and lower 2.5% percentiles of the bootstrapped distributions following Chernick (2008) and Dalby *et al*. (2013). Confidence intervals for Spearman's correlation coefficients were calculated using the Fisher transformation as outlined in Zar (1996).

The significance of mean Jaccard similarity was assessed using the upper and lower critical values published by Real (1999). The critical values provide the probability that an observed Jaccard index value is different from what would be expected at random, given the number of taxa within the two samples.

The significance of Spearman’s Rho was tested against the null hypothesis that species abundance ranks were not associated between samples ($\rho=0$). For all tests, significance was assessed at $\alpha=0.01$ to reduce the chance of Type 1 error associated with multiple comparisons. We used this more conservative significance level as an alternative to the strict adjustments enforced by more commonly used procedures such as Bonferroni correction which can inflate the likelihood of Type 2 errors (Verhoeven *et al*. 2005).

Finally, the relative abundances of individual species and associated 95% confidence intervals were calculated using the “plus-four” method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007). This method is preferred to the standard confidence interval for proportions as it is less likely to produce confidence intervals that are smaller than 95%.

Faunal analysis: site- and time-effects

As the fossil assemblages are located within 500 m of each other, we tested the similarity of the palaeocommunity preserved in each site as a basis for assessing the reliability of observed temporal variation at the species and whole-assemblage levels. This approach was endorsed by Bennington and Bambach (1996), but is rarely applied to vertebrate fossil localities where typically, there is only one assemblage available for a given time period.

Site based sampling effects were calculated for species richness and evenness as the difference in means of the 1000 bootstrap samples for comparisons between units A, B, C and E(*) sampled from the two sites, following Nakagawa and Cuthill (2007) and Dalby *et al*. (2013). We adopted this method as it provides information about the magnitude and precision of effects and is useful when multiple comparisons are being considered (Di Stefano 2004; Nakagawa 2004; Nakagawa and Cuthill 2007). Site-effects on the relative abundances of individual species were quantified using the mean difference in species proportions. Site-based similarity of the beta diversity measures were examined by calculating these measures for all unit comparisons between the two sites (e.g., Wet Cave unit A v. Blanche Cave unit A).

The effects of time-averaging on patterns of variability (time-effects) were examined by studying the assemblages at the two temporal scales available in the deposit: (a) the coarse, macroscale corresponding to broad climatic phases of the last glacial cycle (e.g., marine isotope stage (MIS)-3, the Last Glacial Maximum (LGM) and MIS-2 deglaciation), and (b) the finer, mesoscale of millennia or centuries, enabling variation within these broader climatic phases to be examined. Time-effects on species richness and evenness were quantified as the difference in means of the 1000 bootstrap samples between consecutive units and phases within each site. Time-effects on the relative abundances of individual species were examined using the mean difference in proportions of consecutive units and phases. The beta diversity measures were also calculated for consecutive units and phases.

To examine similarity amongst all units and phases and to assess overall temporal trends at the macro- and mesoscales, we additionally used the unweighted paired-group method of hierarchical cluster analysis based on arithmetic means, using Jaccard and Bray-Curtis similarity (using the bootstrapped sample-size standardised NISP values), and Spearman's Rho (original NISP values), similar to the approach of Belmaker and Hovers (2011). As a multivariate technique, cluster analysis facilitated a comparison of all units and phases, rather than between consecutive units and phases only. Although cluster analysis does not provide a test of significance of the similarities among samples, we used bootstrapping to test the consistency of nodes in the cluster dendrogram (1000 resamples). Nodes of ≥ 95% support were considered to be different from random (Jackson *et al*. 2010). Cluster analysis was performed in PAST version 2.02.

Given the range of depositional and post-depositional processes that can contribute to the heterogeneity of species relative abundances between samples within a single sedimentary horizon (Bennington and Bambach 1996), we additionally examined the significance of temporal trends in species proportions using the Cochran-Armitage test (Chi-square test for linear trend), following Zar (1996) and Cannon (2000). The test was applied at the macroscale on those species that recorded presences in at least three units, and at the mesoscale, on those species that occurred in at least four phases. Cochran-Armitage tests for the effect of sample size on observed trends in proportion data by dividing the total chi-square value into two parts: one that is due to a linear trend in abundance and another due to departure from linearity, such as curvilinear trends (Cannon 2001). The test was performed with the 'Chi-square and Cochran's Calculator' Microsoft Excel macro created by Cannon. We used the Type I error rate of α=0.01 for Cochran's test.

The statistical significance of site and time-effects was established on the a basis that the 95% confidence interval of the effect size did not contain 0. Significant time-effects were additionally judged on the basis that time-effect size was greater than site-effect size (based on overlap of 95% confidence intervals of site and time-effects), following Cumming (2009) and noting the cautions of Schenker and Gentleman (2001). Non-statistically significant changes in community attributes with time were considered as 'noise,' cautioning against over-interpretation of ecological meaning. In contrast, given the extent of sampling variation inherent in fossil assemblages, statistically significant variation was considered to also be ecologically significant ('signal'). We acknowledge that this does not mean that non-statistically significant variation is not ecologically meaningful, only that our confidence in the observed trends is limited by sampling variation.

Palaeoclimatic and environmental context

The faunal data were compared against late Quaternary sea-surface temperatures (SST) reconstructed from marine core MD03-2607 collected from offshore south-eastern South Australia (Lopes dos Santos *et al*. 2012). SSTs were plotted at the temporal resolution of the original core data and as mean values time-averaged over the temporal durations of the units and phases of Wet and Blanche caves (based on the maximum median ages of the upper and lower unit and phase boundaries; Table 6.1). Mean SST time-averaged over the upper and lower 95% hpd ranges of the top and bottom boundaries of the units and phases, respectively, resulted in almost identical values as those time-averaged within the median ages.

Pollen data from a sediment core collected from the 3rd chamber of Blanche Cave were used as a proxy for the broad types of vegetation local to the Naracoorte Caves over the last glacial cycle (Darrénougué *et al*. 2009). Mean percentages of woody, herbaceous and woody-herbaceous taxa were calculated from samples corresponding to each of units A, B, C and E*. The Naracoorte Cave speleothem growth record was used as an indicator of effective moisture availability over the late Quaternary for this locality (Ayliffe *et al*. 1999).

Results

Data summary

Thirty-nine small mammal taxa were identified from 6,749 specimens from Wet Cave and 7,161 from Blanche Cave units A, B, C and E* and their associated phases (Table E.1 Appendix E). The total, murid sub-sample adjusted NISP for the assemblages were 11,075 (Wet) and 18,216 (Blanche).

Sampling variation of the local palaeocommunity: site-effects

No significant site-effects on species richness were detected between units A, B, C and E(*) of Wet and Blanche caves (Fig. 6.2; Table 6.3). By comparison, significant site-based sampling variation was evident in the evenness of the assemblages of units A, B and C between the two sites (Fig. 6.2; Table 6.3).

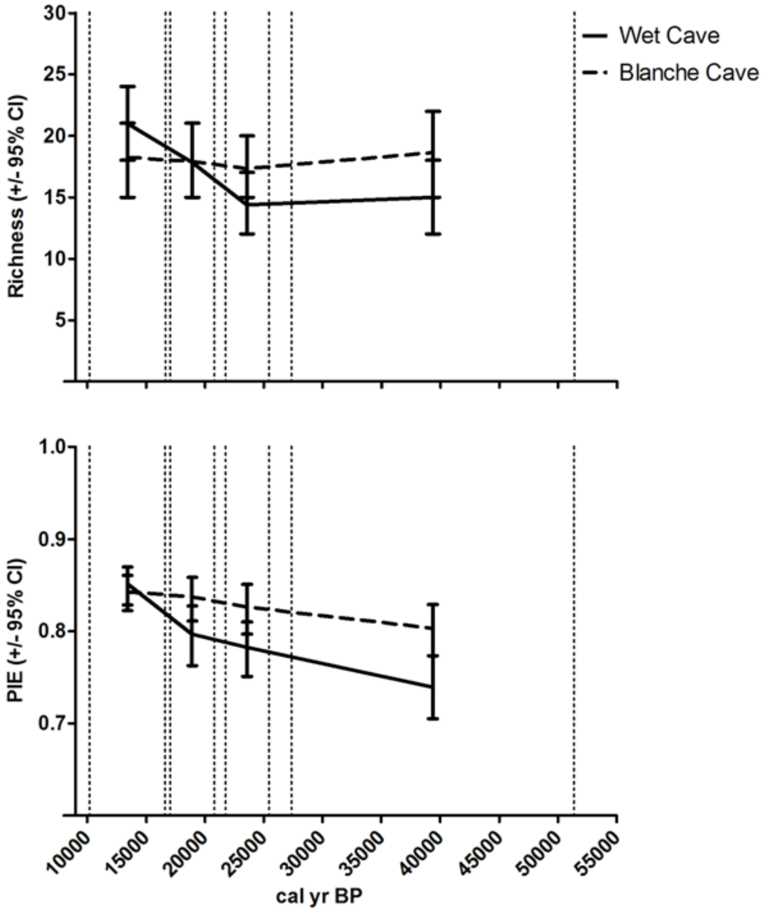

Figure 6.2 Macroscale trends in species richness and evenness (probability of interspecific encounter, PIE) of the small mammal assemblages of Wet and Blanche caves. Values shown are the mean ± upper and lower 2.5% percentiles (equiv. to 95% confidence intervals) of 1000 bootstrap re-samples standardised to a sample size of 303 specimens for all units. Vertical dotted lines indicate the median upper and lower modelled ages of units A, B, C and E(*) from the two sites. Upper and lower 95% highest probability density ranges for these median ages are presented in Table 6.1 and Fig. 6.1.

Table 6.3 Mean site- and time-effect sizes (difference between means) for species richness and evenness (Probability of Interspecific encounter, PIE) of 1000 bootstrap re-samples standardised to a sample size of 303 specimens for all units and phases. 95% confidence intervals are the 2.5% upper and lower percentiles of the bootstrapped mean. Asterisks indicate statistically significant effects where the 95% confidence interval does not include the value zero.

	Comparison	Species richness mean (2.5% percentiles)	PIE mean (2.5% percentiles)
Site-effects	Wet E – Blanche E*	2.747 (-2, 7)	0.008 (-0.023, 0.036)
	Wet C – Blanche C	-0.073 (-4, 4)	-0.040 (-0.082, -0.002)*
	Wet B – Blanche B	-2.937 (-6, 0)	-0.044 (-0.081, -0.006)*
	Wet A – Blanche A	-3.643 (-8, 1)	-0.064 (-0.108, -0.017)*
Time-effects (macroscale)	Wet E – C	3.174 (-1, 8)	0.054 (0.015, 0.094)*
	Wet C – B	3.429 (-1, 7)	0.015 (-0.028, 0.061)
	Wet B – A	-0.611 (-5, 3)	0.043 (-0.001, 0.086)
	Blanche E* – C	0.354 (-4, 5)	0.006 (-0.025, 0.036)
	Blanche C – B	0.565 (-3, 4)	0.011 (-0.023, 0.046)
	Blanche B – A	-1.317 (-6, 3)	0.023 (-0.015, 0.062)
Time-effects (mesoscale)	E6 - E5	4.030 (0, 8)	-0.039 (-0.081, 0.001)
	E5 - E4	1.123 (-2, 4)	0.014 (-0.021, 0.046)
	E4 - E3	1.476 (-1, 4)	-0.002 (-0.037, 0.032)
	E3 - E2	0.141 (-2 2)	0.023 (-0.011, 0.057)
	E2 - E1	1.362 (-1, 4)	0.014 (-0.027, 0.057)
	E1 - C2	-4.494 (-8, -1)*	-0.046 (-0.085, -0.009)*
	C2 - C1	-1.129 (-5, 3)	-0.022 (-0.055, 0.010)
	C1 - B1	0.501 (-3, 4)	0.022 (-0.014, 0.057)
	B1 - A4	-1.950 (-6, 2)	-0.017 (-0.052, 0.015)
	A4 - A3	0.800 (-4, 6)	0.015 (0.016, 0.046)
	A3 - A2	-0.145 (-5, 5)	0.046 (0.007, 0.087)*
	A2 - A1	1.311 (-4, 6)	-0.002 (-0.046, 0.044)

Jaccard similarity and rank-order abundance correlations for the units compared between Wet and Blanche caves were higher than expected at random, reflecting highly similar assemblage composition and structure between the two sites (Table 6.4). Mean Bray-Curtis similarities between Wet and Blanche caves were greater than 0.75 (Table 6.4). The similarity of the assemblages from Wet and Blanche caves for each of these beta-diversity measures was reflected in the dendrograms of the cluster analysis; however in all cases, units E and E* were separated on the first or second node with 100% bootstrap support (Fig. 6.3).

Site-effect sizes on the relative abundances of individual species were variable as shown in Figure 6.4 and Table E.2 (Appendix E). Species proportions in Blanche Cave fell within a maximum range of 15% of those recorded in Wet Cave for all units.

Table 6.4 Similarity index values (Jaccard and Bray-Curtis) and Spearman’s rank-order correlations between contemporaneous units of Wet and Blanche caves. For Jaccard and Bray-Curtis similarity, the data presented are the mean of 1000 bootstrap re-samples standardised to a sample size of 303 specimens for all and 95% confidence intervals are the 2.5% upper and lower percentiles of the bootstrapped mean. 95% confidence intervals for Spearman’s Rho were calculated using the Fisher transformation. All Jaccard similarity index values and Spearman’s ranks are significantly higher than expected at random (α=0.01). No significance test is available for Bray-Curtis similarity.

	Jaccard mean (2.5% percentiles)	# species in pair	Spearman’s Rho mean (95% CI)	Bray-Curtis mean (2.5% percentiles)
Wet E-Blanche E*	0.581 (0.458, 0.708)	33	0.702 (0.493, 0.835)	0.758 (0.721, 0.797)
Wet C-Blanche C	0.621 (0.478, 0.765)	29	0.831 (0.696, 0.909)	0.841 (0.795, 0.889)
Wet B-Blanche B	0.707 (0.550, 0.833)	22	0.853 (0.733, 0.922)	0.801 (0.763, 0.839)
Wet A-Blanche A	0.635 (0.478, 0.790)	36	0.585 (0.326, 0.762)	0.824 (0.781, 0.871)

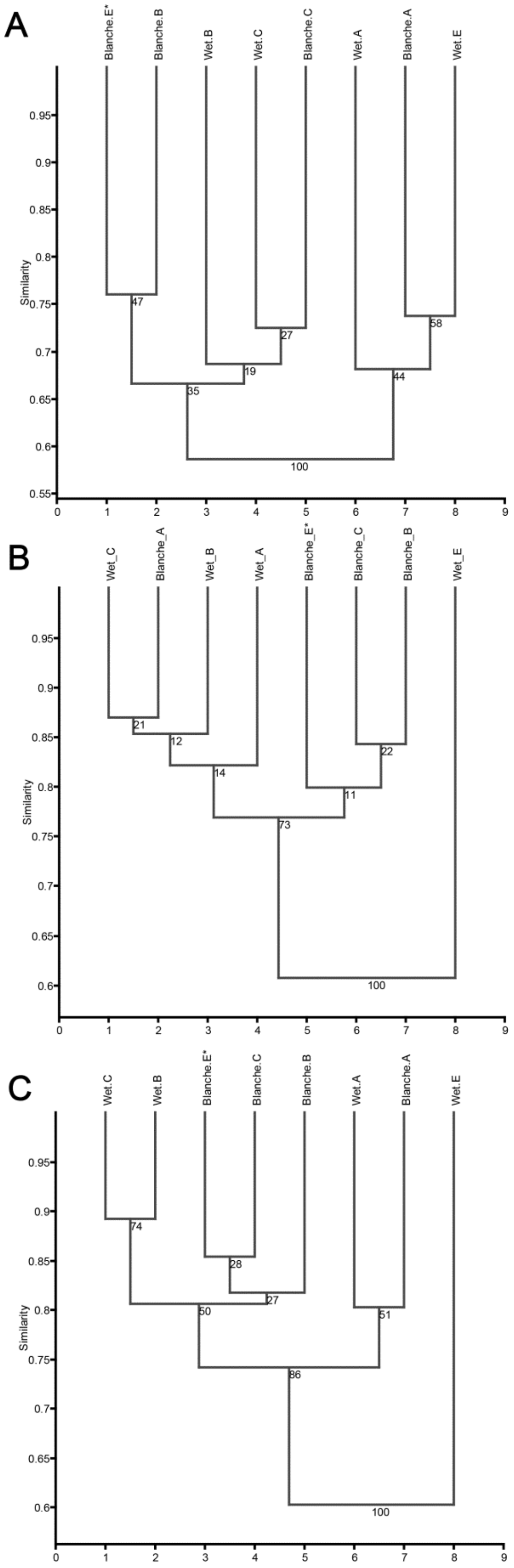

Figure 6.3 Unweighted paired-group mean dendrograms of units A, B, C and E(*) of Wet and Blanche caves, clustered based on (A) Jaccard similarity, (B) Spearman's Rho and (C) Bray-Curtis similarity. Jaccard and Bray-Curtis similarity measured from mean number of specimens of each taxon in a sample based on 1000 bootstrap re-samples standardised to a total sample size of 303 specimens. Spearman's Rho calculated from total sample for each unit. The bootstrap probability of each node is based on 1000 re-samples.

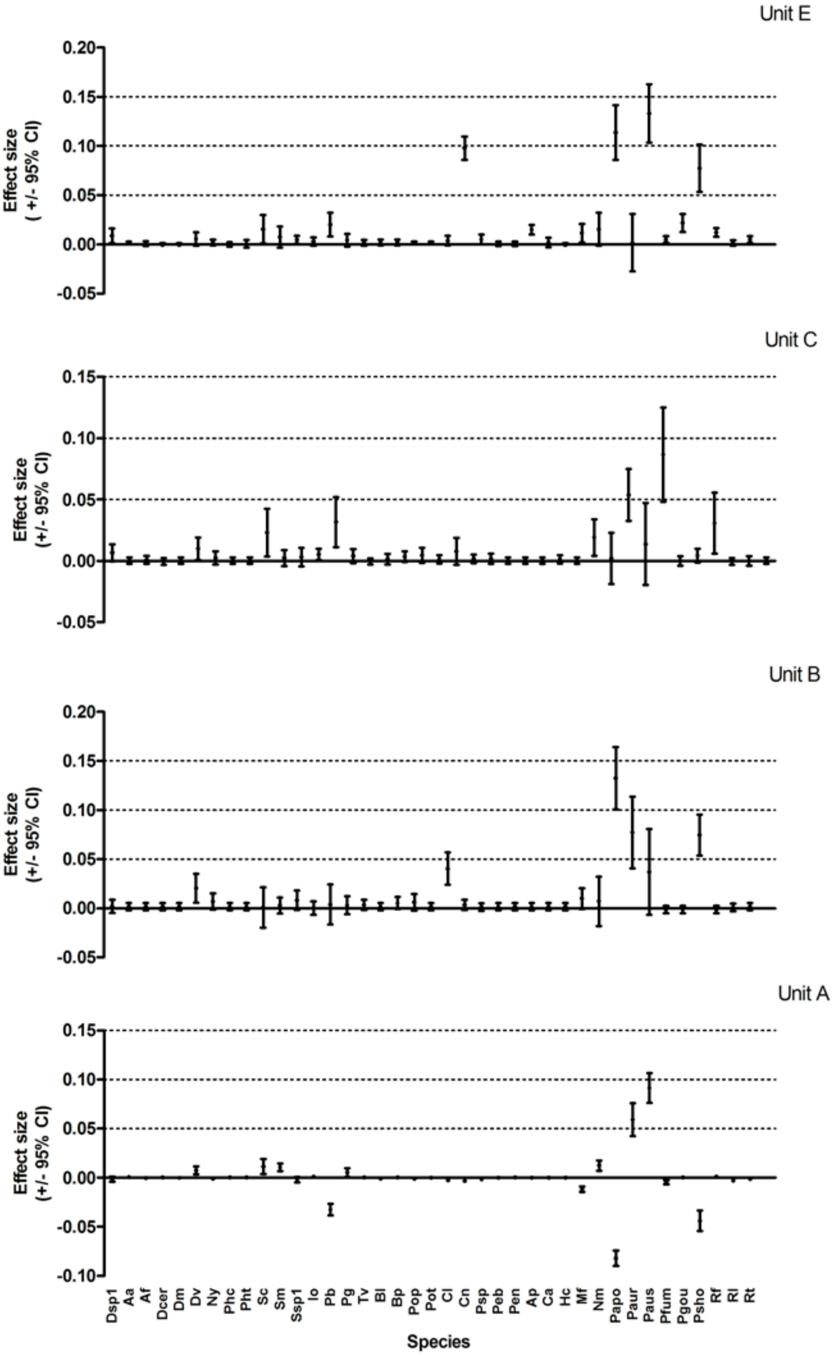

Figure 6.4 Mean ± 95% confidence interval of site-effect size (difference between means) of species proportions in Blanche Cave compared with Wet Cave. Confidence intervals were calculated using the “plus four” method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007). Species codes are presented in Table E.1 (Appendix E).

Macroscale time-effects on palaeocommunity metrics

Species richness and Jaccard similarity showed no significant macroscale variation through either Wet or Blanche caves (Figs. 6.2 and 6.5; Tables 6.3 and 6.5). Significant macroscale time-effects on evenness, rank-order abundance and Bray-Curtis similarity were detected only between Wet Cave units C and E (Table 6.5; Fig. 6.5). These time-effects were reflected in the cluster analysis which showed that Wet Cave unit E was more different in terms of species abundances and structure to Wet and Blanche cave units A, B and C than the latter were to each other, with 100% bootstrap support (Fig. 6.3).

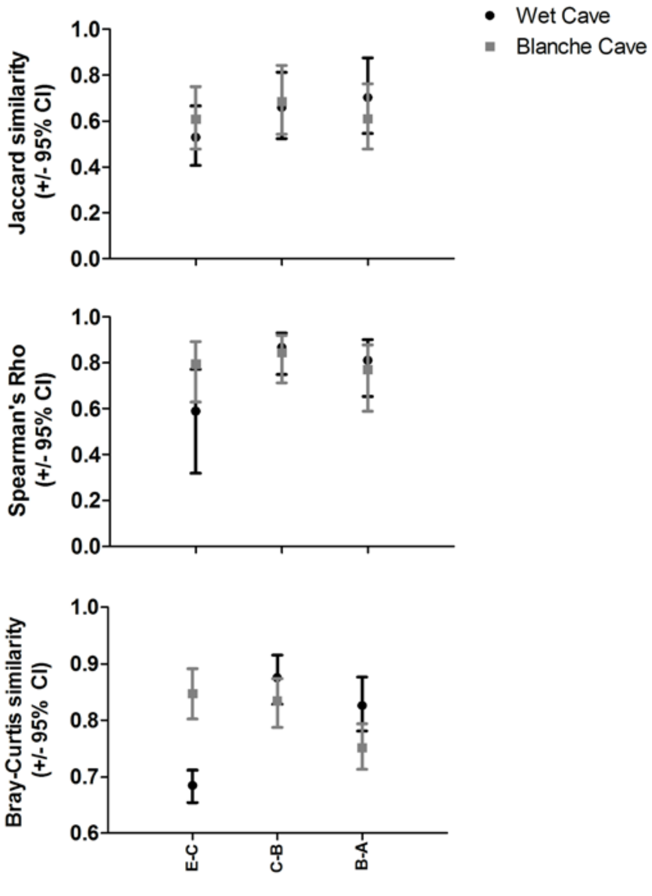

Figure 6.5 Jaccard and Bray-Curtis similarity indices and Spearman rank-order abundance correlations (Spearman's Rho) between adjacent units of Wet and Blanche caves. All metrics except Spearman's Rho are presented as the mean ± upper and lower 2.5% percentiles (equiv. to 95% confidence intervals) of 1000 bootstrap re-samples standardised to a sample size of 303 specimens for all units. Spearman's Rho calculated from total sample for each unit and 95% confidence intervals calculated using the Fisher transformation (Zar 1996).

Mesoscale time effects on palaeocommunity metrics

At the mesoscale, species richness declined from phase C2 to E1 and ranged at the 95% confidence level from -8 to -1 taxa (Fig. 6.6; Table 6.3). Evenness was more variable than species richness at this finer temporal scale and there were two significant time-effects on community evenness: an increase in evenness from phase A2 to A3 and a decrease from phase C2 to E1. Although these values were statistically significant, they were comparable to site-effect sizes on evenness (Table 6.3).

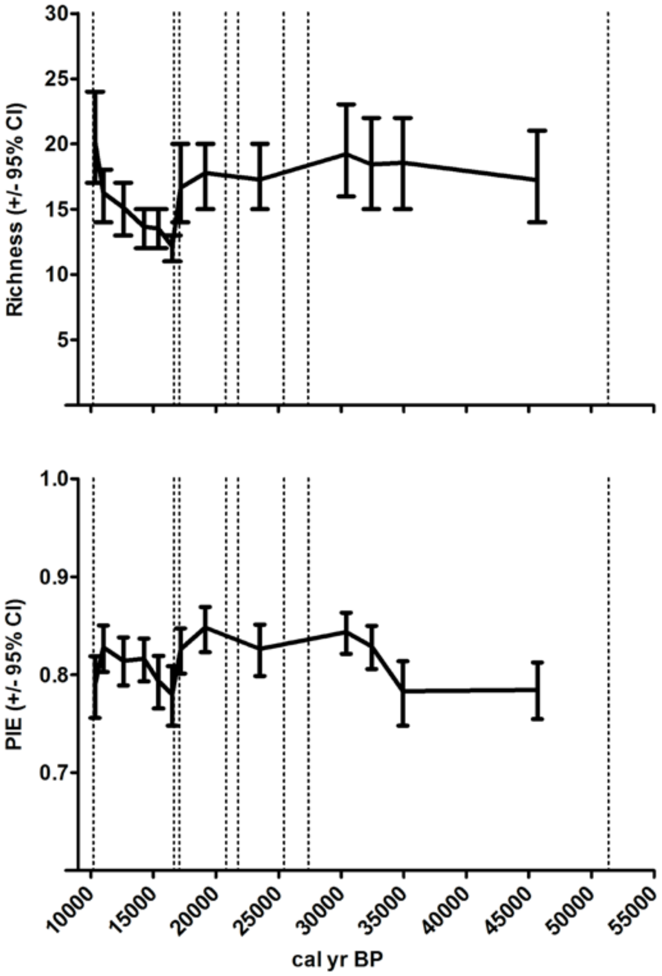

Figure 6.6 Mesoscale trends in species richness and evenness (probability of interspecific encounter, PIE) of the small mammal assemblages of Wet and Blanche caves. Values shown are the mean ± upper and lower 2.5% percentiles (equiv. to 95% confidence intervals) of 1000 bootstrap re-samples standardised to a sample size of 303 specimens for all phases. Vertical dotted lines indicate median upper and lower modelled ages of the phases from Wet and Blanche caves. Upper and lower 95% highest probability density ranges for these median ages are presented in Table 6.1 and Fig. 6.1.

Jaccard similarity was higher than expected at random between phases A1 to C2 (Table 6.5; Fig. 6.7). The lowest compositional similarity (Jaccard index) occurred between phases E1 and C2 but was not significantly different from random and fell within the range of site-effects measured from unit C in Wet and Blanche caves. The Jaccard similarity values of E4-E3, E5-E4 and E6-E5 were also non-significant (Table 6.5). In the cluster analysis based on Jaccard similarity, phases A1 to A4 were separated from B1 to E5 with 100% bootstrap support (Fig. 6.8). Phase E6 was separated from phases E1 to E5 (100% support) while the separation of phases E1 to E4 from B1 to C2 was poorly supported (9%).

Table 6.5 Similarity index values and Spearman Rank correlations of adjacent units and phases at the macro- and mesoscales, respectively, through Wet and Blanche caves. All mean Jaccard similarity index values and Spearman's ranks are significantly higher than expected at random (p<0.01) with the exception of Jaccard similarity of Wet Cave unit E-C and phases E6-E5, E5-E4, E4-E3 and E1-C2 (indicated by 'NS').

	Jaccard mean (2.5% percentiles)	Spearman's Rho mean (95% CI)	Bray-Curtis mean (2.5% percentiles)
Wet Cave E-C	0.530 (0.407, 0.666) NS	0.590 (0.320, 0.771)	0.684 (0.654, 0.711)
Wet Cave C-B	0.659 (0.524, 0.813)	0.867 (0.751, 0.931)	0.875 (0.828, 0.915)
Wet Cave B-A	0.702 (0.545, 0.875)	0.811 (0.655, 0.901)	0.826 (0.781, 0.876)
Blanche Cave E*-C	0.609 (0.478, 0.750)	0.795 (0.628, 0.892)	0.847 (0.802, 0.891)
Blanche Cave C-B	0.685 (0.542, 0.842)	0.845 (0.713, 0.919)	0.834 (0.787, 0.873)
Blanche Cave B-A	0.611 (0.478, 0.762)	0.771 (0.589, 0.878)	0.751 (0.713, 0.793)
E6-E5	0.544 (0.423, 0.682) NS	0.664 (0.425, 0.816)	0.680 (0.653, 0.710)
E5-E4	0.581 (0.476, 0.706) NS	0.717 (0.505, 0.848)	0.804 (0.759, 0.856)
E4-E3	0.610 (0.500, 0.734) NS	0.762 (0.575, 0.873)	0.812 (0.767, 0.861)
E3-E2	0.850 (0.688 1.000)	0.950 (0.903, 0.975)	0.851 (0.806, 0.896)
E2-E1	0.722 (0.600, 0.857)	0.859 (0.737, 0.927)	0.882 (0.830, 0.927)
E1-C2	0.540 (0.421, 0.666) NS	0.685 (0.467, 0.824)	0.778 (0.734, 0.826)
C2-C1	0.687 (0.550, 0.850)	0.871 (0.758, 0.933)	0.840 (0.881, 0.797)
C1-B1	0.718 (0.591, 0.850)	0.866 (0.749, 0.931)	0.816 (0.779, 0.854)
B1-A4	0.602 (0.478, 0.750)	0.763 (0.577, 0.874)	0.808 (0.763, 0.858)
A4-A3	0.634 (0.480, 0.810)	0.844 (0.711, 0.919)	0.887 (0.846, 0.942)
A3-A2	0.680 (0.524, 0.850)	0.909 (0.826, 0.953)	0.821 (0.781, 0.868)
A2-A1	0.662 (0.500, 0.824)	0.964 (0.929, 0.982)	0.879 (0.832, 0.921)

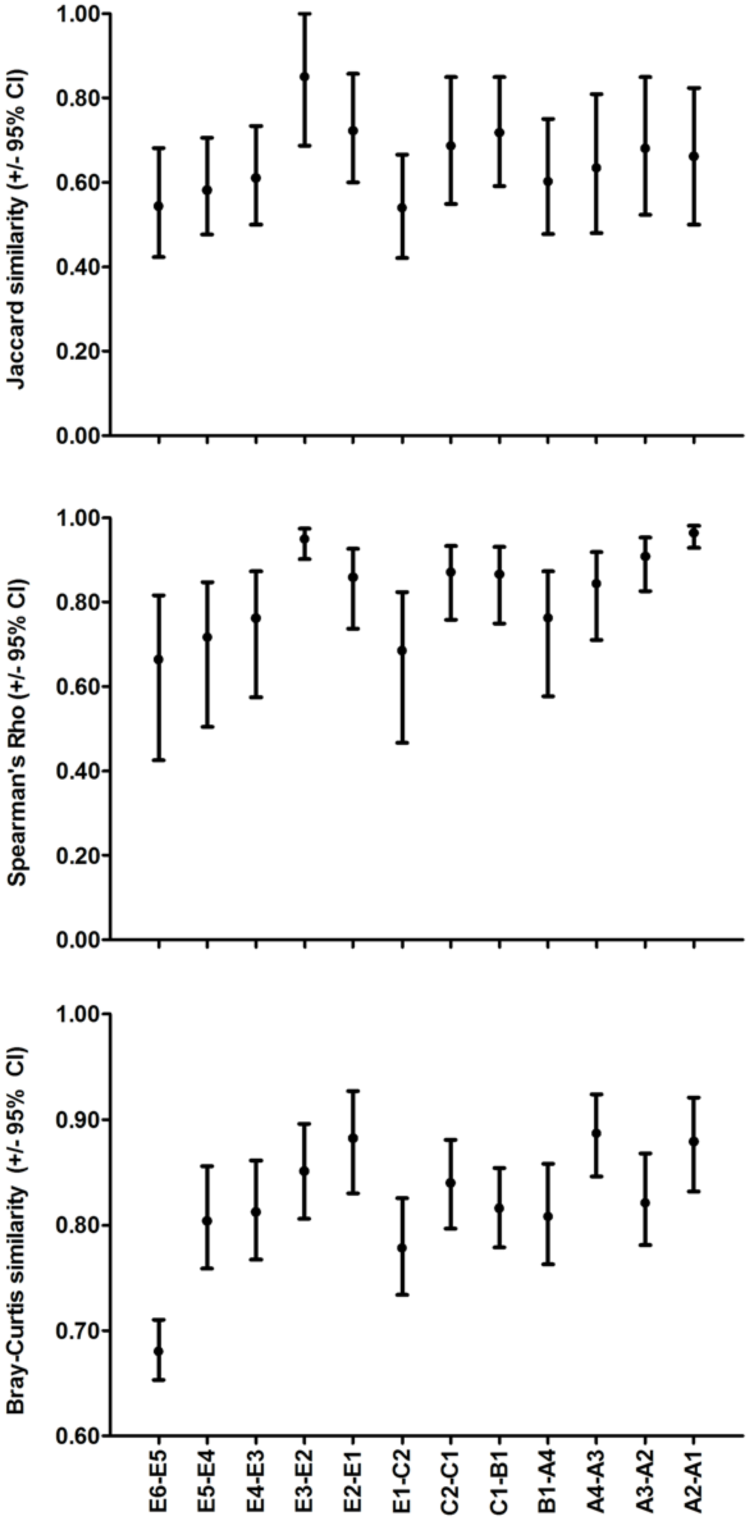

Figure 6.7 Jaccard and Bray-Curtis similarity and Spearman rank-order abundance correlations (Spearman's Rho) of adjacent phases of Wet and Blanche caves. All metrics except Spearman's Rho are presented as the mean ± upper and lower 2.5% percentiles (equiv. to 95% confidence intervals) of 1000 bootstrap re-samples standardised to a sample size of 303 specimens for all phases. Spearman's Rho calculated from total sample for each phases and 95% confidence intervals calculated using the Fisher transformation (Zar 1996).

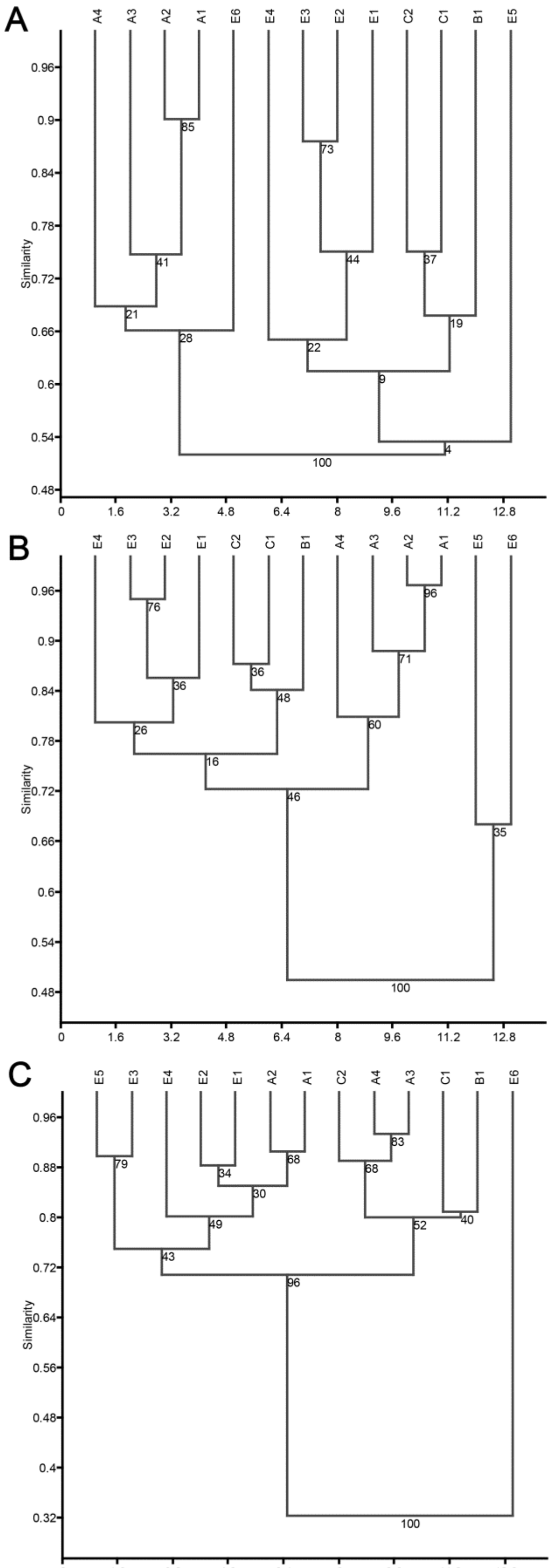

Figure 6.8 Unweighted paired-group mean dendrograms of phases from Wet and Blanche caves, clustered based on (A) Jaccard similarity, (B) Spearman's Rho and (C) Bray-Curtis similarity. Jaccard and Bray-Curtis similarity measured from mean number of specimens of each taxon in a sample based on 1000 bootstrap re-samples standardised to a total sample size of 303 specimens. Spearman's Rho calculated from total sample for each unit. Bootstrap probability of each node based on 1000 re-samples are presented.

The rank-order abundance correlations of phases A1 to C2 were high and ranged between 0.763 and 0.964 (Fig. 6.7). A decline in correlation of 0.186 occurred from phases C2-C1 to E1-C2 (Table 6.5), reflecting a similar temporal trend as the Jaccard similarity index (Fig. 6.7). In the cluster analysis there was only 16% bootstrap support for the separation of phases C2 and E1 based on rank-order abundance, contrasting with phases E5 and E6 which together were separated from all other phases with 100% bootstrap support. The rank-order abundance correlation of units E1 and C2 also fell within the range of the site-effect associated with unit C for this metric (Table 6.4).

Bray-Curtis similarity was more variable at the mesoscale than Jaccard similarity and Spearman's Rho as reflected in the cluster analysis which identified three separate groups (phase E6; phases A3 to C2; phases A1 to A2 and E1 to E5) with bootstrap support of 100% and 96%, respectively (Fig. 6.8). The separation of phase E6 from all other phases in the cluster analysis is consistent with the low Bray-Curtis similarity measured between phases E5 and E6 (Table 6.5) and shows that relative abundance of species in phase E6 were more different to all other phases than would be expected at random.

Time-effects on individual species relative abundances

For nearly all taxa, the magnitude of site-effects on the relative abundance of individual species exceeded any macroscale time-effect, severely limiting the extent to which temporal variation in relative species abundances within individual sites could be examined (Tables E.2–E.5 Appendix E). In addition, significant macroscale linear trends in relative abundance were detected for only *c.* 35% of the Blanche Cave taxa which occurred in three or more units (Table E.6 Appendix E). Wet Cave provided more reliable estimates of macroscale trends in species proportions, with 57% of taxa demonstrating significant linear trends in this site (Table E.6 Appendix E). Only five species had significant linear trends in both assemblages (*Sminthopsis murina, Perameles gunnii, Notomys mitchellii, Pseudomys auritus* and *Pseudomys australis*), and in all cases, the patterns of variation with time were similar, despite significant differences in relative abundance values between the two sites for some units (Fig. 6.9; Table E.6).

In addition to the five species which demonstrated significant and similar trends in abundance through the Wet and Blanche Cave sequences at the macroscale, significant linear trends at this temporal resolution were detected for a further 10 species which occurred in at least three units of one of the two sites (Fig. 6.10). Significant linear trends at the mesoscale were demonstrated by 15 of 32 species identified from four or more phases (Table E.7 Appendix E; Fig. 6.11).

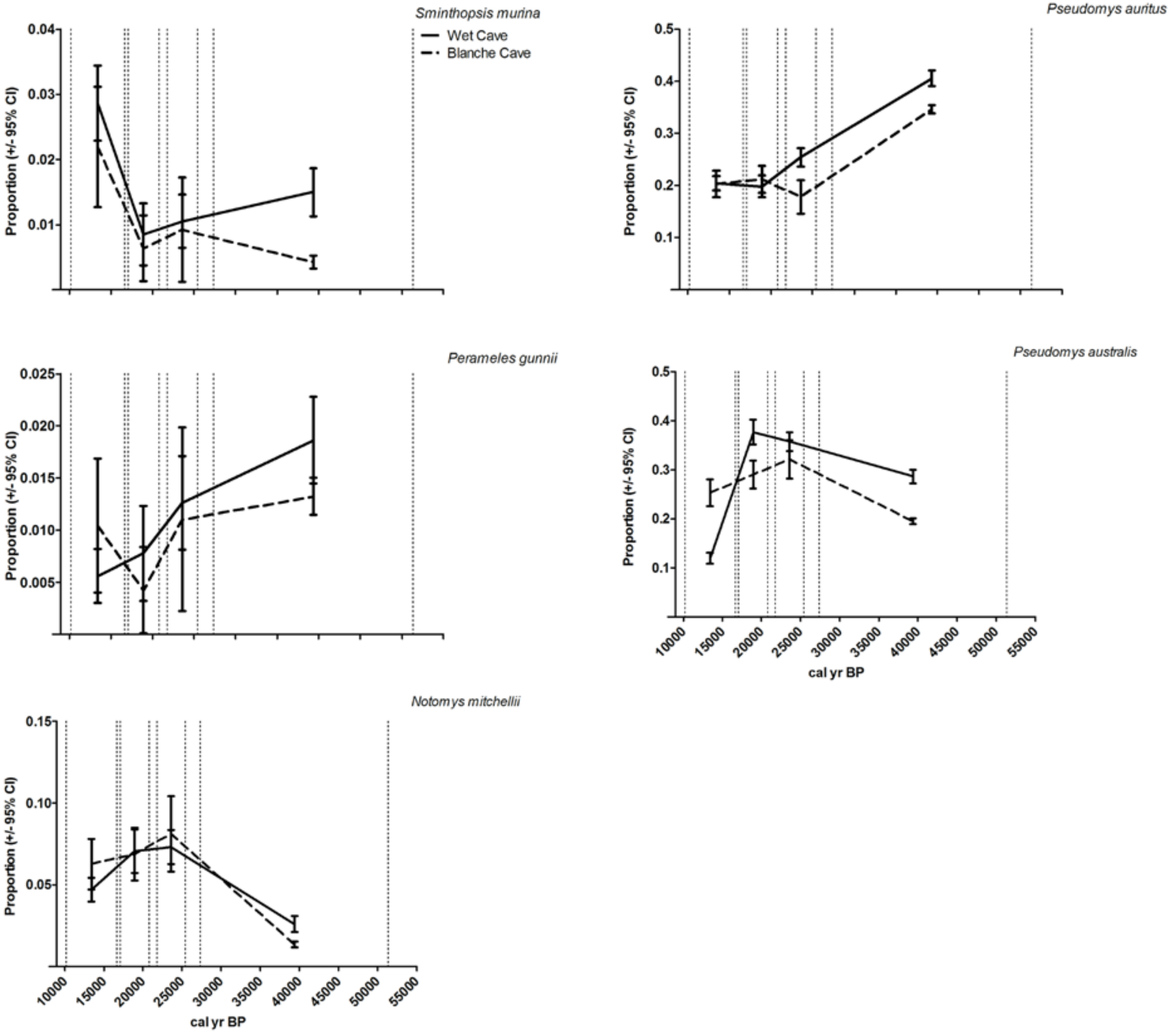

Figure 6.9 Mean ± 95% confidence interval of species proportions demonstrating significant linear trends (α=0.01) at the macroscale according to Cochran's test in both Wet and Blanche caves. Confidence intervals were calculated using the "plus four" method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007). Vertical dotted lines indicate median upper and lower modelled ages of the phases from Wet and Blanche caves. Upper and lower 95% highest probability density ranges for these median ages are presented in Table 6.1 and Fig. 6.1.

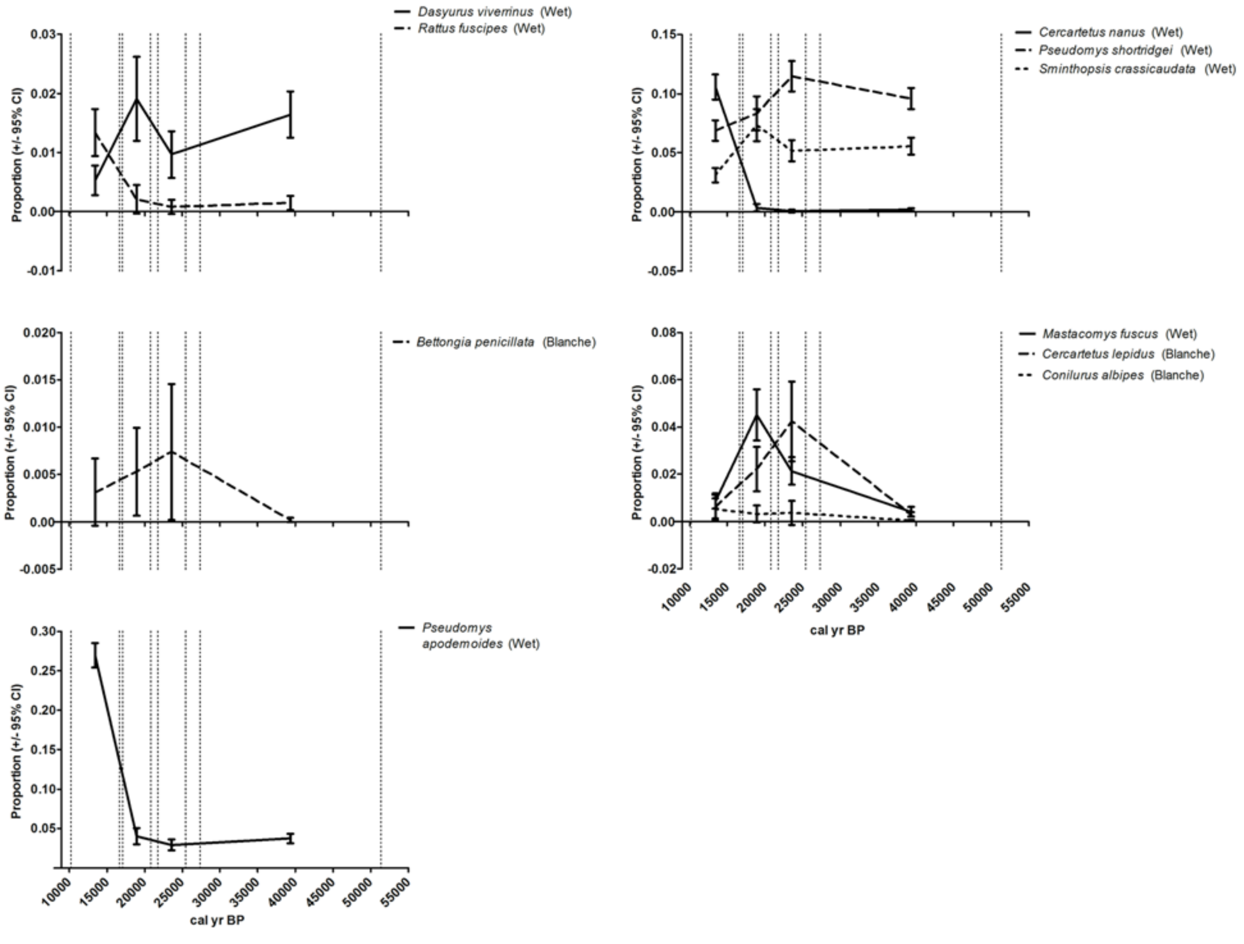

Figure 6.10 Mean ± 95% confidence interval of species proportions demonstrating significant linear trends (α=0.01) at the macroscale in either Wet or Blanche Cave. Confidence intervals were calculated using the "plus four" method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007). Vertical dotted lines indicate median upper and lower modelled ages of the phases from Wet and Blanche caves. Upper and lower 95% highest probability density ranges for these median ages are presented in Table 6.1 and Fig. 6.1.

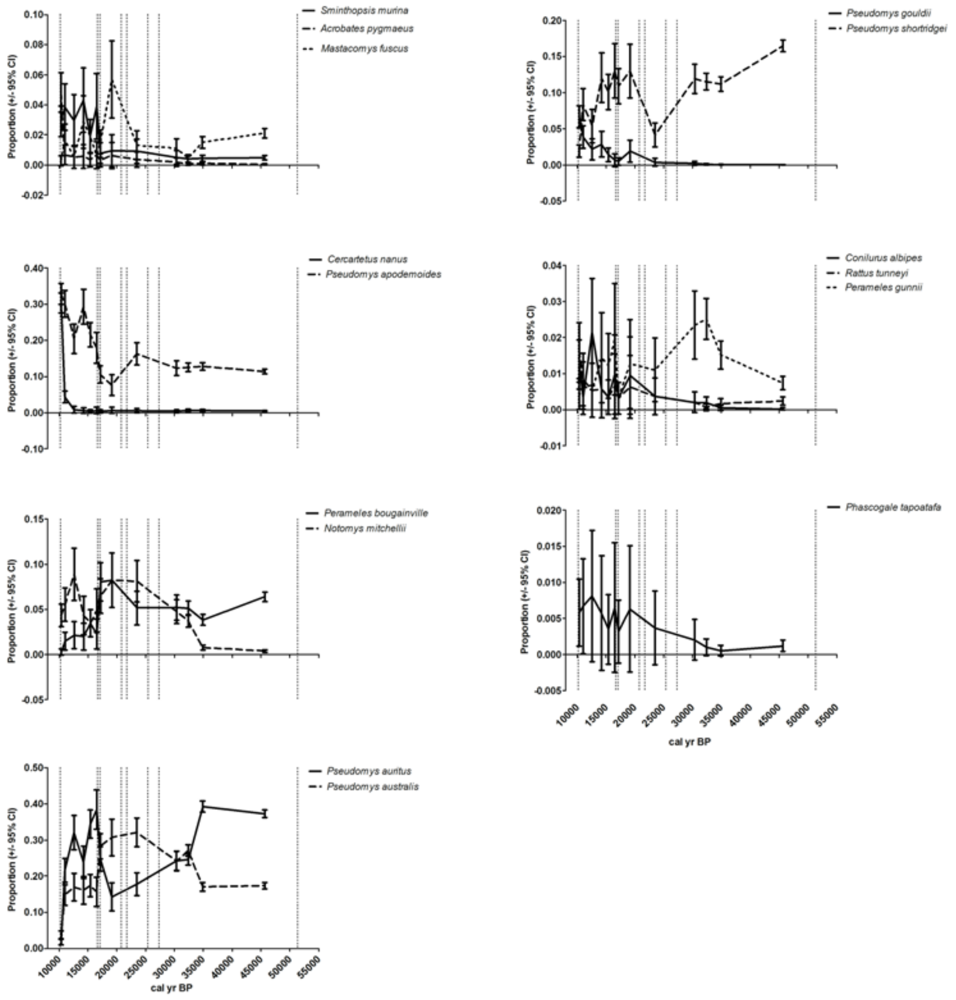

Figure 6.11 Mean ± 95% confidence interval of species proportions demonstrating significant linear trends (α=0.01) at the mesoscale (phases A4–A1, B, C2–C1 of Blanche Cave, and phases E6–E1 of Wet Cave). Confidence intervals were calculated using the "plus four" method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007). Vertical dotted lines indicate median upper and lower modelled ages of the phases from Wet and Blanche caves. Upper and lower 95% highest probability density ranges for these median ages are presented in Table 6.1 and Fig. 6.1.

Discussion

Similarity of Wet and Blanche Cave fossil assemblages: palaeocommunity variables

The lack of statistically significant site-effects on species richness, composition and abundance ranks, and high Bray-Curtis index values of the assemblages from Wet and Blanche caves shows that overall, the two sites provided similar palaeocommunity samples for each time period represented by units A, B, C and E(*). This demonstrated similarity is consistent with expectations based on their spatial proximity, similar temporal span and accumulation-mode (tytonid owls; Macken and Reed 2013; Macken *et al*. 2013b). By comparison, significant differences in assemblage evenness and the relative abundances of individual species between the sites revealed sampling effects not evident in the metrics based on species presence/absence and rank-order data.

Quantifying variability in local palaeocommunities is critical for testing patterns of stasis and/or change in palaeocommunities across space and time (Bennington and Bambach 1996). Thus, the similarity of palaeocommunity variables measured from the assemblages of units A, B and C of Wet and Blanche caves suggests that any temporal variability and/or stability observed in these metrics reflects real patterns with time at the macroscale.

We note that the similarity of whole-assemblage variables measured directly between Wet Cave unit E and Blanche Cave unit E* is surprising given that they are not temporally equivalent (unit E* overlaps, but does not cover the entire temporal period represented in Wet Cave unit E; Table 6.1; Macken *et al*. 2013b). One reason for the similarity between these units may be the mixing of bone material of Pleistocene and Holocene ages in unit E*. As shown by St Pierre *et al*. (2012), Holocene aged speleothem (calcium carbonate) straws and charcoal are present in Blanche Cave layers 1 and 3 which correspond to unit E* (Table E.1 Appendix E). However, Pleistocene aged charcoal samples are also present in layers 1 to 3. The mixed age of materials in these layers suggests that reworking occurred during or following deposition. Site disturbance by human activity is the likely cause of such mixing in the upper layers of the Blanche Cave deposit as the site has a long history of visitation by European settlers in the region. In particular, guano collection in

Blanche Cave may have stripped the younger Holocene aged sediments from the study site, resulting in disturbance to the Pleistocene aged layers that are today represented by the top layers of the deposit (Darrénougué *et al*. 2009). Alternatively, layers 1 to 3 may be Holocene aged and contaminated with Pleistocene aged material as a result of the site disturbance. Further dating of materials from the upper layers in Blanche Cave is required to understand the full extent and nature of reworking that may have occurred over the history of the site. However, regardless of the specific processes involved, the mixed age of sediments, and potentially of fossil material in unit E*, may have increased the time-averaging of fossil faunas in this section of Blanche Cave. Such mixing of faunas of different ages can inflate species richness by increasing the likelihood of sampling rare fauna (Hadly 1999), and/or by the consolidation of faunas from separate environmental and climatic periods (Graham 1985). This greater time-averaging of the unit E* faunas may account for the apparent similarity in whole-assemblage attributes between this assemblage and that from Wet Cave unit E.

We also note that there are differences in the magnitude and significance of time-effects between units E and C of Wet Cave and units E* and C of Blanche Cave. This variation reveals sampling effects not captured by the alpha or beta diversity metrics measured as site-effects alone. For example, divergence in the temporal trends associated with units E and E* is evident in the cluster analyses, where units E and E* are relatively more different to each other than units A, B and C. Of particular note is Bray-Curtis similarity which shows that the relative abundances of species from Wet Cave units C to E are more different than from Blanche Cave unit C and E*, consistent with expectations based on the known temporal-inequality of units E and E* (Table 6.5). Given the sampling limitations of Blanche Cave unit E*, we do not provide any further evaluation of temporal trends between units C and E* from this site.

Similarity of Wet and Blanche Cave fossil assemblages: relative abundance of individual species

While the palaeocommunity variables are similar between Wet and Blanche caves, the relative abundances of individual species varied between contemporaneous units. This is not surprising given the diverse range of processes involved in fossil accumulation and which can contribute to spatial heterogeneity in fossil occurrences within and among sites. Differences in the relative abundances of species between contemporaneous units in Wet and Blanche caves are consistent with other studies that have found that fossil specimens are not evenly distributed across a single sedimentary horizon or across suitable habitat patches in living communities (e.g., Brown *et al*. 1995). For example, Bennington and Bambach (1996) found that replicate samples of fossil molluscs and brachiopods from marine shales had different underlying species abundance distributions, suggesting that time-averaging in the shales was not long enough to reduce spatial variability in the relative abundances of species within an assemblage. This heterogeneity may result from patchiness in the living community, taphonomic processes and/or sampling error.

In the case of Wet and Blanche caves, taphonomic processes and sampling error are expected to account for the site-based differences observed, rather than patchiness in the living community. While it is expected that individuals of populations would have been patchily distributed in the Pleistocene landscape around the caves, such patchiness would have had a limited effect on the distribution of the relative abundances of species in the assemblages given the sampling mode (transport of animal remains to the caves by owls).

The influences of other biases such as variation in bone and/or teeth preservation are commonly observed in fossil assemblages (e.g., Fernandez-Jalvo and Andrews 1992). To address these taphonomic concerns, Bobe *et al*. (2002) compared the percentage occurrence of different skeletal-elements against taxonomic variability through time to establish the extent to which changes in the abundances of species may have been caused by taphonomic and/or ecological processes. Such an approach was not suitable for the assemblages from Wet and Blanche caves where, given the density of bone material, only cranio-dental specimens were identified. Additionally, the bias towards small mammals throughout both sequences shows that the primary taphonomic filter (tytonid owls) remained similar through the last glacial cycle, when both the whole assemblage, including mammals with body mass >2.5 kg (McDowell 2001; Laslett 2006) and only the small mammal component (Fig E.3 Appendix E) are considered.

The Cochran-Armitage tests and relative magnitude of site- and time-effects show that, for the majority of species, temporal trends in the relative abundances of individual species could not be used to establish the stability or otherwise of species populations through time. This lack of confidence in the relative abundance trends arises both as a result of the sampling variance between the two sites and inadequate sample sizes between consecutive units within single sites. However, of particular note is that for those species where significant temporal trends were detected in both sites, the trends were the same or very similar (Fig. 6.3). These results suggest that where sampling was adequate, trends in species proportions were preserved in the same way in the two deposits, regardless of the sampling variation between them. This suggests that such trends are biologically significant.

Macro- versus mesoscale patterns of natural variation, persistence and intrinsic thresholds of change

To assess the ecological significance of temporal change observed in ecological variables measured from the assemblages of Wet and Blanche caves, we integrated the numeric hierarchy of Rahel (1990) and terminology of Bennington and Bambach (1996; Table 6.2). According to Bennington and Bambach (1996), after site-effects are accounted for, if two samples have statistically different species abundance distributions, they may be assumed to have come from different palaeocommunity types (Table 6.2). However, as noted by Rahel (1990), the relative abundances of species within a community may be highly variable with time while other variables such as rank-order abundance and composition remain unchanged. Further, Hadly and Barnosky (2009) suggested that while changes in the relative abundances of species are the “early warning signal” of environmental impacts on species (p. 47), they also argued that changes in relative abundance alone do not constitute significant change from a normal baseline of variation operating at the species level within a palaeocommunity. Rather, based on evidence from fossil and modern assemblages, they suggested that variation in the relative abundances of species is the normal type of response to climate change and other disturbances across different temporal scales.

Given these perspectives and the observation that relative abundances were poorly sampled in the Wet and Blanche caves, we used the more conservative ecological variable of rank-order abundance to assess the stability of the palaeocommunity through last glacial cycle. This metric lies in the middle of Rahel's (1990) hierarchy. An ecological driver of stability in abundance ranks may be synchrony of changes in the relative abundance of species within a community in response to disturbance. This may reflect similar responses of individual species to environmental or climatic changes (Rahel, 1990). However, individualistic responses of populations (species) to climate change are more common and lead to composite effects on communities (Stewart 2008). Of particular interest then was whether the relative abundance of species through the last glacial cycle varied individually and beyond thresholds operating within the palaeocommunity to lead to a new rank-order abundance structure, and hence, a new palaeocommunity type?

In taking this approach, we acknowledge that Bennington and Bambach (1996) cautioned against the use of non-parametric analysis of rank-order abundances. They argued that even small differences in the NISP values of species between samples makes them susceptible to accepting the null hypothesis ($\rho=0$, no association between samples) when there is, in fact, an association or correlation of species ranks between them. However, Spearman's Rho is commonly used in the analysis of fossil assemblages, particularly to assess the fidelity of live-dead assemblages (e.g., Kidwell 2001; Terry 2010a, b). It has also been used in ecological studies (e.g., Rabonsky *et al*. 2011) and has been suggested as a useful measure for detecting early signs of change in ecological assemblages (Magurran and Henderson 2010). Further, the alternative parametric ANOVA suggested by Bennington and Bambach (1996) was not suitable for the present study as only a limited number of replicates was available for the macroscale analysis (n=2), while only single samples were available for each phase at the mesoscale.

This lack of sample replication is common in the study of vertebrate fossil assemblages, where sample(s) are collected from quadrats or grids non-randomly positioned within a depositional environment (e.g., river channel or cave floor), as was the case for Wet and Blanche caves. Despite the collection of samples from multiple quadrats in some vertebrate studies, they are rarely treated as independent replicates as (a) specimens from different quadrats may have come from the same individual, (b) samples from nearby quadrats are commonly pooled to increase sample size until additional sampling effort is unlikely to recover new taxa ("sampling to redundancy"; Lyman 2008, p. 143), and (3) there is often a limited capacity to temporally correlate specimens between sites due to varying depositional histories, temporal coverage and time-averaging. These and other sampling issues and strategies associated with vertebrate fossil assemblages are discussed in more detail elsewhere (e.g., Lyman 2008; Terry 2009).

Palaeocommunity reorganisation

Within the range of sampling variation observed between Wet and Blanche caves, the macro- and mesoscale analyses suggest that a single palaeocommunity type persisted from 51.4 to 17.1 kyr BP (95% CI: 60.0 to 16.7 kyr BP). This stability is observed despite evidence for significant temporal variation (based on 95% CI and time-effect > site-effect) in the relative abundances of some taxa over this time. By comparison, the low rank-order abundance correlation of units C and E in Wet Cave and separation of these units in the cluster analysis based on this variable with 100% bootstrap support suggests that the palaeocommunities from these two time periods may be significantly different.

Palaeocommunity reorganisation between these units is reflected at the mesoscale in the significant decline in species richness from phase C2 to E1. Species richness does not appear in Rahel's (1990) hierarchy but reflects community-level variation at a scale consistent with composition as both of these metrics are based on species presence/absence data. The variation in the presence of individual species within the palaeocommunity likely reflects the dispersal of species from the region proximal to the caves during phase E1, rather than local extinction: species absent from phase E1 return to the Wet Cave record in one of phases E2 to E6 or the Holocene samples of Robertson Cave entrance chamber (pers. obs.). Only one species may have gone locally extinct over the transition of phase C2 to E1 (*Bettongia gaimardi*) as this species is not known from younger fossil assemblages of the Naracoorte Caves. Thus, despite our lack of confidence in the trends observed in the relative abundances of individual species, the significant decline in species richness from phase C2 to E1 reflects re-organisation of the palaeocommunity and the emergence, at least during phase E1, of a new palaeocommunity type from that of the previous *c.* 33 kyrs. We also note that the mean decline in species richness of five (based on the sample-size standardised data; 95% CI: 1 to 8) from phase C2 to E1 is the same as the decline in species richness of a small mammal assemblage over the Pleistocene–Holocene transition in Samwell Cave, northern California (Blois *et al*. 2010). The loss of species observed in the Samwell Cave sequence at the end of the Pleistocene was coincident with a decline of *c*. 0.15 in Jaccard similarity and *c*. 0.06 in Bray-Curtis similarity. These changes were interpreted as reflecting a reorganisation of the palaeocommunity at the end of the Pleistocene (Blois *et al*. 2010). As the values measured from Samwell Cave are almost identical to the differences between these metrics observed in the assemblages from Wet and Blanche caves from phase C2 to E1, we interpret a similar degree of palaeocommunity reorganisation in the Naracoorte small mammal faunas following the last glacial maximum.

Interestingly, the high and statistically significant compositional similarity and rank-order abundance correlation of phases E1 and E2, and phases E2 and E3 suggest a period of relative stability in the palaeocommunity from *c*. 16.7 to 14.0 kyr BP (95% CI: 17.1 to 12.7). This is followed by a possible second reorganisation of the palaeocommunity from phase E5 to E6, 10.8 and 10.5 kyr BP (95% CI: 11.2 to 10.9 kyr BP). The evidence for this second reorganisation is the low mean rank-order abundance correlation of these phases when compared with the other phases; although unlike the first significant episode of palaeocommunity change, the second is not associated with a significant change in species richness.

Palaeoclimatic and environmental thresholds

It is common for palaeoenvironmental reconstructions to be based on the contemporary distribution and niche space of the species identified in a fossil assemblage. Such properties are then used to infer the local extrinsic and intrinsic factors associated with a palaeocommunity at the time of accumulation. However, geographic range and niche contraction as a result of human mediated landscape change is expected to severely limit the accuracy of palaeoenvironmental reconstructions using this technique (e.g., Belyea 2007; Bilney *et al*. 2010). Consequently, we are cautious in inferring the environmental, climatic and biological correlates of the small mammal palaeocommunities from the fauna themselves and instead contrast them against independent records of palaeoclimatic and environmental conditions (Fig. 6.12).

As we have only used a narrow range of palaeoclimatic and environmental records, we acknowledge that they may not best explain the palaeocommunity changes observed in the Naracoorte record. The palaeoclimatic and environmental data presented and discussed here were selected on the basis of their proximity to the Naracoorte Caves, temporal coverage and chronological resolution. As such, while they provide a reference to local and regional temperature, effective precipitation and vegetation using a range of proxies, they do not cover all the extrinsic factors that are expected to interact together to drive palaeocommunity variability through time. For example, as examined by Broughton *et al*. (2008), increased seasonality may be more closely related to changes in vertebrate palaeocommunities through species competitive processes, preceding impacts related to temperature thresholds. However, at the present time there are no proxy data for seasonality available for late Quaternary south-eastern South Australia, limiting us to the palaeoclimatic and environmental data presented in Figure 6.12.

Macroscale trends in SST, vegetation types and speleothem growth phases show that palaeoclimatic and environmental conditions were variable through MIS-3 and MIS-2 (*c*. 51.4 to 17.1 kyr BP). The early glacial periods of MIS-3 and MIS-2 are characterised by two periods of high effective moisture availability (Ayliffe *et al*. 1998) and a trend towards lower mean SSTs (although, fine resolution SST data show high variability through units A, B and C; Fig. 6.12; Lopes dos Santos *et al*. 2012). The temporal variability in effective precipitation demonstrated in these records is also reflected in the sedimentary records of lakes in south-eastern South Australia and south-western Victoria (Dodson 1975; Dodson 1977; Cook 2009).

During the early glacial period, lacustral phases in the Murray Darling Basin and palaeochannels that fed the Willandra lakes systems in south-eastern Australia were characterised by periods of large, high energy flows and high lake levels, driven by winter snowmelts from the Snowy Mountains (Bowler *et al*. 2007; Bowler *et al*. 2012). Palaeoclimate records reflect the influence of seasonal processes on deposition in these environments (Kemp and Spooner 2007; Macken *et al*. 2013a;

Petherick *et al*. 2013). By comparison, if there were changes in local or regional effective precipitation and/or seasonality, they had minimal impact on the sediment type and deposition of sediments forming unit A in Wet and Blanche caves over the later stages of MIS-3 (Macken *et al*. 2013a).

The pollen data from Blanche Cave reveal a trend towards increasing relative abundance of woody taxa (e.g., Eucalyptus, Casuarina, Acacia and Banksia) at the expense of herbaceous (e.g., Poaceae) and woody-herbaceous taxa (e.g., Asteraceae) from units A to B. A more dramatic change in vegetation-types is evident from unit B to C, with a decline in the relative abundance of woody taxa by *c.* 25%, while herbaceous taxa increased by *c.* 10% and woody-herbaceous by *c.* 15% (N.B., The genera listed for each of the vegetation groupings was sourced from D'Costa and Kershaw (1997)). Pollen records examined from lakes Bolac and Turungmoroke in south-western Victoria reflect a similar trend of vegetation community change, where open-grassland steppe encroached upon woodlands towards the end of MIS-3 and into MIS-2 (Cook 2009). Shifts towards open grasslands over the LGM are exhibited in a number of pollen cores across Australia (Turney *et al*. 2006; Petherick *et al*. 2013); although, Petherick *et al*. (2013) noted sites in south-east Queensland and northern NSW that exhibit higher percentages of Casuarinaceae than those from southern Australia at the time of the LGM. They also noted the Lake Surprise record of south-western Victoria which recorded a peak in *Eucalyptus* over the LGM (Builth *et al*. 2008).

Given the variation in pollen signals from across these sites and the limited resolution of pollen data currently published from Blanche Cave, the timing of vegetation changes associated with the last glacial cycle from the Naracoorte region is difficult to interpret. The shift from a positive to negative moisture budget at *c.* 20 kyr BP reflected in the speleothem record (Ayliffe *et al*. 1998) and/or the rapid increase in SST over the accumulation of unit C from *c.* 18.7 kyr BP (Lopes dos Santos *et al*. 2012) may have contributed to the apparent changes in the dominant vegetation types in the Blanche Cave pollen record observed from unit B to unit C. Finer temporal scale pollen analysis using the distinct pollen groupings (rather than broad vegetation types) is required to temporally constrain the vegetation changes and allow a more meaningful comparison with the fossil faunas and other palaeoclimatic data.

Interestingly, there is no evidence for a change in small mammal palaeocommunity type from units B to C (or phases B1 to C2) despite the noted vegetation changes and shift towards relative aridity during the accumulation of unit C. Community composition and structure are influenced by a combination of intrinsic (e.g., body size, physiology, niche breadth, dispersal) and extrinsic factors (e.g., climate conditions, habitat availability, food supply) along with biotic interactions (e.g., competition, predation; Munguía *et al*. 2008; Benton 2009). Given the palaeoclimatic and environmental variability observed through units A to C, the maintenance of a single palaeocommunity type through MIS-3 and the LGM is expected to reflect intrinsic processes of compensation by variation in the survival, reproduction, interspecific interactions and dispersal of populations within the palaeocommunity (Brown and Lomolino 1998; Magurran and Henderson 2010).

We note that the extent of time-averaging in the fossil data at both the macro- and mesoscales is far greater than the palaeoclimatic record of SSTs available in the nearby marine core. As discussed by Stenseth and Mysterus (2005) and Blois and Hadly (2009), time-averaging of fossil faunas, when compared with climatic and other environmental records, often weakens the ‘signal’ of climate effects on faunas and limits the detectability of the impacts of short term climate fluctuations in fossil or ecological records. Hopley and Maslin (2010) refer to this as ‘climate-averaging’, where more than one climatic regime or episode is averaged across a single phase of bone-accumulation. Thus, we stress here that the persistence of the palaeocommunity through units A to C is evident only at the temporal scales available in the deposits and does not preclude ecologically significant changes that may have occurred at finer temporal scales.

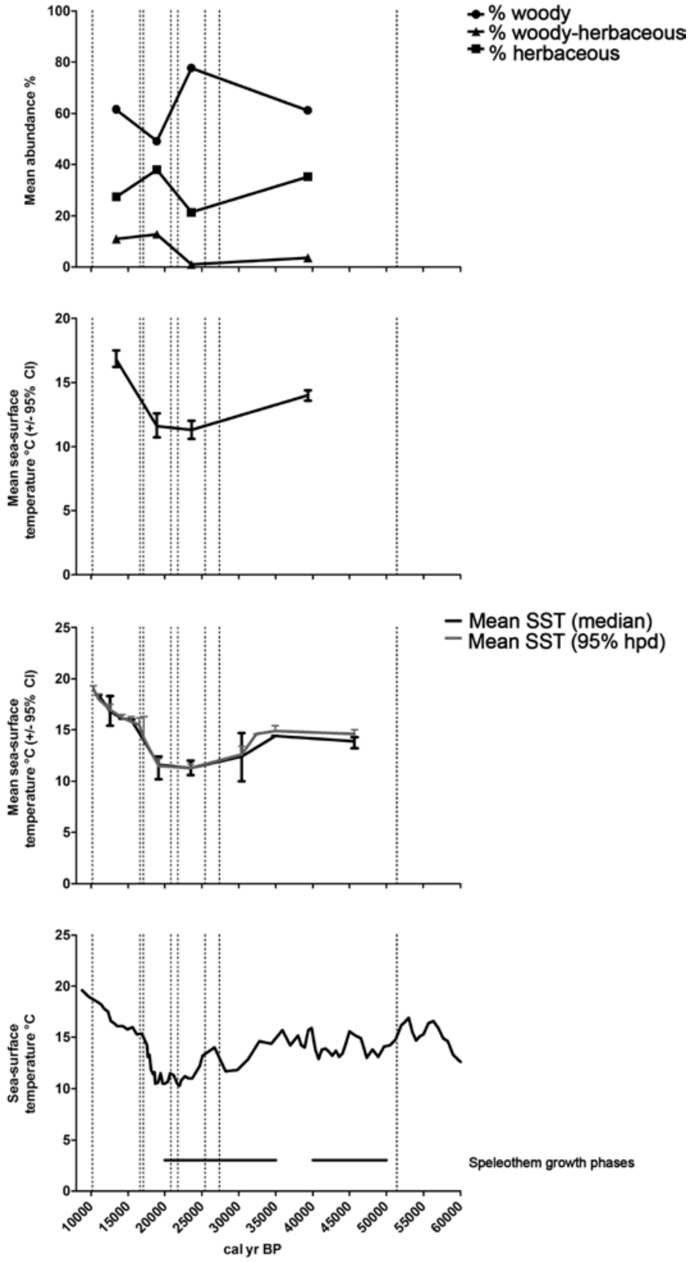

Figure 6.12 Palaeoenvironmental and palaeoclimatic data for the last glacial cycle. Pollen record was sampled from a core collected from Blanche Cave 3rd Chamber (Darrénougué *et al*. 2009). Values represent mean abundance of samples corresponding to each of units A, B, C and E* (unit A, n=6; unit B, n=1; unit C, n=3; unit E*, n=3). Sea-surface temperatures (°C) from Lopes dos Santos *et al*. (2012) were reconstructed from U_{37}^{k} of the alketones of core MD03-2607, collected from offshore south-eastern South Australia on the Murray Canyons. Mean values were calculated for temperature estimates within the median upper and lower modelled ages of units A, B, C and E(*) and phases A1–E6 (Table 6.1) and were very similar to mean ages calculated within the upper and lower 95% hpd ranges (unit A, n=31; unit B, n=10; unit C, n=12; unit E*, n=13). Speleothem growth record reproduced from Ayliffe *et al*. (1998) and indicates phases of effective precipitation (rainfall > evapotranspiration). Vertical dotted lines indicate median upper and lower modelled ages of the phases from Wet and Blanche caves. Upper and lower 95% highest probability density ranges for these median ages are presented in Table 6.1 and Fig. 6.1.

These limitations are evident in attempts to understand the palaeoclimatic and environmental correlates of the occurrence of rare taxa within the assemblages. Of interest is the single occurrence of the Mulgara (*Dasycercus* sp. indet.) in Wet Cave unit C (Macken and Reed 2013). The species is represented by a single left maxilla (FU20934) and a left dentary in the re-worked unit D of Wet Cave, which was excluded from the analysis (FU20933; Macken and Reed 2013). *Dasycercus* spp. (*D. blythi* and *D. cristicauda*) are today found in the arid central-western and central portions of Australia, respectively (Van Dyck and Strahan 2008). However, given the resolution of the fossil data and speleothem growth record, it is not possible to associate the occurrence of *Dasycercus* sp. indet. with specific palaeoclimatic conditions. Unfortunately, no finer temporal resolution for Wet Cave unit C is currently available given the homogeneous nature of the sediments and the resolution and precision of the chronological model (Macken *et al*. 2013a, b). However, the presence of a *Dasycercus* specimen suggests that landscape features facilitated the dispersal of the species from its core range to south-eastern South Australia over the LGM or in the immediately post-LGM deglaciation period.

The macroscale pattern of palaeocommunity reorganisation between units C and E is coincident with an a return of woody vegetation to a similar proportion as observed in unit A, while the % of herbaceous vegetation declined and woody-herbaceous remained constant. These environmental and ecological changes are also correlated with higher SSTs than observed through MIS-3 and the LGM, and local drying as evidenced by the lack of speleothem growth from *c.* 20 kyr BP (Fig. 6.12). In the Samwell assemblage, changes in species richness and evenness were strongly correlated with climate change over the glacial-interglacial transition at the end of the Pleistocene, reflecting both direct and indirect climatic drivers of faunal change at this locality (Blois *et al*. 2010). However, in the Naracoorte Cave faunas examined here, the significant decline in species richness from 17.1 to 16.7 kyr BP (95% CI: 17.4 to 15.6 kyr BP) is not directly temporally correlated with the rapid increase in SST beginning 18.4 kyr BP observed in marine core MD03-2607 (Fig. 6.12; Lopes dos Santos *et al*. 2012), or the shift from a positive to negative moisture budget from *c.* 20 kyr BP (Ayliffe *et al*. 1998). It instead lags the onset of warming and drying by *c.* 1 to 3 kyrs, based on the 95% CI of the median ages associated with transition from phase C2 to E1 and appears to have been associated with sea-surface temperatures warming beyond 16°C, rather than warming per se. The second likely palaeocommunity shift evident in the low rank-order abundance structure of phases E5 and E6, *c.* 10.8 to 10.5 kyr BP (95% CI: 11.2 to 10.9 kyr BP), is associated with mean SSTs becoming warmer than 18°C.

Given the current groupings of the pollen data, it is not possible to assess if the species that composed the vegetation communities varied throughout the last glacial cycle (e.g., Casuarinaceae versus *Eucalyptus*). Such changes may have been more directly associated with the observed small mammal palaeocommunity changes than can be inferred from the current vegetation groupings. Further, based on the current pollen data, the small mammal palaeocommunity appears to have been more directly influenced by palaeoclimatic conditions than by change in the % dominance of vegetation groupings.

Previous palaeoenvironmental reconstructions for the Naracoorte region were based on the habitat preferences of the faunas preserved in the fossil assemblages. These reconstructions have commonly reflected a wide range of vegetation communities that are assumed to have persisted as a "mosaic" through glacial-interglacial cycles of the Quaternary (e.g., Fraser and Wells 2006; Laslett 2008). However, in a review of palaeovegetation of temperate Australia, Dodson and Ono (1997) noted that for areas of diverse topography, it can be difficult to reconstruct the diversity of habitat types formerly present at different times in the past. Despite this limitation, they note that such patches may be significant as refugia for plant species during periods of climate stress. The persistence of different vegetation communities in topographic refugia is also likely to have been important for the long-term persistence of faunas as well, such as the small mammal palaeocommunity of the early glacial period and LGM and as noted for faunas from southern Australia by Byrne (2008). Further research into the local vegetation of the Naracoorte area over this period will be valuable for more deeply exploring the relationship between the mammal faunas and habitat types at this locality, and hence, vegetation thresholds of the small mammal palaeocommunities and individual species through the Pleistocene.

Conclusions

The detection of ecologically significant variation in the assemblages from Wet and Blanche caves was dependent upon both the temporal and ecological scale of observation. When contrasted against other palaeocommunity records where whole-scale faunal turnover resulted in compositionally dissimilar assemblages (e.g., Hocknull *et al*. 2007), the small mammal palaeocommunity of late Quaternary Naracoorte appears to have been highly stable and persistent. However, using a nested numeric hierarchy revealed temporal variation across ecological variables of the fossil assemblages, with at least one episode of significant palaeocommunity reorganisation over the post-LGM deglaciation.

Palaeocommunity reorganisation occurred at 17.1 to 16.7 kyr BP, 1–3 kyr after the commencement of post-glacial warming from 18.4 kyr BP and local drying from *c.* 20 kyr BP. This palaeocommunity shift was correlated with SSTs warming beyond 16°C and dry conditions when compared with the previous *c.* 33 kyr BP. A likely second palaeocommunity reorganisation event was recorded at 10.8 to 10.5 kyr BP, correlated with SSTs warming past 18°C and continued relative aridity. These patterns provide some insight into the likely extrinsic thresholds for the successive palaeocommunities of the Naracoorte region through the last glacial cycle. However, further research is required to reveal the relationships between the small mammal fauna, local vegetation and habitat characteristics that are expected to have exerted strong controls on the survival, reproduction, interspecific interactions and dispersal of populations across the region.

Whole community-level variables measured from the assemblages of Wet and Blanche caves were highly consistent between the two sites for temporally equivalent units. This limited site-based sampling variation provided a robust and reliable record of whole-palaeocommunity change with time. By comparison, our analysis showed that the relative abundances of individual species in the deposits were affected by sampling variation and the patchy distribution of specimens across bedding plains or stratigraphic horizons. These observations cautioned against using changes in the relative abundance of individual species to infer individual species responses to climate change. However, where the relative abundances of individual species were adequately and consistently sampled in the two sites, there was evidence for large magnitude changes in the abundances of some species, while others persisted at low abundance for the majority of the record.

Ecological thresholds operating within the palaeocommunity maintained the rank-order abundance distribution of species within the palaeocommunity, despite evidence for variation in the relative abundances of some species and palaeoclimatic and vegetation change through the early glacial period and LGM from 51.7 to 17.1 kyr BP. We suggest that change in the abundances of species reflects intrinsic and community level processes in response to climatic and environmental change and were within thresholds that maintained the palaeocommunity type through this time.

The Wet and Blanche cave records also reflect the ability of the palaeocommunity to recover species following a severe disruption. This may be related to an inherent ability of the broader ecosystem to resist or recover from disturbance. For example, connectivity of habitats and suitable patches, which are today observed to be critical factors in species dispersal and migration, was likely a feature of the south-eastern South Australia ecosystem through the last glacial cycle.

From a biodiversity conservation perspective, the long-term records from Wet and Blanche caves strengthen arguments for a focus on the interaction of intrinsic and extrinsic thresholds operating on communities and individual species across multiple scales (du Toit 2010). Unfortunately, the majority of the small mammals that formed the successive palaeocommunity types through the last glacial cycle are no longer present in south-eastern South Australia today (Robinson *et al*. 2000). However, the Naracoorte record reveals a remarkable capacity for some species to persist either at very low abundance, or to maintain populations despite severe increases and decreases in population size and/or density, in response to opportunities within the community and/or environment across different time scales.

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7. Concluding Discussion

The motivating questions for this thesis were drawn from a wide range of ecological literature and relate to knowledge gaps that hamper conservation efforts, particularly those associated with climate change. These questions were:

(a) How do ecosystems respond in the short and long-term to disturbance,
(b) What is the natural range of variation exhibited by ecosystems at different temporal and spatial scales, and
(c) What are the limits of resilience, or thresholds beyond which ecosystems change state?

As argued throughout this thesis, palaeoecological assemblages such as those of the Naracoorte Caves are particularly useful for addressing these questions given their long-temporal span and the preservation of large samples of natural archives representing ecosystem composition, condition and character through time. However, before these questions can be assessed from any palaeoecological assemblage, firm temporal and stratigraphic constraints are required, as well as a thorough understanding of the diversity represented within a deposit, its taphonomic biases and representativeness of the living ecosystem from which it was sampled.

This thesis was structured around aims and objectives to establish the ecological, temporal, analytical and sampling frameworks of Late Quaternary aged small mammal assemblages of the Naracoorte Caves, to allow the questions identified above to be explored. While the questions themselves were not identified as specific aims of the thesis, the success of the thesis may be judged by the ability of the research as a whole to address them in relation to the small mammal faunas of Wet and Blanche caves.

Here, the main findings associated with the research presented in the thesis are summarised, with limitations and directions for future work identified. The significance of the work is also explored. These discussions are then followed by a synthesis of the findings of the thesis in relation to the three, overarching questions identified above.

Stratigraphic and temporal analyses (chapters three and four)

Assessment of the stratigraphic profile of Wet Cave provided the basis for the age-depth models presented in chapter four and the macroscale faunal analyses presented in chapter six. Through a review of all available sedimentary, stratigraphic and chronological data, six units (A, oldest to F, youngest) were identified within the Wet Cave profile. In describing these units, a more thorough and accurate comparison to the stratigraphic profiles of Blanche Cave 3rd Chamber and RCIC could be made than had previously been available. Further, the sedimentary descriptions for Wet Cave were used to identify local palaeoclimatic conditions in comparison to the broader palaeoclimate context of the last glacial cycle across south-eastern Australia. This comparison provided not only the palaeoclimatic context for the faunal assemblages of Wet and Blanche caves examined in the thesis, but allowed for divergences between localities at both a regional and local scale in terms of climate conditions and processes to be identified. The additional radiocarbon determinations for Wet Cave presented in chapter three were also useful as they provided information about the extent of re-working in the Wet Cave sequence and extra data for the age-depth models.

The greatest limitation to the research presented in chapter three was the loss of the excavated section of Wet Cave to floods at the end of 2010, following commencement of the thesis project. As a result, no additional sedimentary or chronological sampling could be completed as had been planned. This limited the review of the Wet Cave sequence to data that had been collected by a range of researchers over a period of 5 years from 1997 to 2001. However, despite this limitation, the breadth, quality and quantity of data previously collected from the Wet Cave sequence were sufficient for the identification of the sedimentary units completed here. Further sedimentary analyses, had they been possible, would have focussed on geochemical analyses to refine the palaeoclimatic interpretation of the sediments and to test the stratigraphic divisions based primarily on the physical characteristics of the sediments (texture, composition and colour).

Future research in Wet Cave could involve the extraction of a sediment core from the entrance chamber to obtain samples for geochemical analysis, as was completed for Blanche Cave 3rd Chamber (Darrénougué *et al*., 2009). The core samples could also be used to test for the presence of pollen grains in the Wet Cave sediments. As the entrance chamber of Wet Cave has a large open roof entrance, it may have accumulated pollen grains in a similar way as Blanche Cave 3rd Chamber. If pollen were preserved in Wet Cave, it would provide a valuable comparison against the Blanche Cave record to test for the influence of sampling and taphonomic biases on pollen preservation and observed temporal variation in local vegetation patterns.

Additional charcoal for dating may also be collected from a sedimentary core sampled in the entrance chamber of Wet Cave. As discussed in chapter four, the resolution of the age-depth model for Wet Cave would be greatly improved if more radiocarbon determinations were available. Of particular use would be additional samples from units B, C and F as these units currently have only one or two radiocarbon determinations. Additional samples may improve the precision of the modelled boundaries for these units and the 95% confidence ranges for the duration and hiatus estimates associated with these layers. Additional samples from unit F are also required to assess the degree of reworking of Holocene and Pleistocene aged materials in the upper layers of the Wet Cave sequence.

While extensive radiocarbon dating of bone material from Blanche Cave was unsuccessful due to the poor preservation of collagen (E. Reed, pers. comm.), the potentially younger age of bones in unit F of Wet Cave (<1000 years) may mean that they could be dated and be used to test for the extent of reworking at the top of the sequence. No faunal analyses were completed on the faunas from unit F given the evidence for reworking indicated by the available ^{14}C ages and sedimentary data. However, if the faunas were found to be only minimally reworked by dating the bones directly, they would be valuable as a late Holocene aged sample of local small mammals. The faunas identified from the entrance chamber of Robertson Cave (chapter five) provide the only reliable Holocene aged fauna for the Naracoorte Caves at the present time (although the Holocene component was not differentiated from the Pleistocene component in the current research). Additional assemblages would be of value for comparative analyses and improving our estimates of faunal diversity given the likely differences in accumulation mode between the Wet Cave and RCEC assemblages.

The age-depth models for Wet and Blanche caves presented in chapter four are the first Bayesian models developed for vertebrate fossil assemblages in Australia. They were critical for the faunal analyses presented in chapter six as they facilitated a robust and statistically-based correlation of the Wet and Blanche cave sequences using estimates of the ages of the upper and lower boundaries of the sedimentary units and layers of the two sites.

Through the integration of *prior* information into the models, a thorough appraisal of the stratigraphy of Blanche Cave was also completed. This assessment of the Blanche Cave stratigraphy was new and contrasted with earlier analyses of the sequence as the age-depth models were constructed using layer data compiled during excavation by E. Reed (pers. comm.), rather than the sedimentary core sampled by Darrénougué *et al.* (2009) or the 5 cm spits excavated by Laslett (2006).

Assessment of the stratigraphic information associated with the 27 layers individually sampled from Blanche Cave grid squares A3 and B3 identified seven 'phases.' These phases were interpreted as independent samples of bone and sediment accumulation that could be differentiated from each other on the basis of their sedimentary characteristics. The modelled ages of the upper and lower boundaries of these phases, along with the lenses identified in unit E of Wet Cave, provided the basis for the finer, mesoscale analysis of the fossil assemblages presented in chapter six. Correlation of these phases to units A, B, C and E in Wet Cave provided the basis for defining the stratigraphic extent of these units in Blanche Cave, and hence, the comparative faunal analyses.

The primary limitation of the age-depth models is the poor resolution (low precision) of the modelled ages for the boundaries within the sequences. As discussed in chapter four, the resolution could only be improved by further dating of the Wet and Blanche cave sequences. Ironically, Blanche Cave may be one of the best dated Late Pleistocene fossil sequences in Australia, with 40 radiocarbon determinations spread across the one metre depth profile of the studied section. Of these, six were excluded from the model prior to its construction as they were so outlying (of Holocene age) that they prevented the model from running. A further two were identified as outliers in the model with 92 and 95% probability. However, the primary constraint on the precision of the modelled ages is that there are few ^{14}C ages relative to the temporal span of the deposit (*c*. 36,000 years).

Future work to develop the age-depth model for Blanche caves could incorporate other dating information that is available for this site, including U/Th dating of speleothem straws (St Pierre *et al.*, 2009, 2012) and OSL dating of sand grains (Darrénougué *et al.*, 2009). The Bayesian age-depth models developed in the current work excluded these additional data given the uncertainties associated with speleothem straw deposition into the sedimentary deposit and the systematic off-set of the OSL ages with the radiocarbon determinations (Darrénougué *et al.*, 2009). However, if these issues were resolved, the additional data may help to refine the modelled ages for the Blanche Cave boundaries. As these additional materials are not available for the Wet Cave sequence, additional radiocarbon samples would be of most use in this site and, as previously noted, should focus on units B, C and F.

Another limitation to the age-depth models is the uncertainty regarding the modelled upper boundary for layer one in Blanche Cave and its correlation to Wet Cave. The model prior applied to the top of the Blanche Cave sequence strongly affected the modelled age for the top of layer one. The chosen prior was used on the basis of the presence of *Pinus* pollen in the sediments, suggesting recent contamination with allochthonous materials, including dusts and sands. However, the model prior and the limited number of ^{14}C determinations available for layer one resulted in the age of the layer being poorly represented by the model, as judged in light of evidence that the Holocene aged layers of the deposit had been stripped by human activity (Darrénougué *et al.*, 2009). Additional radiocarbon samples for this layer and an alternative model with a different *prior* for the top boundary of Blanche Cave may resolve this problem.

A final limitation of the age-depth model and stratigraphic analyses associated with the Blanche Cave sequence is the uncertainty regarding the extent and process of reworking in layers four to nine. A total of 1779 small mammal specimens were identified from these layers in grid square A3 of the Blanche Cave deposit; however, given the mixed age of charcoal and straws in these layers, they were excluded from the faunal analyses. It is currently unclear if these layers are

Pleistocene aged with contamination by Holocene straws and charcoal or if they are Holocene aged with Pleistocene contamination. Given the Pleistocene age for layers one and three, the latter is considered more likely. However, further investigation is required to resolve which of these scenarios best explains the processes of deposition and disturbance at the top of the Blanche Cave sequence. Regardless of which scenario is correct, there is a high chance that the faunas are also of mixed age, limiting their usefulness to the faunal analyses completed in the thesis.

Late Quaternary small mammal faunas of the Naracoorte Caves (chapters five and six)

The small mammal faunas preserved in the Late Quaternary aged assemblages of Wet, Blanche and RCIC were first examined by McDowell (2001) and Laslett (2006) and published in composite lists compiled by Reed and Bourne (2000, 2009). The significance of the faunas in these sites is demonstrated by their use in establishing the former, pre-European distribution of the following extant mammal faunas: *Conilurus albipes* (McDowell and Medlin, 2009), *Pseudomys shortridgei* (Kemper *et al.*, 2010), *Cercartetus* spp. (Harris and Goldingay, 2005; Harris, 2006, 2009a, b; Harris and Garvey, 2009) and *Petauroides volans* (Harris and Maloney, 2010).

Despite these applications, the long-term patterns of occurrence of small mammal faunas in the fossil assemblages of the Naracoorte Caves had not previously been explored. As highlighted in chapter five, a critique of the former species lists for Naracoorte Cave deposits showed that eight small mammal species (six Dasyuridae and two Potoroidae) were absent from the Late Pleistocene–Holocene aged deposits but present in older assemblages. A further three species (all small possums) were absent from deposits of >50 kyr BP, but present in those <50 kyr BP. If real, these observed patterns suggested that there was a turnover of small mammal species in the region in the Late Pleistocene prior to the last glacial cycle that had hitherto been either ignored or unnoticed by previous investigators.

The updated species list for the Late Quaternary presented in chapter five represents the results of a systematic re-assessment of the fossil assemblages from these caves using both previously examined samples (Wet Cave), new samples (Blanche Cave, Wet Cave) and new sites (RCEC). The identification of the faunas from these deposits was completed as part of the research for this thesis to: (a) assess the accuracy of previous faunal lists and (b) ensure that data collection and species identifications were standardised across the sites in preparation for the analyses presented in chapter six.

The implications of the revised taxonomic lists for the Late Pleistocene–Holocene aged deposits of the Naracoorte Caves are significant. As discussed in chapter five, the new faunal lists show that seven species had been previously unrecognised in the deposits. Of these, five accounted for the eight absences apparent in the earlier species lists. The two additional taxa identified in the current study represent new records for the Naracoorte Caves and the south-east region of South Australia (*Dasycercus* sp. indet and *Pseudomys novaehollandiae*).

The absence of *Cercartetus concinnus* from the Naracoorte fossil record as shown in chapter five is of particular interest as the species is the most common of the pygmy possums found in the region today. Unlike other pygmy possums and species with east-west distributions across Southern Australia (e.g., *Phascogale tapoatafa*: Spencer *et al*., 2001; *Pseudomys shortridgei*: Salinas *et al*., 2009), *C. concinnus* populations are genetically similar across their range, suggesting recent connectivity and/or range expansion (Osborne and Christidis, 2002; Pestell *et al.*, 2008). The previous published fossil data for the Naracoorte Caves (Reed and Bourne, 2000) suggested that *C. concinnus* populations were present in south-eastern Australia during the Pleistocene, conflicting with the phylogeographic data. As a consequence, the described biogeographic history for the species was ambiguous and has remained unresolved (Pestell *et al.*, 2008).

The revision of the fossil occurrence data from the Naracoorte Caves presented in chapter five suggests that *C. concinnus* was not present in the region during the Quaternary up to *c*. 1,000 years before present. This finding, in combination with a review of the contemporary and Quaternary distribution of *C. concinnus* (Fig. 7.1; Appendix F), is more consistent with the model of recent range expansion indicated in the phylogenetic data. From a biogeographic perspective, the combined phylogeographic and revised fossil data suggest that *C. concinnus* was confined to southern Western Australia and Kangaroo Island (M. McDowell, pers. comm.) from at least the Late Pleistocene. Populations on mainland South Australia, Victoria and New South Wales are therefore hypothesised to have been established during the Holocene from either Western Australia and/or Kangaroo Island. However, targeted phylogenetic and phylogeographic sampling of individuals from populations across the species range is required to confirm this hypothesis. Biogeographic processes, especially the role and location of habitat refugia and barriers/facilitators to dispersal have consequences for the management and conservation of *C. concinnus* into the future. A comparative analysis to compare the phylogeographic patterns in *C. concinnus* with other pygmy possums and species with east-west distributions warrants future investigation.

New faunal data for the Naracoorte Caves was also presented in chapter five in the species list for the entrance chamber of Robertson Cave. As the site is under ongoing investigation by E. Reed (pers. comm.), no further analysis of the RCEC faunas were completed in the current thesis. However, the small mammals from this site will be useful in future studies as a comparison against the inner chamber of Robertson Cave to assess local variation in accumulation, taphonomy and diversity. Further, initial dating of the RCEC deposit shows that it contains Holocene aged material, with an immediately pre-European component. As noted earlier, this is significant as the Holocene-aged samples from Wet Cave may have been contaminated with Pleistocene sediments and bone, limiting their usefulness as indicators of the faunas for this period. Thus, the Holocene aged RCEC faunas provide a temporal extension from the deposits studied here from Wet and Blanche caves.

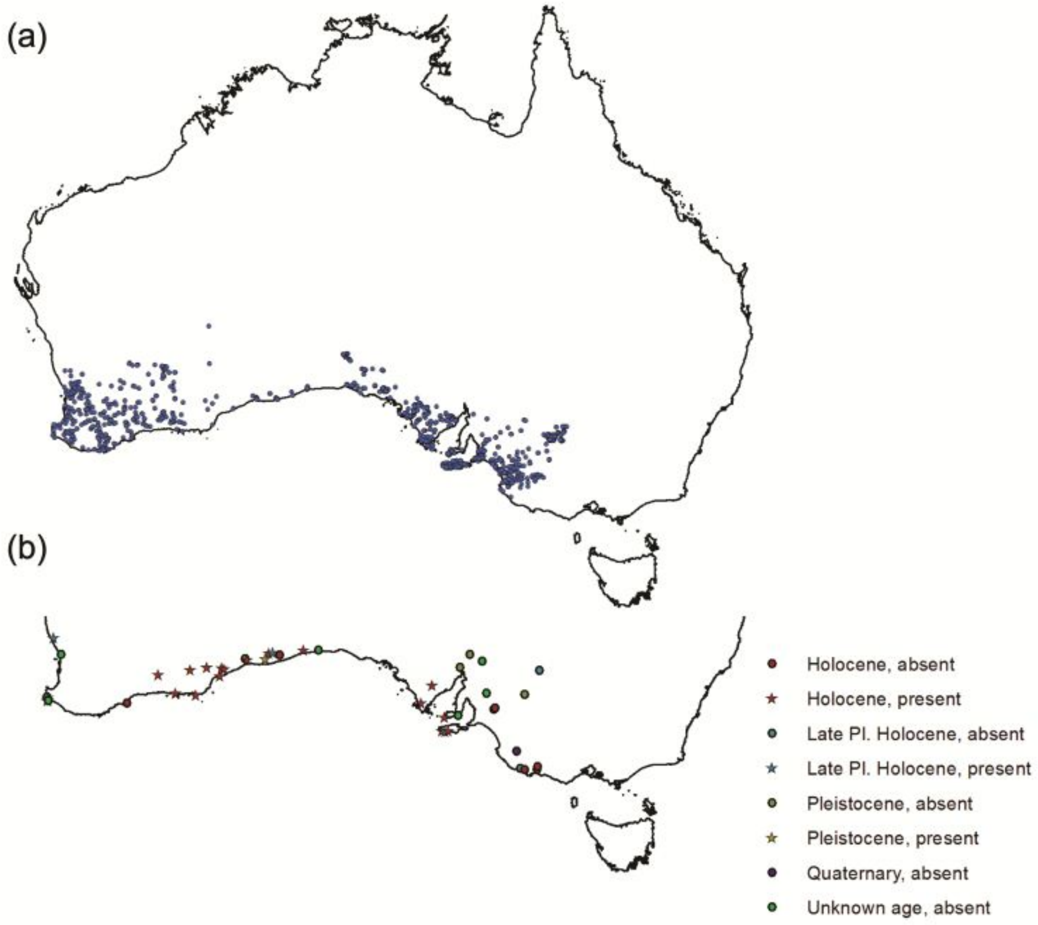

Figure 7.1 (a) Contemporary (post-European arrival to present) distribution of *C. concinnus*, compiled from museum collection data and observation records available from the Atlas of Living Australia and (b) fossil distribution (Pleistocene to Holocene) of *C. concinnus*. Sites where *C. concinnus* has been identified are indicated by stars. Sites where other small faunas have been identified, but *C. concinnus* is not recorded are indicated by the small circles. For details of data compilation, refer to Appendix F.

The research presented in chapter five deliberately ignored temporal patterns within the examined assemblages. While this may be considered a limitation of the work, temporal patterns were thoroughly examined in chapter six. The primary aim of chapter five was to provide an up-to-date list of the small mammal faunas of Late Pleistocene–Holocene Naracoorte for the research community and to detail the sampling protocols used to generate the faunal databases for the studied assemblages. Given the significance of the fossil assemblages in providing pre-European and Pleistocene distributions for extant and extinct faunas, it is imperative that the underlying data (that is, taxonomic lists) are continually revised and checked for accuracy.

Additionally, the fossil specimens for Wet Cave were formally assigned field numbers only and the original database was no longer available (M. McDowell, pers. comm.). All specimens identified in the current study were registered to either the Flinders University Fossil Register or the SAM Palaeontology Collection, under the direction of E. Reed. Electronic databases of the specimens and their registrations have been produced as part of this thesis and have been integrated into the collection management systems of the SAM (M. Binnie) and Flinders University (E. Reed and A. Macken). These processes are critical for the accountability of the research presented in the thesis and to facilitate access and interpretation by others.

As *c*. 23,500 specimens were identified from the assemblages of Wet, Blanche and Robertson Cave entrance chamber, there is no doubt that there are some errors in the identification of some specimens examined for this thesis. However, all attempts were made to ensure that identifications were accurate through the use of comparative specimens from a wide range of collections (including both modern and fossil), reference to descriptions in the literature and discussions with other researchers experienced in small mammal identification. As some taxonomic groups are more difficult to identify to species level than others, it is suggested that future work target the following groups to more clearly define diagnostic characters and intraspecific variation: *Pseudomys auritus* versus *Pseudomys australis*, and *Pseudomys novaehollandiae* versus *Pseudomys apodemoides*. The two undiagnosed

Dasyuridae taxa (Dasyuridae sp. 1 and *Sminthopsis* sp. 1) also clearly require further examination to assess if they are known or new taxa.

In chapter six, the sedimentary, stratigraphic, chronological and species diversity data were integrated for the faunal analyses. Chapter six addressed the primary aims of the thesis relating to the detection and assessment of natural variation in the small mammal assemblages of Wet and Blanche caves, and the relationship between variation and resilience.

The faunal analyses were structured around a comparison of site versus temporal variation of different palaeocommunity metrics through time. This approach enabled an assessment of the statistical significance of temporal variation across all metrics. The use of an *a priori* defined ecological hierarchy combining the metric scale of Rahel (1990) and terminology of Bennington and Bambach (1996) provided a novel basis for assessing the ecological significance of observed variability.

There were a number of key findings from the faunal analyses, summarised below:

1. **The small mammal palaeocommunity was stable through the early glacial period and LGM, *c.* 51.4 to 17.1 kyr BP**. This stability was observed despite changes in palaeoclimatic and environmental conditions at different temporal scales and suggests that such changes were within limits that could be tolerated by the palaeocommunity either through adaptation, resilience and/or intrinsic population processes. The resilience of the palaeocommunity to the LGM contrasts with a general assumption that this period was associated with local declines in biodiversity in Australia (McDowell *et al.*, 2013). The lack of significant palaeocommunity change at the LGM observed in the Wet and Blanche caves faunas may reflect the influence of either local refugial dynamics or that a resilient faunal community was already established by the start of the early glacial period. Alternatively, climatic and environmental conditions at the LGM may not have differed greatly from those of the preceding 10,000 years, for which

there is evidence of fluctuating but sustained cool mean temperatures (Lopes dos Santos *et al*., 2012).

2. **At least one significant palaeocommunity reorganisation was detected over the post-LGM deglaciation**. This palaeocommunity reorganisation was evidenced by a statistically significant decline in species richness from *c*. 17.1 to 16.7 kyr BP and was correlated with SSTs warming beyond 16°C. A second possible change in palaeocommunity type was indicated by a decline in rank-order abundance of the palaeocommunity from *c*. 10.8 to 10.5 kyr BP and was associated with a continued warming of mean SSTs past 18°C. These observations reflect palaeoclimatic thresholds of successive palaeocommunity types for small mammals of south-eastern South Australia. The first palaeocommunity reorganisation lagged behind the onset of post-glacial warming, suggesting that temperature thresholds may be more important in structuring faunal communities than shifts towards warming or cooling per se.

3. **For some variables, site-based sampling variation was similar to, or greater than, temporal variation.** This limited the significance that could be drawn from observed changes through the depositional sequences and was particularly the case for individual species proportions. For the majority of species, random sampling effects obscured temporal effects, cautioning against the use of species proportions to assess species responses to past palaeoclimatic and environmental changes. It also cautions against the use of species abundances as a basis for palaeoenvironmental reconstructions. However, in some cases, individual species relative abundances were adequately sampled. The similarity observed between the relative abundance trends of species between Wet and Blanche caves also suggests that in some cases, changes in relative abundances are accurately represented in fossil assemblages. These findings advocate the use of a range of statistical tests to discern those trends that may be considered ecologically significant and those that represent ‘noise’. If palaeoecological trends are to be used to inform biodiversity conservation strategies, it is imperative that the observed data are robust and critically evaluated.

4. **Mesoscale analyses revealed significant change that was obscured or ‘time-averaged’ at the macroscale.** While the macroscale analyses revealed palaeocommunity reorganisation between units C and E in Wet Cave, the mesoscale analyses showed that significant palaeocommunity changes occurred at discrete times over the deglacial period. The two timescales available in the deposits provided the first opportunity to compare longer term trends (e.g., early glacial versus LGM versus deglaciation) against shorter-term climate and environmental fluctuations both for the Naracoorte Caves and other vertebrate fossil sites in Australia.

Each of these findings leads to new research questions that may be explored in future analysis of the Wet and Blanche caves faunas, and those of other deposits of the Naracoorte Caves. Of interest is the relationship between palaeocommunity restructuring and local vegetation dynamics. The published pollen record for Blanche Cave provides only a coarse reference to local vegetation; however, a more detailed and finely resolved pollen record is available and is in preparation by E. Reed (pers. comm.). Cross-correlation of the palaeocommunity types with the detailed pollen record will enable a test for environmental thresholds in terms of a range of new variables including dominant canopy species (e.g., *Eucalyptus* versus *Banksia*) dominant understorey composition (e.g., shrubby heath versus grassland) and relative vegetation density (e.g., open versus closed woodland) at a finer palynological and temporal scale.

Despite the caution applied to interpretation of the relative abundances of individual species in the thesis, a suite of new questions may be examined for those taxa where the data are more reliable. Of particular interest is the relative role of intrinsic (such as metapopulation dynamics, local adaptation) versus extrinsic processes (e.g., habitat heterogeneity) to the long-term persistence of individual species through the Quaternary in south-eastern South Australia. As noted in the thesis, the faunas preserved in the Naracoorte Caves are commonly used to argue for the preservation of a mosaic of vegetation types proximal to the caves through the Quaternary. This observation is significant to discussions of biogeographic refugia in southern Australia, which are considered to be places that have maintained a range of habitat types through periods of climate stress (Byrne, 2008). The diverse and complex topography of south-eastern South Australia is expected to have played an important role in maintaining habitat heterogeneity and hence, the long-term persistence of individual taxa. However, no specific tests of this hypothesis have been made nor have other factors such as evolutionary adaptation (e.g., change in body size or dietary breadth) been examined.

Future research will test the relative role of extrinsic and intrinsic processes in the long-term persistence of individual small mammal species through the Late Quaternary. This will also involve identifying potential environmental and intrinsic correlates of the observed increases in abundance of *Sminthopsis murina*, *Pseudomys apodemoides* and *Cercartetus nanus* over the deglacial period. Each of these taxa maintained a presence within the region during MIS-3 and the LGM, but at low relative abundance when compared with other species and their later expansions (Fig. 6.11). The drivers of concurrent declines in relative abundance of *Perameles bougainville* and *Pseudomys australis* are also of interest.

The relative abundance data for these species and others adequately sampled in Wet and Blanche Caves could also be used to examine habitat-faunal associations of the past. Cross-correlation of individual species with the high-resolution pollen record will enable a test of the stability of plant-faunal associations through time and a comparison against species contemporary habitat preferences to examine how much niche contraction or change has occurred as a result of European landscape disturbance. A fire history for the Late Quaternary from charcoal sequences in the deposits could also be used as a basis for identifying temporal patterns in species-fire interactions.

Another area of future research for the Naracoorte Caves is to define the composition and structure of the Holocene palaeocommunity and determine how local faunas responded to increased regional seasonality and continuing warming through this period (Kemp *et al.*, 2012; Lopes dos Santos *et al.*, 2012). Of particular interest is to identify the timing and environmental correlates of local extinction of small mammal species that persisted through Pleistocene climate changes but which are now absent from south-eastern South Australia (e.g., *Pseudomys auritus* and *Pseudomys australis*).

Future research directions will also involve more comparative faunal analyses to assess longer-term patterns of palaeocommunity variability and the structure of successive faunal communities through the Pleistocene by comparing the faunas of Wet and Blanche caves with those of Cathedral Cave and Grant Hall. Spatial-temporal patterns of palaeocommunity structure could also be examined through a comparison of the Wet and Blanche Cave faunas with those from the two deposits in Robertson Cave. The excavation of other Late Quaternary aged fossil sites within the Naracoorte Caves by E. Reed (pers. comm.) presents further opportunities to explore palaeocommunity variability and responses to climatic and environmental change at different time scales, likely to enhance our understanding of the patterns and drivers observed in the current thesis.

An important future research direction is to link palaeocommunity patterns observed in the Naracoorte Caves to other localities to assess spatial-temporal patterns of species occurrence and palaeocommunity structure. Target locations include south-western Victoria and the Lower South East of South Australia, and the Murray Mallee region, forming a latitudinal gradient south and north of the Naracoorte Caves, respectively. The aim of this research will be to determine patterns of latitudinal range contraction and expansion of individual taxa to better understand the spatial dynamics associated with the responses of individual species and palaeocommunity types to climate change.

Final Synthesis

The theoretical relationship between natural variation and resilience provided a framework for the research presented in this thesis. These concepts are increasing being applied to biodiversity conservation strategies, but rarely are baseline data on the constraints, processes and patterns of changes in diversity in response to disturbances across different temporal, spatial and ecological scales available. Palaeoecological assemblages are increasingly recognised as a source of information on the types of changes and responses that occur across scales within ecological communities through time. However, rarely are theoretical and statistical frameworks used in the assessment of temporal patterns of change in palaeoecology, despite the arguments forwarded by Erwin (2009) and Rull (2012).

In the analysis of the Late Quaternary fossil assemblages of Wet and Blanche caves presented here, concepts relating to natural variation and resilience provided a way of linking observations in the fossil record to current and future biodiversity conservation strategies. This was achieved primarily by addressing key knowledge gaps about the normal types of response to different patterns of environmental and climatic change, and the time scales over which they are expressed. Of particular focus for this thesis were the responses of the small mammal palaeocommunity to both short and long-term patterns of climate change, the natural range of variation exhibited by the small mammal palaeocommunity at different ecological and temporal scales and the limits of resilience, or thresholds beyond which the palaeocommunity shifted to a new state.

The main finding of the thesis in relation to these questions is that patterns of variation observed in fossil records are highly dependent upon the scales at which they are measured. This was not unexpected in light of the discussions presented in the literature review. However, the research presented here provides the first quantification of these differences in the study of vertebrate fossil assemblages of the Naracoorte Caves and Australia more broadly.

The assemblages of Wet and Blanche caves show that palaeocommunity types (defined by a given rank-order abundance structure) can be persistent for thousands of years during periods of highly variable climatic conditions, even at different scales of time-averaging. The persistent palaeocommunity type of the early glacial and LGM periods reflects the resilience of the palaeocommunity in terms of structure, richness and composition to frequent temperature fluctuations within the range of *c*. 10 to 16°C (SSTs; Lopes dos Santos *et al.*, 2012) combined with broad scale restructuring of vegetation communities. This suggests that it is not disturbance per se that leads to shifts between community/ecosystem states, but disturbance beyond thresholds within which particular states can persist. A similar conclusion was drawn by Rodriguez (2004) based on observed ecological stability of mammal communities in the Mediterranean during the Early to Middle Pleistocene. A key priority of research on contemporary ecosystems should then be to model and predict thresholds within which community structures can be maintained.

At the finer temporal scale available in the deposits, the small mammal assemblages showed that state shifts may or may not be preceded by gradual palaeocommunity changes. For example, beta diversity measures at the mesoscale indicated a gradual decline in similarity between the successive palaeocommunity samples through phases E1 to E5, culminating in a shift to a new palaeocommunity type at phase E6. This is not surprising given the nature of the climate thresholds detected for the palaeocommunities. In both cases of palaeocommunity change, the thresholds were associated with continued warming, rather than short-term fluctuations in temperatures as was observed over the early glacial period and LGM. However, in comparison to the second palaeocommunity reorganisation, the first significant change in palaeocommunity type was not the result of a gradual trend. It instead occurred as an abrupt decline in species richness, without prior indication of changes operating within the palaeocommunity. These contrasting patterns reflect the influence of both intrinsic and extrinsic responses of the small mammal faunas to climate change.

Intrinsic responses are associated with non-linear ecological processes, thresholds and tipping points (Williams *et al.*, 2011). Such responses are characterised by variable timings and rates of change among species and localities in response to progressive climate change. Intrinsic responses are expected to best explain the palaeocommunity shift observed between phases E5 and E6 at the end of the Pleistocene. Evidence for non-synchronous rates and timing of changes among species through the deglaciation is reflected in Fig 6.11. For example, both *Pseudomys apodemoides* and *Cercartetus nanus* increased in relative abundance over the deglacial period. However, the increase in relative abundance in *P. apodemoides* began from phase C2. By comparison, the abundance of *C. nanus* remained at very low levels until it rapidly increased between phase E5 and E6. While asynchronous fluctuations in species relative abundances are evident through the early glacial period and LGM, they were insufficient to lead to a new rank-order abundance structure within the palaeocommunity as a whole.

In contrast to intrinsic responses, extrinsic ecological changes are driven by external, abrupt climate changes and are characterised by synchronous responses of species within and between localities (Williams *et al.*, 2011). While not all species demonstrated a significant change in relative abundance between phases C2 and E1, the significant decline in species richness observed shows that the ranges of a number of species contracted away from the Naracoorte Caves region at the same time.

These contrasting intrinsic and extrinsic responses to climate change show that there may or may not be early warnings for community level shifts. In comparison to Hadly and Barnosky (2009) who argued that changes in species abundance signal environmental and climatic impacts on communities, species relative abundances in the assemblages of Wet and Blanche caves were not always associated with the palaeoclimatic and environmental variables. They were also not always statistically significant or ecologically significant in terms of impacts at higher levels of community-structure. This suggests that changes in the relative abundances of individual species may not best reflect the nature of palaeoenvironmental changes of the past or be a reliable indicator for future climate change or other environmental effects. Instead, measures that take account of species abundances within a community as a whole may be more reliable indicators of community changes.

However, where the relative abundances of individual species were more reliably sampled, they provide evidence for individualistic species responses to past disturbances. These asynchronous changes in species abundances observed in the Wet and Blanche cave assemblages suggest that future climate change will impact on species within communities in different ways, even if they are considered to have similar ecological niches and tolerance ranges. A similar finding has been found in studies from other continents (e.g., Stewart, 2008; Stewart *et al.*, 2009). From a biodiversity conservation perspective, this suggests that species responses to disturbances may be unpredictable, arguing for regional evaluation of population distributions, size and connectivity. Maintaining the capacity of individuals to disperse to new habitats and/or sustain populations across a range of localities is expected to be critical strategies for building not only the resilience of individual species, but communities. The latter emerges as a result of the asynchrony of changes in individual species. Clearly then, synchronous changes in the relative abundances of individual species may be used to identify communities at risk of structural change.

These observations advocate for biodiversity conservation approaches that monitor the abundances of individual species across their range and the structure of local communities. In combining these two strategies, multiple ecological and spatial scales are considered. At the present time, many longer-term programs monitor species presence/absence only. This is because it is time consuming and more difficult to measure species abundances. However, the fossil assemblages of Wet and Blanche caves show that the composition of a community may be stable for very long periods of time, even with the sporadic occurrence of vagrants (e.g., *Dasycercus* sp.) or rare taxa. Further, some species may persist at very low abundance over multiple sampling periods (e.g., *Cercartetus nanus*) before dramatically increasing or decreasing in abundance. Presence/absence data cannot provide insight into these types of changes.

In contrast to the approach adopted in this thesis, other palaeoecological studies have focussed on the ecological traits and functions represented in a fossil assemblage to define palaeocommunity types and hence, examine variability through time (e.g., Rodriguez, 2004). These approaches stem from a prevailing trend that, regardless of the species that fill ecological niches within a given ecosystem through time, ecosystems generally demonstrate long term structural and functional persistence (Rodriguez, 2004; Hadly and Barnosky, 2009). As such, ecosystems may be best defined by their ecological traits, rather than on a taxonomic basis.

Palaeocommunities were defined in this thesis based on taxonomic rather than ecological traits because taxonomic based diversity and composition of the study assemblages were poorly understood. Further, any approach that used ecological traits would be severely limited by the bias in the fossil assemblages towards small mammals. As a consequence of this bias, the diversity and richness of functional groups is restricted by the poor representation of large mammals (body mass .2.5 kg) in the assemblages and the exclusion of non-mammalian faunas from this study. Nonetheless, there is an important question that arises from these contrasting approaches and that is, how do we recognise or define ‘normal’ or ‘problematic’ patterns of variation in species composition and richness if the trophic and size structure of the community remains constant through time, and visa-versa? Ultimately, the answer to this question is best informed by the values of society regarding goals. In particular, the relative importance of preserving ecosystem functions versus communities and species. For example, Walker (1992) argues that it is more effective to manage for ecosystem function than individual species. In contrast, the Australian Draft Biodiversity Conservation Strategy identifies the retention of biodiversity values and critical ecosystem functions as the first of six priorities to build ecological resilience. This presents a challenging conflict between the conservation of individual species and maintaining ecosystem structure and function. Palaeoecological information about the relationship between taxonomic and ecological variability and resilience are imperative to addressing this conflict.

Finally, it is important to acknowledge that the temporal scales of the fossil assemblages clearly exceed the time-scales over which ecosystems can be monitored by researchers today and the rate at which anthropogenic climate change is expected to impact on local communities. However, the macro- and mesoscale trends documented in Wet and Blanche caves provide a backdrop against which decadal trends may be compared. Seasonal fluctuations in species abundances and the boom-bust cycles common in many Australian small mammals reflect natural variation within yearly and decadal time periods. Research programs that can nest these shorter term patterns within broader temporal scales will be critical for identifying and mediating climate-change impacts into the future.

Appendix A

The following manuscript was prepared as a conference review following the 2011 annual meeting of the Ecological Society of Australia. It draws upon research presented within the conference that used palaeoecological techniques and archives to address ecological and conservation problems. The aim of the review was to highlight the shared research goals and themes of palaeoecological and ecological studies as observed by myself and the co-authors during the conference. The manuscript is awaiting revisions following initial peer review.

Contribution of Authors

Amy Macken:

- Initiated and lead the collaborative review.
- Liaised with co-authors regarding structure and content of the review.
- Facilitated co-author contributions through the development of a question sheet.
- Prepared the manuscript for publication.

Patrick Moss

- Mentored Amy Macken in leading the collaborative project.
- Provided advice and ideas on the structure of the review.
- Contributed content and ideas to the manuscript.
- Provided comment on the final manuscript.

Graeme Armstrong

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The importance of the past: the palaeoecological context of modern landscapes

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Abstract

There has long been disconnect between ecological and palaeoecological researchers, with relatively limited attempts to integrate datasets to address key research and/or management issues associated with the Australasian landscape. However, the 2011 conference of the Ecological Society of Australia observed interchange between ecologists and palaeoecologists, particularly through the shared research themes of landscape change and the impacts of past climates and human activities in shaping modern systems. In this review, we explore these common themes using examples of palaeoecological research presented at the conference. We aim to highlight the contribution that palaeoecological research has made to both (a) our understanding of how populations, species and landscapes are shaped across different spatial and temporal scales, and (b) to informed decision making for the conservation and restoration of ecosystems. Existing collaborations between palaeoecology and ecology show that there is increasing recognition in

Australasia of the contribution of long-term data from palaeoecological records. The critical component of these integrative projects is that they bring together people from different research disciplines, organisations and management roles, rather than simply relying on published data or literature to provide complementary perspectives. We suggest that such collaborations are most successful when they involve a broad range of people to overcome the challenges associated with integrating data across different time-scales and interpreting findings in terms relevant to both past, present and future ecological systems.

Keywords conservation, ecology, long-term, palaeoecology, Quaternary

Introduction

Palaeoecology is concerned with the study of "natural archives" of past environments preserved in sedimentary and geological settings such as wetlands, marine sediments, archaeological sites and caves (Smol, 2010). While palaeoecological records are commonly used as proxies to reconstruct past climates (e.g., Hesse *et al.*, 2004) they also provide a means of examining ecological and evolutionary change over time (e.g., Hocknull *et al.*, 2007; Keith *et al.*, 2009). Despite the broad range of applications argued for long-term palaeoecological data, such perspectives are relatively under-utilised in ecological and/or conservation research in Australasia.

Poor integration of palaeoecological, ecological and conservation research is commonly attributed to factors such as (a) limited understanding by palaeoecologists of the data needs of resource managers, (b) publication in palaeoecology specific journals and (c) the use of discipline-specific terminology and data presentation (Willis *et al.*, 2005; Jackson and Sax, 2010). It is also suggested that the management implications of palaeoecological data may not always be appreciated by palaeoecologists or the wider ecological-research community (Willis *et al.*, 2005; Lyman, 2006).

The 2011 Annual Conference of the Ecological Society of Australia (ESA) included a palaeoecological symposium entitled, "The importance of the past: the palaeoecological context of modern landscapes." The aim of the symposium was to examine the role of past environmental processes in shaping modern landscapes and the contribution that this information can make to landscape management and conservation. Palaeoecological research was also presented in other symposia during the conference, highlighting an increased recognition within the ecological research community of the value of long-term data provided by palaeoecology and the desire of palaeoecologists to communicate their research directly with ecologists.

In contrast to Manning *et al.* (2009) who suggest that the research themes of palaeoecology, ecology, biogeography and conservation biology are commonly treated independently of one another, the 2011 ESA conference highlighted significant overlap in the research aims of palaeoecologists and ecologists in Australasia more generally. We suggest that this represents greater coherence between our disciplines than commonly recognised. In their review of the contribution of palaeoecology to nature conservation, Vegas-Vilarrúbia *et al.* (2011) argued that “ecology and palaeoecology are simply different approaches with a common objective” (p. 2362). While this objective is more broadly described as increasing our “ecological understanding of the biosphere” (Vegas-Vilarrúbia *et al.*, 2011, p. 2362), we suggest that palaeoecology and ecology share research goals that may be defined more specifically. Our focus here is on common research goals and themes that emerged within the 2011 ESA conference: (1) characterising the drivers and ecological impacts of landscape change, (2) defining benchmarks and baselines in ecological systems to understand natural variability, and (3) increasing our knowledge of the evolutionary and ecological history of communities, species and local populations. Common to these themes is the goal of improving decision making for ecosystem management and restoration.

In this review we discuss palaeoecological research presented at the 2011 ESA conference relating to these themes. We provide a synthesis of the types of ecological questions common to a range of symposia at the conference and provide a summary of recent palaeoecological insights into natural systems that have the potential to inform decision making for the management of ecosystems. In the final section, we describe current collaborations between palaeoecologists and ecologists relevant to Australasia. We acknowledge the importance of high-resolution, accurate and precise temporal constraints on palaeoecological data but give only minor attention to the chronological methods associated with each study, instead focussing on the types of research questions that can be addressed using palaeoecological records. We direct readers to the associated publications which discuss chronological methods for each study and other reviews which examine temporal scaling issues more explicitly (e.g., Bennington *et al.*, 2009).

We acknowledge that this review provides only a limited snapshot of both palaeoecological research presented at the conference and across Australasia more generally; however, our intention is to promote continued engagement between palaeoecologists and ecologists through research collaborations, increase support for palaeoecological research aimed at generating information for management and conservation and to promote the role of palaeoecology within ecological forums such as the ESA.

Changing Landscapes

The 2011 ESA organising committee set a guiding theme for the conference of "ecology in changing landscapes." This theme highlights the value of integrating knowledge of natural systems across biological and spatial scales and the need to build the capacity of ecosystems, and ecologists, to respond to increasingly rapid change in the future.

Research presented in symposia as diverse as "Restoring Australia's top-order predator communities", "Poised between population irruption and collapse – what does the ecology of *Callitris* teach us about Australian environmental history?", "Carbon and soil ecology", "Restoration – a structural and functional approach", "Threatened marine species", "Fire" and "Changing ecology at the top – Australian alpine biodiversity" addressed questions associated with (1) the ecological role of taxa within landscapes, (2) the impact of disturbances on ecological interactions, processes and functions at a landscape scale, (3) landscape-scale drivers of species and habitat distributions, and (4) fire–landscape dynamics.

These questions were also addressed in the palaeoecology symposium. In many cases, the palaeoecological research was driven by specific management problems suggesting that palaeoecological studies in Australasia, while valuable for contextualising modern landscapes, also play a role in targeting specific landscape-scale problems confronting land managers, ecologists and conservation agencies. For example, JW’s paper characterised the ecosystem functions performed by extinct taxa and the long-term effects of their absence from the landscape, providing a baseline against which the impacts of introduced herbivores in New Zealand could be assessed.

New Zealand has many introduced large herbivores which are regarded as pests as they severely alter vegetation community structure and composition. However, prior to human settlement (13th C), New Zealand’s terrestrial ecosystems were occupied by large avian herbivores, including nine species of Moa. Their rapid extinction soon after human arrival left vegetation communities in an unnatural state, with severely reduced levels of herbivory. Consequently, vegetation communities at the time of European arrival may not be an appropriate baseline from which to evaluate present day vegetation changes caused by introduced species.

The diets of Moa and other extinct avian herbivores and the vegetation communities in which they foraged were studied to provide a more suitable baseline to assess the impacts of introduced herbivores. The primary technique involved in this research was palaeodietary analysis of coprolites (fossil faeces). Ancient DNA extracted from coprolites was used to identify the herbivore species associated with given samples and the plant species that made up the herbivore’s diet. Plant species consumed by the extinct herbivores were also identified from leaf fragments contained within the coprolites, while pollen provided further dietary details and general information about feeding habitats (Wood *et al.*, 2008; 2012a; 2012b). In addition to the palaeodiet reconstructions, insights were gained about the role of the extinct herbivores as pollinators and seed dispersers. For example, the presence of intact seeds within coprolites provided evidence of seed dispersal and the high abundance of pollen from taxa that are bird or insect pollinated was used to infer possible pollination (particularly in fauna known to consume nectar).

Key findings included the identification of seed dispersal syndromes in rare plant species. Palaeoecological data also showed that some rare plants (e.g., spring annual herbs) were once relatively common and were dispersed by Moa (Rogers and Overton, 2007; Wood *et al.*, 2008). The rarity of the palaeodiet plant species in contemporary New Zealand landscapes is mainly attributed to the extinction of avian herbivores and the introduction of competitive grasses (Rogers and Overton, 2007). Interestingly, the rare plant species today appear to benefit from disturbance by rabbits and sheep, which are perhaps replacing some of the functions once provided by birds (e.g., seed dispersal, grazing competing plants, deposition of nutrients in dung; Rogers and Overton, 2007).

Research in the palaeoecology symposium was also concerned with reconstructing pre-human fire regimes to examine how fire has shaped particular landscapes and to assist in the development of appropriate fire management programs. The role of anthropogenic fire in the Australian landscape is both significant and highly controversial. Scientific views range from the ‘fire-stick farming’ hypothesis of Jones (1969), which suggests that human burning practices are fundamental to the modern Australian environment, i.e., shift to more fire-adapted ecosystems and increased soil erosion (e.g., Gammage, 2011), through to those who suggest that long-term natural climatic factors control the fire regimes (e.g., Mooney *et al.*, 2011). Intermediate views are also widely endorsed (e.g., Kershaw *et al.*, 2003; Moss *et al.*, 2007), with alterations in late Quaternary fire regimes being attributed a combination of natural climatic and anthropogenic forces, with regional factors playing a key role.

Notions of pre-European fire regimes continue to shape debates over natural resource management in Australia. For example, it has been suggested that a shift towards Aboriginal ‘fire-stick farming’ methods (i.e., low intensity and frequent fires) would reduce conflagrations that significantly impact contemporary Australian environments (Select Committee into the Recent Australian Bushfires, 2003). However, as reflected in the abstract of GA, there is little doubt that fire management strategies associated with European settlement of Australia over the last 200+ years have had a significant impact at a local and continental scale (Mooney *et al.*, 2011).

Through an analysis of the population genetics of three sympatric Spinifex (*Triodia*) species, GA examined how fire has shaped the Kimberley region of north-western Australia, providing a fire-frequency baseline against which the current fire management could be compared. Chloroplast microsatellites and coalescent analysis was used to infer the historical demography of three *Triodia* species and ultimately, their historical sympatry in the Kimberley. Coalescent analysis uses the haplotype diversity among sampled individuals to determine the time to most recent common ancestor (Tmrca) of the sampled populations. Multiplying the Tmrca by the generation time, in this case a fire event, revealed that the three species had been present in the landscape for millennia. To assess if the species had also been in sympatry during this time, consensus tree topologies were examined for evidence for serial founder effects at the edge of the species range (Excoffier and Ray 2008; Kuhner, 2009), taking account the potential dispersal rate given particular life histories.

The results suggested that the three *Triodia* species, from different functional groups, had coexisted under the same fire regime since the late Pleistocene (Armstrong, 2011). The three species, each with a different life history strategy (obligate seeder, facultative resprouter and obligate resprouter) were then used to populate a spatial model and allowed to compete under a range of different fire frequencies and scales. The model gave a clear result that these species could persist in sympatry only when the mean fire interval was centred around 5 years and over a range of spatial scales (Armstrong and Phillips, 2012).

While they used different palaeoecological techniques, the studies of JW and GA point to the shared objectives of landscape-scale ecological and palaeoecological research in Australasia. The capacity of palaeoecological research to address specific management issues stems from the provision of temporal information regarding a particular problem often beyond the time scales available in traditional ecological studies. Within the theme of changing landscapes, the key findings of palaeoecological research presented across the conference suggest that a combination of natural and human factors is needed to fully explain alterations in landscapes over the Late Quaternary period, and hence pre-European landscapes. Such interplay of natural and human factors in shaping modern landscapes over many millennia is reflected not only in the palaeoecological record, but as noted by BG, is evident in the life-histories of living taxa which reflect evolutionary adaptations towards Aboriginal land-use, such as fire, plant trading and collection techniques (Gott, 2005). It also suggests it is unlikely there is a single explanation for continental variations in Late Quaternary environments, emphasising the need for regional and site-specific studies. Integration of palaeoecological and ecological research which provide data on landscape dynamics at varying spatial and temporal scales presents perhaps the best means of contextualising modern landscapes and elucidating the factors that shape their character, processes and functions through time.

Such insights may also provide a framework from which to identify and assess landscape-scale management strategies. In comparison to the extent of change that has occurred to landscapes since European settlement, the impacts of current management actions are often negligible. Palaeoecological records may provide alternative and new strategies and should stiffen our resolve to at least consider broad-scale and sometimes dramatic responses. For example, as argued by Peter Latz in the “Talks on the Wildside” session of the conference, management of wild populations of introduced herbivores such as camels could be designed to achieve ecological benefits such as the regulation of vegetation and fire. Such a perspective provides an alternative to the management of feral and pest animals separate from the goal of landscape-scale ecosystem-process management.

Benchmarks and Baselines

Palaeoecological research into landscape-scale processes described in the former section is closely related to the theme of “benchmarks and baselines.” The examples discussed were concerned with establishing baseline ecological conditions for current management. In this section, we explore palaeoecological research that has enabled critical parameters and constraints within ecological systems to be discerned. In particular, we focus on palaeoecological research concerned with documenting natural variability within ecological systems.

Natural variability is a key trait of many ecosystems, contributing to their long-term resilience to disturbance, including climate change (e.g., Walker *et al.*, 2004).

Integration of concepts of natural variability into management plans is becoming more common, particularly as it is increasingly recognised that a ‘single state’ is an unrealistic goal in natural systems which fluctuate over time, and where even small scale environmental perturbations may lead to ecological shifts (Landres *et al.*, 1999; Parmesan and Yohe, 2003; Folke *et al.*, 2004). By providing long-term perspectives of ecological systems spanning multiple decades to several millennia, palaeoecological data can make a significant contribution to management programs by determining the full range of conditions exhibited by a natural system (e.g., Froyd and Willis, 2008; Hadly and Barnosky, 2009).

Ecosystem variables which may be elucidated by long-term palaeoecological studies include (a) the environmental, climatic and anthropogenic drivers of change, (b) the frequency of extreme events, (c) initial points of change in a given system, (d) ecological thresholds, and (e) patterns of response, particularly when a given threshold is breached. Baseline information that incorporates these variables is critical for revealing conditions prior to impact (e.g., pre-European condition or impacts following a disturbance or implementation of a given management strategy), trajectories of change and signs of recovery.

Research issues relating to the theme of “benchmarks and baselines” were explored in symposia on ecological restoration and management under climate change (e.g., “Modelling, pattern and prediction,” “New approaches to conservation in a changing climate – species translocations as an adaptive strategy,” “Ecological Monitoring,” and “Restoration – a structural and functional approach”), highlighting the widespread need for information on the nature, variability and structure of baseline conditions in natural systems. We summarise here two palaeoecological studies presented within the palaeoecology symposium which contribute this type of information for two freshwater systems in south eastern Australia.

Research presented by RG aimed to understand long-term changes across decades that have occurred in the Murray-Darling Basin as a result of combined anthropogenic and climatic pressures. However, it also provided an opportunity to gain an understanding of how the system has responded to change at a centennial scale. Over the past 200 years since European settlement of Australia, the Murray-Darling Basin has undergone significant changes in land use and water management (Davis *et al.*, 2001). There is little doubt the system is still responding to these changes, in concert with a highly variable climate which makes the determination of a baseline condition extremely difficult. Many wetlands are now so far removed from their ‘natural condition’ that restoration attempts are largely futile (Gell, 2010).

While state switches in the wetlands of the river have been well documented (e.g., Ogden, 2000; Reid *et al.*, 2007; Reid, 2008), little attention has been given to the water-quality history of wetlands on the river and how the sediments from these environments may be best studied to reveal pre- and post- European condition. RG’s research was particularly concerned with the following questions: How has water quality in the Sinclair Flat wetland of the lower River Murray changed following European settlement and how does the present ecological condition of the wetland compare to its historical range of variability?

The palaeoecological archives utilised in this research were diatoms sampled within sedimentary cores from the study locality. Diatoms are unicellular micro algae found in fresh water and marine systems. Many diatom species have narrow tolerance limits which make them useful bioindictors and, as a result, they are commonly used to monitor present day environmental conditions (e.g., Cook *et al.*, 2010; Ziemann and Schulz, 2011). Preservation of the silica cell walls of diatoms in sedimentary sequences makes them useful palaeoecological proxies to reconstruct the biological, physical and chemical variables of water bodies through time. By providing information on a wide range of variables, diatoms are particularly valuable as they enable the interaction of different abiotic and biotic factors to be evaluated.

Historical changes to Sinclair Flat from the diatom record show a gradual transition from a clear-water system favouring benthic species in the 1920s when river regulation was introduced, to a plankton dominated system in the 1950s. By the 1960s, the Sinclair Flat was characterised by higher concentrations of epiphytic diatoms suggesting increased macrophytic cover. Today, the wetland is a turbid, nutrient enriched and mesosaline lagoon, attesting to the degraded state of the lower River Murray (Grundell *et al.*, 2012). Importantly, the long-term record from Sinclair Flat revealed a gradual change in river conditions following river regulation, rather than a single, short-term impact (Grundell *et al.*, 2012). Consequently, intermittent sampling is unlikely to have revealed the ecological response of the system, enforcing the need for long-term studies of natural systems for detecting trends and natural variability in complex ecological systems.

The second example is the current research of PD into the ecological function of lakes of the Western Plains, Victoria through the last 5000 years. Many studies have reconstructed Pleistocene climate variability in this region through the use of bioindicators such as pollen, diatoms and ostracods (e.g., Gell *et al.*, 1994; Jones *et al.*, 2001; Kershaw *et al.*, 2004). These studies have revealed the close relationship between changes in salinity and lake water levels to climate and climate variability in this system; however, the impact of catchment and climatic changes on primary productivity and producers remains largely unknown. The research of PD aims to address this knowledge gap by examining primary productivity and phototrophic community structure, measured from fossil pigments preserved in the lake sediments.

At a local scale, drivers of change in primary producers in the lake systems are expected to include local nutrient enrichment from diffuse and point sources of sewage, agriculture and industrial wastes within the catchment. At a regional scale, the pervasive nature of atmospheric nitrogen pollution is increasingly recognised as a mechanism of change in lake systems while global climatic change is likely to impact the nature and function of lakes via altered inputs of energy and other materials.

Pigments produced by aquatic plants, algae and photosynthetic bacteria are useful bioindicators as they represent the entire phototrophic community with a high degree of taxon specificity (Wright and Jeffrey, 1997; Leavitt and Hodgson, 2001). In PD’s current research, fossil pigments from the sediment cores will be detected using High-performance Liquid Chromatography, an advanced technique that can separate, qualify and quantify individual pigments in a sample (e.g., Chen *et al.*, 2001; Leavitt and Hodgson, 2001). Additional palaeoecological proxies (diatoms and pollen) will also be correlated with the pigment data.

As these examples demonstrate, tracking environmental and ecological changes in sediment records through time can reveal the impacts of human activity and natural processes on ecological and environmental systems. They are also critical in providing benchmarks and baselines against which managers can evaluate the degree to which their restoration efforts are successful. Such baselines give insight into the key constraints operating on natural systems at decadal to millennial time scales, depending on the preservation and nature of the depositional environment.

In a recent review Batterbee *et al.* (2011) noted that palaeoecological records, particularly those of freshwater systems, can provide an extension of long-term monitoring data-sets. In some cases, palaeoecological records from sedimentary deposits overlap in age with long-term monitoring programs, enabling cross-validation between them (Batterbee *et al.*, 2011). This is particularly relevant to the palaeolimnological studies discussed here, where high resolution records of seasonal to decadal conditions are commonly preserved in the finely laminated sediments of freshwater systems. These records are particularly useful for the investigation of human driven effects on natural systems that commonly operate over short time frames.

Evolution and Ecology of Diversity

As discussed for “benchmarks and baselines”, many research questions associated with the theme of “evolution and ecology of diversity,” are common to the first section which was concerned with “changing landscapes.” This overlap arises because of the inherent links between ecosystem processes, landscape dynamics, species geographic ranges and the distribution of diversity. In this section, we examine the relationships between diversity at a given locality, the geographic ranges of individual taxa and the evolutionary, ecological and historical factors that shape them through time.

David Bowman’s opening plenary session set a vibrant tone for the conference, encouraging continued curiosity of the natural world to drive ecological research.

He also challenged delegates to continue to develop and further their research into the processes that structure ecosystems, rather than focussing solely on documenting diversity. He argued that describing diversity is relatively easy in comparison to the increasingly vital need to understand the interactions and constraints which control diversity.

Palaeoecological research presented at the conference shows that palaeoecological techniques have the potential to inform on ecological processes and, contrary to general perceptions, commonly addresses complex ecological questions relating to species interactions and their relationship with abiotic factors that shape the distribution of diversity in the long-term. However, the examples also show that information about past diversity is valuable as a baseline against which the extent and rates of change in diversity of a given locality can be determined. Such descriptions may be the only source of information from which we can identify at-risk species and habitats and to provide a context when considering assertive conservation actions such as translocations.

The presentation of MM in the palaeoecology symposium provides an example of palaeoecological research concerned with reconstructing the past temporal and spatial distribution of vertebrate faunas and the diversity of mammal communities through time. Vertebrate fossil assemblages are preserved in a wide range of environments and geological settings such as lake and riparian deposits, rock shelters and caves, dune blowouts and human structures such as buildings and eaves (e.g., Price and Sobbe, 2005; Hocknull *et al.*, 2007; McDowell and Medlin, 2009). The remains of vertebrates accumulate in these settings through natural attrition such as pitfall entrapment into caves, death of inhabiting animals, mass-death events, post-death transport of bone material and predatory accumulation by owls and other raptors, humans or carnivorous mammals and reptiles (e.g., Reed and Bourne, 2000; McDowell and Medlin, 2009).

MM highlighted the specific utility of late Holocene aged vertebrate fossil assemblages, those that span the last few thousand years, as indicators of pre-European faunas for specific localities. These ‘young’ fossil assemblages often fill knowledge gaps about the occurrence and distribution of vertebrates immediately prior to European arrival. These gaps occur due to the incomplete and poor historical documentation of faunal biogeography and biased museum collections which often do not include rare or cryptic species. Specific applications of vertebrate fossil data discussed by MM included detecting new species (e.g., Start *et al.*, 2012) and tracking the contraction and expansion of species ranges in response to European landscape modification (e.g., Baynes and McDowell, 2010; McDowell and Medlin, 2010). Drawing on his own research, MM noted in his presentation that present populations rarely reflect the pre-European biogeography of most species and warns of the dangers of baseline slip (McDowell *et al.*, 2013).

While these studies are primarily concerned with documenting past diversity as a means of assessing the extent of change in species occurrences, distribution and communities through time, they also provide an important basis for elucidating the drivers of species and community level changes through time. For example, the relative abundances of taxa within fossil assemblages are commonly assessed through a stratigraphic sequence to identify ecological change. Correlation of fossil sequences with climatic data can provide clues to the potential drivers of such changes (e.g., Prideaux *et al.*, 2007; Macken *et al.*, 2012). Studies which track the occurrence of species through the fossil record may also reveal not only those species that have been most impacted by past climatic and/or environmental changes, but also those species most resilient (e.g., Macken *et al.*, 2012). Through the integration of a range of natural archives such as vertebrate fossils, pollen and diatoms, relationships between these parameters may be elucidated. Greater synthesis of phylogenetic data from living populations and extinct taxa with fossil occurrences also presents an opportunity to improve our understanding of the biogeography of modern taxa and the evolutionary and ecological factors that have shaped their distributions through time. Such collaborations may present the only means of improving our knowledge of the biogeography of key taxa and populations as there remain significant gaps in the Quaternary fossil record and because of the severe underestimation of species niches and geographic ranges in modern landscapes (e.g., Bilney *et al.*, 2010).

Linkages between Palaeoecology and Ecology

The central theme of the 2011 conference ("ecology in changing landscapes") recognised a need to (a) increase our knowledge of how natural systems respond to rapid change particularly associated with human landscape modification and climate change, and (b) empower ecologists, conservation practitioners and land managers in their decision making in the management of landscapes undergoing rapid change. As shown here, many of the palaeoecological studies presented at the conference were directly driven by, or could be applied to, management and/or ecological restoration problems.

In many cases, the connection between palaeoecological research and conservation management arose directly from collaborations involving a wide range of research and management organisations. For example, within New Zealand's Landcare Research institute, a small number of palaeoecologists work within a large team of ecologists on various collaborative projects. Examples of recent projects include vegetation and fire history reconstructions and diet and habitat analyses for the endangered South Island Takahe (e.g., Wilmshurst, 2003). Landcare Research is also currently involved in collaborations with Maori iwi in the Northland region, using pollen archives to guide restoration planting. Another New Zealand example is the Arawai Käkäriki (Green Waterway) programme of the Department of Conservation (DOC), aimed at understanding and restoring three of New Zealand's most significant wetland/freshwater sites with the collaboration of the scientific and wider community. A major focus of the programme is research to guide vegetation restoration and the development of best-practice management and monitoring tools. DOC are working with a paleoecologist (CW) to determine pre-human impact fire variability, natural vegetation cover and baseline conditions in the lakes and wetlands prior to Maori and European impacts.

The Collaborative Research Network of the University of Ballarat, through the Regional Landscape Change program, provides an example of a research collaboration between palaeoecologists and ecologists with a specific focus on (a) understanding climate variations over the last 2000 years, (b) identifying sites that are sensitive to climatic change and to discern the relative impact of climate and human-driven catchment changes on their conditions, and (c) examine the management implications of climate change on habitat and biodiversity restoration and freshwater system health. We also note the successful ARC funded Environmental Futures Network (2005–2010) which brought scientists from a broad range of environmental disciplines together with land managers to (a) describe the current status of biodiversity in Australia, (b) identify the evolutionary, ecological and climatic factors that have shaped current ecosystems through time and (c) collate information for management planning.

Other collaborations or partnerships have been driven more directly by land management organisations or stakeholders who have engaged the skills and knowledge of palaeoecologists to support the development of management plans. For example, land managers and government and private companies responsible for appropriate management of grassland ecosystems of south east Queensland and north west Tasmania have enlisted a palaeoecologist (PM) to examine fire history and human and natural impacts as drivers of change in these environments. The aim of this research is to develop management plans to better conserve grassland ecosystems, particularly through fire management. Partnerships have also arisen where the work of palaeoecologists has reached a wide audience and generated interest in its potential to enhance management planning. For example, work of MM on the pre-European mammal faunas of Yorke Peninsula in South Australia has generated interest from managers who are developing a Conservation Action Plan for the region.

These examples demonstrate the wide range of partnerships that may emerge between palaeoecologists, ecologists and land managers. Common to all is the facilitation of active engagement and partnership of people from a wide range of backgrounds and we suggest that this remains a critical factor in the development and success of collaborations. Yet despite these examples, the need to continually promote cross-disciplinary engagement remains, particularly in the face of limited funding opportunities and the complexity of management problems faced by governments, conservation organisations and ecosystems. This need is reflected in data on the number of palaeoecological talks presented at ESA conferences over the last 11 years (Fig. 1). These data show that palaeoecology has been only a minor feature of past ESA conferences, signalling the potential for increased participation by palaeoecologists in the future. Palaeoecology-based talks are also commonly linked to palaeoecology symposia, suggesting that palaeoecologists may not always directly associate their research within the context of broader ecological research themes of the conferences and/or a disconnection between ecological and palaeoecological research networks. Given these trends, we make the following suggestions to stimulate new dialogue about cross-disciplinary collaborations and engagement between ecologists and palaeoecologists:

- ***Increased support for cross-disciplinary research projects***
  Palaeoecological research presented at the conference and existing research programs that engage palaeoecologists and ecologists provide evidence for the contribution that collaborative projects can make when addressing complex ecological problems. Cross-disciplinary collaborations are critical for addressing large scale management issues such as climate change, fire management and water security but can also be valuable for local or regional scale conservation actions. Through direct engagement of palaeoecologists with land managers, ecologists and other organisations involved in conservation, palaeoecological data may be more easily interpreted and applied to ecological problems. However, a significant need for financial support for such collaborations exists. Wider acceptance of the contribution that palaeoecological data makes to management decision making may assist in securing research funding. Such funding is often limited for palaeoecological research as it is often considered a descriptive, rather than applied science. The examples discussed here challenge this perception.

- ***Continued promotion and integration of palaeoecological research in ecological organisations such as the Ecological Society of Australia.***
  A positive aspect of the 2011 conference was that palaeoecological research was not restricted to the palaeoecology symposium, but was integrated within a range of symposia (e.g., “Poised between population irruption and collapse – what does the ecology of *Callitris* teach us about Australian environmental history?”, “Plant ecology”, and in an open session). The confidence of palaeoecologists to attend ecological forums and to present palaeoecological data to a wide audience is imperative for continued

> engagement and promotion of the contribution of palaeoecology to broader ecological issues. Through involvement in ecological forums, palaeoecologists also have the opportunity to stay in touch with current management concerns and to consider and discuss the applications of palaeoecological data in these contexts.

We also recognise that there are challenges in establishing collaborations across disciplines, particularly those associated with integrating data across different time-scales. The temporal resolution of data from some palaeoecological studies is too coarse for some questions. It is incumbent on palaeoecologists to be realistic about what a given natural archive can reveal. Engagement with ecologists on these issues is crucial to help identify what contributions can be made, and the scale at which the information is useful. Another challenge is the often urgent need for conservation action or the development of a management plan which are often generated much more quickly than palaeoecological (or other ecological) data. We suggest that it is important to identify the objectives and timelines of all stakeholders early in a collaborative project. Greater publishing of palaeoecological research for access by a wider audience is required, but more importantly, active engagement of people is most crucial for the successful integration, interpretation and application of research across the shared themes of ecology and palaeoecology.

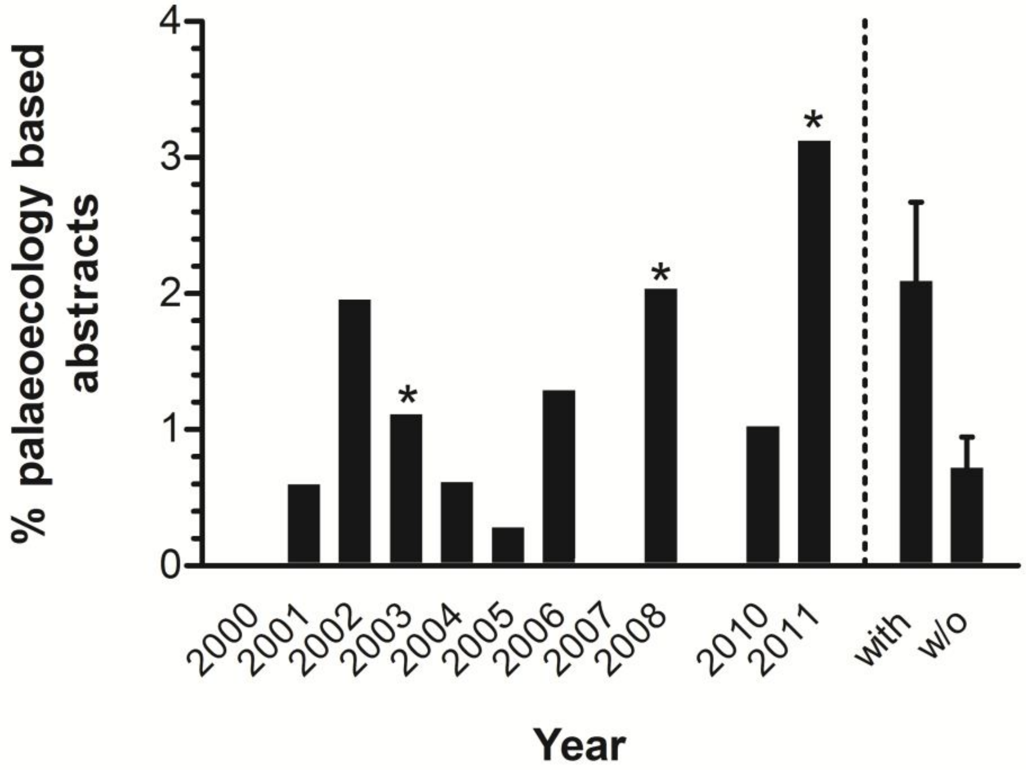

Figure A.1 Proportion of palaeoecology based abstracts presented at annual conferences of the Ecological Society of Australia (ESA) from 2000 to 2011. The proportions of palaeoecology based talks during conferences with and without (w/o) palaeoecology themed symposia are also presented. Error bars for the symposium data show standard errors (with n=3, w/o n=6). Asterisks indicate years during which the conference included a palaeoecology symposium. An abstract was considered to be palaeoecology based if it included analysis or discussion of sediment-based natural archives (e.g., pollen, diatoms) and/or phylogeographic techniques. As the 2009 ESA conference was combined with the 10th International Congress of Ecology, it was excluded from the analysis.

Conclusion

The common research themes between palaeoecological and ecological research presented at the 2011 ESA conference reflect a high degree of cross-over between these often separated disciplines. Palaeoecological research presented at the conference provides examples of the contribution that long-term records can make to our understanding of natural systems and to our management decision making. The shared research themes also reflect the importance of current ecological research and problems faced by land managers in directing palaeoecological research.

As palaeoecologists, there is inherent value for us in engaging with the ecological research community and the ESA; in many cases we share the goal of providing information that can be used to make appropriate and effective decisions for the conservation of species, landscapes and ecological processes. Continued engagement of palaeoecology and ecology through the ESA annual conference, both within and outside of palaeoecology specific symposia, and the development of research collaborations will strengthen the linkages between our disciplines. As demonstrated in the examples discussed here, increased participation and collaboration can also make significant contributions to informed and appropriate ecosystem management and restoration.

Acknowledgements

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Appendix B

Table B.1 Excavation intervals of the Wet Cave stratigraphic sequence. Depth below datum (D/D) from excavation data sheets (D. Bartholomeusz and students of Flinders University 1997 to 1998) and sedimentary profile (McDowell, 2001). Sediment colour and description modified from McDowell (2001). Grain size distributions from Forbes & Bestland (2007); Radiocarbon ages from Pate *et al.* (2002, 2006) are indicated in italics and were determined from charcoal sampled *in situ*. Radiocarbon ages in the current study were determined from charcoal samples sorted from bulk material of individual excavation layers. Calendar ages before present (cal y BP) were calibrated in OxCal4.1 (Bronk Ramsey 2009) using the INTCAL09 calibration curve (Reimer *et al.* 2009).

								Grain Size Distribution (%)				
Pit	**Layer**	**Interval**	**D/D cm**	**Unit**	**Forbes & Bestland (2007) sample code***	**Sediment colour**	**Description****	**> Coarse sand (>0.5 mm)**	**Medium to fine sand (0.5–0.3 mm)**	**Very fine sand to very coarse silt (0.3–0.1 mm)**	**< Coarse silt (<0.1 mm)**	**cal y BP**
2	1	1	0 to -7			7.5YR3/1	Very dark grey silts with moderately sorted, medium sized, sub-rounded quartz grains and orange clay clasts.					
2	2	1	-7 to -20			7.5YR3/2	Dark brown silt with moderately sorted, medium sized, sub-rounded quartz forming clean sandy laminations.					
2	2	2	-20 to -21.5			7.5YR3/2	Dark brown silt with moderately sorted, medium sized, sub-rounded quartz forming clean sandy laminations.					
2	2	3	-21.5 to -24			7.5YR3/2	Dark brown silt with moderately sorted, medium sized, sub-rounded quartz forming clean sandy laminations.					13,308 – 12,958
2	3	1	-24 to -30	F		7.5YR2.5/2	Very dark brown silt with moderately sorted, medium sized, sub-rounded quartz forming clean sandy laminations.					
2	3	2	-30 to-34			7.5YR2.5/2	Very dark brown silt with moderately sorted, medium sized, sub-rounded quartz forming clean sandy laminations.					
2	3	3	-34 to -39			7.5YR2.5/2	Very dark brown silt with moderately sorted, medium sized, sub-rounded quartz forming clean sandy laminations.					
2	4	1	-39 to -52		Wp1d	7.5YR3/3	Dark brown silt with moderately sorted, medium sized, sub-rounded quartz forming clean sandy laminations overlying a degraded flowstone. Sediment sample Wp1d also contained	12.1	43.3	21.5	23.1	*735 – 569 (D/D -41cm)*

Pit	Layer	Interval	D/D cm	Unit	Forbes & Bestland (2007) sample code*	Sediment colour	Description**	Grain Size Distribution (%)				cal y BP
								> Coarse sand (>0.5 mm)	Medium to fine sand (0.5–0.3 mm)	Very fine sand to very coarse silt (0.3–0.1 mm)	< Coarse silt (<0.1 mm)	
							milky white non-clastic material.					
2	5	1	-52 to -60	E	Wp1h	7.5YR2.5/3	Very dark brown clayey, silty sand with moderately sorted, medium sized, sub-rounded quartz grains and limestone gravel.	1.6	27.6	65.9	4.9	10,486 – 10,242
2	5	2	-60 to -83			10YR6/4	Light yellow brown clayey sand with moderately sorted, medium sized, sub-rounded polished quartz grains.					*11,204 – 10,662 (D/D -64cm)*
2	6	1	-83 to -87			7.5YR4/1	Dark grey silty sand with moderately sorted, medium sized, sub-rounded polished quartz grains.					
2	6	2	-87 to -94			10YR6/4	Light yellow moderately sorted, medium sized, sub-rounded polished quartz clayey sand.					14,882 – 13,990
2	6	3	-94 to -100			7.5YR4/1	Dark grey silty sand with moderately sorted, medium sized, sub-rounded polished quartz grains.					
2	6	4	-100 to -110			10YR6/4	Light yellow, moderately sorted, medium sized, sub-rounded polished quartz clayey sand.					16,881 – 16,352
1	5	1	-110 to -132	D		7.5YR5/6	Mottled orange and brown, poorly sorted, medium sized, sub-rounded sandy clay.					
1	5	2	-132 to -134			7.5YR5/6	Mottled orange and brown, poorly sorted, medium sized, sub-rounded sandy clay.					*17,421 – 16,759 (D/D -134cm)*
1	5	3	-134 to -135			7.5YR5/6	Mottled orange and brown, poorly sorted, medium sized, sub-rounded sandy clay.					
1	5	4	-135 to -140			7.5YR5/6	Mottled orange and brown, poorly sorted, medium sized, sub-rounded sandy clay.					
1	5	5	-140 to -142			7.5YR5/6	Mottled orange and brown, poorly sorted, medium sized, sub-rounded sandy clay.					
1	5	6	-142 to -150			7.5YR5/6	Mottled orange and brown, poorly sorted, medium sized, sub-rounded sandy clay.					
1	6	1	-150 to -159			10YR8/6	Yellow, well sorted, medium sized, rounded quartz sand with polished grains and dark brown silty laminations.					
1	6	2	-159 to -162			10YR8/6	Yellow, well sorted, medium sized, rounded quartz sand with polished grains and dark brown silty laminations.					
1	6	3	-162 to -164			10YR8/6	Yellow, well sorted, medium sized, rounded quartz sand with polished grains and dark brown silty laminations.					

								Grain Size Distribution (%)				
Pit	Lay-er	Inter-val	D/D cm	Unit	Forbes & Bestland (2007) sample code*	Sediment colour	Description**	> Coarse sand (>0.5 mm)	Med-ium to fine sand (0.5–0.3 mm)	Very fine sand to very coarse silt (0.3–0.1 mm)	< Coarse silt (<0.1 mm)	cal y BP
1	6	4	-164 to -167	C		10YR8/6	Yellow, well sorted, medium sized, rounded quartz sand with polished grains and dark brown silty laminations.					
1	6	5	-167 to -170		W 2	10YR8/6	Yellow, well sorted, medium sized, rounded quartz sand with polished grains and dark brown silty laminations.	0.5	52.5	45.7	1.3	*18,465 – 16,610 (D/D -170cm)*
1	6	6	-170 to -187			10YR8/6	Yellow, well sorted, medium sized, rounded quartz sand with polished grains and dark brown silty laminations.					
1	6	7	-187 to -192		W 4	7.5YR4/6	Brown clayey sand with moderately sorted, medium sized, rounded, polished quartz grains.	2.9	33.6	56.3	7.2	25,031 – 24,442
1	6	8	-192 to -198			10YR8/6	Yellow, well sorted, medium sized, rounded clayey quartz sand with polished grains.					
1	6	9	-198 to -205	B		10YR7/6	Yellow, well sorted, medium sized, rounded clayey quartz sand with polished grains.					*23,890 – 22,390 (D/D -199cm)*
1	6	10	-205 to -212		W 8	10YR5/6	Yellow-brown clayey sand with well sorted, medium sized, rounded, polished quartz grains.	3.0	33.5	53.2	10.2	
1	6	11	-212 to -220			7.5YR5/8	Brown clayey sand with moderately sorted, medium sized, rounded polished quartz grains.					
1	6	12	-220 to -229		W 10	2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.	13.6	23.9	41.8	20.7	*30,944 – 26,339 (D/D -223cm)*
1	7	1	-229 to -231			2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.					
1	7	2	-231 to -233			2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.					
1	7	3	-233 to -246			2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.					*36,280 – 34,546 (D/D -234cm)*
1	7	4	-246 to -257			2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.					*39,939 – 36,654 (D/D -249cm)/* *23,005 – 24,446 (D/D -252cm)*
1	7	5	-257 to -267	A		2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.					
1	7	6	-267 to -276			2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with					*45,984 – 43,334 (D/D*

Pit	Layer	Interval	D/D cm	Unit	Forbes & Bestland (2007) sample code*	Sediment colour	Description**	Grain Size Distribution (%)				cal y BP
								> Coarse sand (>0.5 mm)	Medium to fine sand (0.5–0.3 mm)	Very fine sand to very coarse silt (0.3–0.1 mm)	< Coarse silt (<0.1 mm)	
							sandy laminations.					*-269cm)*
1	7	7	-276 to -290			2.5YR4/6	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.					... *– 45,693 (D/D -276cm)*
1	7	8	-290 to -305			2.5YR2.5/4	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.					
1	7	9	-305 to -350		W 15 (-335 cm)	2.5YR2.5/4	Dark red, well sorted, medium sized, rounded sandy clay with sandy laminations.	4.3	26.2	45.3	24.3	*39,648 – 35,157 (D/D -320cm)/* 10,415 – 10,225

* Forbes & Bestland (2007) incorrectly labelled the samples from Pit 2 as Pit 1 and visa-versa.

** Medium grain size in description = 0.25–0.5 mm.

Appendix C

Table C.1 Chronological order (oldest to youngest) of Wet and Blanche Cave `Phase Boundaries` based on 50% probability threshold.

	`Boundary`		`Boundary`
1.	Blanche Layer 27 bottom	39.	Blanche Layer 11 bottom
2.	Wet Unit A bottom	40.	Blanche Layer 12 bottom
3.	Blanche Layer 27 top	41.	Blanche Layer 12 top
4.	Blanche Layer 26 bottom	42.	Blanche Layer 13 top
5.	Blanche Layer 14 bottom	43.	Blanche Layer 11 top
6.	Blanche Layer 26 top	44.	Blanche Layer 10 top
7.	Blanche Layer 25 bottom	45.	Blanche Layer 8 bottom
8.	Wet Unit D bottom	46.	Blanche Layer 9 bottom
9.	Blanche Layer 25 top	47.	Blanche Layer 9 top
10.	Blanche Layer 24 bottom	48.	Blanche Layer 6 bottom
11.	Blanche Layer 24 top	49.	Blanche Layer 5 bottom
12.	Blanche Layer 23 bottom	50.	Blanche Layer 4 bottom
13.	Blanche Layer 22 bottom	51.	Blanche Layer 7 bottom
14.	Wet Unit D top	52.	Blanche Layer 7 top
15.	Blanche Layer 21 bottom	53.	Blanche Layer 8 top
16.	Wet Unit A top	54.	Blanche Layer 5 top
17.	Wet Unit B bottom	55.	Blanche Layer 6 top
18.	Blanche Layer 23 top	56.	Blanche Layer 4 top
19.	Blanche Layer 21 top	57.	Wet Unit E bottom
20.	Blanche Layer 22 top	58.	Blanche Layer 3 bottom
21.	Blanche Layer 20 bottom	59.	Wet Lens 2: 6/4 top
22.	Blanche Layer 20 top	60.	Wet Lens 2: 6/3 bottom
23.	Blanche Layer 19 bottom	61.	Wet Lens 2: 6/3 top
24.	Blanche Layer 19 top	62.	Wet Lens 2: 6/2 bottom
25.	Blanche Layer 14 top	63.	Wet Lens 2: 6/2 top
26.	Blanche Layer 16 bottom	64.	Wet Lens 2: 6/1 bottom
27.	Blanche Layer 15 bottom	65.	Wet Lens 2: 6/1 top
28.	Wet Unit B top	66.	Blanche Layer 3 top
29.	Blanche Layer 17 bottom	67.	Wet Lens 2: 5/2 bottom
30.	Blanche Layer 18 bottom	68.	Blanche Layer 2 bottom
31.	Wet Unit C bottom	69.	Wet Lens 2: 5/2 top
32.	Blanche Layer 16 top	70.	Wet Lens 2: 5/1 bottom
33.	Blanche Layer 15 top	71.	Blanche Layer 2 top
34.	Blanche Layer 17 top	72.	Blanche Layer 1 bottom
35.	Blanche Layer 18 top	73.	Blanche Layer 1 top
36.	Wet Unit C top	74.	Wet Unit E top
37.	Blanche Layer 13 bottom	75.	Wet Unit F bottom
38.	Blanche Layer 10 bottom	76.	Wet Unit F top

Table C.2 Pairs of `Boundaries` between Wet and Blanche Caves that are statistically similar at 68.2% and/or 95.4% probability.

`Boundaries`	`Difference` range			
	68.2%		95.4%	
Blanche_Cave_Layer_27_bottom to Wet_Cave_Unit_A_bottom	-6044	3841	-10979	6900
Blanche_Cave_Layer_27_top to Wet_Cave_Unit_A_bottom	1664	7646	-886	11828
Blanche_Cave_Layer_23_top to Wet_Cave_Unit_A_top	-3968	-773	-5412	1386
Blanche_Cave_Layer_22_top to Wet_Cave_Unit_A_top	-5579	-2345	-6726	3314
Blanche_Cave_Layer_22_top to Wet_Cave_Unit_B_bottom	-6897	-4658	-7890	1502
Blanche_Cave_Layer_21_bottom to Wet_Cave_Unit_A_top	-5328	-1708	-6639	1752
Blanche_Cave_Layer_21_bottom to Wet_Cave_Unit_B_bottom	-6872	-3964	-7493	316
Blanche_Cave_Layer_21_top to Wet_Cave_Unit_A_top	-4569	-399	-5808	3270
Blanche_Cave_Layer_21_top to Wet_Cave_Unit_B_bottom	-6115	-2479	-6947	1096
Blanche_Cave_Layers_21_to_23_top to Wet_Cave_Unit_A_top	-3720	640	-5124	4002
Blanche_Cave_Layers_21_to_23_top to Wet_Cave_Unit_B_bottom	-5146	-1351	-6680	1589
Blanche_Cave_Layer_20_bottom to Wet_Cave_Unit_A_top	178	3694	-2329	5209
Blanche_Cave_Layer_20_bottom to Wet_Cave_Unit_B_bottom	-1322	1644	-3812	3143
Blanche_Cave_Layer_20_top to Wet_Cave_Unit_B_bottom	119	1984	-684	4110
Blanche_Cave_Layer_20_top to Wet_Cave_Unit_B_top	-3445	-717	-5915	163
Blanche_Cave_Layer_19_bottom to Wet_Cave_Unit_B_bottom	497	2588	-116	4712
Blanche_Cave_Layer_19_bottom to Wet_Cave_Unit_B_top	-3139	-248	-5404	972
Blanche_Cave_Layer_19_top to Wet_Cave_Unit_B_top	-900	1980	-3295	2810
Blanche_Cave_Layer_19_top to Wet_Cave_Unit_C_bottom	-4751	-2004	-5340	853
Blanche_Cave_Layers_15_to_18_bottom to Wet_Cave_Unit_B_top	84	2843	-2400	3582
Blanche_Cave_Layers_15_to_18_bottom to Wet_Cave_Unit_C_bottom	-3860	-1165	-4439	1496
Blanche_Cave_Layer_18_bottom to Wet_Cave_Unit_B_top	1877	4814	-583	5529
Blanche_Cave_Layer_18_bottom to Wet_Cave_Unit_C_bottom	-1971	942	-2986	3435
Blanche_Cave_Layer_18_top to Wet_Cave_Unit_C_bottom	-790	1811	-1329	4347
Blanche_Cave_Layer_18_top to Wet_Cave_Unit_C_top	-1245	-20	-2018	798
Blanche_Cave_Layer_17_bottom to Wet_Cave_Unit_B_top	1596	4500	-891	5168
Blanche_Cave_Layer_17_bottom to Wet_Cave_Unit_C_bottom	-2294	606	-3249	3092
Blanche_Cave_Layer_17_top to Wet_Cave_Unit_C_bottom	-1279	1226	-1607	3792
Blanche_Cave_Layer_17_top to Wet_Cave_Unit_C_top	-1765	-640	-2301	364
Blanche_Cave_Layer_16_bottom to Wet_Cave_Unit_B_top	541	3185	-1900	3885
Blanche_Cave_Layer_16_bottom to Wet_Cave_Unit_C_bottom	-3421	-899	-3830	1724
Blanche_Cave_Layer_16_top to Wet_Cave_Unit_B_top	1680	4540	-677	5513
Blanche_Cave_Layer_16_top to Wet_Cave_Unit_C_bottom	-2228	502	-2653	3056
Blanche_Cave_Layer_15_bottom to Wet_Cave_Unit_B_top	831	3499	-1620	4154
Blanche_Cave_Layer_15_bottom to Wet_Cave_Unit_C_bottom	-3130	-567	-3616	2014
Blanche_Cave_Layer_15_top to Wet_Cave_Unit_B_top	2249	4991	-93	5808
Blanche_Cave_Layer_15_top to Wet_Cave_Unit_C_bottom	-1714	905	-2110	3430
Blanche_Cave_Layer_15_top to Wet_Cave_Unit_C_top	-2250	-956	-2798	94
Blanche_Cave_Layers_15_to_18_top to Wet_Cave_Unit_C_bottom	-549	1988	-1041	4546

Boundaries	Difference range			
	68.2%		95.4%	
Blanche_Cave_Layers_15_to_18_top to Wet_Cave_Unit_C_top	-982	148	-1780	936
Blanche_Cave_Layer_14_bottom to Wet_Cave_Unit_A_bottom	11260	28460	-6930	30521
Blanche_Cave_Layer_14_bottom to Wet_Cave_Unit_A_top	-10468	4935	-28887	5550
Blanche_Cave_Layer_14_bottom to Wet_Cave_Unit_B_bottom	-12253	2825	-30626	3515
Blanche_Cave_Layer_14_top to Wet_Cave_Unit_B_top	-1797	3217	-3788	5558
Blanche_Cave_Layer_14_top to Wet_Cave_Unit_C_bottom	-5392	-319	-6578	2268
Blanche_Cave_Layers_10_to_13_bottom to Wet_Cave_Unit_C_bottom	-231	2487	-760	6121
Blanche_Cave_Layers_10_to_13_bottom to Wet_Cave_Unit_C_top	-659	406	-1785	3816
Blanche_Cave_Layers_10_to_13_bottom to Wet_Cave_Unit_E_bottom	-918	-253	-2414	236
Blanche_Cave_Layer_13_bottom to Wet_Cave_Unit_C_bottom	-135	2215	-401	4804
Blanche_Cave_Layer_13_bottom to Wet_Cave_Unit_C_top	-539	359	-1135	1231
Blanche_Cave_Layer_13_bottom to Wet_Cave_Unit_E_bottom	-810	-247	-1641	24
Blanche_Cave_Layer_13_top to Wet_Cave_Unit_C_bottom	-61	2296	-314	4915
Blanche_Cave_Layer_13_top to Wet_Cave_Unit_C_top	-465	423	-1050	1350
Blanche_Cave_Layer_13_top to Wet_Cave_Unit_E_bottom	-740	-189	-1567	126
Blanche_Cave_Layer_12_bottom to Wet_Cave_Unit_C_bottom	-132	2229	-409	4823
Blanche_Cave_Layer_12_bottom to Wet_Cave_Unit_C_top	-536	372	-1160	1233
Blanche_Cave_Layer_12_bottom to Wet_Cave_Unit_E_bottom	-814	-230	-1650	45
Blanche_Cave_Layer_12_top to Wet_Cave_Unit_C_bottom	-58	2312	-320	4930
Blanche_Cave_Layer_12_top to Wet_Cave_Unit_C_top	-465	438	-1069	1361
Blanche_Cave_Layer_12_top to Wet_Cave_Unit_E_bottom	-747	-173	-1571	158
Blanche_Cave_Layer_11_bottom to Wet_Cave_Unit_C_bottom	-102	2284	-374	4966
Blanche_Cave_Layer_11_bottom to Wet_Cave_Unit_C_top	-506	399	-1197	1366
Blanche_Cave_Layer_11_bottom to Wet_Cave_Unit_E_bottom	-777	-213	-1672	74
Blanche_Cave_Layer_11_top to Wet_Cave_Unit_C_bottom	-31	2358	-297	5035
Blanche_Cave_Layer_11_top to Wet_Cave_Unit_C_top	-440	470	-1096	1457
Blanche_Cave_Layer_11_top to Wet_Cave_Unit_E_bottom	-720	-144	-1574	185
Blanche_Cave_Layer_10_bottom to Wet_Cave_Unit_C_bottom	-148	2262	-445	4966
Blanche_Cave_Layer_10_bottom to Wet_Cave_Unit_C_top	-554	377	-1307	1341
Blanche_Cave_Layer_10_bottom to Wet_Cave_Unit_E_bottom	-826	-231	-1751	49
Blanche_Cave_Layer_10_top to Wet_Cave_Unit_C_bottom	-48	2323	-307	4956
Blanche_Cave_Layer_10_top to Wet_Cave_Unit_C_top	-455	445	-1064	1387
Blanche_Cave_Layer_10_top to Wet_Cave_Unit_E_bottom	-735	-166	-1571	160
Blanche_Cave_Layers_10_to_13_top to Wet_Cave_Unit_C_bottom	4	2432	-275	5170
Blanche_Cave_Layers_10_to_13_top to Wet_Cave_Unit_C_top	-413	529	-1150	1625
Blanche_Cave_Layers_10_to_13_top to Wet_Cave_Unit_E_bottom	-709	-89	-1592	307
Blanche_Cave_Layers_10_to_13_top to Wet_Cave_Lens_2_6_4_top	-1084	-280	-1989	12
Blanche_Cave_Layers_04_to_09_bottom to Wet_Cave_Unit_C_bottom	61	3051	-313	7969

Boundaries	Difference range			
	68.2%		95.4%	
Blanche_Cave_Layers_04_to_09_bottom to Wet_Cave_Unit_C_top	-401	795	-1185	5940
Blanche_Cave_Layers_04_to_09_bottom to Wet_Cave_Unit_E_bottom	-651	149	-2084	1925
Blanche_Cave_Layers_04_to_09_bottom to Wet_Cave_Lens_2_6_4_top	-1034	-68	-2285	350
Blanche_Cave_Layers_04_to_09_bottom to Wet_Cave_Lens_2_6_3_bottom	-1814	-529	-2727	131
Blanche_Cave_Layer_09_bottom to Wet_Cave_Unit_C_top	-105	851	-664	1714
Blanche_Cave_Layer_09_bottom to Wet_Cave_Unit_E_bottom	-410	259	-1171	604
Blanche_Cave_Layer_09_bottom to Wet_Cave_Lens_2_6_4_top	-767	75	-1631	311
Blanche_Cave_Layer_09_bottom to Wet_Cave_Lens_2_6_3_bottom	-1560	-360	-2226	12
Blanche_Cave_Layer_09_top to Wet_Cave_Unit_C_top	110	1036	-458	1919
Blanche_Cave_Layer_09_top to Wet_Cave_Unit_E_bottom	-191	427	-985	820
Blanche_Cave_Layer_09_top to Wet_Cave_Lens_2_6_4_top	-568	234	-1456	511
Blanche_Cave_Layer_09_top to Wet_Cave_Lens_2_6_3_bottom	-1340	-160	-2028	184
Blanche_Cave_Layer_08_bottom to Wet_Cave_Unit_C_bottom	159	2581	-129	5152
Blanche_Cave_Layer_08_bottom to Wet_Cave_Unit_C_top	-285	710	-840	1633
Blanche_Cave_Layer_08_bottom to Wet_Cave_Unit_E_bottom	-581	153	-1324	542
Blanche_Cave_Layer_08_bottom to Wet_Cave_Lens_2_6_4_top	-963	-43	-1773	268
Blanche_Cave_Layer_08_top to Wet_Cave_Unit_C_bottom	275	2686	-24	5234
Blanche_Cave_Layer_08_top to Wet_Cave_Unit_C_top	-170	816	-713	1725
Blanche_Cave_Layer_08_top to Wet_Cave_Unit_E_bottom	-470	245	-1228	639
Blanche_Cave_Layer_08_top to Wet_Cave_Lens_2_6_4_top	-828	68	-1686	350
Blanche_Cave_Layer_08_top to Wet_Cave_Lens_2_6_3_bottom	-1618	-401	-2286	30
Blanche_Cave_Layer_07_bottom to Wet_Cave_Unit_C_top	-105	853	-664	1717
Blanche_Cave_Layer_07_bottom to Wet_Cave_Unit_E_bottom	-410	260	-1171	605
Blanche_Cave_Layer_07_bottom to Wet_Cave_Lens_2_6_4_top	-766	75	-1632	312
Blanche_Cave_Layer_07_bottom to Wet_Cave_Lens_2_6_3_bottom	-1559	-360	-2227	13
Blanche_Cave_Layer_07_top to Wet_Cave_Unit_C_top	109	1037	-465	1925
Blanche_Cave_Layer_07_top to Wet_Cave_Unit_E_bottom	-192	427	-989	821
Blanche_Cave_Layer_07_top to Wet_Cave_Lens_2_6_4_top	-568	234	-1458	511
Blanche_Cave_Layer_07_top to Wet_Cave_Lens_2_6_3_bottom	-1341	-160	-2030	184
Blanche_Cave_Layer_06_bottom to Wet_Cave_Unit_C_top	-47	865	-615	1745
Blanche_Cave_Layer_06_bottom to Wet_Cave_Unit_E_bottom	-333	264	-1128	576
Blanche_Cave_Layer_06_bottom to Wet_Cave_Lens_2_6_4_top	-702	79	-1576	285
Blanche_Cave_Layer_06_bottom to Wet_Cave_Lens_2_6_3_bottom	-1498	-325	-2164	1
Blanche_Cave_Layer_06_top to Wet_Cave_Unit_C_top	148	1026	-389	1929
Blanche_Cave_Layer_06_top to Wet_Cave_Unit_E_bottom	-127	409	-947	784

Boundaries	Difference range			
	68.2%		95.4%	
Blanche_Cave_Layer_06_top to Wet_Cave_Lens_2_6_4_top	-505	234	-1405	474
Blanche_Cave_Layer_06_top to Wet_Cave_Lens_2_6_3_bottom	-1289	-139	-1967	162
Blanche_Cave_Layer_05_bottom to Wet_Cave_Unit_C_top	-5	910	-584	1791
Blanche_Cave_Layer_05_bottom to Wet_Cave_Unit_E_bottom	-294	305	-1095	623
Blanche_Cave_Layer_05_bottom to Wet_Cave_Lens_2_6_4_top	-663	117	-1544	325
Blanche_Cave_Layer_05_bottom to Wet_Cave_Lens_2_6_3_bottom	-1457	-284	-2127	42
Blanche_Cave_Layer_05_top to Wet_Cave_Unit_C_top	181	1065	-363	1970
Blanche_Cave_Layer_05_top to Wet_Cave_Unit_E_bottom	-95	445	-915	830
Blanche_Cave_Layer_05_top to Wet_Cave_Lens_2_6_4_top	-475	268	-1373	522
Blanche_Cave_Layer_05_top to Wet_Cave_Lens_2_6_3_bottom	-1255	-105	-1937	201
Blanche_Cave_Layer_04_bottom to Wet_Cave_Unit_C_top	27	919	-540	1800
Blanche_Cave_Layer_04_bottom to Wet_Cave_Unit_E_bottom	-249	311	-1061	616
Blanche_Cave_Layer_04_bottom to Wet_Cave_Lens_2_6_4_top	-623	126	-1507	319
Blanche_Cave_Layer_04_bottom to Wet_Cave_Lens_2_6_3_bottom	-1422	-261	-2089	44
Blanche_Cave_Layer_04_top to Wet_Cave_Unit_C_top	193	1066	-350	1974
Blanche_Cave_Layer_04_top to Wet_Cave_Unit_E_bottom	-79	448	-905	820
Blanche_Cave_Layer_04_top to Wet_Cave_Lens_2_6_4_top	-458	272	-1359	512
Blanche_Cave_Layer_04_top to Wet_Cave_Lens_2_6_3_bottom	-1244	-96	-1922	200
Blanche_Cave_Layers_04_to_09_top to Wet_Cave_Unit_C_top	279	1210	-425	2257
Blanche_Cave_Layers_04_to_09_top to Wet_Cave_Unit_E_bottom	-15	591	-948	1066
Blanche_Cave_Layers_04_to_09_top to Wet_Cave_Lens_2_6_4_top	-1084	-280	-1989	12
Blanche_Cave_Layers_04_to_09_top to Wet_Cave_Lens_2_6_3_bottom	-1165	21	-1906	399
Blanche_Cave_Layer_03_bottom to Wet_Cave_Unit_C_top	525	1528	-15	2413
Blanche_Cave_Layer_03_bottom to Wet_Cave_Unit_E_bottom	193	927	-517	1399
Blanche_Cave_Layer_03_bottom to Wet_Cave_Lens_2_6_4_top	-169	733	-1005	1100
Blanche_Cave_Layer_03_bottom to Wet_Cave_Lens_2_6_3_bottom	-925	300	-1613	734
Blanche_Cave_Layer_03_bottom to Wet_Cave_Lens_2_6_3_top	-1610	-395	-2040	260
Blanche_Cave_Layer_03_top to Wet_Cave_Unit_E_bottom	501	1342	-209	1787
Blanche_Cave_Layer_03_top to Wet_Cave_Lens_2_6_4_top	143	1127	-689	1505
Blanche_Cave_Layer_03_top to Wet_Cave_Lens_2_6_3_bottom	-603	675	-1305	1147
Blanche_Cave_Layer_03_top to Wet_Cave_Lens_2_6_3_top	-1264	-3	-1759	674
Blanche_Cave_Layer_02_bottom to Wet_Cave_Lens_2_6_4_top	628	1553	-271	1841
Blanche_Cave_Layer_02_bottom to Wet_Cave_Lens_2_6_3_bottom	-140	1115	-858	1526

Boundaries	Difference range			
	68.2%		95.4%	
Blanche_Cave_Layer_02_bottom to Wet_Cave_Lens_2_6_3_top	-817	414	-1314	1097
Blanche_Cave_Layer_02_bottom to Wet_Cave_Lens_2_6_2_bottom	-1215	-289	-1691	410
Blanche_Cave_Layer_02_top to Wet_Cave_Lens_2_6_4_top	929	1920	-324	3148
Blanche_Cave_Layer_02_top to Wet_Cave_Lens_2_6_3_bottom	191	1519	-770	2611
Blanche_Cave_Layer_02_top to Wet_Cave_Lens_2_6_3_top	-479	840	-1110	2109
Blanche_Cave_Layer_02_top to Wet_Cave_Lens_2_6_2_bottom	-889	96	-1397	1599
Blanche_Cave_Layer_02_top to Wet_Cave_Lens_2_6_2_top	-1491	-364	-2884	796
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_6_4_top	1050	2271	-198	6805
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_6_3_bottom	301	1870	-622	6255
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_6_3_top	-305	1251	-954	5770
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_6_2_bottom	-707	503	-1256	5306
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_6_2_top	-1401	-4	-2820	4331
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_6_1_bottom	-2551	-527	-3680	3381
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_6_1_top	-3521	-1530	-4126	2504
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_5_2_bottom	-4036	-2763	-4447	1602
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_5_2_top	-4302	-3434	-4814	1044
Blanche_Cave_Layer_01_bottom to Wet_Cave_Lens_2_5_1_bottom	-4574	-3758	-5058	813
Blanche_Cave_Layer_01_bottom to Wet_Cave_Unit_E_top	-5006	-3995	-6345	712
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_6_3_top	-20	15108	-55	15199
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_6_2_bottom	-404	14557	-429	14608
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_6_2_top	-1119	14052	-1182	14094
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_6_1_bottom	-2314	13049	-2386	13184
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_6_1_top	-3184	12030	-3224	12159
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_5_2_bottom	-3694	11244	-3719	11290
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_5_2_top	-4075	10853	-4099	10885
Blanche_Cave_Layer_01_top to Wet_Cave_Lens_2_5_1_bottom	-4336	10531	-4357	10555
Blanche_Cave_Layer_01_top to Wet_Cave_Unit_E_top	-4781	10265	-4823	10287
Blanche_Cave_Layer_01_top to Wet_Cave_Unit_F_bottom	-13459	3290	-13592	8028
Blanche_Cave_Layer_01_top to Wet_Cave_Unit_F_top	-14537	431	-14563	477

Appendix D

Marsupial dental nomenclature follows Luckett (1993), except premolars, which are referred to as $P^1/_1$, $P^2/_2$, $dP^3/_3$, $P^3/_3$ for simplicity, ignoring dental homology where the 1st and 2nd premolars are considered deciduous. Upper dentition is indicated by the superscript tooth number (e.g., M^1); lower dentition by subscript tooth number (e.g., M_1). Terminology of dental morphology follows Cramb and Hocknull (2010). Dentary terminology follows Rich (1991). Higher systematics for mammals follows Aplin and Archer (1987).

Systematic Palaeontology

Supercohort Marsupialia Illigeri, 1811 *sensu* Cuvier, 1817
Cohort Australidelphia Szalay, 1982

Order Dasyuromorphia Gill, 1872 *sensu* Aplin and Archer, 1987
Family Dasyuridae Goldfuss, 1820 *sensu* Waterhouse, 1838

Genus in det.
sp. 1
Fig. D.1–D.3
Referred Material. FU9002, 9025, 14365, 14368, 14374, 14375, 14378, 17381, 14384, 14386, 14390, 14392, 14394, 14397, 14400, 14639, 14646, 20886–20875, 20877, 20878, 20887–20894, 20896, 20897. SAM P47383, 47412, 47546, 47566, 47572, 47625, 47629, 47638, 47645.

Description. FU20889 *Left dentary (alveoli for* $I_{1\text{-}3}$, C_1, P_2; $P_{1,3}$, $M_{1\text{-}4}$*, present);*
FU14374 *Left dentary (no teeth present)*

Molar tooth row length 6.75 mm; premolar row length 3.26 mm. Ventral border of horizontal ramus moderately convex; tapers anteriorly from anterior end of P_3. Ascending ramus rises at a steep angle to the horizontal ramus. Coronoid process tapers posteriorly to a broad point. Mandibular notch rounded-square in shape. Mental foramen ventral to anterior end of M_1. Canine alveolus oval in occlusal outline. Posterior ends of P_1 and P_2 contacts anterior end of P_2 and P_3 respectively.

Posterior end of P_3 contacts anterior end of M_1. Premolars oval in occlusal outline; well-developed posterior cusps present on each premolar. Smaller anterior cusps present on P_1 and P_2 only. Buccal cingulids poorly developed. Antero-posterior length of P_2 longer than P_1, which is slightly longer than P_3. Medial cusps of P_{1-3} positioned over anterior portion of each tooth and approximate height of protoconids of molar tooth row. M_{1-4} with narrow but well developed anterior cingulids. Broader, well developed posterior cingulids present on M_{1-3}. Entoconids absent. Hypoconid antero-posteriorly compressed; interior angle acute so that it appears narrow in occlusal view. Trigonids of M_{1-3} longer antero-posteriorly and broader than talonids. No talonid basin on M_4 which is reduced to single cusp (hypoconid). Protoconid tallest cusp on M_{1-4} followed by metaconid except M_4 where metaconid and paraconid approximate the same height. Weakly developed notches present between anterior and posterior alveoli of M_{1-4}.

Remarks. Specimens comparable with both *Sminthopsis* and *Antechinus*, but generic diagnosis hampered by presence of notches between molars, a character more typically observed in *Antechinus*. Lack of premolar crowding and overall similar size of premolars is more typical of *Sminthopsis*. Acute inner angle of hypoconid more typical of *Sminthopsis* than *Antechinus*. Specimens distinguished from *Phascogale calura* by un-crowded and non-reduced P_3; distinguished from *Antechinomys laniger* by more steeply angled horizontal ramus and broader expansion of rear of dentary from massateric fossa.

Larger over-all size and molar and premolar row lengths contrast with *Sminthopsis crassicaudata*, *S. murina* and *S. leucopus*. Absence of entoconids on molars also distinguishes these specimens from *S. crassicaudata*, *Antechinus flavipes, A. agilis* and *A. stuartii*. Support for unique identity from *A. agilis, A. stuartii* and *A. minimus* supported by single cusped talonid of M_4 (Van Dyck, 2002). Lack of premolar spacing also suggests Dasyuridae sp. 1 is unique from *S. leucopus.*

Comparative Specimens. *Antechinomys laniger* SAM M22202, M22633. *Antechinus agilis* SAM M23166; AM M33343, AM M33930. *A. flavipes* SAM M4747, M5800, M7512. *A. minimus* SAM M10176, M13377, M11941, M22405. *A. stuartii* SAM M7500, M7501, M14143. *Phascogale calura* SAM M3151.

Sminthopsis crassicaudata SAM M7562, M7566. *S. leucopus* AM M13272, SAM M8594. *S. murina* SAM M6469, M7941, M16606.

Figure D.1 Left dentary of Dasyuridae sp. 1 (FU20889), buccal view.

Figure D.2 Left dentary of Dasyuridae sp. 1 (FU20889), occlusal view.

Figure D.3 Left dentary of Dasyuridae sp. 1 (FU14374), buccal view.

Genus *Antechinus* Macleay, 1841

Antechinus sp. cf. *A. agilis* Dickman, Parnaby, Crowther and King, 1998

Figs. D.4–D.6

Referred Material. FU14393. 14398, 20916, 20930, 20886, 20895, 20927; SAM P47433.

Description. FU20886 *Left dentary (alveoli for I_3, C_1, P_{1-3}, M_1; M_{2-4} present)* Posterior end of dentary broken off, preserving only the horizontal ramus and the anterior portion of the ascending ramus and massateric fossa. Ventral border of horizontal ramus moderately convex and tapers anteriorly from posterior end of M_1. Bone on buccal edge of alveoli for P_3 is bulged as permanent premolar is un-erupted. Notch present between alveoli of M_1. No spaces between posterior and anterior alveoli of adjacent premolars indicating crowded premolar row. Mental foramen ventral to posterior alveolus of M_1 is antero-posteriorly elongated so that it appears oval in shape. Smaller, oval shaped mental foramen is present ventral to alveoli for P_2. M_3 displaced buccally from M_2 and M_4 to reveal lingual edges of molar roots and alveoli. Short, columnar entoconids present on M_2 and M_3. Trigonid and talonid of similar width on M_2 and M_3. Talonid of M_4 buccal-lingually compressed; hypoconid and hypoconulid moderately developed. Protoconid tallest cusp on M_{2-4}, followed by metaconid and paraconid on M_2 and M_3. Paraconid approximates the metaconid height on M_4. Narrow anterior and posterior cingulid present on M_2 and M_3.

FU20930 *Right maxilla (P^{1-3}, M^{1-4} present).*

Canine and incisors unpreserved in specimen which is broken off at the anterior alveolus for P^1. Infraorbital foramen dorsal of posterior alveolus of M^1. Premolars oval in occlusal outline and crowded. P^2 and P^3 have well-developed buccal and lingual cingula. These are weakly developed on P^1. P^1 shorter in height and width than P^2, which is shorter in height and width than P^3. Medial cusp the most prominent, positioned anterior of the centre of each premolar. P^1 and P^2 orientated antero-lingual to P^3 which is in-line with lateral line of molar stylar cusps. No anterior crista on molars. Molars also have poorly developed posterior crista which are worn in the specimen to a broad, posterior-facing surface. Well-developed, narrow anterior cingula on M^{1-4}; posterior cingula present on M^{1-3}. M^1 anterior cingulum extends to trigon basin. Stylar cusp D broad in M^1, reduced in size in M^2 and smallest on M^3. Metacone most prominent cusp on $M^{1\text{-}3}$; paracone shorter than stylar cusp D. Metaloph notch lingual of metaconule of M^1 and M^2. M^4 is shaped like a transverse bar in occlusal outline, posterior edge rounded with wear.

Remarks. Smaller overall molar size and molar row length of specimen is more similar to *A. agilis/A. stuartii* than *A. flavipes, A. swainsonii* and *A. minimus* which are generally larger overall. Presence of small, columnar entoconid on M_3 contrasts with *A. flavipes* which typically lacks an entoconid on M_3 (Dickman *et al.*, 1998). Talonid of M_4 in *A. flavipes* only made up of one cusp (reduced hypoconid), compared with two in *A. agilis, A. stuartii* and *A. minimus* (Van Dyck, 2002). Anterior cingulum of M^1 in *A. agilis/A. stuartii* extends into trigon basin; terminates at base of paraconid in *A. flavipes*.

Only minor maxillary, dentary and dental characters distinguish *A. agilis* from *A. stuartii* (Dickman *et al.*, 1998; Crowther, 2002). As a result of the poor preservation and fragmentary nature of the fossil specimens, distinguishing the two species based on these characters is very difficult. Differentiation is also confounded by the high degree of morphological and size variability observed between populations of *A. agilis* and *A. stuartii* (Crowther, 2002). However, based on the current distribution of the two species, it is assumed that the specimens are more likely to be of *A. agilis* than *A. stuartii*. This assumption is supported by the presence of cingulated upper premolars of specimen FU20930, such that they appear shorter and wider than in *A. stuartii* (Dickman *et al.*, 1998; Crowther, 2002).

Comparative specimens. *Antechinus agilis* SAM M23166; AM M33343, AM M33930. *A. flavipes* SAM M4747, M5800, M7512. *A. minimus* SAM M10176, M13377, M11941, M22405. *A. stuartii* SAM M7500, M7501, M14143. *A. swainsonii* SAM M7047, M15075.

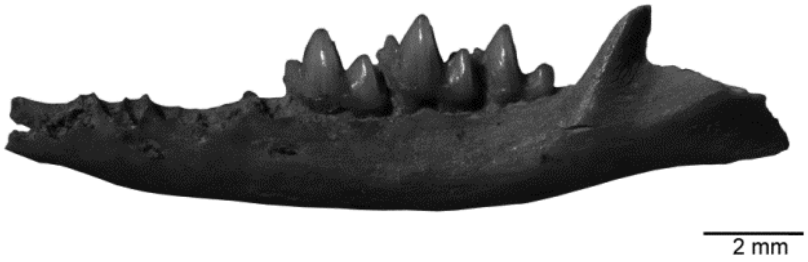

Figure D.4 Left dentary of *Antechinus* sp. cf. *A. agilis* (FU20886), buccal view.

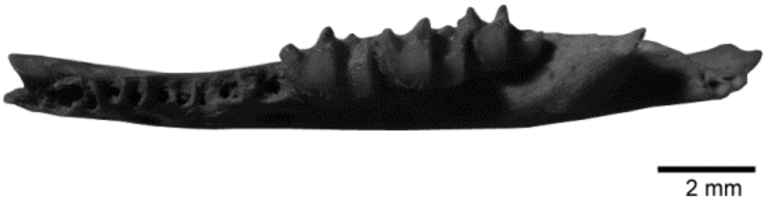

Figure D.5 Left dentary of *Antechinus* sp. cf. *A. agilis* (FU20886), occlusal view.

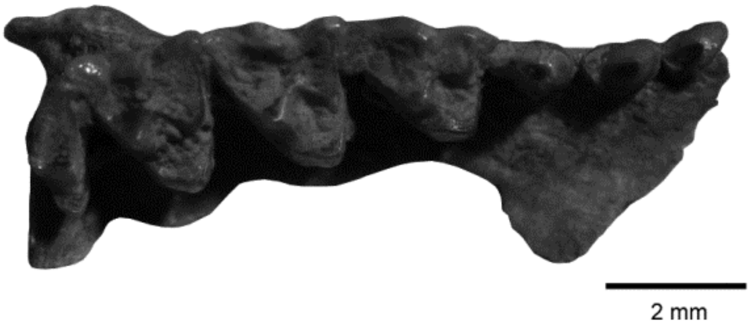

Figure D.6 Right maxilla of *Antechinus* sp. cf. *A. agilis* (FU20930), occlusal view.

Genus *Dasycercus* Peters, 1875

***Dasycercus* sp. indet.**

Fig. D.7–D.9

Referred Material. FU20933, 20934.

Description. FU20933 *Left dentary (alveoli for I_3 and C_1; P_{1-2}, M_{1-4}, present)* Ascending ramus rises at a steep angle to the horizontal ramus. Coronoid process broad; tip broken off specimen. Ventral border of horizontal ramus moderately convex, tapers anteriorly from posterior end of P_2 along broad symphysis. Antero-buccal end of dentary broken off to reveal anterior alveolus of P_1, C_1 and I_3. Two mental foramen in dentary, one ventral to posterior root of P_1 and one ventral to posterior root of M_1. Two premolars only. P_1 slightly quadrate and P_2 oval in occlusal outline; both with well-developed lingual and buccal cingulid. Posterior edge of P_2 ventral to anterior edge so that buccal and lingual cingulid dip dorsa-posteriorly in lateral view. Single, anteriorly aligned medial cusp on P_{1-2}. Anterior and posterior cristid connects cusp to highly reduced anterior and posterior cingulid. P_2 medial cusp taller than P_1 and more antero-posteriorly compressed to form sharper point. Molars with well-developed anterior cingulid. Posterior and buccal cingulid well-developed on M_{1-3}. Entoconids absent on lower molars. Paraconid absent in M_1 such that the trigonid is laterally compressed and tapers anteriorly. Protoconid of M_1 in line with medial cusps of P_{1-2}; lingually offset from protoconids on M_{2-4}. Hypoconulid approximately the same height as metaconid of M_1. Hypocristid angled transverse to molar tooth row, postero-buccal of hypoconid. It angles sharply posteriorly half way between the hypoconid and hypoconulid, in line with the protoconid, so that it appears sharply curved in occlusal view. Talonid basins of M_2 and M_3 narrower antero-posteriorly than trigonid. Hypoconid shorter than the metaconid of M_{2-3}. Hypocristid forms a straight crest connecting the hypoconid to the hypoconulid, *en echelon* to the molar tooth row. No talonid basin on M_4; reduced to single cusp (hypoconid). M_4 metaconid broken on specimen.

FU20934 *Left maxilla (alveoli for C^1 and P^1; P^2, M^{1-3}present,).*

Alveolus for canine is large, moderately laterally compressed. Infraorbital foramen dorsal of metacone of M^1. Anterior alveolus for P^1 peg like; posterior alveolus antero-posteriorly compressed so that it appears laterally elongated in occlusal outline. P^2 oval to semi-quadrate in occlusal outline. Posterior edge of tooth ventral to anterior edge so that buccal and lingual cingula dip dorsa-posteriorly in lateral view. Single large, centrally aligned medial cusp. No anterior or posterior cusps. Posterior crista joins medial cusp to rear of tooth where buccal and lingual cingula contact. Lingual cingulum present anterior and posterior of base of medial cusp. Buccal cingulum well defined along base of medial cusp, from anterior to posterior edges of the tooth. M^{1-3} appear sub-triangular in occlusal outline with narrow, reduced anterior cingula. Buccal cingula absent. Base of protocone of M^{1-2} broad to form a roughly square antero-lingual corner with contact to small, notch-like posterior cingulum in occlusal outline. Posterior cingulum absent on M^3; base of protocone antero-posteriorly compressed and deep buccal indent present. Paracone and stylar cusp B of M^1 fused. Metacone prominent, directly antero-lingual of stylar cusp D. M^2 metacone prominent, taller than stylar cusp D, which is taller than the paracone, which is taller than the protocone. Stylar cusp B approximates height of paracone in M^{2-3}. In M^3, the paracone is taller than stylar cusp D, which is columnar. Paracone and stylar cusp B directly in line on M^2 such that postparacrista is straight and perpendicular to the molar tooth row in occlusal view. Paracone postero-lingual of stylar cusp B on M^3; postparacrista curved postero-buccal in occlusal view. Small protoconule on preprotocrista of M^{2-3}.

Remarks. *Dasycercus* sp. indet. is distinguished from the similarly sized *Phascogale tapoatafa* by the absence of (d) $P^3/_3$, absence of posterior cingulum on M^3 and highly reduced anterior cingula on all upper molars. The absence of entoconids on lower molars also excludes *Phascogale*. In *Dasyuroides byrnei*, the stylar shelf of the upper molars is more posteriorly elongated between stylar cusps D and E than *Dasycercus*. Metastylar corner of M^3 more laterally compressed in *Dasyuroides byrnie*. Skull of *Dasyuroides byrnei* has larger palatal foramen.

Woolley (2005) suggested that the two species of *Dasycercus* could be distinguished by morphological characters, including the single dental character of two upper premolars in *D. blythi* and three in *D. cristicauda*. However, a high degree of intraspecific variability for this trait has been observed within fossil and modern collections (Van Dyck and Strahan, 2008; McDowell and Medlin, 2010). As a result, the specimens from Wet Cave can be identified to genus level only.

Comparative specimens. *Dasycercus cristicauda* SAM M2773, M2784, M2796, M3113. *Dasycercus blythi* SAM M2773. *Dasyuroides byrnie* SAM M9489, M13908, M13910. *Phascogale tapoatafa* SAM M1635, M7522, M21128.

Figure D.7 Left dentary of *Dasycercus* sp. indet. (FU20933), buccal view.

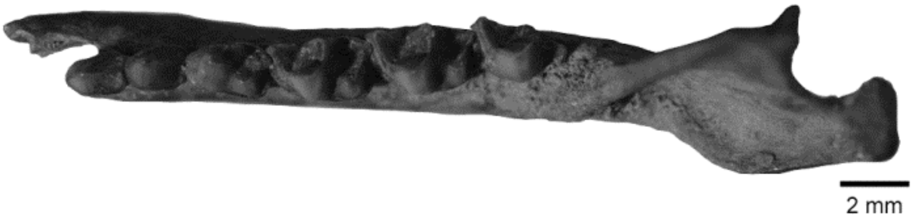

Figure D.8 Left dentary of *Dasycercus* sp. indet. (FU20933), occlusal view.

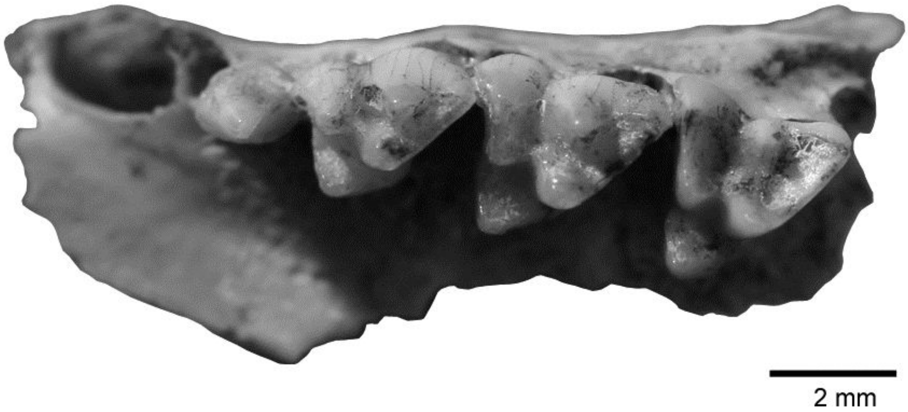

Figure D.9 Left maxilla of *Dasycercus* sp. indet. (FU20934), occlusal view.

Genus *Dasyurus* Geoffroy, 1796

Dasyurus maculatus Kerr, 1792

Fig. D.10–D.13

Referred Material. FU14362, 14140; SAM P47387, 47392, 47424, 47633, 47641.

Description. FU14140 *Left dentary (alveoli for $I_{1\text{-}3}$; C_1 present; alveoli for $P_{1\text{-}2}$, $M_{1\text{-}2}$, anterior alveolus for M_3)*

Partial juvenile dentary; posterior end broken off from anterior alveolus of M_3. Symphysis broad and extends from anterior alveolus of M_1 to anterior end of dentary. Mental foramen ventral to posterior alveolus of M_1; smaller mental foramen ventral to posterior alveoli of P_1 and P_2. C_1 partially erupted. Alveoli for premolars angled antero-lingual to tooth row; suggest relatively long, broad premolar teeth, with P_2 approximating the length of M_1. P_1 shorter than P_2; anterior alveolus of P_1 connected to alveolus of C_1. Notches present between anterior and posterior alveoli of M_1 and M_2; alveoli as wide as dentary. Width of dentary expands from M_1 such that anterior alveolus of M_3 is twice as broad as anterior alveolus of M_1.

FU14362 *Right M_3.*

Anterior and posterior roots intact. Trigonid, talonid and anterior, posterior and buccal cingulid as in left M_2. Protoconid tallest, most prominent cusp, followed by paraconid and metaconid which approximate the same height. Hypoconid only half as tall as metaconid. Paracristid notch well defined and positioned buccally of metacristid notch which is lingual of centre of metacristid. Internal angle at hypoconid approaches 90 degrees; small notch in centre of hypocristid. Entoconid extends conically from broad base, posterior to line drawn down centre of talonid. Entocristid notch well defined.

FU14362 (batch) *Left M^2.*

Approximates right-angled triangle in occlusal outline. Anterior cingulum complete and extends from stylar cusp A to base of protoconule. Notch in centre of paraloph; metaloph notch well defined buccal of metaconule. Buccal indent mid-way between stylar cusps B and D; buccal indent at posterior edge of stylar cusp D. Crista connects stylar cusp D and metacone; this divides the stylar shelf into anterior and posterior halves. Metacone tallest cusp, followed by stylar cusp D, paracone, stylar cusp B and protocone.

Remarks. *Dasyurus* cranio-dental characters are described by Archer (1976), together with a key of specific dental characters to differentiate the *Dasyurus* species. Character states for a range of cranio-dental features for *D. maculatus* are listed by Wroe *et al.* (2000).

Many features identified in the key of Archer (1976) are unpreserved in fossil specimens, or in this case, relate to the upper dentition which is under-represented in the assemblage when compared with specimens of the lower dentition. However, the larger size of *D. maculatus* teeth distinguishes them from the smaller *D. viverrinus* and *D. geoffroii*. Differentiation of fossil specimens of *D. maculatus* is also supported by observations of *D. maculatus*, *D. viverrinus* and *D. geoffroii* specimens made during the course of this project. M_{1-4} posterior cingulids are weakly developed and a buccal cingulid is absent on *D. viverrinus*. The hypoconulid of M_2 and M_3 is more posteriorly elongated in *D. viverrinus* than *D. maculatus.* The ascending ramus of *D. geoffroii* tapers dorsally such that the anterior edge is more re-curved and the coronoid process narrower, with a rounder posterior-facing point than observed in *D. viverrinus* which has a broader ascending ramus and coronoid process. Coronoid process constricted to a posterior-facing fine point in *D. viverrinus*. Maxilla and dentaries of *D. geoffroii* are typically smaller than *D. viverrinus*; however, tooth size is comparable with *D. viverrinus*. *D. geoffroii* is also unique in possessing a small diastema between I^1 and I^2; however, premaxilla are rarely preserved in fossil assemblages.

Character states identified in Archer (1976) that differentiate *D. maculatus* from *D. viverrinus* are: moderately spatulate crowns on the upper incisors, broader premolars; lack of shear-occlusion of upper and lower premolars; upper molars approximately as wide as they are long; M^3 paracone and metacone almost approximated in size; anterior cingulum of M^{1-4} complete and moderately developed posterior cingulum on upper molars. The only lower dentition character identified by Archer (1976) to distinguish the two species is the sub-equal height of the metaconid on M_4 compared with the paraconid; however, expression of this trait in *D. viverrinus* is variable within the species.

Comparative specimens. *Dasyurus geoffroii* SAM M79, M3066, M3067, M10123. *D. maculatus* SAM M2085, M7211, M10989. *D. viverrinus* SAM M6213, M7213, M7220, M15012.

Figure D.10 Left dentary of *Dasyurus maculatus* (FU14140), buccal view.

Figure D.11 Right M_3 of *Dasyurus maculatus* (FU14362), buccal view.

Figure D.12 Right M_3 of *Dasyurus maculatus* (FU14362), lingual view.

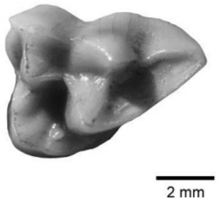

Figure D.13 Left M^2 of *Dasyurus maculatus* (batch 5U6 A3:L22), occlusal view.

Genus *Phascogale* Temminck, 1824

***Phascogale calura* Gould, 1844**

Fig. D.14–D.16

Referred Material. FU20641, 20645, 20657; SAM P47432.

Description. SAM P47432 *Left maxilla (alveolus for C^1; P^{1-3}, M^{1-4}present).* Gen. et sp. cf. *Phascogale calura.*

Anterior portion of maxilla complete with suture to premaxilla visible as a narrow groove. Infraorbital foramen dorsal of anterior half of M^1. Alveolus for C^1 large, broader than premolars and length approximates combined length of P^{1-2}. P^{1-3} with well-developed buccal and lingual cingula. Posterior end of P^1 rounded in occlusal outline, tapers to antero-buccally inclined tip. P^2 oval in occlusal outline with slight lateral compression at the middle of the buccal and lingual sides. Anterior end of P^3 broader than posterior end in occlusal outline. Medial cusps of P^{1-3} tall, weighted over anterior portion of each respective tooth. Posterior crista connects tip of medial cusp with small posterior cusp of P^{1-3}.

M^1 stylar cusp A contacts buccal side of posterior cusp of P^3. Well-developed anterior cingula on M^{1-4}. Posterior cingula present on M^{1-4}; extends postero-buccally on M^{1-3} to form a very thin ledge of enamel ventral of metacone and which extends to half-way along the length of the metacrista. Stylar cusp B and paracone of M^1 are separated by a short paracrista. M^{1-2} metacone approximates the height and size of stylar cusp D. Metacone of M^3 is slightly taller and broader than stylar cusp D. Stylar cusp B and the paracone approximate the same height on M^{1-2}. Anterior border of M^{2-4} approximately 90 degrees to buccal border of molar tooth row. Inside angle of M^{2-3} protocone antero-posteriorly compressed so that molars are triangular in occlusal view but not equilateral; trigon basin circular in occlusal outline. M^{2-3} postparacrista v-shaped as lingual angle between paracone and metacone is acute. M^4 paracone largest cusp; transverse bar in occlusal outline with short posterior projection of the highly reduced metacone.

FU20645 *Left Dentary (alveoli for M_{2-4})*

Anterior end of dentary broken off from M_2. Ascending ramus broken off at just above the level of the tooth row. Ventral border of horizontal ramus convex. Mental foramen ventral of anterior alveolus of M_2. Contact between anterior and posterior alveoli of $M_{2\text{-}3}$ with notches.

Remarks. As noted by Lundelius and Turnbull (1978), differentiation of maxillary fragments of *Phascogale calura* and *Antechinus flavipes* can be problematic. *P. calura* maxillae are generally larger overall than *A. flavipes* with broader premolars and a larger canine. Narrower antero-posterior width of M^2 trigon observed in *P. calura* than *A. flavipes*; however, further taxonomic investigation is required to confirm reliable upper dental characters to differentiate these species.

Dentary of *P. calura* is more easily distinguished from *A. flavipes* by broader premolars, antero-posteriorly longer molars and broad, rounded tip of coronoid process. Entoconids on lower dentition better developed than in *A. flavipes*, presence of which differentiates this species from *A. laniger* which has no entoconids.

Comparative Specimens. *Antechinomys laniger* SAM M22202, M22633. *Antechinus flavipes* SAM M4747, M5800, M7512. *Phascogale calura* SAM M3151. *Phascogale tapoatafa* SAM M1635; M7522; M21128.

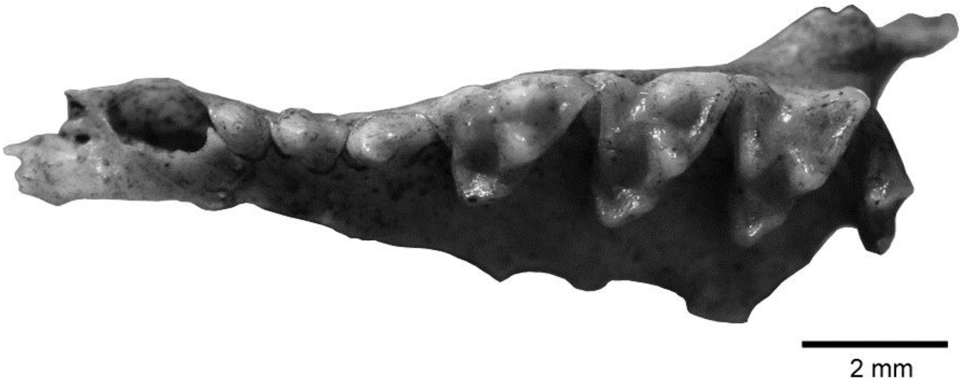

Figure D.14 Left maxilla of Gen. et sp. cf. *Phascogale calura* (SAM P47432), occlusal view.

Figure D.15 Left dentary of *Phascogale calura* (FU20645), buccal view.

Figure D.16 Left dentary of *Phascogale calura* (FU20645), occlusal view.

Genus *Sminthopsis* Thomas, 1886

sp. 1

Fig. D.17

Referred Material. FU14364, 14367, 14369, 14371–14373, 14376, 14379, 14383, 14387, 14389, 14391, 14395, 14396, 14399, 14404, 20655, 20658, 20665, 20786, 20879, 20898–20901, 20903–20915, 20917, 20919, 20928, 20932. SAM P47382, 47407, 47418, 47425, 47547, 47559, 47573, 47648.

Description. FU14395 *Left maxilla (alveoli for* C^1*,* $P^{1,2}$*;* P^3*,* M^{1-4} *present).*

Infraorbital foramen dorsal of anterior half of M^1, extending antero-posteriorly to posterior end of P^3. Premaxillary vacuity extends to, and rarely extends beyond, posterior edge of C^1. Canine alveolus oval in occlusal outline; twice as broad as P^1, and twice as long antero-posteriorly. P^1 and P^3 oval in occlusal outline. $P^3 > P^2 > P^1$ in antero-posterior length and in height (P^2 height observed in other specimens). Small anterior cusp present on P^1; posterior cusp only moderately developed. Medial cusp most prominent, positioned anterior of centre of premolar mass. Moderately developed lingual cingula on P^1 extend from posterior to anterior cusp. Buccal cingula extend anteriorly from posterior cusp to base of medial cusp. P^3 medial cusp most prominent, positioned over anterior end of premolar. Height of medial cusp approximates M^{1-3} metacone height. No anterior cusp, but well developed posterior cusp present. As a result, posterior end of P^3 appears v-shaped in lateral view. Posterior cristid connecting medial to posterior cusp has been worn to a broad, flat occlusal surface. Posterior cusp contacts metastylar indent of M^1. P^3 has poorly developed buccal and lingual cingula. Interdental fenestrae moderately to well developed between M^{1-4}. No posterior cingula on M^{1-4}; anterior cingula present, extend only to midpoint between stylar cusp A and paracone on $M^{3,4}$. M^1 stylar cusp B and paracone connected by short paracrista. Antero-posterior length of paracone narrow so that inner angle is acute in occlusal view, contrasts with broader angle of metacone in M^{1-3}. Metacone and stylar cusp D approximate the same height in $M^{1,2}$; stylar cusp D not as high as metacone on M^3.

Remarks. Specimens identified as *Sminthopsis* by absence of posterior cingula on M^{1-3}, contrasting with *Phascogale* and *Antechinus*. Although *A. minimus* does not have posterior cingula on the upper molars, specimens are distinguished from this species by overall molar shape which is antero-posteriorly compressed. Distinguished from *Antechinomys laniger* by shorter and narrower premaxillary vacuity, and lack of spacing between canine and premolars.

Specimens compared with all available *Sminthopsis* species represented in the SAM mammal collection, but character state observed to be unique from known species. *Sminthopsis* sp. 1 differentiated from the southern Australian species *S. crassicaudata*, *S. murina* and *S. leucopus* by longer molar and premolar row length and large canine alveolus. Size and shape of P^3 also distinguishes specimens from *S. murina* and *S. crassicaudata*. Lack of premolar spacing also contrasts with *S. leucopus* and short premaxillary vacuity supports differentiation from *S. crassicaudata* and *S. murina.*

Comparative specimens. *Antechinomys laniger* SAM M22202, M22633. *Antechinus agilis* SAM M23166; AM M33343, AM M33930. *A. flavipes* SAM M4747, M5800, M7512. *A. minimus* SAM M10176, M13377, M11941, M22405. *A. stuartii* SAM M7500, M7501, M14143. *A. swainsonii* SAM M7047, M15075. *Phascogale calura* SAM M3151. *Sminthopsis crassicaudata* SAM M7562, M7566. *S. leucopus* AM M13272, SAM M8594. *S. murina* SAM M6469, M7941, M16606.

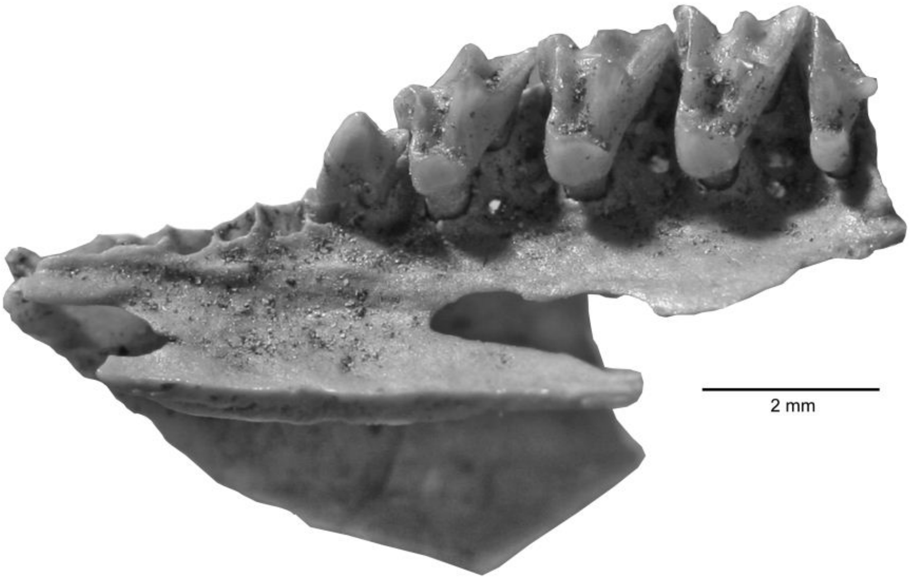

Figure D.17 Left maxilla of *Sminthopsis* sp. 1 (FU14395), occlusal view.

Table D.1 Reference literature used to aid in the taxonomic identification of cranio-dental fossil specimens from the study assemblages. Species identifications were also based on observations made from museum specimens, as described in the main text.

Family	**Reference Literature**
Peramelidae	Freedman, L. 1965. Skull and tooth variation in the genus Perameles. Part I: Anatomical features. *Records of the Australian Museum* **27,** 147–165.
Potoroidae	Finlayson, H.H. 1938. On a new species of Potorus (Marsupialia) from a cave deposit on kangaroo island, South Australia. *Transactions of the Royal Society of South Australia* **62,** 132–140.
	Merrilees, D. and Porter, J.K. 1979. *Guide to the identification of teeth and some bones of native land mammals occurring in the extreme south west of Western Australia*. Western Australian Museum, Perth.
	Smith, M.J. 1971. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. I. Potoroinae (Macropodidae), Petauridae and Burramyidae (Marsupialia). *Transactions of the Royal Society of South Australia* **95,** 185–198.
Burramyidae / Pseudocheiridae / Petauridae / Acrobatidae	Archer, M. 1984. The Australian marsupial radiation. In: *Vertebrate Zoogeography and Evolution in Australasia*. M. Archer and G. Clayton (eds.), pp. 633–808. Hesperian Press, Merrickville, New South Wales.
Muridae	Baynes, A. and McDowell, M.C. 2009. *Dichotomous key for the identification of the native rodents of south eastern South Australia.* Unpublished Report. Flinders University of South Australia.
	Watts, C.H.S. and Aslin, H.J. 1981. *The rodents of Australia.* Angus and Robinson Publishers, Australia.

Appendix E

Table E.1 Division of sedimentary layers from Wet and Blanche Cave into units (macroscale) and phases (mesoscale). The fossil assemblages within sedimentary layers were pooled to create samples representing each unit and phase. The number of identified specimens (NISP) is shown for each sample and is the final, sub-sample corrected value. Wet and Blanche Cave layers are described in Macken *et al*. (2013b).

Unit	**Wet Cave**		**Blanche Cave**		**Phase**	**Wet Cave**		**Blanche Cave**	
	Layers	**NISP**	**Layers**	**NISP**		**Layers**	**NISP**	**Layers**	**NISP**
E	2:5/1 – 2:6/4	3208	1 and 3 *(Unit E*)*	955	**E6**	2:5/1	1031		
					E5	2:5/2	592		
					E4	2:6/1	367		
					E3	2:6/2	344		
					E2	2:6/3	571		
					E1	2:6/4	303		
C	1:6/1 – 1:6/6	1412	10 – 18[#]	941	**C2**			10 – 13	629
					C1			15 – 18	312
B	1:6/7 – 1:6/11	2379	19 – 20	539	**B1**			19 – 20^	539
A	1:6/12 – 1:7/9	4076	21 – 27	15781	**A4**			21 – 23	977
					A3			24	2937
					A2			25	3817
					A1			26 – 27^	8050

^Due to the low NISP values, specimen data from layer 20 (NISP = 7) were pooled with those from layer 19 to create phase B1, and layer 27 data (NISP = 145) was pooled with layer 26 to form phase A1. Blanche Cave layers nine to four represented a single depositional block from which individual phases of accumulation could not be differentiated (Macken *et al*., 2013b). [#] Layer 14 was excluded from the analysis as it contains reworked material.

Table E.2 Mean ± 95% confidence intervals of site-effect size (difference between means) of Blanche Cave species proportions compared with those of Wet Cave for units A, B, C and E(*). Confidence intervals were calculated using the “plus four” method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007). Species name codes listed for reference to Fig. 6.4 of main text.

		Unit E(*)			**Unit C**			**Unit B**			**Unit A**		
	Species code	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Dasyuridae sp. 1	Dsp1	0.008	0.016	0.001	0.007	0.014	0.000	0.002	0.008	-0.005	-0.001	0.001	-0.004
Antechinus sp. cf. *A. agilis*	Aa	0.001	0.003	-0.001	0.000	0.003	-0.002	0.001	0.005	-0.002	0.001	0.001	0.000
Antechinus flavipes	Af	0.001	0.003	-0.002	0.001	0.004	-0.002	0.001	0.005	-0.002	0.000	0.000	-0.001
Dasycercus sp. indet.	Dcer	-0.001	0.001	-0.003	0.000	0.003	-0.003	0.001	0.005	-0.002	0.000	0.001	0.000
Dasyurus maculatus	Dm	-0.001	0.001	-0.003	0.000	0.003	-0.002	0.001	0.005	-0.002	0.000	0.000	-0.001
Dasyurus viverrinus	Dv	0.005	0.012	-0.001	0.010	0.019	0.001	0.020	0.035	0.006	0.007	0.011	0.003
Ningaui yvonneae	Ny	0.002	0.005	-0.001	0.002	0.008	-0.003	0.007	0.015	-0.002	-0.001	0.000	-0.002
Gen et sp. cf. *Phascogale calura*	Phc	0.000	0.002	-0.003	0.000	0.003	-0.002	0.001	0.005	-0.002	0.000	0.001	0.000
Phascogale tapoatafa	Pht	0.001	0.005	-0.003	0.000	0.003	-0.002	0.001	0.005	-0.002	0.000	0.001	-0.001
Sminthopsis crassicaudata	Sc	0.015	0.030	0.001	0.023	0.042	0.004	0.001	0.021	-0.020	0.011	0.019	0.004
Sminthopsis murina	Sm	0.007	0.018	-0.003	0.002	0.009	-0.004	0.003	0.011	-0.006	0.011	0.014	0.007
Sminthopsis sp. 1	Ssp1	0.004	0.008	0.000	0.003	0.011	-0.004	0.008	0.018	-0.002	-0.002	0.001	-0.005
Isodon obesulus	Io	0.003	0.007	-0.001	0.005	0.010	0.001	0.000	0.007	-0.007	0.001	0.003	-0.001
Perameles bougainville	Pb	0.020	0.032	0.008	0.032	0.052	0.011	0.004	0.024	-0.017	-0.033	-0.027	-0.038
Perameles gunnii	Pg	0.004	0.011	-0.003	0.004	0.010	-0.002	0.003	0.012	-0.006	0.005	0.010	0.001
Trichosurus vulpecula	Tv	0.001	0.004	-0.002	0.000	0.002	-0.003	0.003	0.008	-0.002	0.000	0.001	0.000
Bettongia lesueur	Bl	0.001	0.003	-0.001	0.000	0.002	-0.003	0.001	0.005	-0.002	0.000	0.001	0.000
Bettongia penicillata	Bp	0.002	0.005	-0.001	0.001	0.006	-0.003	0.001	0.005	-0.002	-0.001	0.000	-0.002
Potorous platyops	Pop	0.002	0.005	-0.001	0.004	0.008	-0.001	0.005	0.011	-0.001	0.000	0.001	0.000
Potorous tridactylus	Pot	0.001	0.003	-0.001	0.005	0.011	-0.002	0.006	0.014	-0.003	-0.001	0.000	-0.002
Cercartetus lepidus	Cl	0.001	0.003	-0.001	0.001	0.005	-0.002	0.001	0.005	-0.002	0.000	0.001	0.000
Cercartetus nanus	Cn	0.004	0.008	-0.001	0.008	0.019	-0.003	0.040	0.057	0.024	-0.003	-0.002	-0.004

		Unit E(*)			Unit C			Unit B			Unit A		
	Species code	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Pseudocheirus peregrinus	Psp	0.098	0.110	0.086	0.002	0.005	-0.002	0.003	0.008	-0.002	-0.003	-0.002	-0.005
Petaurus breviceps	Peb	0.005	0.010	0.000	0.002	0.006	-0.002	0.001	0.005	-0.003	-0.002	-0.001	-0.003
Petaurus norfolcensis	Pen	0.000	0.003	-0.002	0.000	0.003	-0.002	0.001	0.005	-0.002	0.000	0.001	-0.001
Acrobates pygmaeus	Ap	0.000	0.003	-0.002	0.000	0.003	-0.002	0.001	0.005	-0.002	0.000	0.001	0.000
Conilurus albipes	Ca	0.015	0.020	0.010	0.000	0.003	-0.002	0.001	0.005	-0.002	0.000	0.000	-0.001
Hydromys chrysogaster	Hc	0.002	0.007	-0.003	0.001	0.005	-0.002	0.001	0.005	-0.002	0.000	0.000	-0.001
Mastacomys fuscus	Mf	-0.001	0.001	-0.003	0.000	0.003	-0.002	0.001	0.005	-0.002	0.000	0.001	0.000
Notomys mitchellii	Nm	0.011	0.021	0.002	0.019	0.034	0.004	0.010	0.020	-0.001	-0.012	-0.009	-0.014
Pseudomys apodemoides	Papo	0.015	0.032	-0.002	0.002	0.023	-0.019	0.007	0.032	-0.018	0.012	0.017	0.007
Pseudomys auritus	Paur	0.114	0.141	0.086	0.054	0.075	0.033	0.132	0.164	0.101	-0.082	-0.075	-0.090
Pseudomys australis	Paus	0.001	0.030	-0.028	0.014	0.047	-0.020	0.077	0.114	0.041	0.059	0.076	0.042
Pseudomys fumeus	Pfum	0.133	0.163	0.103	0.087	0.125	0.048	0.037	0.081	-0.007	0.091	0.106	0.076
Pseudomys gouldii	Pgou	0.005	0.008	0.002	0.000	0.004	-0.004	-0.001	0.002	-0.005	-0.005	-0.002	-0.007
Pseudomys shortridgei	Psho	0.022	0.031	0.012	0.004	0.010	-0.001	-0.001	0.002	-0.005	0.000	0.001	0.000
Rattus fuscipes	Rf	0.077	0.101	0.053	0.031	0.056	0.006	0.074	0.095	0.054	-0.044	-0.033	-0.054
Rattus lutreolus	Rl	0.012	0.016	0.008	0.000	0.003	-0.003	-0.001	0.002	-0.005	0.001	0.002	0.000
Rattus tunneyi	Rt	0.001	0.004	-0.001	0.000	0.004	-0.004	0.001	0.004	-0.003	-0.003	-0.002	-0.004

Table E.3 Mean ± 95% confidence intervals of macroscale-effect size (difference between means) of species proportions in Wet Cave. Confidence intervals were calculated using the "plus four" method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007).

		Wet E-C			**Wet C-B**			**Wet B-A**	
	Mean	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Dasyuridae sp. 1	0.001	0.005	-0.002	-0.001	0.003	-0.005	-0.001	0.002	-0.005
Antechinus sp. cf. *A. agilis*	0.000	0.001	-0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Antechinus flavipes	-0.001	0.002	-0.003	0.002	0.004	-0.001	0.000	0.001	-0.001
Dasycercus sp. indet.	-0.001	0.001	-0.003	0.001	0.003	-0.001	0.000	0.001	-0.001
Dasyurus maculatus	0.000	0.001	-0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Dasyurus viverrinus	-0.013	-0.006	-0.021	0.009	0.017	0.001	-0.007	-0.001	-0.012
Ningaui yvonneae	-0.003	0.000	-0.005	0.000	0.004	-0.003	0.002	0.004	0.000
Gen et sp. cf. *Phascogale calura*	0.001	0.002	-0.001	0.000	0.002	-0.001	0.000	0.001	-0.001
Phascogale tapoatafa	0.002	0.004	0.000	0.000	0.002	-0.001	0.000	0.001	-0.001
Sminthopsis crassicaudata	-0.042	-0.027	-0.057	0.022	0.038	0.005	-0.004	0.007	-0.015
Sminthopsis murina	0.021	0.028	0.013	-0.002	0.004	-0.008	-0.005	0.001	-0.010
Sminthopsis sp. 1	0.000	0.005	-0.005	0.001	0.006	-0.004	-0.001	0.003	-0.005
Isodon obesulus	-0.005	-0.001	-0.009	0.001	0.006	-0.004	0.003	0.006	0.000
Perameles bougainville	-0.033	-0.022	-0.045	-0.007	0.007	-0.021	0.032	0.042	0.022
Perameles gunnii	-0.002	0.003	-0.007	-0.005	0.001	-0.011	-0.006	0.000	-0.012
Trichosurus vulpecula	0.000	0.002	-0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Bettongia lesueur	-0.003	0.000	-0.006	0.003	0.006	0.000	0.000	0.001	-0.001
Bettongia penicillata	0.000	0.001	-0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Potorous platyops	-0.003	0.000	-0.005	-0.001	0.003	-0.004	0.003	0.005	0.000
Potorous tridactylus	0.000	0.001	-0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Cercartetus lepidus	-0.012	-0.006	-0.018	0.013	0.019	0.007	0.000	0.001	-0.001
Cercartetus nanus	0.102	0.113	0.091	0.002	0.005	0.000	-0.001	0.000	-0.003

	Wet E-C			Wet C-B			Wet B-A		
	Mean	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Pseudocheirus peregrinus	0.000	0.002	-0.002	0.001	0.003	-0.002	0.001	0.002	-0.001
Petaurus breviceps	0.000	0.002	-0.002	0.000	0.002	-0.001	-0.001	0.001	-0.002
Petaurus norfolcensis	0.000	0.002	-0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Acrobates pygmaeus	0.015	0.020	0.011	0.000	0.002	-0.001	0.000	0.001	-0.001
Conilurus albipes	0.005	0.008	0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Hydromys chrysogaster	0.000	0.001	-0.002	0.000	0.002	-0.001	0.000	0.001	-0.001
Mastacomys fuscus	-0.036	-0.025	-0.047	0.024	0.036	0.011	0.017	0.023	0.011
Notomys mitchellii	-0.023	-0.008	-0.038	-0.003	0.014	-0.020	0.047	0.058	0.035
Pseudomys apodemoides	0.230	0.248	0.211	0.011	0.023	-0.002	-0.008	0.001	-0.017
Pseudomys auritus	0.006	0.031	-0.019	-0.056	-0.029	-0.083	-0.151	-0.128	-0.175
Pseudomys australis	-0.257	-0.229	-0.285	0.019	0.051	-0.013	0.071	0.095	0.048
Pseudomys fumeus	0.004	0.007	0.000	0.002	0.004	-0.001	-0.003	-0.001	-0.005
Pseudomys gouldii	0.032	0.039	0.025	0.002	0.004	-0.001	0.000	0.001	-0.001
Pseudomys shortridgei	-0.014	0.003	-0.031	-0.031	-0.012	-0.051	0.019	0.034	0.003
Rattus fuscipes	0.012	0.016	0.007	0.001	0.003	-0.001	-0.001	0.001	-0.002
Rattus lutreolus	0.000	0.003	-0.003	0.001	0.004	-0.002	0.001	0.002	-0.001
Rattus tunneyi	0.005	0.008	0.002	0.000	0.002	-0.001	0.000	0.001	-0.001

Table E.4 Mean ± 95% confidence intervals of macroscale-effect size (difference between means) of species proportions in Blanche Cave. Confidence intervals were calculated using the “plus four” method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007).

	Blanche E*-C			**Blanche C-B**			**Blanche B-A**		
	Mean	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Dasyuridae sp. 1	0.003	0.012	-0.006	0.004	0.013	-0.005	-0.001	0.005	-0.007
Antechinus sp. cf. *A. agilis*	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.002	0.005	-0.002
Antechinus flavipes	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.001	0.005	-0.003
Dasycercus sp. indet.	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.002	0.005	-0.002
Dasyurus maculatus	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.001	0.005	-0.002
Dasyurus viverrinus	0.002	0.011	-0.007	-0.021	-0.006	-0.037	0.021	0.035	0.006
Ningaui yvonneae	-0.003	0.002	-0.009	-0.004	0.005	-0.013	0.008	0.016	0.000
Gen et sp. cf. *Phascogale calura*	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.002	0.005	-0.002
Phascogale tapoatafa	0.002	0.006	-0.002	-0.001	0.003	-0.005	0.001	0.005	-0.002
Sminthopsis crassicaudata	-0.004	0.015	-0.023	-0.002	0.021	-0.025	0.008	0.027	-0.011
Sminthopsis murina	0.016	0.026	0.005	-0.002	0.006	-0.011	0.003	0.011	-0.004
Sminthopsis sp. 1	-0.007	-0.001	-0.014	-0.003	0.008	-0.015	0.005	0.015	-0.005
Isodon obesulus	0.003	0.008	-0.001	-0.004	0.002	-0.011	0.004	0.010	-0.002
Perameles bougainville	-0.045	-0.024	-0.066	0.029	0.054	0.003	-0.004	0.014	-0.023
Perameles gunnii	0.006	0.013	-0.001	-0.006	0.003	-0.015	-0.004	0.004	-0.012
Trichosurus vulpecula	0.001	0.005	-0.003	-0.003	0.003	-0.008	0.003	0.009	-0.002
Bettongia lesueur	0.000	0.004	-0.004	0.000	0.005	-0.004	0.000	0.004	-0.003
Bettongia penicillata	-0.002	0.003	-0.007	-0.001	0.006	-0.009	0.005	0.012	-0.001
Potorous platyops	-0.006	-0.001	-0.012	-0.002	0.008	-0.012	0.008	0.016	0.000
Potorous tridactylus	-0.001	0.003	-0.005	0.000	0.005	-0.004	0.002	0.005	-0.002
Cercartetus lepidus	-0.016	-0.006	-0.026	-0.019	0.000	-0.038	0.038	0.054	0.021
Cercartetus nanus	0.006	0.012	0.000	-0.003	0.003	-0.008	-0.001	0.004	-0.006

	Blanche E*-C			Blanche C-B			Blanche B-A		
	Mean	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Pseudocheirus peregrinus	0.003	0.009	-0.003	0.001	0.006	-0.004	0.000	0.004	-0.004
Petaurus breviceps	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.001	0.004	-0.003
Petaurus norfolcensis	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.002	0.005	-0.002
Acrobates pygmaeus	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.002	0.005	-0.002
Conilurus albipes	0.002	0.007	-0.003	0.000	0.005	-0.004	0.002	0.005	-0.002
Hydromys chrysogaster	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.002	0.005	-0.002
Mastacomys fuscus	-0.006	0.008	-0.019	0.014	0.028	0.001	-0.004	0.005	-0.013
Notomys mitchellii	-0.006	0.016	-0.028	-0.012	0.016	-0.040	0.066	0.089	0.043
Pseudomys apodemoides	0.062	0.092	0.033	-0.068	-0.032	-0.104	0.042	0.073	0.010
Pseudomys auritus	-0.009	0.028	-0.045	0.034	0.076	-0.007	-0.169	-0.136	-0.202
Pseudomys australis	-0.037	0.003	-0.077	-0.031	0.018	-0.080	0.126	0.166	0.086
Pseudomys fumeus	-0.001	0.003	-0.005	0.000	0.005	-0.004	-0.006	-0.002	-0.010
Pseudomys gouldii	0.006	0.014	-0.003	0.005	0.011	-0.002	0.002	0.005	-0.002
Pseudomys shortridgei	0.032	0.063	0.002	0.074	0.100	0.048	-0.100	-0.082	-0.117
Rattus fuscipes	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.002	0.005	-0.002
Rattus lutreolus	-0.001	0.003	-0.005	0.000	0.005	-0.004	-0.002	0.002	-0.006
Rattus tunneyi	0.000	0.003	-0.003	-0.001	0.003	-0.005	0.000	0.004	-0.003

Table E.5 Mean ± 95% confidence intervals of mesoscale-effect size (difference between means) of species proportions. Confidence intervals were calculated using the “plus four” method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007).

	E6-E5			**E5-E4**			**E4-E3**			**E3-E2**		
	Mean	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Dasyuridae sp. 1	-0.001	0.003	-0.005	-0.006	0.003	-0.016	-0.006	0.009	-0.022	0.004	0.019	-0.011
Antechinus sp. cf. *A. agilis*	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Antechinus flavipes	0.003	0.009	-0.002	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Dasycercus sp. indet.	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Dasyurus maculatus	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Dasyurus viverrinus	-0.009	0.000	-0.018	0.001	0.015	-0.013	0.005	0.018	-0.008	0.002	0.012	-0.007
Ningaui yvonneae	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Gen et sp. cf. *Phascogale calura*	0.002	0.007	-0.003	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Phascogale tapoatafa	0.000	0.007	-0.007	0.000	0.009	-0.010	0.003	0.012	-0.007	0.001	0.008	-0.005
Sminthopsis crassicaudata	-0.028	-0.012	-0.045	-0.031	-0.001	-0.061	0.030	0.063	-0.002	-0.004	0.022	-0.030
Sminthopsis murina	-0.009	0.009	-0.027	0.010	0.032	-0.013	-0.013	0.013	-0.040	0.023	0.046	0.000
Sminthopsis sp. 1	-0.003	0.005	-0.010	-0.010	0.005	-0.024	0.010	0.026	-0.005	-0.003	0.008	-0.014
Isodon obesulus	0.001	0.006	-0.003	-0.001	0.005	-0.007	-0.003	0.007	-0.013	0.004	0.013	-0.005
Perameles bougainville	-0.012	-0.002	-0.021	-0.006	0.011	-0.022	0.002	0.021	-0.018	-0.016	0.004	-0.036
Perameles gunnii	-0.002	0.004	-0.009	0.002	0.010	-0.005	-0.009	0.004	-0.021	0.001	0.015	-0.013
Trichosurus vulpecula	0.000	0.005	-0.004	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Bettongia lesueur	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Bettongia penicillata	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Potorous platyops	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Potorous tridactylus	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Cercartetus lepidus	0.000	0.005	-0.004	-0.006	0.003	-0.016	0.005	0.016	-0.006	-0.001	0.007	-0.008
Cercartetus nanus	0.261	0.293	0.229	0.037	0.054	0.019	0.003	0.012	-0.007	0.001	0.008	-0.005

Pseudocheirus peregrinus	0.001	0.006	-0.003	-0.004	0.004	-0.012	0.003	0.012	-0.007	0.001	0.008	-0.005
Petaurus breviceps	0.000	0.005	-0.004	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Petaurus norfolcensis	-0.002	0.003	-0.007	0.001	0.008	-0.006	0.000	0.008	-0.008	0.001	0.008	-0.005
Acrobates pygmaeus	0.042	0.057	0.028	0.002	0.010	-0.005	0.000	0.008	-0.008	0.001	0.008	-0.005
Conilurus albipes	0.010	0.017	0.003	-0.017	-0.003	-0.032	0.016	0.031	0.001	0.001	0.008	-0.005
Hydromys chrysogaster	-0.001	0.003	-0.005	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Mastacomys fuscus	-0.013	-0.003	-0.023	0.012	0.024	0.001	-0.023	-0.006	-0.041	0.009	0.028	-0.011
Notomys mitchellii	-0.011	0.011	-0.033	-0.033	0.001	-0.067	0.046	0.082	0.011	0.007	0.033	-0.018
Pseudomys apodemoides	0.027	0.074	-0.020	0.098	0.153	0.043	-0.089	-0.026	-0.152	0.077	0.136	0.019
Pseudomys auritus	-0.198	-0.164	-0.232	-0.104	-0.046	-0.162	0.083	0.148	0.017	-0.107	-0.047	-0.166
Pseudomys australis	-0.111	-0.080	-0.141	-0.022	0.026	-0.069	0.009	0.063	-0.045	-0.014	0.036	-0.063
Pseudomys fumeus	0.017	0.026	0.008	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Pseudomys gouldii	0.029	0.050	0.007	0.018	0.039	-0.003	-0.007	0.015	-0.029	0.014	0.033	-0.005
Pseudomys shortridgei	-0.064	-0.041	-0.088	0.031	0.063	-0.001	-0.067	-0.026	-0.108	0.019	0.061	-0.023
Rattus fuscipes	0.035	0.048	0.023	0.001	0.008	-0.006	0.000	0.008	-0.008	0.001	0.008	-0.005
Rattus lutreolus	0.005	0.011	-0.001	-0.001	0.005	-0.007	0.000	0.008	-0.008	0.001	0.008	-0.005
Rattus tunneyi	0.009	0.019	-0.001	0.004	0.012	-0.004	0.000	0.008	-0.008	0.001	0.008	-0.005

		E2-E1			**E1-C2**			**C2-C1**			**C1-B1**	
	Mean	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Dasyuridae sp. 1	0.004	0.016	-0.008	-0.005	0.008	-0.017	0.002	0.015	-0.012	0.004	0.016	-0.008
Antechinus sp. cf. *A. agilis*	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Antechinus flavipes	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Dasycercus sp. indet.	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Dasyurus maculatus	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Dasyurus viverrinus	-0.006	0.006	-0.018	0.000	0.014	-0.013	0.000	0.013	-0.013	-0.020	-0.002	-0.038

Ningaui yvonneae	-0.002	0.006	-0.009	0.000	0.008	-0.008	-0.010	0.004	-0.023	0.003	0.018	-0.011
Gen et sp. cf. *Phascogale calura*	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Phascogale tapoatafa	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Sminthopsis crassicaudata	0.006	0.032	-0.021	-0.008	0.018	-0.035	-0.019	0.012	-0.051	0.012	0.045	-0.021
Sminthopsis murina	-0.019	0.005	-0.042	0.030	0.052	0.008	0.000	0.011	-0.011	-0.001	0.010	-0.012
Sminthopsis sp. 1	-0.008	0.008	-0.024	0.007	0.023	-0.009	-0.003	0.011	-0.018	0.000	0.015	-0.016
Isodon obesulus	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	-0.002	0.006	-0.011
Perameles bougainville	0.013	0.035	-0.008	-0.060	-0.033	-0.086	0.000	0.036	-0.037	0.030	0.065	-0.005
Perameles gunnii	-0.006	0.011	-0.022	0.015	0.029	0.000	-0.008	0.003	-0.019	0.000	0.014	-0.013
Trichosurus vulpecula	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	-0.001	0.008	-0.009
Bettongia lesueur	-0.002	0.006	-0.009	0.000	0.008	-0.008	0.000	0.008	-0.008	0.001	0.009	-0.006
Bettongia penicillata	-0.002	0.006	-0.009	-0.001	0.007	-0.010	-0.002	0.009	-0.012	0.001	0.012	-0.010
Potorous platyops	-0.002	0.006	-0.009	-0.005	0.005	-0.014	-0.002	0.011	-0.014	0.000	0.014	-0.013
Potorous tridactylus	-0.002	0.006	-0.009	0.000	0.008	-0.008	0.000	0.008	-0.008	0.001	0.009	-0.006
Cercartetus lepidus	0.000	0.008	-0.008	-0.016	-0.003	-0.028	-0.010	0.012	-0.031	-0.012	0.013	-0.037
Cercartetus nanus	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	-0.001	0.008	-0.009
Pseudocheirus peregrinus	-0.002	0.006	-0.009	0.000	0.008	-0.008	-0.003	0.007	-0.013	0.005	0.014	-0.005
Petaurus breviceps	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Petaurus norfolcensis	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Acrobates pygmaeus	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Conilurus albipes	-0.005	0.005	-0.014	0.005	0.015	-0.005	-0.005	0.005	-0.014	0.005	0.014	-0.005
Hydromys chrysogaster	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Mastacomys fuscus	0.014	0.027	0.002	-0.009	0.001	-0.020	-0.041	-0.015	-0.068	0.043	0.069	0.016
Notomys mitchellii	-0.013	0.015	-0.040	-0.017	0.013	-0.048	-0.016	0.019	-0.052	0.000	0.038	-0.038
Pseudomys apodemoides	0.038	0.092	-0.017	0.072	0.121	0.023	0.031	0.069	-0.006	-0.088	-0.046	-0.130
Pseudomys auritus	-0.040	0.027	-0.107	0.136	0.200	0.072	0.107	0.158	0.056	-0.036	0.014	-0.086

Pseudomys australis	0.019	0.070	-0.032	-0.128	-0.074	-0.182	-0.024	0.038	-0.086	-0.015	0.049	-0.079
Pseudomys fumeus	-0.002	0.006	-0.009	0.000	0.008	-0.008	0.000	0.008	-0.008	0.001	0.009	-0.006
Pseudomys gouldii	0.009	0.020	-0.002	0.000	0.008	-0.008	-0.013	0.002	-0.027	0.014	0.028	0.000
Pseudomys shortridgei	-0.028	0.016	-0.073	0.020	0.065	-0.025	-0.020	0.024	-0.064	0.088	0.128	0.047
Rattus fuscipes	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006
Rattus lutreolus	-0.002	0.006	-0.009	0.000	0.008	-0.008	0.000	0.008	-0.008	0.001	0.009	-0.006
Rattus tunneyi	-0.002	0.006	-0.009	0.002	0.009	-0.005	-0.002	0.005	-0.009	0.001	0.009	-0.006

	B1-A4			**A4-A3**			**A3-A2**			**A2-A1**		
	Mean	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**	**Mean**	**Upper 95%**	**Lower 95%**
Dasyuridae sp. 1	0.000	0.008	-0.007	-0.005	0.001	-0.011	0.001	0.006	-0.003	0.004	0.008	0.001
Antechinus sp. cf. *A. agilis*	0.001	0.005	-0.003	0.000	0.003	-0.002	0.000	0.001	-0.001	0.000	0.001	-0.001
Antechinus flavipes	0.001	0.005	-0.003	0.000	0.002	-0.002	0.000	0.001	-0.002	0.000	0.002	-0.001
Dasycercus sp. indet.	0.001	0.005	-0.003	0.001	0.003	-0.001	0.000	0.001	-0.001	0.000	0.001	0.000
Dasyurus maculatus	-0.002	0.003	-0.008	0.003	0.007	-0.001	0.001	0.002	-0.001	0.000	0.001	0.000
Dasyurus viverrinus	0.014	0.030	-0.002	0.002	0.010	-0.007	0.004	0.009	-0.002	0.004	0.007	0.000
Ningaui yvonneae	0.008	0.017	0.000	0.000	0.002	-0.002	-0.001	0.001	-0.002	0.000	0.002	-0.001
Gen et sp. cf. *Phascogale calura*	0.001	0.005	-0.003	0.001	0.003	-0.001	0.000	0.001	-0.001	0.000	0.001	0.000
Phascogale tapoatafa	0.001	0.005	-0.003	0.000	0.003	-0.002	0.000	0.001	-0.001	-0.001	0.000	-0.002
Sminthopsis crassicaudata	-0.026	-0.001	-0.051	0.019	0.038	0.000	0.002	0.013	-0.010	0.029	0.037	0.020
Sminthopsis murina	0.003	0.012	-0.005	0.000	0.005	-0.004	0.000	0.003	-0.003	-0.001	0.002	-0.003
Sminthopsis sp. 1	0.005	0.016	-0.006	-0.003	0.004	-0.009	-0.001	0.004	-0.006	0.006	0.010	0.002
Isodon obesulus	0.001	0.009	-0.006	0.001	0.006	-0.003	0.001	0.004	-0.001	0.000	0.001	-0.001
Perameles bougainville	-0.001	0.022	-0.024	0.000	0.016	-0.016	0.013	0.023	0.003	-0.026	-0.018	-0.034
Perameles gunnii	-0.013	-0.001	-0.026	-0.002	0.008	-0.013	0.010	0.017	0.003	0.008	0.012	0.003
Trichosurus vulpecula	0.002	0.007	-0.004	0.002	0.005	-0.001	0.000	0.001	-0.001	0.000	0.001	-0.001

Bettongia lesueur	-0.006	0.000	-0.013	0.006	0.012	0.001	0.000	0.002	-0.002	0.001	0.003	-0.001
Bettongia penicillata	0.005	0.011	-0.002	0.001	0.003	-0.001	0.000	0.001	-0.001	0.000	0.001	0.000
Potorous platyops	0.006	0.015	-0.003	0.001	0.005	-0.002	0.000	0.002	-0.002	0.001	0.002	-0.001
Potorous tridactylus	0.001	0.005	-0.003	0.000	0.002	-0.002	0.001	0.002	-0.001	0.000	0.001	0.000
Cercartetus lepidus	0.032	0.050	0.015	0.003	0.009	-0.003	0.002	0.005	-0.001	0.001	0.003	-0.001
Cercartetus nanus	0.001	0.007	-0.006	-0.003	0.001	-0.008	0.000	0.004	-0.004	0.001	0.004	-0.001
Pseudocheirus peregrinus	-0.001	0.004	-0.006	0.001	0.005	-0.002	-0.001	0.001	-0.003	0.001	0.002	-0.001
Petaurus breviceps	0.001	0.005	-0.003	0.000	0.002	-0.002	0.000	0.001	-0.002	0.000	0.001	-0.001
Petaurus norfolcensis	0.001	0.005	-0.003	0.000	0.003	-0.002	0.000	0.001	-0.001	0.000	0.001	0.000
Acrobates pygmaeus	0.001	0.005	-0.003	0.001	0.003	-0.001	0.000	0.001	-0.002	0.000	0.001	-0.001
Conilurus albipes	0.001	0.005	-0.003	-0.001	0.002	-0.003	0.001	0.003	0.000	0.000	0.001	0.000
Hydromys chrysogaster	-0.001	0.004	-0.006	0.003	0.006	-0.001	0.000	0.001	-0.001	0.000	0.001	0.000
Mastacomys fuscus	0.001	0.012	-0.010	0.006	0.013	-0.001	-0.011	-0.006	-0.015	-0.006	-0.001	-0.011
Notomys mitchellii	0.033	0.059	0.007	0.010	0.025	-0.005	0.029	0.037	0.022	0.004	0.007	0.000
Pseudomys apodemoides	0.039	0.077	0.002	-0.003	0.021	-0.027	-0.003	0.013	-0.018	0.014	0.026	0.001
Pseudomys auritus	-0.066	-0.024	-0.108	-0.004	0.027	-0.035	-0.147	-0.125	-0.169	0.020	0.039	0.001
Pseudomys australis	0.079	0.127	0.032	-0.030	0.002	-0.061	0.101	0.121	0.081	-0.004	0.011	-0.018
Pseudomys fumeus	0.000	0.004	-0.005	-0.005	-0.001	-0.009	-0.001	0.003	-0.005	-0.002	0.001	-0.006
Pseudomys gouldii	0.001	0.005	-0.003	0.001	0.003	-0.001	0.000	0.001	-0.001	0.000	0.001	0.000
Pseudomys shortridgei	-0.078	-0.052	-0.105	0.003	0.027	-0.020	0.003	0.018	-0.012	-0.053	-0.040	-0.066
Rattus fuscipes	-0.003	0.003	-0.009	0.005	0.009	0.000	0.000	0.001	-0.001	0.000	0.001	0.000
Rattus lutreolus	-0.011	-0.003	-0.019	0.009	0.016	0.001	-0.001	0.002	-0.004	0.003	0.005	0.000
Rattus tunneyi	0.001	0.005	-0.003	0.001	0.003	-0.001	-0.001	0.000	-0.003	-0.001	0.001	-0.002

Table E.6 Chi-square statistics for Cochran's test of linear trend for species proportions at the macroscale (units A, B, C and E) of Wet and Blanche Caves. Cochran's test was only performed on those species in Wet and Blanche which occurred within three or more units. χ^2 is the normal chi-square test statistic which is divided into two components: χ_t^2 is chi-square for linear trend; χ_d^2 is chi-square for departure from linear trend (e.g., may be curvilinear). Significance assessed at α=0.01.

	Cochran's Test											
	Wet Cave						**Blanche Cave**					
Species	χ^2 **(df = 3)**	p	χ_t^2 **(df = 1)**	p	χ_d^2 **(df = 2)**	p	χ^2 **(df = 3)**	p	χ_t^2 **(df = 1)**	p	χ_d^2 **(df = 2)**	p
Dasyuridae sp. 1	2.417	0.490	0.870	0.351	0.275	0.872	4.598	0.204	3.070	0.080	1.528	0.466
Antechinus flavipes	5.763	0.124	4.078	0.043	1.685	0.431						
Dasyurus viverrinus	26.791	0.000	14.485	0.000	12.306	0.002	20.780	0.000	0.422	0.516	20.359	0.000
Ningaui yvonneae							19.085	0.000	3.050	0.081	16.035	0.000
Sminthopsis crassicaudata	43.105	0.000	15.713	0.000	27.392	0.000	0.905	0.824	0.329	0.566	0.577	0.750
Sminthopsis murina	42.120	0.000	17.434	0.000	24.687	0.000	45.201	0.000	30.609	0.000	14.592	0.001
Sminthopsis sp. 1	0.640	0.887	0.167	0.682	0.473	0.789	6.558	0.087	2.820	0.093	3.738	0.154
Isoodon obesulus	12.524	0.006	0.696	0.404	11.829	0.003	4.772	0.189	0.473	0.492	4.299	0.117
Perameles bougainville	101.337	0.000	4.814	0.028	96.523	0.000	19.236	0.000	0.792	0.374	18.444	0.000
Perameles gunnii	31.227	0.000	29.919	0.000	1.308	0.520	11.264	0.010	7.585	0.006	3.679	0.159
Trichosurus vulpecula							7.652	0.054	2.083	0.149	5.570	0.062
Bettongia lesueur							1.145	0.766	0.478	0.489	0.667	0.716
Bettongia penicillata							40.105	0.000	18.420	0.000	21.685	0.000
Potorous platyops	16.421	0.001	0.177	0.674	16.244	0.000	23.050	0.000	2.006	0.157	21.044	0.000
Cercartetus lepidus							184.689	0.000	36.038	0.000	148.650	0.000
Cercartetus nanus	812.791	0.000	594.182	0.000	218.609	0.000	6.078	0.108	0.555	0.456	5.523	0.063

	Cochran's Test											
	Wet Cave						**Blanche Cave**					
Species	χ^2 **(df = 3)**	***p***	χ_t^2 **(df = 1)**	***p***	χ_d^2 **(df = 2)**	***p***	χ^2 **(df = 3)**	***p***	χ_t^2 **(df = 1)**	***p***	χ_d^2 **(df = 2)**	***p***
Pseudocheirus peregrinus	3.714	0.294	3.658	0.056	0.056	0.972	5.786	0.123	2.685	0.101	3.101	0.212
Conilurus albipes							19.158	0.000	15.995	0.000	3.163	0.206
Mastacomys fuscus	141.229	0.000	9.769	0.002	131.460	0.000	6.497	0.090	2.420	0.120	4.077	0.130
Notomys mitchellii	91.432	0.000	17.161	0.000	74.270	0.000	306.883	0.000	239.272	0.000	67.610	0.000
Pseudomys apodemoides	1360.069	0.000	988.100	0.000	371.969	0.000	25.613	0.000	3.378	0.066	22.235	0.000
Pseudomys auritus	455.529	0.000	376.273	0.000	79.256	0.000	208.741	0.000	172.856	0.000	35.885	0.000
Pseudomys australis	554.467	0.000	224.925	0.000	329.542	0.000	106.470	0.000	64.456	0.000	42.014	0.000
Pseudomys fumeus	15.802	0.001	3.768	0.052	12.034	0.002						
Pseudomys shortridgei	37.746	0.000	21.278	0.000	16.468	0.000	50.749	0.000	3.398	0.065	47.351	0.000
Rattus fuscipes	81.586	0.000	57.013	0.000	24.573	0.000						
Rattus lutreolus	3.431	0.330	3.410	0.065	0.021	0.990						

Table E.7 Chi-square statistics for Cochran's test of linear trend, measured at the mesoscale through the Wet and Blanche Cave sequences. Cochran's test was only performed on those species that occur in four of more phases. χ^2 is the normal chi-square test statistic which is divided into two components: χ_t^2 is chi-square for linear trend; χ_d^2 is chi-square for departure from linear trend (e.g., may be curvilinear). Significance assessed at α=0.01.

Species	χ^2 **(df = 3)**	***p***	χ_t^2 **(df = 1)**	***p***	χ_d^2 **(df = 2)**	***p***
Dasyuridae sp. 1	29.846	0.003	2.079	0.149	27.767	0.004
Antechinus flavipes	15.756	0.203	0.706	0.401	15.050	0.180
Dasyurus viverrinus	51.549	0.000	0.810	0.368	50.739	0.000
Ningaui yvonneae	39.413	0.000	1.262	0.261	38.151	0.000
Phascogale tapoatafa	26.650	0.009	8.132	0.004	18.518	0.070
Sminthopsis crassicaudata	146.664	0.000	1.749	0.186	144.916	0.000
Sminthopsis murina	218.348	0.000	161.766	0.000	56.582	0.000
Sminthopsis sp. 1	23.119	0.027	0.288	0.592	22.831	0.019
Isoodon obesulus	11.777	0.464	0.038	0.845	11.739	0.384
Perameles bougainville	161.698	0.000	94.068	0.000	67.630	0.000
Perameles gunnii	96.851	0.000	8.359	0.004	88.492	0.000
Trichosurus vulpecula	12.356	0.417	0.800	0.371	11.557	0.398
Bettongia lesueur	34.069	0.001	1.799	0.180	32.270	0.001
Bettongia penicillata	52.826	0.000	1.456	0.228	51.369	0.000
Potorous platyops	30.759	0.002	0.429	0.513	30.331	0.001
Potorous tridactylus	17.142	0.144	0.138	0.710	17.004	0.108
Cercartetus lepidus	229.817	0.000	3.052	0.081	226.765	0.000
Cercartetus nanus	4410.114	0.000	1734.401	0.000	2675.713	0.000
Pseudocheirus peregrinus	6.063	0.913	1.259	0.262	4.804	0.940
Petaurus breviceps	5.813	0.925	2.521	0.112	3.292	0.986
Acrobates pygmaeus	800.397	0.000	305.796	0.000	494.601	0.000

Species	χ^2 **(df = 3)**	***p***	χ_t^2 **(df = 1)**	***p***	χ_d^2 **(df = 2)**	***p***
Conilurus albipes	182.061	0.000	80.035	0.000	102.026	0.000
Mastacomys fuscus	104.401	0.000	19.599	0.000	84.802	0.000
Notomys mitchellii	491.593	0.000	255.473	0.000	236.121	0.000
Pseudomys apodemoides	606.184	0.000	477.065	0.000	129.119	0.000
Pseudomys auritus	902.392	0.000	503.134	0.000	399.258	0.000
Pseudomys australis	461.570	0.000	37.524	0.000	424.046	0.000
Pseudomys fumeus	53.986	0.000	3.646	0.056	50.340	0.000
Pseudomys gouldii	889.826	0.000	622.570	0.000	267.256	0.000
Pseudomys shortridgei	306.866	0.000	199.469	0.000	107.397	0.000
Rattus lutreolus	43.658	0.000	0.192	0.661	43.466	0.000
Rattus tunneyi	101.184	0.000	25.074	0.000	76.110	0.000

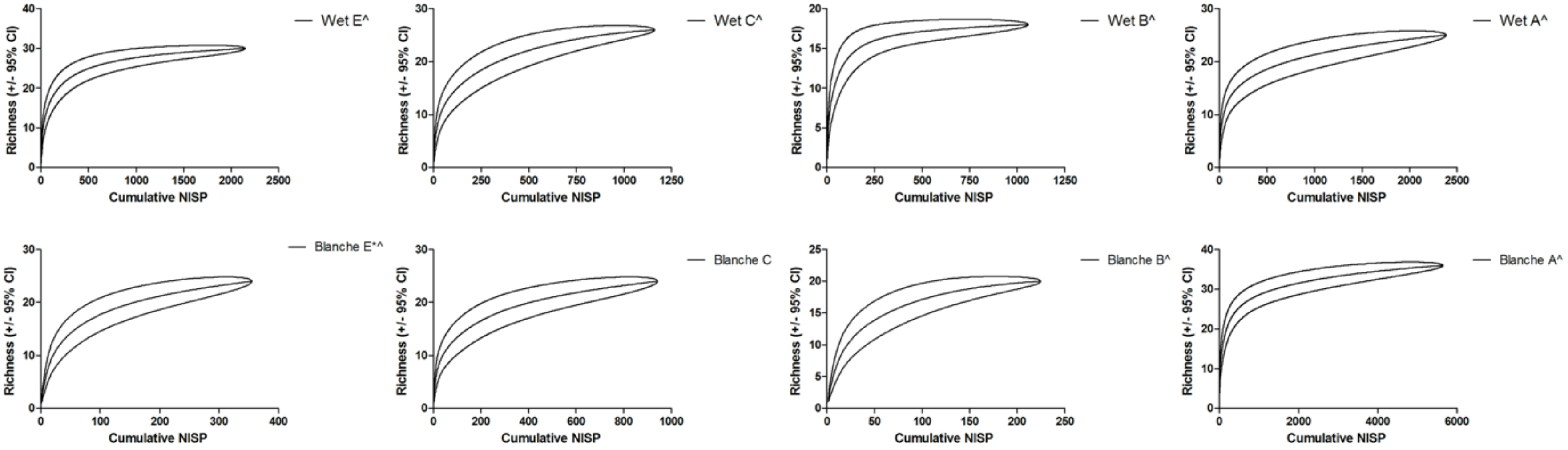

Figure E.1 Rarefaction curves of number of identified specimens (NISP) and species richness for all units of Wet and Blanche caves. ^Indicates those units that contain samples in which Murids were sub-sampled.

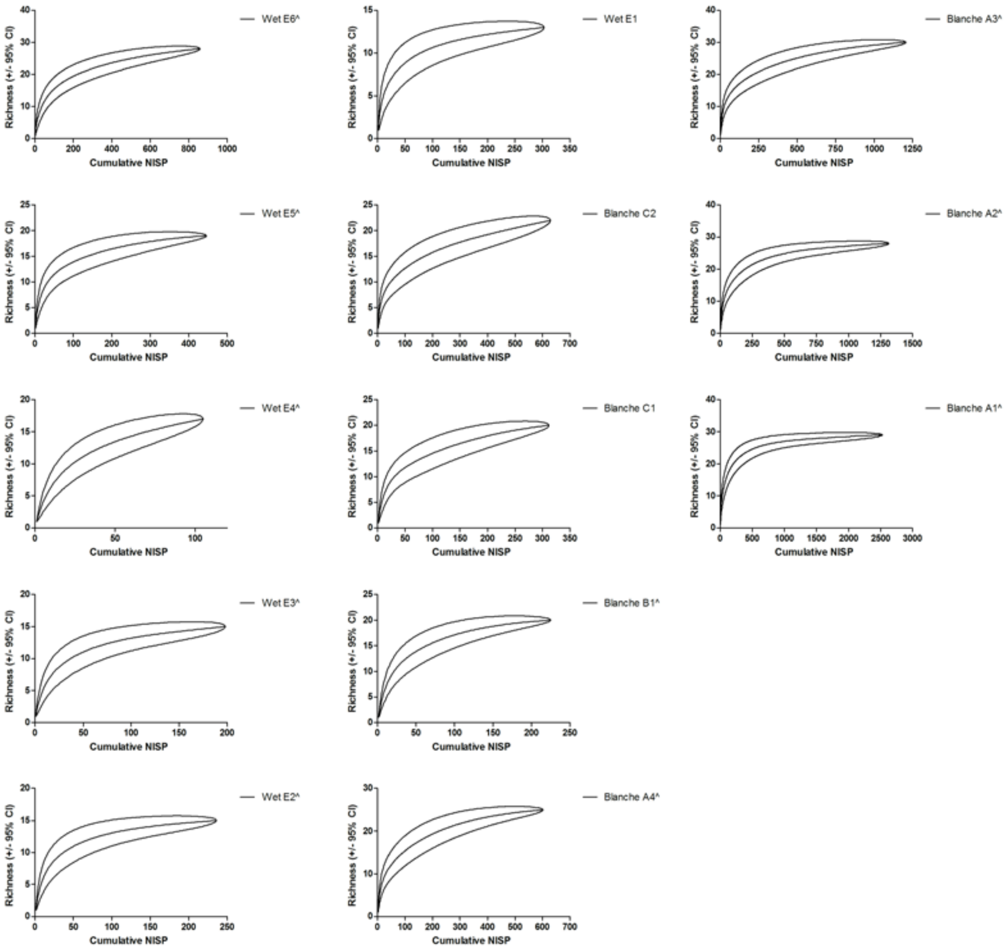

Figure E.2 Rarefaction curves of number of identified specimens (NISP) and species richness for all phases of Wet and Blanche caves. ^Indicates those units that contain samples in which Murids were sub-sampled

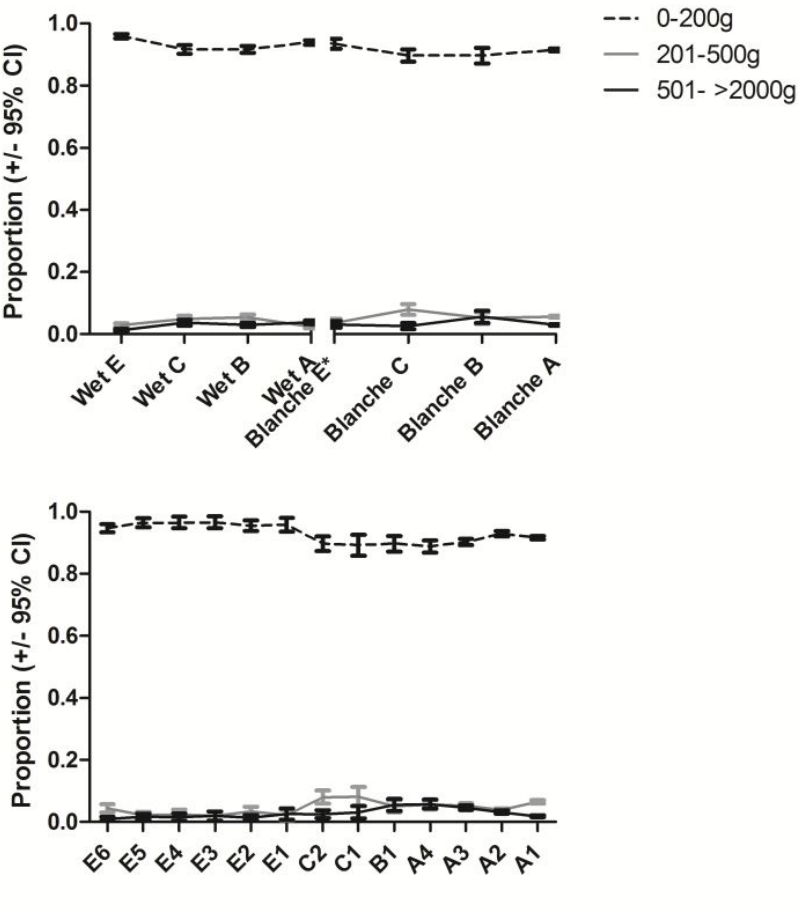

Figure E.3 Body mass distribution of small mammal taxa (body mass ≤2.5 kg) in the Wet and Blanche Cave units and phases. Data presented are the mean ± 95% confidence interval, calculated using the “plus four” method as outlined in Agresti and Caffo (2000) and Moore and McCabe (2007).

Appendix F

Spatio-temporal distribution of *Cercartetus concinnus*

Contemporary (post-European arrival to present)

The contemporary distribution of *C. concinnus* was compiled from records of specimens held in Australian and international museums and research institutions (Table F.1). Collection data were compiled from the Atlas of Living Australia (ALA) database and were vetted against data supplied from the institutions directly. The ALA also provided observational data, providing spatial occurrence points not covered by the specimen records.

Spatial distribution maps were generated in ArcMap v10.1 (Fig. 7.1, main text). Only specimens or observations in both the museum and ALA databases that had latitude and longitudinal data were plotted in the distribution maps. Of the 2218 records of *C. concinnus* available across the combined museum and ALA database, 2115 had latitude and longitude reference points. Of these, 42 were marked as 'spatially suspect,' leaving 2073 data points for the distribution map.

C. concinnus is the most widespread of the pygmy possums in Australia, with a distribution spanning southern Australia from south-west Western Australia to the Murray mallee region of Victoria and New South Wales. The Nullarbor was thought to form a barrier between eastern and western Australian populations, providing support for Wakefield's (1963) split of *C. concinnus* into two subspecies. However, despite the lack of detection of *C. concinnus* in surveys of the Nullarbor region in 1984 (McKenzie and Robinson, 1987), specimens were available from this region for the phylogenetic analyses performed by Pestell *et al.* (2008). Harris (2009) also noted specimens of *C. concinnus* collected from the Nullarbor Plain and Great Victoria Desert, challenging the previous assumption of a disjunct distribution of *C. concinnus* across southern Australia. Within the data compiled from the ALA and museum collections, 219 records are associated with the Nullarbor, Hampton and Great Victoria Desert Interim Biogeographic Regionalisation for Australia (IBRA) regions. These records clearly verify the presence of the species across this once considered distributional ‘gap.’ The records associated with these regions were collected between 1974 and 2012.

Another interesting feature of the contemporary distribution of *C. concinnus* is the history of its detection in the Murray Mallee region of south-western New South Wales (NSW). The first record for *C. concinnus* in NSW was associated with a specimen collected from near Gol Gol on the River Murray in 1958 (NMV C 2848). A second specimen was collected from the Mallee Cliffs Conservation Park in 1996 (AM M32456), prompting the listing of *C. concinnus* as an endangered species in NSW under the Threatened Species Conservation Act 1995.

Following its listing, a recovery plan was developed for *C. concinnus* in NSW and surveys were conducted to determine the distribution and size of populations within the state (NPWS, 2001). A total of 306 records of *C. concinnus* are available in the combined museum and ALA database in the Murray Mallee region of NSW, dating from 1996 to 2008.

Fossil (Pleistocene to Holocene)

Quaternary-aged fossil occurrence data for *C. concinnus* were compiled from the published literature. Latitude and longitudinal data for fossil localities were sourced from the Geoscience Australia Place Name Search and published sources. Only a limited number of fossil collections have been dated and in many cases, the resolution of the dating prohibits fine-scale analysis of fossil occurrences with time. As a result, the fossil distribution map was divided into the following time-periods:

1. Quaternary (2.6 myr to immediate pre-European arrival)
2. Pleistocene (2.6 myr to 11 kyr BP)
3. Late Pleistocene–Holocene (126 kyr to immediately pre-European arrival and/or present day), and
4. Holocene (11 kyr to immediately pre-European arrival and/or present day).

Where minimum and/or maximum radiocarbon or other radiometric data were available, these were used to constrain the specimens into one of these four time-periods. For some sites, no dating was available but the age of the specimens was inferred by the original authors through fossil association (e.g., presence of megafauna to infer Pleistocene age), taphonomic features (e.g., condition and discolouration of bone material) and association with geological formations. Where no age data were available, sites were marked as ‘unknown,’ but likely span any part of the Quaternary.

Fossil sites located within or near to the contemporary range of the species from which small animal remains have been recovered (e.g., rodents, lizards, bats and frogs), but which have not yielded identified specimens of *C. concinnus* were also plotted. This approach allowed for a comparison of the fossil distribution of *C. concinnus* against all documented fossil sites within the modern range of the species. It is recognised that the absence of the species from a fossil site may not represent the true absence of the species from the palaeocommunity sampled in the deposit. The lack of detection of *C. concinnus* may be due to a common bias in the early study of Pleistocene fossil sites towards larger mammals, particularly the megafauna given the significance of their Pleistocene extinction. For many sites, this bias resulted in poor detection, preservation or records of smaller mammals that co-occurred with the larger megafauna. Therefore, the fossil distribution data serve as a comparison against the species’ contemporary distribution to generate biogeographic hypotheses that can be tested using phylogeographic data, as well as to identify fossil sites for future re-examination.

Table F.1 Australian and international museums and institutions (and associated acronyms) that provided specimen data for *Cercartetus concinnus* with latitude and longitude and collection year data.

Institution
American Museum of Natural History, New York, USA
Australian Museum, Sydney, Aust.
Australian National Wildlife Collection (CSIRO), Aust.
Museum of Comparative Zoology, Harvard University, Washington, USA
The Field Museum, Chicago, USA
Museum Victoria, Melbourne, Aust.
Natural History Museum, London, UK
Queensland Museum, Brisbane, Aust.
Smithsonian National Museum of Natural History, Washington, USA
South Australia Museum, Adelaide, Aust.
Western Australian Museum, Perth, Aust.

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