Palaeoecology and preliminary taphonomy of the Robertson Cave entrance chamber fauna, Naracoorte

Thesis submitted in accordance with the requirements of the University of Adelaide for an Honours Degree in Environmental Geoscience

Patrick Ray Tavasci October 2018



PALAEOECOLOGY AND PRELIMINARY TAPHONOMIC ANALYSIS OF THE ROBERTSON CAVE ENTRANCE CHAMBER FAUNA, NARACOORTE

PALAEOECOLOGY OF ROBERTSON CAVE

ABSTRACT

The entrance chamber of Robertson Cave contains the most complete Holocene vertebrate deposit yet found at Naracoorte Caves, South Australia. The deposit dates from ~946 to 24090 Cal yr BP, spanning the 'youngest' part of the ~500,000 year Naracoorte fossil record. This study examined previously unstudied entrance chamber material, focussing primarily on the mammal fauna. Fossils were first sorted for diagnostic specimens and then identified to taxon. Taphonomic analysis of bone breakages, corrosion, manganese staining and hairline fracturing were completed. Statistical significance of faunal community composition across 12 excavation layers was analysed using chi-squared tests, along with comparisons between a similar, contemporaneous site; Wet Cave, and the modern mammal faunas for the region. Rarefaction was undertaken to ensure that the sample size from the deposit was sufficient to assess community structure. Palaeoecological analysis revealed the mammal fauna was composed largely of small herbivores and insectivores, with larger herbivores and only two larger carnivores. Assessment of the abundance of Anura in comparison with the mammalian fauna showed that in excavation layers 3 and 4, there was a much higher ratio of mammals; particularly Muridae, to Anura, which correlates to \sim 3819 to 10224 years ago. Taphonomic analysis of corrosion and breakages suggest the faunal assemblage was accumulated primarily as an owl deposit, aligning with prior work. The owl species was likely Tvto novaehollandiae, as indicated by the prev size range. Limited manganese staining and hairline fracturing of the bones suggest the cave environment remained relatively dry over time and has not experienced frequent significant wetting and drying. The inferred vegetation for the area immediately around the cave entrance was open, dry sclerophyll forest. Additionally, open mallee heathland was likely present in the region. Overall, Robertson Cave has a well-preserved diverse fossil assemblage that warrants further research.

KEYWORDS

Palaeoecology, palaeontology, taphonomy, Naracoorte, Robertson Cave, fossil, fauna, Holocene, Pleistocene

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INTRODUCTION

The Naracoorte Caves World Heritage Site represents, across multiple fossil deposits, a record of fauna forming a near-complete record for that area over the past ~500ka (Macken, Prideaux, & Reed, 2012; Macken & Reed, 2013; Reed & Bourne, 2000). These deposits offer insight into not only the past fauna, but also the palaeoclimate and palaeoecology of the South East of South Australia, allowing these caves both in and around the world heritage site to reconstruct that area of Australia back through time from the modern day.

Much of the work at Naracoorte has focussed on the Pleistocene megafaunal deposits (Macken et al., 2012; Moriarty, McCulloch, Wells, & McDowell, 2000; Prideaux et al., 2007). Due to the focus on the megafauna and the date of the megafaunal extinction, there has been less focus on younger fossil deposits, particularly those that span the Holocene. This has been addressed in recent years with the excavation of late Quaternary deposits in Wet Cave, Blanche Cave and Robertson Cave (Macken & Reed, 2013; McDowell, 2001; Reed & Bourne, 2009; Reed, 2012).

The objective of this study is to further the understanding of the past faunas and climate of Naracoorte by analysing a vertebrate fossil sample from the entrance chamber of Robertson Cave, which represents the most complete Holocene fossil record yet discovered at Naracoorte (E. H. Reed, personal communication, 2018). The site spans from 946 to 24090 median Cal yr BP (Grealy et al., 2016; E. H. Reed, personal communication, 2018), with the vertebrate deposits formed from the accumulation of owl pellets. Some of the excavated sample had previously been examined by Macken and Reed (2013). Unstudied material from the site will be the focus of the current study.

The specific aims of the study are to determine the accumulation mode/s of the cave; identify to taxon as much of the excavated bone material as possible; analyse this material for which portions of them are represented and what taphonomic features they have; and lastly, to use the identifications to infer the palaeoecology of the region and compare other faunas with the one recorded in the entrance chamber of Robertson Cave.

In order to assess post-European settlement biodiversity loss, the uppermost Holocene layer of the Robertson Cave entrance chamber faunal assemblage will be compared with the present-day fauna of the Naracoorte region. To do this, the fossil material was analysed to understand the faunal composition, taking into consideration the accumulation mode for the cave, and the implications following this analysis are explored with respect to fauna and climate, and in comparison with modern fauna and other Naracoorte deposits. It is expected that European settlement at this time had a significant impact on the faunal assemblage, especially as a result of land clearing for agricultural use.

BACKGROUND

Robertson Cave consists of two chambers, an entrance chamber and an inner chamber. The entrance chamber has two roof window entrances, each less than six metres across, registered in the Australian Speleological Federation Karst Index Database as 5U17 and 5U18 respectively.

Window entrances are formed when the roof of a cave becomes too thin to remain standing, and collapses, leaving a circular opening, with only a thin layer of rock, in this case (and typically) limestone, between the inside of the cave and the surface above it (Reed, 2012). Each of the entrances to Robertson Cave has a short drop of less than three metres to the modern sediment floor of the cave. Figure 1 shows a map of the cave, indicating the location of the dig site for the material used in this study, as well as the location of the entrances. It is important to note the entrance type, as this will determine how fauna will interact with the cave. A cave such as this one, with two window entrances of this size can serve as a roost for both bats and owls.



5U17 ROBERTSON CAVE

Surveyed by L. Reed and M. Kouklina 2004, drawn by D. Grindley, adapted from CEGSA Map No. 4014, September 2007.

Figure 1: Map of Robertson Cave, Naracoorte, indicating the entrances and excavation site (E. H. Reed, personal communication, 2018).

Robertson Cave is today known for being a wintering cave for bats, as well as sometimes serving as a roost for owls. Window entrances, no matter what the size, may still act as pitfall traps to some species (Reed, 2012). This means that the potential fossil sources for Robertson Cave are from bats using the cave, owl pellets and from fauna falling into the cave.

The fossil assemblage from the entrance chamber of Wet Cave, a similar fossil site at Naracoorte, will be compared to that of Robertson Cave. The entrance chamber excavation of Wet Cave dates from between 45,984 and 43,334 to 735 and 569 years ¹⁴C Cal yr BP; however the upper Holocene-aged layers of the deposit were mixed to some degree (Macken, McDowell, Bartholomeusz, & Reed, 2013; Macken & Reed, 2013).

The Robertson Cave entrance chamber deposit has previously undergone radiocarbon dating of all excavation layers in this section (E. H. Reed, personal communication, 2018). Analysis of the sediment sources for the inner chamber deposit were undertaken by Forbes and Bestland (2007) and Forbes, Bestland, Wells, and Krull (2007). Half of the excavated material was analysed from a biodiversity standpoint (Macken & Reed 2013), and Grealy et al. (2016) undertook a study analysing aDNA from Robertson Cave, which was primarily an example to show that this was possible at the Naracoorte caves and what methods were involved.

Many of the caves in the Naracoorte region have already had studies regarding the palaeoecology and taphonomy, but Robertson, largely, has not. This study aims to expand knowledge of late Quaternary faunas (particularly during the Holocene), while also addressing what the fauna was like recently, allowing for comparisons between the

ecology now and what it was like prior to European settlement in the region. The earliest excavated record will also show how the Last Glacial Maximum impacted on the Naracoorte fauna, and give a window into how the changing climate during this period was affected through time.

METHODS

EXCAVATION AND SORTING

The fossil material was excavated by E. Reed in 2011, by strata in 5 cm layers, to a total depth of one metre (Macken & Reed, 2013). The pit consisted of two one-metre adjacent grid squares; 1 and 2, which were each quartered into four square sections A, B, C and D (E. H. Reed, personal communication, 2018). This study focussed on the previously unexamined grid square 2 material.

After excavation, the material was wet screened to remove most of the fine loose sediment (E. H. Reed, personal communication, 2018). For this study, 54 bags of previously screened bulk material were sorted using brushes and forceps, separating bones from the remainder of the material. Small fragments and/or unidentifiable bone elements were left in the bulk material. The aim of the sorting process was to separate out diagnostic elements that could be identified to taxon.

IDENTIFICATION

Once sorted, the material was identified as precisely as possible. This was completed using comparisons with published works on the species present, guided by previous work on the Robertson Cave fauna (Macken & Reed, 2013), and comparison specimens housed in the Mammal Collection of the South Australia Museum. This study primarily focussed on the mammal material, with some non-mammals identified to family level, notably Anura.

All *Pseudomys* and *Notomys* material was identified from maxillae only, though their dentaries were still counted, but not identified beyond family.

Notomys mitchellii and *Pseudomys gouldii* cannot be distinguished from each other without the presence of the upper first molar (J. Treloar, personal communication, 2018). In the raw data, cf. *Psuedomys gouldii* and cf. *Notomys mitchellii* were listed separately, but for the analyses, the indeterminate identifications are combined with the confirmed species values for this reason.

Similarly, *Pseudomys apodemoides* can never be identified with total certainty from maxillae material, as it is often identical to *Pseudomys novaehollandiae* (J. Treloar, personal communication, 2018). The latter can be distinguished at times from *P. apodemoides*, as it may have a cusp on the first molar. If the first molar or a cusp is absent, *P. apodemoides* is indistinguishable from *P. novaehollandiae* using maxillae (J. Treloar, personal communication, 2018). Where this was the case, the species was counted as *Pseudomys* sp. cf. *apodemoides* for all instances, and is referred to *Pseudomys apodemoides* within the results.

TAPHONOMIC ANALYSES

Three methods were used in the analysis of the taphonomy:

Bone breakage - A slightly modified version of the classification scheme used by Lloveras et al. (2008), who assign classifications to different element types of bone based on which sub-sections of them remain. This was modified by adding an extra class to their mandible classifications to accommodate for a particular combination of preserved sections that was left out of their method. Where minor fracturing was present, for example, a small chip missing out of the back of a mandible branch, this was still counted as being complete as this was the best fitting representation classification.

	1	2	3	4	5	6	7
Long bones and metapodial	6	6	5				
Innominate			2			En se	D
Scapula	e se	É	NS.		U.		
Mandible	S	J.				2	
Cranium		L		1	10		

Figure 2: Table of element representation by present and fractured components, modified from Lloveras, L., Moreno-Garcia, M., & Nadal, J. (2008). Taphonomic study of leporid remains accumulated by the Spanish Imperial Eagle (*Aquila adalberti*). *Geobios, 41*, 91-100. Note that only mandible and cranium rows were used in this study. For the mandible row; 1 is complete, 2 is incisive part only, 3 is mandible body and incisive part, 4 is mandible body only, 5 is mandible body and branch, 6 is condylar process only, and 7 is incisive part, mandible body and branch. For the Cranium row; 1 is complete, 2 is premaxilla only, 3 is incpremaxilla and maxilla, 4 is maxilla only, 5 is maxilla with zygomatic arch and 6 is neurocranium or zygomatic arch only.

Corrosion - The presence or absence of both corrosion and hairline fractures were

measured for each element of bone present per bag of material from the deposit.

Manganese staining - Lastly, manganese staining of the bones was noted, as these are indicators of water presence in the caves to varying degrees (López-González et al., 2006). To do this, bones were recorded as having one of five degrees of manganese coverage. The first of these was None, meaning 0% coverage. This was followed by Very Minimal which covered the range of >0% to \leq 10%. This was followed by Minimal, >10% to \leq 25%; then Low, >25% to \leq 50%; followed by Intermediate, >50% to \leq 75%; then High, >75% to <100%; and lastly, Total, with 100% coverage.

PALAEOECOLOGICAL ANALYSES

The number of identified specimens (NISP) was calculated using the identified material, which was used to calculate the minimum number of individuals (MNI), which in turn were used to calculate the relative abundance of these species.

Using these values, and the known habitats inhabited by these species, today or in the past, the general floral ecology of the region was inferred.

The program R (R: A language and environment for statistical computing, 2013) and its package Rcmdr (Fox & Bouchet-Valat, 2018) were used to undertake both rarefaction and chi-squared tests.

Rarefaction was used through the 'vegan' package in R (Oksanen et al., 2018) to calculate the total diversity of the population, compared with the sampled values, using rarefaction curves. This ensures that the excavation is of a sufficient size to capture a realistic snapshot of the species in the environment at that time in the past.

Chi-squared tests were used to test if assemblages between layers and between other assemblages are significantly different. MNI values were used for all comparisons except for comparing the Robertson Cave entrance chamber assemblage to the Wet Cave excavation assemblage, where presence/absence data were used.

Modern species assemblage data was gathered using NatureMaps, a free online ecological data tool provided by the South Australian Government (NatureMaps, 2018). Specifically, NatureMaps was employed by using the 'Fauna Tools' option, creating a simple species list using a manually chosen selection area (NatureMaps, 2018). As owls are known to hunt up to 50 km from their roost, the selection area was made to be an approximately 100 km wide square (as no circle option is available), using the inprogram scale bar (NatureMaps, 2018; E. H. Reed, personal communication, 2018). This square was approximately centred on Robertson Cave, in order to gather the closest available data to what fauna could be found within the hunting range of an owl roosting there (E. H. Reed, personal communication, 2018). The species list generated was refined to only native mammalian species, as this was the only taxon that were identified to species level from the fossil deposit. These values were then normalised against the total MNI in Layer 1, before undertaking chi-squared tests. As only one bat species was found in the entire deposit, Layer 1 was also compared to the modern species assemblage with the bat data removed, to ensure this difference was not incorrectly distorting the statistical difference between the two species assemblages.

OBSERVATIONS AND RESULTS

ROBERTSON CAVE

This deposit is made up of dark brown, fine sand; with a high degree of contemporaneous plant material in the upper four layers (Grealy et al. 2016), which continues into the lower layers to a much lesser extent.

There were significant numbers of insect casings in the uppermost layers of the deposit, and were present in most layers, as well as some insect exoskeleton pieces preserved, mainly in the upper two layers.

The top five layers of the deposit also preserve snail shells, which are quite rare in the Naracoorte fossil record, and likely only appear in these layers as they are the most well-preserved layers, simply by being the youngest.

An interesting sidenote is that bracken abruptly appears in the record in Layer 4.

FAUNAL RESULTS

The results of the chi-squared tests undertaken, shown in Table 1 indicate that Layers 1 and 2 are not statistically different from each other, as are Layers 3 and 4, and Layers 9, 10, 11 and 12. Layers 5, 6, 7 and 8 are each distinct from all other layers.

Layer 1 is distinct from the modern Naracoorte region species assemblage – the data for which is the faunal record for an approximate 50 kilometre range from Robertson Cave, as this is the potential range of hunting owls (though it should be noted that the

assemblage changes minimally when taken from the data of the 50 km surrounding the cave and when restricted to exclusively within the Naracoorte National park).

Spagios Assemblage	Chi-Squared Test Results							
species Assemblage	X-squared	df	p-value					
Robertson Cave entrance vs Wet Cave	2	34	1					
Modern Assemblage vs Layer 1	60.729	39	0.01449					
Modern Assemblage vs Layer 1 – No bats	43.083	26	0.01893					
Layer 1 vs Layer 2	44.37	44	0.456					
Layer 2 vs Layer 3	66.578	43	0.01206					
Layer 3 vs Layer 4	45.247	42	0.338					
Layer 4 vs Layer 5	102.47	37	4.634E-08					
Layer 5 vs Layer 6	48.454	30	0.01785					
Layer 6 vs Layer 7	56.284	31	0.003606					
Layer 7 vs Layer 8	46.097	25	0.006254					
Layer 8 vs Layer 9	71.148	34	0.0001959					
Layer 9 vs Layer 10	28.469	37	0.8416					
Layer 10 vs Layer 11	15.638	34	0.997					
Layer 11 vs Layer 12	17.547	29	0.953					

 Table 4: Table of chi-squared test results for all comparisons of fauna. Layer values refer to Grid

 Square 2, Robertson Cave entrance refers to the whole entrance chamber dig.

Figure 3 shows the rarefaction curves for each layer of grid square 2 of the deposit, including the total for all layers; calculated from the MNI values of each layer. The results show that at this sample size, across the whole deposit, most of the species present will be observed within grid square 2 of the excavation.



Sample Size

Figure 3: Rarefaction output graph from Rcmdr (Fox & Bouchet-Valat, 2018) for each layer of the grid square 2, including the total, showing an asymptotic curve, indicating sufficient sample size.



Figure 4: Ratio of the MNI of Anura to both Muridae and Mammalia in the Robertson Cave entrance chamber excavation, grid square 2.

Unexpectedly, it was observed that there is a spike in the ratio of Anura to both mammals and more so Muridae within layers 3 and 4 of the deposit. This is the first time this occurrence has been noted from the Naracoorte fossil record. This has been graphed using MNI values in Figure 4.

Though not recorded, it was also observed that the majority of the Peramelidae found in this study were juvenile.

Table 2 shows the MNI values for every identified mammalian specimen in this grid

square across every layer of the deposit, including totals where appropriate for genera

and families, and includes a combined total for each layer and for each species across all

layers.

Data for Order Anura are also included within this table. Overall number of specimens is higher in the uppermost layers of the deposits, with less material from the lower layers. Muridae is the most abundant identified family in the deposit, with *Pseudomys australis* being the most common species in the deposit.

Table 5: Minimum Number of Individuals (MNI) values for all Anura and identified mammal specimens within grid square 2 of the excavation, including totals for each genus and family identified. MNI for totals were calculated by accounting for each individual species, as well as any individuals identified to genus or family respectively, where they add duplicate elements to increase the MNI.

Order			Layer	1	2	3	4	5	6	7	8	9	10	11	12	Total
Anura				18	41	65	75	18	6	3	2	1	1	2	1	233
Family	Genus	species														
Acrobatidae	Acrobates	pygmaeus		0	0	0	0	0	2	0	0	0	0	0	0	2
Burramyidae	Cercartetus	lepidus		0	0	2	2	1	0	1	0	2	4	2	0	14
		nanus		0	2	1	0	0	0	1	0	0	1	0	0	5
		Total		1	3	4	4	2	0	2	0	2	5	2	0	25
Dasyuridae	Antechinus	agilis		0	0	0	1	0	0	0	0	1	1	0	0	3
		flavipes		0	1	1	0	0	0	3	0	1	1	0	0	7
		Total		0	3	2	1	0	0	3	0	2	2	0	0	13
	Dasyurus	maculatus		2	1	0	0	0	0	0	0	0	0	0	0	3
		viverrinus		4	5	4	0	0	0	1	1	2	1	1	1	20
		Total		6	6	4	0	0	0	1	1	2	1	1	1	23
	Ningaui	yvonneae		0	4	0	1	3	1	1	0	1	1	1	0	13

	Phascogale	calura	0	2	2	0	1	1	0	0	0	0	0	0	6
		tapoatafa	0	1	0	1	0	0	0	0	1	0	0	0	3
		Total	0	3	2	1	1	2	0	0	1	0	0	0	10
	Sminthopsis	crassicaudata	1	0	0	1	0	0	0	0	3	2	2	0	9
		murina	3	5	1	0	0	3	0	0	3	0	1	0	16
		Total	4	5	1	1	0	4	0	0	4	2	3	0	24
	Total		10	23	9	5	7	8	5	2	13	7	5	2	96
Macropodidae	Macropus		0	1	0	0	1	0	0	0	0	0	0	0	2
Miniopteridae	Miniopterus	orianae bassanii	0	4	5	4	2	1	0	0	1	0	0	0	17
Muridae	Conilurus	albipes	2	4	4	1	1	0	0	0	0	1	0	0	13
	Mastacomys	fuscus	0	1	0	0	1	4	2	1	3	0	0	0	12
	cf. Notomys	mitchellii	0	0	1	0	1	0	0	0	0	1	0	3	6
	Notomys	mitchellii	2	0	0	0	2	0	0	2	0	1	1	0	8
	Pseudomys	apodemoides	6	9	4	3	9	9	2	4	4	3	3	1	57
		auritus	0	4	0	0	2	12	6	9	2	4	3	3	45
		australis	1	8	2	1	5	13	6	6	6	6	5	2	61
		fumeus	2	5	1	1	4	13	1	5	3	3	1	1	40
		cf. gouldii	0	4	1	0	6	4	1	0	4	0	1	0	21
		gouldii	0	0	0	2	0	0	0	1	1	1	0	0	5
		novaehollandiae	0	1	1	0	0	0	0	0	0	0	0	0	2
		shortridgei	1	4	2	3	3	3	4	2	1	5	3	0	31
		Total	10	35	11	10	29	53	20	27	21	22	16	7	261
	Rattus		2	1	1	1	0	0	0	0	0	0	0	0	5
	Total		22	53	27	16	39	61	25	33	25	28	18	10	357
Peramelidae	Isoodon	obesulus	0	0	0	1	0	0	0	0	0	1	0	0	2
	Perameles	bougainville	2	2	2	1	0	1	0	0	1	2	1	1	13
		gunnii	1	5	2	0	2	2	6	0	4	3	2	0	27
		Total	3	7	4	1	2	3	6	0	5	5	3	1	40
	Total		5	10	6	3	2	4	6	0	6	8	3	1	54
Petauridae	Petaurus	breviceps	2	0	0	2	0	0	0	0	0	0	0	0	4
		norfolcensis	2	0	0	0	0	0	0	0	0	0	0	0	2
		Total	4	0	0	2	0	0	0	0	0	0	0	0	6
Phalangeridae	Trichosurus	vulpecula	1	1	3	0	1	0	0	0	0	0	0	0	6
Potoroidae	Bettongia	gaimardi	1	2	0	0	0	0	0	0	0	0	0	1	4
		lesueur	0	0	0	0	0	0	0	0	0	0	1	0	1
		Total	1	3	0	0	0	0	0	0	0	0	1	1	6
	Potorous	tridactylus	0	0	1	0	0	0	0	0	1	0	0	0	2
	Total		1	3	3	0	0	0	0	0	1	0	1	1	10
Pseudocheiridae	Pseudocheirus	peregrinus	0	1	2	1	0	0	0	0	0	0	0	0	4
Vombatidae			1	0	0	0	0	0	0	0	0	0	0	0	1
Total Marsupials				46	32	19	15	15	13	2	23	20	11	4	223
Total Mammals				99	59	35	54	76	38	35	48	48	29	14	580
Total with Anura	63	140	124	110	72	82	41	37	49	49	31	15	813		

The relative abundances shown in Table 3 give matching results to Table 2. 10.52% of all individuals in the grid square being *Pseudomys australis* and 61.55% of the species in the deposit falling into the family Muridae. This is a vast majority, with the second-most abundant family being Dasyuridae with only 16.55%. The second most abundant species, however, is not the first by a very wide margin; *Pseudomys apodemoides* has 9.83% of the individuals in the deposit.

Table 6: Table of relative abundances in percentage of species per layer of the Robertson Cave entrance chamber excavation, grid square 2, including total. All values calculated from MNI values as shown in Table 2.

Layer	1	2	3	4	5	6	7	8	9	10	11	12	Total
Acrobates pygmaeus						2.63							0.34
Cercartetus lepidus			3.39	5.71	1.85		2.63		4.17	8.33	6.90		2.41
Cercertetus nanus		2.02	1.69				2.63			2.08			0.86
Cercartetus Total	2.22	3.03	6.78	11.43	3.70		5.26		4.17	10.42	6.90		4.31
Antechinus agilis				2.86					2.08	2.08			0.52
Antechinus flavipes		1.01	1.69				7.89		2.08	2.08			1.21
Antechinus Total		3.03	3.39	2.86			7.89		4.17	4.17			2.24
Dasyurus maculatus	4.44	1.01											0.52
Dasyurus viverrinus	8.89	5.05	6.78				2.63	2.86	4.17	2.08	3.45	7.14	3.45
<i>Dasyurus</i> Total	13.33	6.06	6.78				2.63	2.86	4.17	2.08	3.45	7.14	3.97
Ningaui yvonneae		4.04		2.86	5.56	1.32	2.63		2.08	2.08	3.45		2.24
Phascogale calura		2.02	3.39		1.85	1.32							1.03
Phascogale tapoatafa		1.01		2.86					2.08				0.52
Phascogale Total		3.03	3.39	2.86	1.85	2.63			2.08				1.72
Sminthopsis crassicaudata	2.22			2.86					6.25	4.17	6.90		1.55
Sminthopsis murina	6.67	5.05	1.69			3.95			6.25		3.45		2.76
Sminthopsis Total	8.89	5.05	1.69	2.86		5.26			8.33	4.17	10.34		4.14
Dasyuridae Total	22.22	23.23	15.25	14.29	12.96	10.53	13.16	5.71	27.08	14.58	17.24	14.29	16.55
Macropus		1.01			1.85								0.34
Miniopterus orianae bassanii		4.04	8.47	11.43	3.70	1.32			2.08				2.93
Conilurus albipes	4.44	4.04	6.78	2.86	1.85					2.08			2.24
Mastacomys fuscus		1.01			1.85	5.26	5.26	2.86	6.25				2.07
Notomys mitchellii	4.44		1.69		5.56			5.71		4.17	3.45	21.43	2.41
Pseudomys apodemoides	13.33	9.09	6.78	8.57	16.67	11.84	5.26	11.43	8.33	6.25	10.34	7.14	9.83
Pseudomys auritus		4.04			3.70	15.79	15.79	25.71	4.17	8.33	10.34	21.43	7.76
Pseudomys australis	2.22	8.08	3.39	2.86	9.26	17.11	15.79	17.14	12.50	12.50	17.24	14.29	10.52

Pseudomys fumeus	4.44	5.05	1.69	2.86	7.41	17.11	2.63	14.29	6.25	6.25	3.45	7.14	6.90
Pseudomys gouldii		4.04	1.69	5.71	11.11	5.26	2.63	2.86	10.42	2.08	3.45		4.48
Pseudomys novaehollandiae		1.01	1.69										0.34
Pseudomys shortridgei	2.22	4.04	3.39	8.57	5.56	3.95	10.53	5.71	2.08	10.42	10.34		5.34
Pseudomys Total	22.22	35.35	18.64	28.57	53.70	69.74	52.63	77.14	43.75	45.83	55.17	5	45.00
Rattus	4.44	1.01	1.69	2.86									0.86
Muridae Total	48.89	53.54	45.76	45.71	72.22	80.26	65.79	94.29	52.08	58.33	62.07	71.43	61.55
Isoodon obesulus				2.86						2.08			0.34
Perameles bougainville	4.44	2.02	3.39	2.86		1.32			2.08	4.17	3.45	7.14	2.24
Perameles gunnii	2.22	5.05	3.39		3.70	2.63	15.79		8.33	6.25	6.90		4.66
Peremeles Total	6.67	7.07	6.78	2.86	3.70	3.95	15.79		10.42	10.42	10.34	7.14	6.90
Peramelidae Total	11.11	10.10	10.17	8.57	3.70	5.26	15.79		12.50	16.67	10.34	7.14	9.31
Petaurus breviceps	4.44			5.71									0.69
Petaurus norfolcensis	4.44												0.34
Petaurus Total	8.89			5.71									1.03
Trichosurus vulpecula	2.22	1.01	5.08		1.85								1.03
Bettongia gaimardi	2.22	2.02										7.14	0.69
Bettongia lesueur											3.45		0.17
<i>Bettongia</i> Total	2.22	3.03									3.45	7.14	1.03
Potorous tridactylus			1.69						2.08				0.34
Potoroidae Total	2.22	3.03	5.08						2.08		3.45	7.14	1.72
Pseudocheirus peregrinus		1.01	3.39	2.86									0.69
Vombatidae	2.22												0.17

Table 4: All distribution values refer to species presence or absence in the South East region of South Australia. Modern refers to the species being present there today; Former refers to the species having no modern presence there, but having been recorded there post-Europeansettlement; and Fossil refers to the species only having fossil evidence to show its presence in this region. Distribution data are sourced from *The Mammals of Australia* (2008). Habitat key is as follows: A = All or a wide range of habitats, B = Shrublands, C = Scrub, D = Sedgelands, E = Eucalypt, F = Forest, G = Grassland, H = Heathland, L = Swampland, M = Mallee, P = Alpine Heath, R = Rainforest, S = Sclerophyll and W = Woodland.

Family	Species	Habitat	Distribution
Acrobatidae	Acrobates pygmaeus	Tall F, W	Modern
Durromuidoo	Cercartetus lepidus	M, H, W, wet E	Modern
Burrannyndae	Cercartetus nanus	R, S, tree H	Modern
	Antechinus agilis	F, W, H	Modern
	Antechinus flavipes	A	Modern
	Dasyurus maculatus	Treed habitats, including S, W, C, H	Former
	Dasyurus viverrinus	A, prefers open F, W, open G, P	Former
Dasyuridae	Ningaui yvonneae	Open M, low H, low M C, sandy plains	Modern
	Phascogale calura	Tall trees with dense foliage	Former
	Phascogale tapoatafa	Tall trees, dry S, W	Modern
	Sminthopsis crassicaudata	Open W, low B with suitable plants	Modern
	Sminthopsis murina	W, open F, H, transitional zone to R	Modern
	Conilurus albipes	E open F	Former
Muridae	Mastacomys fuscus	P, sub-P, wet S F, wet D	Fossil
	Notomys mitchellii	Semiarid M with adequate food	Modern

	Pseudomys apodemoides	Dry M H	Modern
	Pseudomys auritus	Open H, dense M, open C	Fossil
	Pseudomys australis	A	Former
	Pseudomys fumeus	A with adequate food	Fossil
	Pseudomys gouldii	Plains and sandy hills	Former
	Pseudomys novaehollandiae	Coastal H, W, open F, paperbark L	Fossil
	Pseudomys shortridgei	Dry H, stringybark open F with H	Modern
	Isoodon obesulus	F, W, B, H	Modern
Peramelidae	Perameles bougainville	Dense C to border of C	Former
	Perameles gunnii	A, prefers open G	Former
Determidee	Petaurus breviceps	Open F	Modern
Petauridae	Petaurus norfolcensis	W and open F	Modern
Phalangeridae	Trichosurus vulpecula	Most trees, prefers F and W	Modern
	Bettongia gaimardi	Open dry F with H or G understorey	Former
Potoroidae	Bettongia lesueur	A except dense vegetation/high rain	Former
	Potorous tridactylus	>60 mm annual rainfall, coastal H, S	Fossil
Pseudocheiridae	Pseudocheirus peregrinus	A with trees	Modern

Of the 32 species present in the grid square, 17 were found to still be present in the South East region of South Australia, as shown in Table 4 along with habitat information, all according to *The Mammals of Australia* (2008). Ten other species had distributions in that area after European settlement of the region, but not in the modern day, and five species were extinct prior to settlement and are only known in the outlined region from fossil sites (*The Mammals of Australia*, 2008).

TAPHONOMIC ANALYSIS RESULTS

A total of 31.57% of identified specimens showed evidence of corrosion. This varied widely across the different layers and species, from 2.7 to 100% of the identified elements of species; and 13.46 to 52.69% of the identified elements within layers, as shown in Table 5.

It should be noted that corrosion was documented as a presence or absence data point for each group of identified elements of a given identification for each bag of material within each layer of the excavation. Therefore, the corrosion percentage here will not align directly with the number of individual identified bones which show corrosion.

Corroded Specimens	1	2	3	4	5	6	7	8	9	10	11	12	Species Total Percent
Antechinus agilis				0/1					1/3	0/1			20.00
Dasyurus viverrinus	0/4	0/7	0/6				0/2		1/3	0/2	1/1	0/1	7.69
Dasyurid Total	0/17	0/31	0/13	0/7	0/9	0/12	1/9	1/1	1/19	0/18	1/6	0/2	2.70
Conilurus albipes	0/2	2/7	1/4	0/1		1/1				0/2			23.53
Mastacomys		1/1			0/1	1/2	0/1	1/1	1/3				44.44
fuscus													
Notomys	1/2		0/1		2/3			0/2		1/3	0/1	0/2	28.57
mitchellii	0/4	2/0	1/4	0/2	0/6	1 /7	0/1	0/4	0/5	0/5	0/4	0/2	0.62
Pseudomys	0/4	5/9	1/4	0/3	0/0	1//	0/1	0/4	0/3	0/3	0/4	0/2	9.02
Pseudomys		1/4			2/3	6/8	2/5	2/6	0/1	1/4	2/4	0/2	43.24
auritus					2.0	0, 0	2.0		0,1	17.		0.1	
Pseudomys	1/1	2/8	1/2	1/1	2/3	8/11	0/5	1/5	2/5	4/7	2/5	0/3	42.86
australis													
Pseudomys	1/2	2/4	1/1	0/1	2/2	8/10	2/2	2/5	4/4	3/3	0/1	0/1	69.44
fumeus	_			0.12	0.12	0/4	0.12	0.12	2/7	0/1	1 /1		26.26
Pseudomys				0/2	2/3	2/4	0/2	0/2	3/1	0/1	1/1		36.36
Pseudomys	0/1	1/4	0/2	1/2	3/3	3/4	0/2	2/2	0/1	4/6	3/3		56.67
shortridgei	0/1	1/-1	0/2	1/2	515	5/1	0/2	212	0/1	1/0	515		50.07
Pseudomys Total	2/8	9/30	18/25	0/7	9/17	26/41	4/18	7/24	9/32	12/26	8/18	0/8	40.94
Muridae total	12/31	34/84	18/41	7/28	27/41	46/73	12/30	16/41	20/42	25/48	18/33	7/22	47.08
Perameles	0/1	0/2	0/1	0/1					0/1	1/4	1/1	0/1	16.67
bougainville													
Perameles gunnii	0/1	0/4	0/1		0/2	2/2	0/3		2/6	0/5	1/5		17.24
Peremeles Total	0/2	0/6	0/4	0/1		2/2	0/3		2/9	1/9	2/6	0/1	16.28
Peramelidae Total	0/5	0/12	0/4	0/4	0/2	3/5	0/4		2/11	2/11	2/7	1/2	14.93
Vombatidae	1/1												100.00
Laver Total	21.67	23.13	24.00	13.46	45 76	52 69	28.26	39 53	30.26	32 53	40.38	28 57	31 57
Percentage	21.07	23.13	27.00	15.40	-13.70	52.07	20.20	57.55	50.20	52.55	10.20	20.57	01.07

Table 5: Table of corroded elements, given in fractions for main data and percentages for column and row totals. Only rows for species with corrosion are shown, as well as appropriate genus and family totals. Layer Total Percentage is for all species within that layer, not just the ones shown. This includes the combined Layer Total Percentage (bottom-right corner).

Manganese staining was observed in reasonably low amounts across the entirety of this deposit. There is a trend of increased manganese staining, starting in Layer 8, more prominent in Layers 7 to 5, and then almost gone in Layer 4. In broad terms, there seems to be less staining in the more recent layers than those before them, which is shown in Figure 5.



Figure 5: Degree of manganese staining on the percentage of elements within each layer.



Figure 6: Graph of the number of each type of fracture observed for all identified specimens from this study. Fracture types 1 to 7 refer to Figure 2. Note that 1 is the absence of fracturing.

The fracturing of identified material within this grid square varied somewhat by species, and of course if it was referring to mandibles or maxillae. Generally, as shown in Figure 6, the fracturing results show that longer bones became fractured, such as Peramelidae mandibles. Smaller mandibles were more likely to be intact, such as Muridae or smaller Dasyurids. Skulls always broke apart, and often the zygomatic arch broke off of maxillae, except in Muridae, where it usually remained attached. There were only 8 instances of hairline fracturing.

DISCUSSION

FAUNA

Given that the majority of species and individuals in the deposit were of a small size, with 31.6% percent of the identified elements showing corrosion, and with 61.56% of the mammals in the deposit being Muridae, within which 47.08% of elements showed corrosion damage; this strongly suggests that the deposit was formed by the accumulation of owl pellets, as expected from prior research (Macken & Reed, 2013). This is supported by the observation that many of the Peramelidae and *Dasyurus viverrinus* individuals were juveniles, as these would more appropriately fit the prey size for the largest owl species in the region that is known to live in caves, the Masked Owl; *Tyto novaehollandiae* (E. H. Reed, personal communication, 2018). Additional supporting evidence for this is that there are only three identified specimens which show corrosion from an individual larger than Peramelidae; one being on a Vombatidae fibula, one on a *Dasyurus viverrinus* right maxilla and lastly, a *Dasyurus viverrinus* left premaxilla. This

suggests that the larger species found within the deposit most likely fell in, rather than being brought in by owls, and the three instances of corrosion noted were simply caused by alternate means other than ingestion, such as drip water within the cave. Due to the lack of observed corrosion on *D. viverrinus* individuals, it may be possible that many fell into the cave as juveniles, due to being less aware of caves.

Further evidence for both owl pellet and pitfall, though primarily owl pellet, accumulation modes for the cave is the fact that some specimens, such as the two of *Macropus* sp. found in this grid square would have been too large for an owl to have brought into the cave.

Interestingly, many of the specimens of the now-extinct *Conilurus albipes* (*The Mammals of Australia*, 2008) did not show any evidence of corrosion, as shown in Table 5. Only *Pseudomys apodemoides* and *Pseudomys novaehollandiae* had lower percentages of corrosion than *C. albipes*, and they are of a much smaller size, and so less readily display corrosion from ingestion. Therefore, it may be that many of the *C. albipes* individuals fell into the cave, as opposed to being brought in by owls.

When *Conilurus albipes* was extant, being last recorded between 1860 and 1862, it was noted that it was not very abundant (*The Mammals of Australia*, 2008). This is, to an extent, contradicted by the fossil record, which shows a higher MNI of *C. albipes* in layers 2 and 3 than any of the lower layers, which is implies that it was not already rare or going extinct, even in Layer 1, which was 946 median Cal yr BP (Grealy et al., 2016; E. H. Reed, personal communication, 2018). It is possible that factors after this, but

prior to European settlement, caused this species to become less abundant, or that the uppermost layers of this deposit were somehow skewed.

It does, however, seem fitting that with European settlement of the regions inhabited by *Conilurus albipes*, land clearing for agriculture followed, resulting in a loss of shelter for the species, as it was described as using low hollows or hollow logs for sleeping and nesting (*The Mammals of Australia*, 2008). Such locations may also have been vulnerable to introduced predators such as foxes, as they were noted as having caused localised extinctions of *Dasyurus viverrinus* across Australia (*The Mammals of Australia*, 2008).

The other now-extinct species that have been found in the entrance chamber are *Potorous platyops, Pseudomys auritus* and *Pseudomys gouldii* (Macken & Reed, 2013; *The Mammals of Australia*, 2008). Interestingly, both *Pseudomys auritis* and *Pseudomys gouldii* occur in Layer 2 of this deposit, but not Layer 1. This alone is not enough to confirm that these species are extinct at this time, given the inconsistency of their appearance in this record, as shown in Table 2, especially with *P. gouldii. Pseudomys auritus*, however, does seem to become less frequent in the uppermost layers than in the lower ones, but again, this is not enough evidence to base assumptions of extinction dates on. It may also be possible that competition from introduced species, as opposed to predation, may have caused some extinction. Without further research, it would seem most likely that these two species went extinct for the same reason as each other; introduced predators, with the same reasoning as previously mentioned to have occurred with *Dasyurus viverrinus (The Mammals of Australia*, 2008).

Despite several species of bat being present in the region (NatureMaps, 2018), only *Miniopterus orianae bassanii*, the Southern Bent Wing Bat, was present in the fossil record of this cave. This suggests that the bats were not present in the deposit due to predation, as if this was the case, it would be expected that other species of bat would appear at least once in the excavation, which is not the case. Additionally, no corrosion was observed on any *M. orianae bassanii* specimen, though this is not especially surprisingly, as the identified mandible and maxillae material from this species are all very small, and therefore are not ideal bones to indicate corrosion. The evidence for *M. orianae bassanii* living in the cave aligns with modern observations of some individuals of using the entrance chamber of this cave as a wintering site (E. H. Reed, personal communication, 2018). This suggests that the usage of the Entrance Chamber of the cave has been consistent, at least in terms of presence or absence of the species, throughout the timeframe of the excavation.

TAPHONOMY

As mentioned, there is a significant amount of corroded material that was identified in this study, as shown in Table 5. This being the cause of owl predation is supported by the fracturing.

Firstly, the breakage types one to seven, as shown in Figure 2 and Figure 6. As would be expected of an owl deposit, larger bones and skulls are damaged and smaller ones are left intact. Besides the Muridae, where the large numbers of type 5 breakages are referring to the identified maxillae, they are quite well preserved, which is reflected in the high numbers of intact material compared to the fractured material. Dasyuridae, which is mostly composed of small species, also shows this pattern. When discounting

less common species, which can have all their elements fractured due to only appearing once or twice, Peramelidae were the most heavily fractured. Being of the largest size range that would likely be prey for any owl in the cave, this is fitting as fracturing representative of predation, especially the heavy damage inflicted in the skulls (Lloveras et al. 2008). Especially in the case of the fracturing of the Peramelidae mandibles, when other, slightly larger mandibles, such as *Dasyurus viverrinus* are entirely unbroken.

Hairline fractures were the other type of fracture graphed in Figure 6. Both hairline fractures and manganese staining are differing signs of a wet environment. Wet caves will more extensively stain manganese into bone material (López-González, et al., 2006), whereas wetting and drying repeatedly can cause hairline fractures in bone.

As shown in Figure 6; there were only eight noted instances of hairline fractures in the identified material, which, combined with the manganese staining results, suggests that the cave was always relatively dry, matching the modern environment within the cave.

The lack of many hairline fractures indicates that the cave has always had stable moisture content, not wet and dry periods. Wet conditions would have resulted in much more extensive manganese staining on bones (López-González, et al., 2006), which was not observed in this deposit, as shown in the manganese results in Figure 5. The dryness within the cave today and in the past explains the high levels of preservation of organic matter within the cave, and given that this material did preserve, the fact that the cave has always been relatively dry is not surprising.

The manganese staining also indicates that the cave was comparatively wetter in the middle layers of the deposit; primarily in Layers 6 to 8, as these layers show greater amounts of manganese staining. Layer 5 is similarly stronger in manganese staining, but

to a lesser degree. Interestingly, this may suggest that when the ratio of Anura and Mammalia changes, as shown in Figure 4, this is the result of a dryer climate.

FAUNAL ASSEMBLAGES

The accumulation mode of the cave may impact the accuracy of comparisons between the faunal assemblage of the cave, and the modern faunal assemblage. The steps taken with the modern faunal data in order to minimise any inaccuracies with comparison are outlined in the method.

In the instance of the comparison between the entrance chambers of Wet Cave and Robertson Cave, presence/absence data are used instead of abundance or count data.

The Wet Cave results in Table 1 show that there is no statistically significant difference between the entrance chambers of these two caves. This is unsurprising, given presenceabsence data was all that was used, and there were only two differences between these datasets, these being the presence of *Dasyurus maculatus* in Robertson Cave and not Wet Cave, and *Hydromys chrysogaster* in Wet Cave and not Robertson Cave (Macken & Reed, 2013). Relative abundance data and perhaps even correlating layers of equal age would be required to further compare and contrast these caves. However, given the data available, and that the caves have an overlapping timeframe, these faunal assemblages are likely to be quite similar between the two caves even when further data is available. This suggests that both caves were formed by the same accumulation method, which was determined to be owl pellets, in previous work on Wet Cave, aligning with the findings of this study, and the past study on the entrance chamber of Robertson Cave (Macken & Reed, 2013; E. H. Reed, personal communication, 2018).

The most unexpected observation was the trend shown in Figure 4; the change in the ratio of Anura to Muridae/Mammalia. As can be seen presently in caves in Naracoorte; Anura enter the caves frequently, without being brought into caves through owl predation. This means that this pattern is more complex than it may at first seem. It is unlikely to be a shift in predation, especially given that many of the Anura bones found would have been from species which are much smaller than the smallest mammalian species (The Mammals of Australia, 2008). An alternative likely explanation, supported by the manganese evidence as discussed, is that there was a shift in climate, resulting in fewer mammalian species in the environment, and more Anura. When accounting for the likely discontinuity between Layers 4 and 5, given the nearly 8000 year gap between the dates for each layer, then it can be said that any major climate event occurring during this time window had the potential to cause the faunal change. Some difficulty is inherent in the overlapping dates for Layers 2 and 3, as this means that it cannot be ascertained with certainty when the influencing factor on the fauna changed back, if it even did. Additionally, bracken makes its first observed appearance in Layer 4. These factors combined make it difficult to determine exactly what happened, as no start date or finish date for this is defined, and the presence of bracken may just be due to its preservation in the record. The continued elevated levels of Anura in Layer 2, before returning to the same number as before in Layer 1 aligns with the mixing of Layers 2 and 3 shown in the dates for the cave.

ENSO events have, for other species, caused extinction events; however, these events occurred from approximately 5-3ka (Brünche-Olsen, Jones, Burridge, & Murchison,

2018), which only covers some of the dates from within the layers showing this pattern. The end date of ~3ka does fit well with the end of the observed pattern here, which, depending on the mixing between the dates of Layers 2 and 3, may match in time. With the current data, it does seem most likely that this type of climactic event was the cause, as ENSO patterns did occur in a similar timeframe (White, Ravelo, & Polissar, 2017; Brünche-Olsen et al., 2018).

ECOLOGY

The palaeoecology of the region, in both terms of fauna (and indirectly, flora) can be inferred using the relative abundance of species and their habitats.

The relative abundance of each species in relation to each other in the deposit is vital for giving a better idea of what the faunal ecology of the area was like. The only caveat in this instance is that the true relative abundances have been filtered through the cave and its accumulation method.

Bearing this in mind, a strong representation for Muridae and other small mammals can be expected, which is the case. Table 3 shows that 61.55% of all the fauna in the cave is from Muridae, followed by the 16.55% of the Dasyurid total, which is mostly small mammals, too. Dasyurids are carnivorous, many of the smaller species insectivorous. Murids are typically herbivorous. Given the larger two species of dasyurids, *Dasyurus maculatus* and *Dasyurus viverrinis*, both being present, this means that there was a sufficient amount of prey for these species, which most likely preyed on the Murids as did the owls. Peramelidae are typically omnivorous but primarily insectivorous, similar to the Dasyurids, a fact that is also true for the *Petaurus* in the deposit.

Having a number of different insectivorous animals in the deposit is not surprising, as there were in fact many insect casings found within the uppermost layers of the deposit, where they were still preserved.

The largest species in the deposit are underrepresented, due to likely only being in the cave as a result of falling in, and so little can be said about the abundances of these relative to the other species, other than, typical of larger species, they are less abundant than their smaller counterparts.

Excluding the previously discussed Dasyurids, all the larger species (*Trichosurus vulpecula*, *Bettongia gaimardi*, *Bettongia lesueur*, *Potorous tridactylus*, *Pseudocheirus peregrinus*, *Macropus* and Vombaditae are herbivorous (*The Mammals of Australia*, 2008).

Overall, this shows a fauna that is composed largely of small herbivores and insectivores, with larger herbivores and only two larger carnivores. This is typical of the modern Australian fauna, although larger predatory species were extant during the older parts of the deposit (Brünche-Olsen et al., 2018; *The Mammals of Australia*, 2008).

Using Table 4, the most likely combination of habitats surrounding the cave can be determined. As it can be confirmed that the largest species in the cave were not brought in by owls, this information can use this to determine the environment directly around the cave entrance by looking at the habitats of these species. Of the specimens identified

to species level, the ones which would have definitely had to fall into the cave are *Dasyurus maculatus, Trichosurus vulpecula, Bettongia gaimardi, Potorous tridactylus, Pseudocheirus peregrinus* and perhaps *Dasyurus viverrinus* and *Bettongia lesueur*. A habitat of open, dry sclerophyll forest suits all of these species (*The Mammals of Australia*, 2008), meaning that this is by far the most likely habitat for the entrance of the cave during the timeframe the deposit was accumulating.

As for species small enough to be brought into the cave through predation by owls, many of these live in woodland habitats, specifically; *Acrobates pygmaeus*, *Cercartetus lepidus*, *Cercartetus nanus*, *Antechinus agilis*, *Antechinus flavipes*, *Sminthopsis crassicaudata*, *Sminthopsis murina*, *Pseudomys australis*, *Pseudomys fumeus*, *Pseudomys novaehollandiae*, *Isoodon obesulus*, *Perameles gunnii*, and *Petaurus norfolcensis* (*The Mammals of Australia*, 2008). Of these, *C. nanus*, *A.agilis*, *A. flavipes*, *P. australis*, *P. fumeus*, *P. gunnii* and *P. norfolcensis* may also have the habitat of open dry sclerophyll forest (*The Mammals of Australia*, 2008), as with the larger species, adding further evidence that this was the environment surrounding the cave entrance.

Of the remaining species, *Phascogale calura*, *Phascogale tapoatafa*, *Conilurus albipes*, *Pseudomys shortridgei*, and *Petaurus breviceps* may all also inhabit an open, dry sclerophyll forest (*The Mammals of Australia*, 2008), which provides further evidence that this was the environment surrounding the entrance of the cave, perhaps for quite a significant portion of the 50 km hunting range of an owl.

Open dry mallee heathland is another habitat that would be potential habitat for *Ningaui yvonneae*, *Notomys mitchellii*, *Pseudomys apodemoides*, and *Pseudomys auritus* which

do not fit any previously mentioned habitat, which also suits *C. lepidus*, *A. agilis*, *A. flavipes*, *D. maculatus*, *D. viverrinus S. murina*, *P. australis*, *P. fumeus*, *P. shortridgei*, *I. obesulus*, *P. gunnii* and *B. lesueur* (*The Mammals of Australia*, 2008). This habitat combination being around the cave entrance is strongly supported by this overlap of species in these habitats.

Mastacomys fuscus is said to inhabit wet sclerophyll forest (*The Mammals of Australia*, 2008), and so potentially lived in this exact condition in the past, or perhaps formerly lived in dry sclerophyll forests as well. Therefore, either *M. fuscus* could also live in the environment around the cave entrance, or there was wet sclerophyll forest within 50 km of the cave, and either of these could be possible.

Similarly, *Perameles bougainville* lives in dense scrub, to border of scrub. Either this habitat range was more extensive in the past, or it scrub was one of the habitats that was within range of the cave.

Lastly, *Pseudomys gouldii* lives exclusively in plains and sandy hills (*The Mammals of Australia*, 2008); it can be assumed that it was living in the Pleistocene dune sand hills around Naracoorte (Forbes & Bestland, 2007).

The downside of using modern habitats to determine past ones is that over long timescales, or due to habitat restrictions, the habitats of a species can change. This analysis assumes largely that the habitats have not changed, but luckily, in this instance, there is little required speculation, as the findings here fit strongly with each other to give an indication of what the region was like in the past.

CONCLUSIONS

The Robertson Cave fauna is both very similar to that of Wet Cave, and more diverse than the modern equivalent, yet ecologically seems very similar, at least given what is represented in the deposit. The species which have gone extinct (either locally or entirely) most likely did so due introduced predators or competition as a result of European settlement. The entrance of the cave was likely in an open, dry sclerophyll forest, with an adjacent or nearby habitat of open dry mallee heathland, perhaps with nearby wet sclerophyll forest and or scrublands.

The entrance chamber of the cave was likely used in the past, as it is today, as a wintering site for *Miniopterus orianae bassanii*, and may have been in a slightly wetter climate during the middle of the accumulation of this excavated record.

This deposit is primarily derived from owl pellets from *Tyto novaehollandiae*, with the exception of some of the larger species found in the deposit.

Robertson Cave yields a well-preserved and, in the context of the Naracoorte Caves, a

uniquely informative fossil deposit, which strongly warrants further research.

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REFERENCES

- BRÜNICHE-OLSEN, A., JONES, M. E., BURRIDGE, C. P., MURCHISON, E. P. (2018). Ancient DNA tracks the mainland extinction and island survival of the Tasmanian devil. *Journal of Biogeography*, *45*, 963-976.
- FORBES, M., & BESTLAND, E. (2007). Origin of the sedimentary deposits of the Naracoorte Caves, South Australia. *Geomorphology*, *86*, 369-392.
- FORBES, M. S., BESTLAND, E. A., WELLS, R. T., & KRULL, E. S. (2007). Palaeoenvironmental reconstruction of the Late Pleistocene to Early Holocene Robertson Cave sedimentary deposit, Naracoorte, South Australia. *Australian Journal of Earth Sciences*, 54, 1-19.
- FOX, J., & BOUCHET-VALAT, M. (2018) Rcmdr: R Commander (Version 2.5-1) [Computer software: R package]. Retrieved from https://cran.r-project.org/web/packages/Rcmdr/index.html
- GREALY, A., MACKEN, A C., ALLENTOFT, M., RAWLENCE, N., REED, E. H., & BUNCE, M. (2016). An assessment of ancient DNA preservation in Holocene-Pleistocene fossil bone excavated from the world heritage Naracoorte Caves, South Australia. *Journal of Quaternary Science*, *31*, 33-45.
- LLOVERAS, L., MORENO-GARCIA, M., & NADAL, J. (2008). Taphonomic study of leporid remains accumulated by the Spanish Imperial Eagle (*Aquila adalberti*). *Geobios*, 41, 91-100.
- LÓPEZ-GONZÁLEZ, F., GRANDAL-D'ANGLADE, A., & VIDAL-ROMANI, J. R. (2006). Deciphering bone depositional sequences in caves through the study of manganese coatings. *Journal of Archaelogical Science*, 33, 707-717.
- MACKEN, A. C., PRIDEAUX, G. J., & REED, E. H. (2012). Variation and pattern in the responses of mammal faunas to Late Pleistocene climatic change in southeastern South Australia. *Journal of Quaternary Science*, *27*, 415-424.
- MACKEN, A. C., MCDOWELL, M. C., BARTHOLOMEUSZ, D. N., & 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., & 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.
- McDowell, M. C. 2001). The analysis of late Quaternary fossil mammal faunas from Robertson Cave (5U17, 18, 19) & Wet Cave (5U10, 11) in the Naracoorte world heritage area, South Australia. (Unpublished master's thesis). University of Adelaide, Adelaide, SA.
- MORIARTY, K. C., MCCULLOCH, M. T., WELLS, R. T., & MCDOWELL, M. C. (2000). Mid-Pleistocene cave fills, megafaunal remains and climate change at Naracoorte, South Australia: towards a predictive model using U-Th dating of speleothems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 159, 113-143.
- The Mammals of Australia (2008). (S. van Dyck & R. Strahan Eds. 3 ed.). Sydney: Reed New Holland.
- NatureMaps (Version 3.0) (2018) [Online only software]. Retrieved from http://spatialwebapps.environment.sa.gov.au/naturemaps/?locale=en-us&viewer=naturemaps
- OKSANEN, J., BLANCHET, F. G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., ... WAGNER, H. (2018) Vegan: Community Ecology Package (Version 2.5-2) [Computer software: R package]. Retrieved from: https://cran.r-project.org/web/packages/vegan/index.html

- PRIDEAUX, G. J., ROBERTS, R. G., MEGIRIAN, D., WESTAWAY, K., HELLSTROM, J., & OLLEY, J. (2007). Mammalian responses to Pleistocene climate change in southeastern Australia. *Geology*, 35, 33-36.
- R: A language and environment for statistical computing (Version 3.5.1) (2013) [Computer software]. Retrieved from http://www.R-project.org
- REED, E. H., & BOURNE, S. J. (2000). Pleistocene fossil vertebrate sites of the South-East region of South Australia. *Transactions of the Royal Society of South Australia*, 124, 61-90.
- REED, E. H., & BOURNE, S. J. (2009). Pleistocene fossil vertebrate sites of the South-East region of South Australia II. *Transactions of the Royal Society of South Australia*, 133, 30-40.
- REED, E. H. (2012). Of mice and megafauna: new insights into Naracoorte's fossil deposits. *Journal of the Australasian Cave and Karst Management Association*, 86, 7-14.
- WHITE, S. M., RAVELO, A. C., POLISSAR, P. J. (2017). Dampened El Niño in the early and mid-Holocene due to insolation-forced warming/deepening of the thermocline. *Geophysical Research Letters*, 45, 316-326.

APPENDIX A: ROBERTSON CAVE ENTRANCE CHAMBER CARBON DATES

Tables of carbon dates and associated information for the study site: the entrance chamber of Robertson Cave (E. H. Reed, personal communication, 2018).

Sample	Excavation	S-ANU#	other	d13C	±	Percent	±	14C	±
name	layer		ID			Modern		age	
						Carbon			
						(pMC)			
RCC5U17-	1	27618	7796	-24.7432	0.608	87.373	0.214	1085	30
1CDL1									
RCC5U17-	2	27619	7797	-23.6277	0.383	73.332	0.177	2490	30
1CDL2									
RCB5U17-	2	27632	7812	-22.2624	0.349	52.783	0.192	5135	40
1CDL2						64.046	0.100		
RCB5U17-	3	27633	7813	-16.7731	0.238	64.046	0.198	3580	35
ICDL3	2	27625	7022	15 7952	0.120	(2 000	0.105	2600	25
ICDI 3	3	2/033	/823	-13./832	0.129	03.888	0.195	3000	33
Dunlicate									
RCC5U17-	3	27620	7798	-24 048	0 567	39.067	0.129	7550	35
1CDL3	5	21020	1150	21.010	0.207	59.007	0.129	1000	55
RCC5U17-	4	27637	7930	-24.2773	0.275	32.187	0.111	9105	40
1CDL4									
RCC5U17-	5	27621	7800	-24.3256	0.612	15.77	0.087	14840	55
1CDL5									
RCC5U17-	6	27623	7801	-31.2762	0.447	15.004	0.081	15235	55
1CDL6									
RCC5U17-	7	27819	7931	-32.1886	1.198	10.984	6.72E-02	17740	55
ICDL7-r	0	27(24	7902	24 (952	0.215	10.5(5	0.0(7	10055	(0)
1CDL 9	8	27624	/803	-24.6852	0.315	10.565	0.06/	18055	60
RCC5U17-	9	27625	7804	_25 501	0.409	9.639	0.064	18700	65
1CDL9	,	27025	7004	-23.371	0.407	7.057	0.004	10770	05
RCC5U17-	10	27626	7805	-21.1276	0.414	8.42	0.061	19880	70
1CDL10					-	-			
RCC5U17-	11	27627	7806	-27.0207	0.42	8.705	0.064	19610	60
1CDL11									
RCC5U17-	12	27629	7807	-25.5249	0.346	8.283	0.071	20010	80
1CDL12									
RCC5U17-	12	27630	7808	-21.9797	0.594	8.223	0.065	20070	70
1CDL12									
Duplicate									

Sample	Unmodelled (cal yr BP)		Confidence			
name			2 sigma			
	from	to	%	median (Cal yr BP)	Calibration curve	material
RCC5U17-	1054	906	95.4	946	SHCal13	charcoal
1CDL1						
RCC5U17-	2705	2358	95.3	2520	SHCal13	charcoal
1CDL2						
RCB5U17-	5926	5731	95.4	5819	SHCal13	bone
1CDL2						
RCB5U17-	3958	3697	95.4	3819	SHCal13	bone
ICDL3						
RCB5U17-	3971	3718	95.4	3852	SHCal13	bone
ICDL3						
Duplicate						
RCC5U17-	8398	8202	95.4	8337	SHCal13	charcoal
1CDL3						
RCC5U17-	10366	10165	95.4	10224	SHCal13	charcoal
1CDL4						
RCC5U17-	18200	17820	95.4	18000	SHCal13	charcoal
1CDL5						
RCC5U17-	18629	18294	95.4	18462	SHCal13	charcoal
1CDL6						
RCC5U17-	21682	21153	95.4	21419	SHCal13	charcoal
ICDL7-r						
RCC5U17-	22038	21584	95.4	21819	SHCal13	charcoal
1CDL8						
RCC5U17-	22831	22421	95.4	22594	SHCal13	charcoal
1CDL9						
RCC5U17-	24114	23625	95.4	23878	SHCal13	charcoal
1CDL10						
RCC5U17-	23840	23318	95.4	23576	SHCal13	charcoal
1CDL11						
RCC5U17-	24282	23774	95.4	24026	SHCal13	charcoal
1CDL12						
RCC5U17-	24323	23863	95.4	24090	SHCal13	charcoal
1CDL12						
Duplicate						

APPENDIX B: ROBERTSON CAVE ENTRANCE CHAMBER NISP AND PRESERVED MATERIAL DATA

Table showing the presence or absence data for varying organic materials found across the deposit, as well as the NISP values for each family from the deposit, with a total.

Data	Itom/Fomily	Layer											
Туре	item/Family	1	2	3	4	5	6	7	8	9	10	11	12
	Insects	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	Y	Ν
Presence	Bracken	Y	Y	Y	Y	Ν	Ν	Ν	Ν	Ν	Ν	Ν	Ν
	Leaves	Y	Y	Y	Y	Y	Y	Y	Y	Y	Ν	Y	Y
	Seed Pods	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Snail Shells	Y	Y	Y	Y	Y	Ν	N	Ν	Ν	N	Ν	Ν
	Agamidae	5	8	2	0	3	1	0	0	0	1	0	0
NISP	Anura (Illia)	31	67	112	119	29	4	4	2	0	0	2	1
	Aves	8	23	12	12	11	26	10	36	16	10	2	10
	Elapidae	33	50	34	39	9	6	6	2	3	0	0	0
	Other Reptilia	4	3	1	0	0	0	2	1	0	1	0	0
	Scinidae	2	4	4	0	2	10	1	5	0	1	3	0
	Muridae	58	153	49	30	113	198	77	103	86	81	49	25
	Acrobatidae	0	0	0	0	0	2	0	0	0	0	0	0
	Burramyidae	1	3	2	5	3	2	2	5	1	7	2	1
	Dasyuridae	20	36	13	8	11	28	23	10	20	17	7	4
	Peramelidae	7	16	6	6	2	13	13	7	14	15	8	7
	Petauridae	4	0	1	3	0	0	0	0	0	0	0	0
	Phalangeridae	1	3	4	0	1	0	0	0	0	0	0	0
	Potoroidae	1	6	3	0	0	0	1	0	0	0	3	2
	Pseudocheiridae	0	1	1	1	0	0	0	0	0	0	0	0
	Miniopteridae	0	5	6	5	2	1	0	0	1	0	0	0
	Vombatidae	1	0	0	0	0	0	0	0	0	0	0	0
	Macropodidae	0	1	0	0	1	0	0	0	0	0	0	0
	Total	176	379	250	228	187	291	139	171	141	133	76	50