Fossil mammals of Caladenia Cave, northern Swan Coastal Plain, south-western Australia

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ABSTRACT – Quaternary palaeoecological research in Western Australia has been focussed primarily around Perth and the extreme south-west, with very little work conducted to the north between 29° and 32°S. Using fossil remains excavated in the 1970s from Caladenia Cave in the East Moore cave area of the northern Swan Coastal Plain, we sought evidence of compositional change in the regional mammal fauna from the mid-Holocene to the present. Loss of *Phascogale calura*, *Perameles bougainville* and *Lagorchestes hirsutus*, species characteristic of semi-arid and arid regions, suggests an increase in rainfall from around 4700 cal. BP. A change to a smaller sieve mesh aperture in the deepest levels of the excavation caused differential recovery which constrained the extent to which ecological inferences could be made. This bias notwithstanding, the Caladenia Cave assemblage suggests major community changes did not characterise the late Holocene, indicating resilience to the impacts of environmental changes prior to European settlement.

KEYWORDS: Holocene, Palaeoecology, Differential Recovery, EM-17

INTRODUCTION

Western Australian vertebrate palaeontology was focussed primarily on the documentation of megafaunal remains until the visit in the mid 1950s by American Fulbright Scholar Ernest L. Lundelius Jr, who initiated the palaeoecological investigation of small mammal assemblages (Lundelius 1957, 1960). Many Western Australian Quaternary cave deposits provide evidence of climatically-driven changes in Late Quaternary species distributions and abundances (Lundelius 1960; Merrilees 1967). Quantitative analyses of small mammal accumulations can provide a more accurate representation of the original communities surrounding a deposit than historical records (Baynes 1979; Lundelius 2006).

Previous studies in south-western Australia have interpreted patterns in climate change from presence/ absence and abundance of 'proxy' species over time (Baynes et al. 1976; Balme et al. 1978; Prideaux et al. 2010). Species such as *Perameles bougainville*, *Bettongia lesueur* and *Petrogale lateralis* are considered indicative of a drier, non-forest environment (Merrilees 1967), whereas *Setonix brachyurus* is considered a proxy for a dense understorey of tall karri forest that requires an annual rainfall of 1000–1200 mm (Baynes et al. 1976; Dortch 2004; Prideaux et al. 2010). These examples demonstrate that changes in climate can be inferred from change in the presence/absence of species characteristic of ecosystems adapted to higher or lower rainfall (see Dortch 2004).

There are very few early historic records of mammals of the northern Swan Coastal Plain, most of the native populations having been devastated by the introduction of cats, foxes and rabbits (see Kitchener et al. 1978 and Wilson et al. 2012). Consequently, fossil assemblages offer the best archives of fauna that originally occupied the region. The study of palaeontological assemblages can generate data that may help model the impacts that future anthropogenic climate change may have

on endemic fauna. Similar work in northern Western Australia and South Australia using Holocene cave sites has been used to extend species records for conservation research in national parks and suggested species rehabilitation sites based on palaeo-distributions (Baynes and McDowell 2010; McDowell et al. 2012). Our investigation of the Caladenia Cave fossil mammal assemblage in 2013 tracked the presence/absence and relative abundances of mammal species through time to detect correlations with extrinsic factors such as climate change. At conception, the investigation was purely exploratory and no hypothesis could be proposed about the presence of particular fauna, or any palaeoecological signals within the resulting data.

SITE

Caladenia Cave (EM-17) is located between the Moore River mouth at Guilderton and Gingin Scarp on the Swan Coastal Plain (Figure 1). It is one of 19 caves known in the East Moore cave area and the only cave excavated for vertebrate remains (Susac 2007). Caladenia Cave is an inclined fissure cave that developed in the Tamala Limestone, a Pleistocene aeolian calcarenite (Bastian 1964).

The discovery of vertebrate remains and their subsequent excavation in Caladenia Cave by amateur palaeontologist Robin Roe in the early 1970s provides the only existing late Quaternary record in the lower Moore River catchment. As Roe's trench was backfilled its precise location could not be determined. However, based on sketches in Roe's notebook (Roe 1971) we were able to determine its approximate location (Figures 2–3).

MATERIALS AND METHODS

SOURCING THE MATERIAL

The fieldwork and excavation conducted by Robin Roe (1970–1975) was initially supervised by Duncan Merrilees (1970–1972), Curator of Palaeontology at the Western Australian Museum, and later assisted by Sandra Sofoulis (1972 until completion). During excavation, Roe and Sofoulis noticed a deterioration of material condition at greater depths and changed the sieve grade to mitigate loss of small specimens (Roe 1974). They used sieves with 3 mm mesh aperture to sieve the sediment from the surface of the deposit down to the base of 'Stone Heap End' and the test pit. For 'Wall End' they changed to a sieve with a 1 mm mesh from 1.48 m to 2.54 m (Groups L to R). Rock and other materials not relevant to the investigation were removed by Roe after sieving. The screen residues were sorted and preliminarily identified by R. P. Hart, K. A. Lance, D. Merrilees and J. K. Porter in the 1970s. Bone specimens were placed in labelled 6 or 12 dram vials and stored by excavation spit. Bird, reptile, fish and archaeological materials were not further investigated in this study.
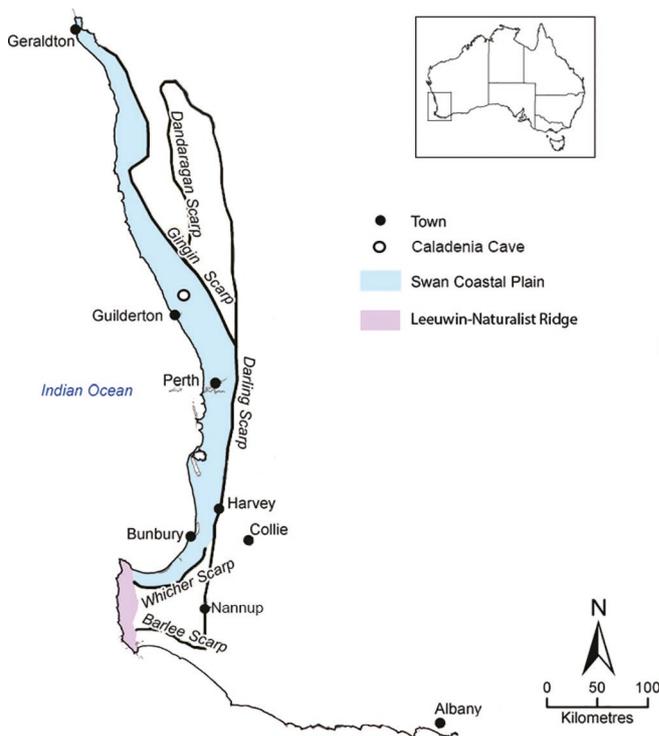
FIGURE 1   Map of the geomorphological features of the southern west coastal region of Australia, showing the location of Caladenia Cave. Image adapted from Barron et al. (2012).

Taphonomic analyses were based on the unidentified bulk-bone fragments, chosen randomly from each data Group (see Table 1) and examined for breakage and digestion damage. Evidence for digestion was recorded as an estimated percentage of the bone surface showing digestive erosion. Breakage was recorded as the percentage remaining of the original complete bone. Material was divided into two faunal size classes (mean adult body weight >250 g and <250 g) to ensure that sieve size bias could be removed from at least the larger species data set. The data were subjected to a Shapiro-Wilk test for normality within each size class. Paired *t*-tests were then conducted in PAST to determine if the two size classes were taphonomically different from one another.

Caladenia Cave was surveyed and mapped in 2013 at grade 44 of the Australian Speleological Federation survey and map standards (Anderson 1997), with width and height measurements recorded every 1 m along the N–S and E–W sections, accurate to the nearest 0.1 m.

CHRONOLOGY

Charcoal samples were collected from most spits, wrapped in foil, labelled and bagged by Roe at the time of excavation. In 2013 samples for dating were chosen based on significant fauna-related events, such as the disappearance of species from the assemblage, or at major stratigraphic boundaries, and at the base and close

to the surface of the deposit, to date the length of the period of accumulation. No charcoal was available above a depth of 700 mm and samples below 2230 mm were contaminated with disturbed material. The charcoal samples were removed from the foil, weighed on an electronic scale, placed in individual polythene bags, and designated a sample number to be sent to Waikato University Radiocarbon Dating Laboratory for dating (liquid scintillation counting).

Another of Roe's charcoal samples was added to resolve an inconsistency within the first group of dates. The small size of the charcoal sample meant that this had to be dated using accelerated mass spectrometry (AMS). Results are *Conventional Age* or *Percent Modern Carbon (pMC)*, following Stuiver and Polach (1977). All material dated from Caladenia Cave was calibrated with OxCal, using the SHCal13 Southern Hemisphere calibration curve (Bronk Ramsey 2009; Bronk Ramsey and Lee 2013; Hogg et al. 2013).

IDENTIFICATION OF MAMMALS

Species nomenclature follows Van Dyck and Strahan (2008) except for the Macropodidae and Rodentia for which taxonomy follows Prideaux and Warburton (2010) and Aplin (2006), respectively. Mammal remains were identified to the lowest taxonomic level possible using museum specimens and published descriptions for comparison. Attempts were made to distinguish between species of *Sminthopsis* using characteristics reported by Archer (1981) and Kitchener et al. (1984). Rodents were identified according to the characteristics reported in Appendix III of Baynes (1979) and his other unpublished notes.

Cranio-dental elements of all mammals were identified. Post-cranial bones (calcanei, humeri, ulnae, femora, scapulae and pelvic elements) of larger mammals (>250 g) were also identified, using the Western Australian Museum fossil reference collection.

FIGURE 2   Plan view of Caladenia Cave. Angles refer to the direction and slope of the floor. Dashed rectangle indicates the approximate position of Roe's trench.
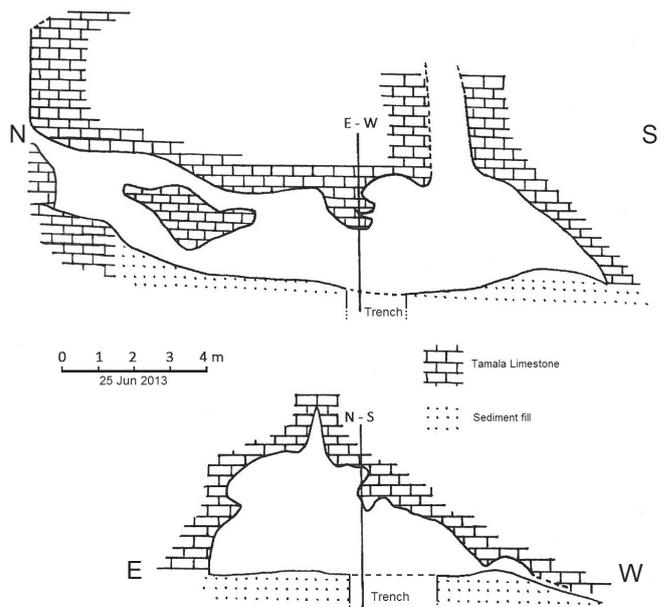
FIGURE 3   Longitudinal and transverse sections of Caladenia Cave. The north-south longitudinal section shows the entrance and edge of the doline on the left. The 'island' of limestone between the roof and floor of the cave is a collapsed part of roof and wall protruding into the section. The entrance slope is supported by large limestone boulders with unknown depths below the surface. The sections show the probable location of the trench inferred from Roe (1971). The protruding section of the ceiling visible in both diagrams is not speleothem development but where part of the ceiling has collapsed leaving an overhang.

TABLE 1   Designated data Groups used in statistical analyses, selected on the sieve size used and the sediment type recorded during excavation. In Groups A–C all spits were originally measured in inches before metric conversion. Surface was 270 mm below the datum. Depth measurements which overlap are due to stratigraphic dip and locations in the three named pit sections ('Stone heap end', test pit and 'Wall end'). The lime-flecked units are from the slumped stratigraphy, some of which was 'disturbed' and so measurements do not reflect the entire slump. The 3 mm sieve Groups I–K from 'Stone Heap End' and the test pit cover the depths also recorded in Groups L–R from 'Wall End'. Spits from 2100–2360 mm are disturbed samples and were excluded. 'Mixed-colour' sediments were not marked in Merrilees' section drawings, but were separated from other spits by Roe and so have been placed in a different Group.

Group	Sieve used	Top of unit (mm)	Base of unit (mm)	Stratigraphic unit	NISP
A	3 mm	270	524	Banded orange and brown sediments	728
B	3 mm	524	625.6	Banded orange and brown sediments	776
C	3 mm	625.6	752.6	Banded orange and brown sediments	737
D	3 mm	755	1050	Brown sediment (1)	672
E	3 mm	1045	1100	Dark brown sediment	537
F	3 mm	1100	1200	Brown sediment (2)	681
G	3 mm	1180	1510	Medium-grained orange sediment	1047
H	3 mm	1290	1340	Light brown bands	61
I	3 mm	1390	1560	Lime-flecked sediment	180
J	3 mm	1540	1980	Mixed colour sediment	227
K	3 mm	1635	2420	Brown sediment (3)	79
L	1 mm	1480	1600	Lime-flecked sediment	773
M	1 mm	1600	1660	Brown sediment (3)	680
N	1 mm	1660	1720	Brown sediment (3)	717
O	1 mm	1720	1840	Brown sediment (3)	767
P	1 mm	1840	1960	Brown sediment (3)	730
Q	1 mm	1960	2100	Brown sediment (3)	644
R	1 mm	2360	2500	Brown sediment (3)	413

TABLE 2   Radiocarbon dates generated by Waikato University Radiocarbon Dating Laboratory from charcoal samples collected during the 1970s Caladenia Cave excavations. The sample codes correspond to Caladenia Cave (CC) and the average depth of the source spit in centimetres (as originally recorded).

Sample code	Depth (mm)	Group	Waikato code	Radiocarbon age (BP)	Calibrated age (cal. BP)
CC100	1000	D	WK37157	2803 ± 68	3037–2750
CC108	1080	E	WK37158	2986 ± 58	3254–2925
CC137	1370	G	WK37159	3544 ± 43	3895–3641
CC154	1540	J	WK37160	3812 ± 45	4296–3979
CC160	1600	J	WK37161	4256 ± 56	4868–4569
CC223	2230	K	WK38730	1346 ± 20	1280–1180
CC231	2310	K	WK37162	1556 ± 34	1489–1316
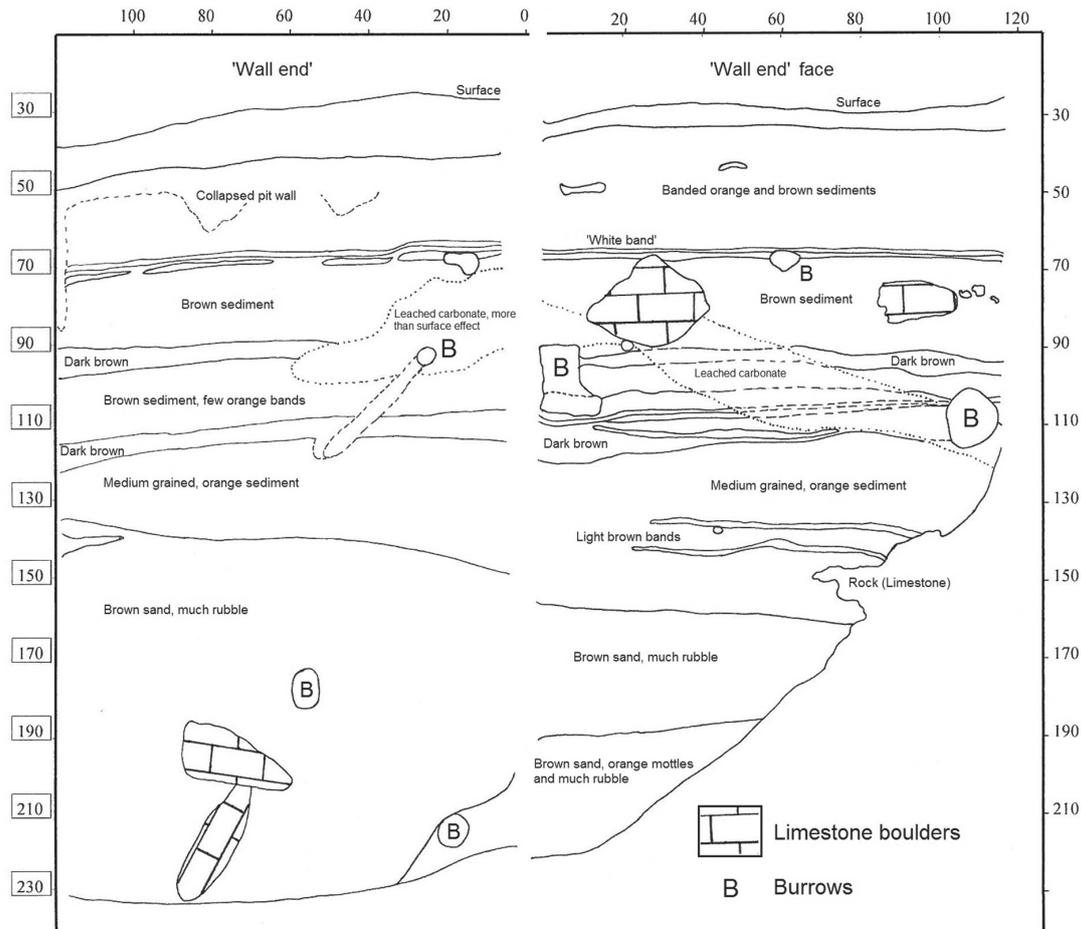
FIGURE 4 Section drawings of 'Wall end' and 'Wall end face', perpendicular faces of the trench. The 0 horizontal point denotes the NW corner of the trench and the datum from which section lines were measured. Burrows in the stratigraphy were either in-filled or contained small frogs. All material from the burrows was labelled disturbed (Roe 1971). All sections were originally sketched by D. Merrilees and redrawn and digitised for this investigation. Illustrations of the other sections are provided in Appendix 2.

PALAEOECOLOGY

Number of Identified Specimens (NISP) was chosen over the Minimum Number of Individuals as the preferred quantitative unit because it is a more robust measure of taxon abundance (Lyman 2008). NISP was calculated by counting all identified specimens (e.g. left and right dentaries and maxillae, and post-cranial material where identified, see Table 3). However, when edentulous jaws were present, isolated teeth were only counted after teeth corresponding to empty alveoli had been subtracted. Data were combined into Groups designated A–R (see Table 1 for details) based on their stratigraphic position, the sieve size used and to ensure sample sizes were robust enough for statistical analyses. Rarefaction curves were generated for each Group (A–R) using PAST (Hammer et al. 2001), to assess the likelihood that additional specimens would yield additional species (Gotelli and Colwell 2001; Hammer

et al. 2001; Lyman and Ames 2007; Hammer and Harper 2008). Correspondence analysis was used to visualise patterns of species abundances in the assemblage.

Body mass statistics were sourced from Van Dyck and Strahan (2008) and the averages were calculated to separate the species into weight classes by 50 g steps. Relative abundance (Ri%) was calculated (NISPspecies/ NISPtotal x 100) to elucidate quantitative differences between Groups. Changes in species diversity between Groups were assessed using the Simpson index of diversity $(1 - \lambda = 1 - \Sigma p_i^2)$, which was calculated for both the full fauna and the fauna that remained after the <50 g species were removed, for comparison. Species <50g were subtracted from all Groups as many were differentially recovered by the 1 mm sieve. Each analysis was conducted in PAST and graphed in Excel. Species habitat guilds were generated from references shown in Table A1, Appendix 1.

TABLE 3 Number of Identified Specimens (NISP) from the Roe excavation in Caladenia Cave, listed by sieve size (3 mm and 1 mm), stratigraphy, Groups, and species.

Sieve	Sediment	Group	Thylacinus cynocephalus	Antechinus flavipes	Dasyurus geoffroii	Parantechinus apicalis	Phascogale calura	Phascogale tapoatafa	Sarcophilus harrisii	Sminthopsis sp. indet	Isoodon obesulus	Perameles bougainville	Cercartetus concinnus	Pseudocheirus occidentalis	Trichosurus vulpecula	Bettongia lesueur	Bettongia penicillata	Potorous platyops	Lagorchestes hirsutus	Macropus eugenii	Macropus fuliginosus	Macropus irma	Setonix brachyurus	Petrogale lateralis	Macroderma gigas	Chalinolobus morio	Falsistrellus mackenziei	Nyctophilus geoffroyi	Nyctophilus gouldi	Hydromys chrysogaster	Mus musculus	Notomys sp. cf. N. mitchelli	Pseudomys albocinereus	Pseudomys fieldi	Pseudomys nanus	Pseudomys occidentalis	Pseudomys shortridgei	Rattus fuscipes	Rattus tunneyi	Total NISP	No. of taxa
3 mm sieve		A	0	15	0	2	0	0	0	205	9	0	0	1	4	0	0	0	0	0	3	4	0	0	0	5	0	0	0	0	0	45	154	2	0	199	41	28	11	728	16
	Banded orange and brown sediments	B	0	37	0	5	0	0	0	244	11	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	1	41	108	9	0	215	53	36	12	776	15
		C	0	44	0	9	0	0	0	215	6	0	0	0	2	0	0	0	0	0	0	1	0	0	5	0	0	0	0	0	0	54	59	12	0	215	56	29	26	737	15
	Brown sediment (1)	D	0	16	1	6	0	0	0	132	27	0	0	0	0	0	4	0	0	0	2	0	0	1	4	3	0	0	1	0	0	31	260	8	0	73	39	36	28	672	19
	Dark brown	E	1	25	1	3	0	0	0	108	3	0	2	0	1	0	3	0	0	0	1	1	0	0	2	3	0	0	0	0	0	25	248	14	0	32	40	10	16	537	20
	Brown sediment (2)	F	0	22	3	5	0	0	0	141	12	0	1	0	3	0	1	2	0	0	1	1	0	0	15	1	0	1	1	0	0	26	242	2	0	49	82	31	39	681	22
	Medium grained orange sediment	G	2	61	3	3	0	1	0	137	30	0	0	1	4	2	8	0	0	3	5	4	2	3	13	0	0	0	0	0	0	53	206	2	0	141	206	55	102	1047	24
	Light brown band	H	0	3	2	0	0	0	0	2	6	0	0	0	0	0	2	0	0	0	0	2	0	0	3	0	0	0	0	0	0	3	8	0	0	18	7	3	1	61	14
	Lime flecked sediment	I	0	9	0	0	0	0	0	33	4	0	0	1	0	0	1	0	0	0	3	3	0	0	0	0	1	1	0	0	0	7	33	1	0	34	27	11	10	180	17
	Mixed colour sediment	J	0	23	2	1	0	0	0	15	9	0	0	4	11	13	10	1	1	0	1	4	0	2	12	0	0	0	0	0	0	12	23	2	0	63	2	12	1	227	23
	Brown sediment (3)	K	0	4	3	2	0	0	0	5	4	0	0	0	1	3	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	6	13	0	0	22	3	6	1	79	16
	Lime flecked sediment	L	0	17	2	3	0	0	0	12	4	3	7	1	0	2	2	1	0	0	0	0	0	0	0	24	0	7	1	0	0	70	500	1	0	90	14	8	4	773	21
1 mm sieve		M	0	15	1	2	0	1	0	14	11	2	5	1	0	4	1	0	0	0	0	0	0	2	2	23	0	4	1	0	0	74	406	0	0	83	9	16	1	680	23
		N	0	10	0	1	0	0	0	11	4	0	2	0	3	1	3	0	0	0	0	0	0	2	1	22	0	1	0	0	0	65	464	2	1	101	11	8	1	717	22
		O	0	7	4	0	0	1	0	8	10	9	2	2	2	5	4	1	1	1	0	0	0	3	0	16	4	2	4	0	0	104	403	6	1	131	24	8	1	767	27
	Brown sediment (3)	P	0	10	7	0	4	0	0	27	17	6	3	2	6	11	5	3	0	1	1	2	1	1	5	12	0	6	1	0	0	85	340	4	0	126	25	20	1	730	28
		Q	0	9	4	2	0	0	0	23	13	8	3	4	8	16	5	0	1	4	0	0	0	2	0	8	1	0	3	0	0	86	305	7	0	99	14	18	0	644	24
		R	0	15	5	1	0	0	0	14	7	0	0	1	5	4	3	0	0	0	0	0	0	2	1	6	2	1	3	0	0	50	204	5	0	55	15	13	1	413	22

RESULTS

SEDIMENTOLOGY AND STRATIGRAPHY

The sedimentary sequence in Caladenia Cave is well stratified. No evidence of reworking of the sediments was observed, except where small burrows occurred (Figure 4). Unfortunately, many of the sediment samples collected by Roe were still damp when placed in vials, causing their paper labels to degrade to the point of illegibility, preventing sedimentological analyses.

CHRONOLOGY

Radiocarbon dates from the sedimentary sequence indicate that the majority of the deposit was undisturbed. Dates CC223 and CC231 are, however, out of sequence (Table 2; Figure 5), probably because of disturbance of sediment by rain washing into the open excavation after a storm (Roe 1974), which would have redeposited much younger material into the trench. All other dates are older and in stratigraphic order, with a high R^2 coefficient once the disturbed dates are excluded (Figure 5).

TAPHONOMY

A majority of the small mammal (<250 g mean adult body weight) material recovered from the excavation was intact with very little, to no digestive erosion (Figure 6) or breakage on crania or long bones (Figure 7). This condition is typical of owl accumulation (Andrews 1990).

Mammalian predators and scavengers, *Sarcophilus harrisii, Thylacinus cynocephalus* and *Homo sapiens,* contributed to the Caladenia Cave assemblage. Evidence of *S. harrisii* includes coprolites and shards of bones of larger, indeterminate marsupials, still with a faecal coating, in Group J. Turtle shell and burnt bones, possible evidence of humans, were found in Group K. All specimens of species >250 g are incomplete, with saw-tooth breakage patterns and higher levels of surface digestive erosion, and many remains of animals larger than 1 kg showed evidence of human use (Monks et al. 2014) (Figure 6). The Shapiro-Wilk tests returned significantly low probabilities that both size classes were not normally distributed (see Appendix 3, Tables A3.1 and A3.3). Paired *t*-tests were then conducted, which highlighted that the two size classes are significantly different from one another taphonomically by both percent completeness and evidence of digestive erosion (p<0.05, see Appendix 3, Tables A3.2 and A3.4).

Species <250 g are generally represented by >90% complete specimens. While much more variable, remains of species >250 g often consisted of bone shards, or broken ends of long bones. Bone completeness of species <250 g generally decreased with depth in the deposit (Figure 7). This was attributed to the weight of the cave fill, trampling and a weakening of the bone
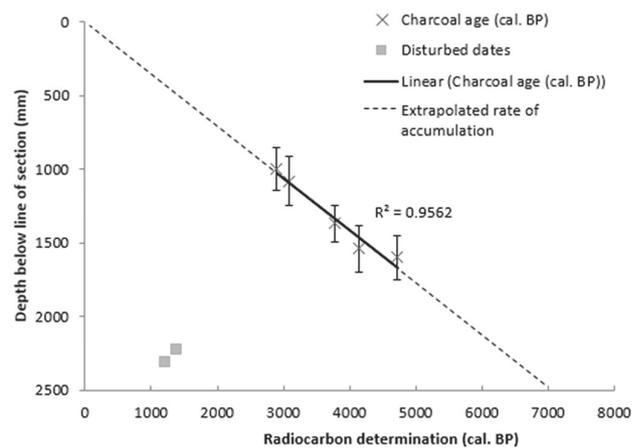
FIGURE 5   Depth-age plot for the deposit in Caladenia Cave. R^2 value does not include the two disturbed dates represented by grey squares.
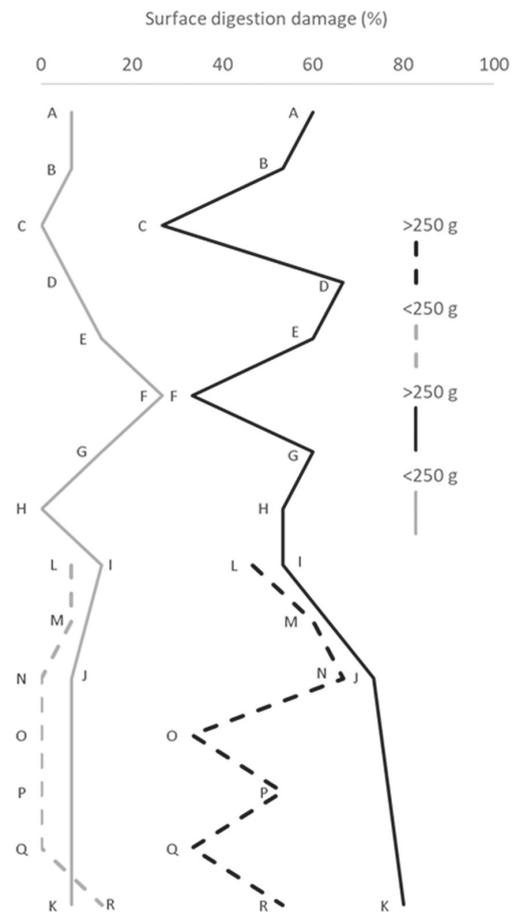
FIGURE 6   The proportion of damage caused by digestion to remains of species <250 g and >250 g. Damage was recorded as percentage of the bone surface showing digestive erosion or bite damage. Solid lines represent the Groups sieved with a 3 mm mesh aperture, dashed lines with a 1 mm aperture.

with age. The specimens recovered from species >250 g appear to have been damaged more by mammalian accumulators such as *S. harrisii*, *T. cynocephalus* and humans before their deposition.

Six burrows were observed in photographs and sketches of the excavation sections. Notable dark staining of all other specimens from the same depth as a single unstained, pale *Mus musculus* specimen is consistent with it having been recovered from a small burrow in the deposit (see Table 3). The mouse may have entered the burrow as a living animal, or its remains could have been reworked from the surface by whatever

FIGURE 7   Bone breakage shown by remains of species <250 g and >250 g. Solid lines represent the Groups sieved with a 3 mm mesh aperture, dashed lines with a 1 mm aperture.

made the burrow. Either could explain its depth in the deposit in relation to its recent (<200 years) invasion of south-western Australia.

Cranio-dental preservation changed through the deposit, from specimens such as intact skulls and splanchnocrania in the upper 1000 mm to mainly small fragments of maxillae and dentaries recovered by the 1 mm sieve in Groups L–M and below. In material from the small sieve mesh aperture (L–R), the ratio of isolated rodent M1s to teeth-bearing bones changed, with most of the NISP counts constituted by molars alone. The mid-range Groups H–K (Figure 8) of the deposit contain higher relative abundances of remains of larger species (>250 g), resulting from natural deaths, scavengers or human accumulation.

The reduction in sieve size by the excavation team, evident in the sharp change in the relative abundance of <50 g species between Groups K and L (Figure 8), caused the differential recovery of smaller species.

FAUNA

A total of 12,407 specimens was identified from the Roe excavation in Caladenia Cave. These have been accessioned into the vertebrate palaeontological collection of the Western Australian Museum under catalogue numbers 13.11.1–13.11.999 and 13.12.1–13.12.617. In most cases only a single catalogue number was allocated to each species from each spit, irrespective of the number of specimens. Only 10,449 specimens were used for statistical analyses due to disturbance of some of the stratigraphy and excavation problems. The biggest change from species presence to absence occurs at approximately 1600 mm (Group J), where the marsupials *Phascogale calura*, *Perameles bougainville* and *Lagorchestes hirsutus* and the placental *Falsistrellus mackenziei* disappear. All of these species were recorded on the basis of jaws or jaw fragments large enough to be retained on a 3 mm sieve, and had their remains been present in the upper part of the deposit, where bone preservation was relatively good, they would have been recovered. The *Falsistrellus mackenziei* specimens have extended the known Holocene northern range limit of the species, which was previously Jandakot at 32°15'S, 115°50'E (Hosken and O'Shea 1995).

No easily distinguished species of *Sminthopsis* such as *Sminthopsis crassicaudata* was identified within the assemblage; other *Sminthopsis* species could not be separated from one another using the descriptions in Archer (1981) or Kitchener et al. (1984).

Sarcophilus harrisii was represented by jaw fragments, isolated teeth and ascribed coprolites. The coprolite specimens, containing small bone fragments, indicate that *Sarcophilus* contributed to the accumulation of vertebrate remains in the cave.
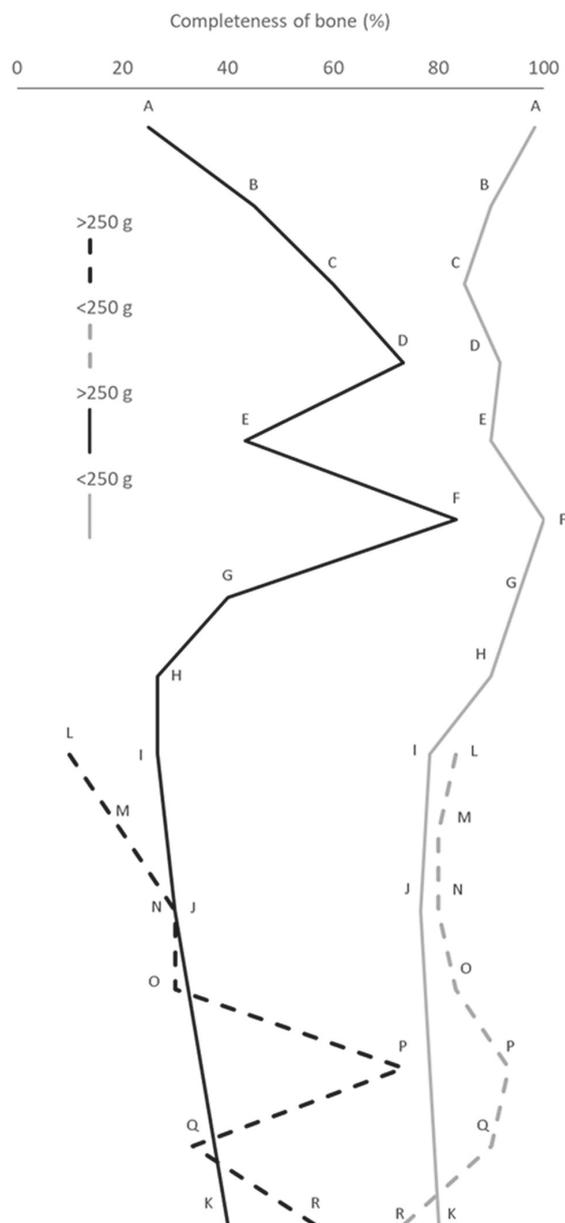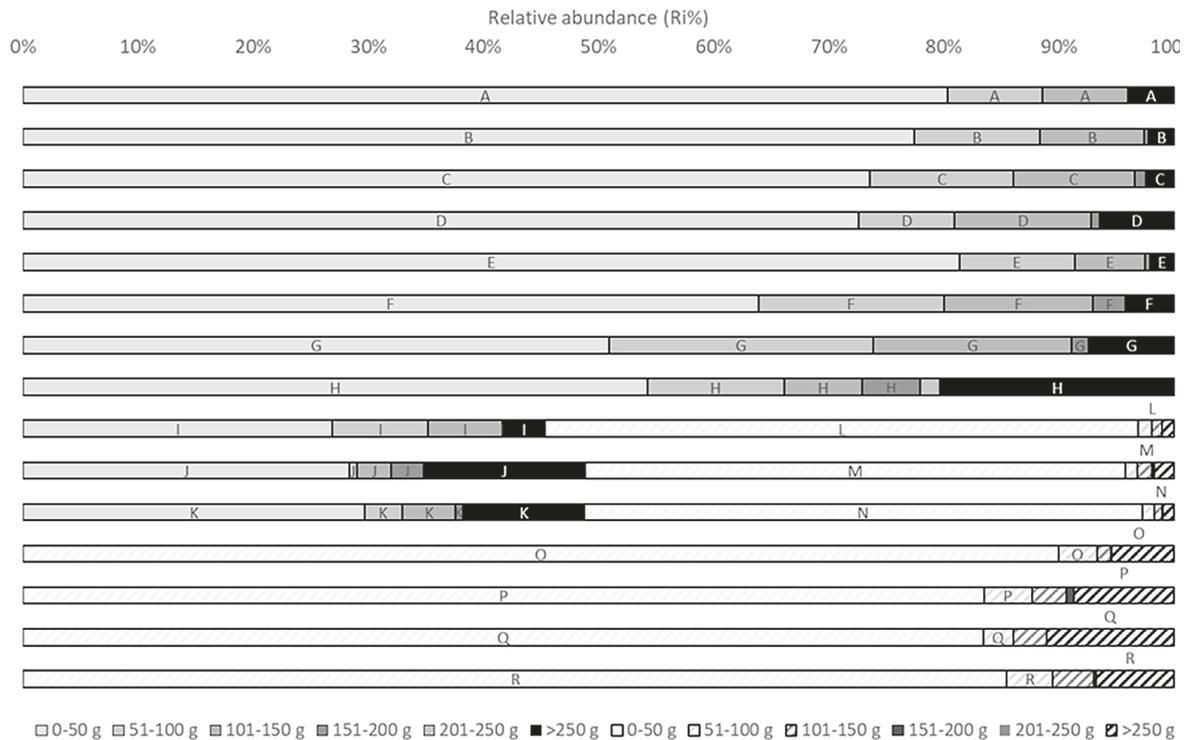
FIGURE 8   The relative abundance of the diagnostic remains recovered from each data Group in Caladenia Cave within allocated average body mass classes.

Evidence of human use of the cave includes hearths described and sketched in Roe's notebooks after a trench wall collapsed (Roe 1974, pp. 39–42). Freshwater mussel shells, turtle shell and fish bones were recovered as well as burnt mammal bone in the lower levels of the deposit (Monks et al. 2014). A fragment of human jaw bone was mentioned in Roe's notebooks (Roe 1971), but cannot be found in the Western Australian Museum collections. Artefacts were also found during the excavation, and catalogued into the Museum archaeological collection (B3086–90, B1979, B1981–82 and A22107–09) providing additional evidence that humans occasionally inhabited the cave.

Three specimens of *Thylacinus cynocephalus* were recovered from the excavation, each at different depths. The chronologically youngest specimen, a right metatarsal III of *Thylacinus cynocephalus* (WA Museum vertebrate palaeontological collection catalogue number 13.11.364) has an associated charcoal age of 3254–2925 cal. BP. All *Thylacinus* specimens were originally identified by Merrilees and confirmed by Thorn with Museum comparative material.

PALAEOECOLOGY

Rarefaction analysis of the NISP data from each Group (see Figures A–R in Appendix 4), indicated that the smallest Group samples, D, E and I, were all still within one standard deviation of the largest samples'

rarefaction curves, and all samples tend towards an asymptote. Group I remained the only sample to not plateau. Therefore, sample sizes and species richness were sufficient for further statistical tests (Gotelli and Colwell 2001; Hammer and Harper 2008).

Correspondence analysis clearly shows a cluster of Groups screened with the 1 mm aperture sieve (circled in Figure 9). The smaller species, such as the microbats, *Pseudomys albocinereus*, and *Phascogale calura* are associated with the 1 mm sieve aperture Groups, while

TABLE 4   Relative abundances of species grouped according to body mass (g) in the 3 mm and 1 mm sieve mesh aperture samples. Body mass data could not be located for some species, therefore Ri% figures do not total 100.

Mass (g)	3 mm (Ri%)	1 mm (Ri%)
0–50	53.90047	86.89071
51–100	9.43340	2.80774
101–150	8.31425	2.22037
151–200	1.52893	0.19437
201–250	0.15771	0.03963
>250	8.75636	5.44026
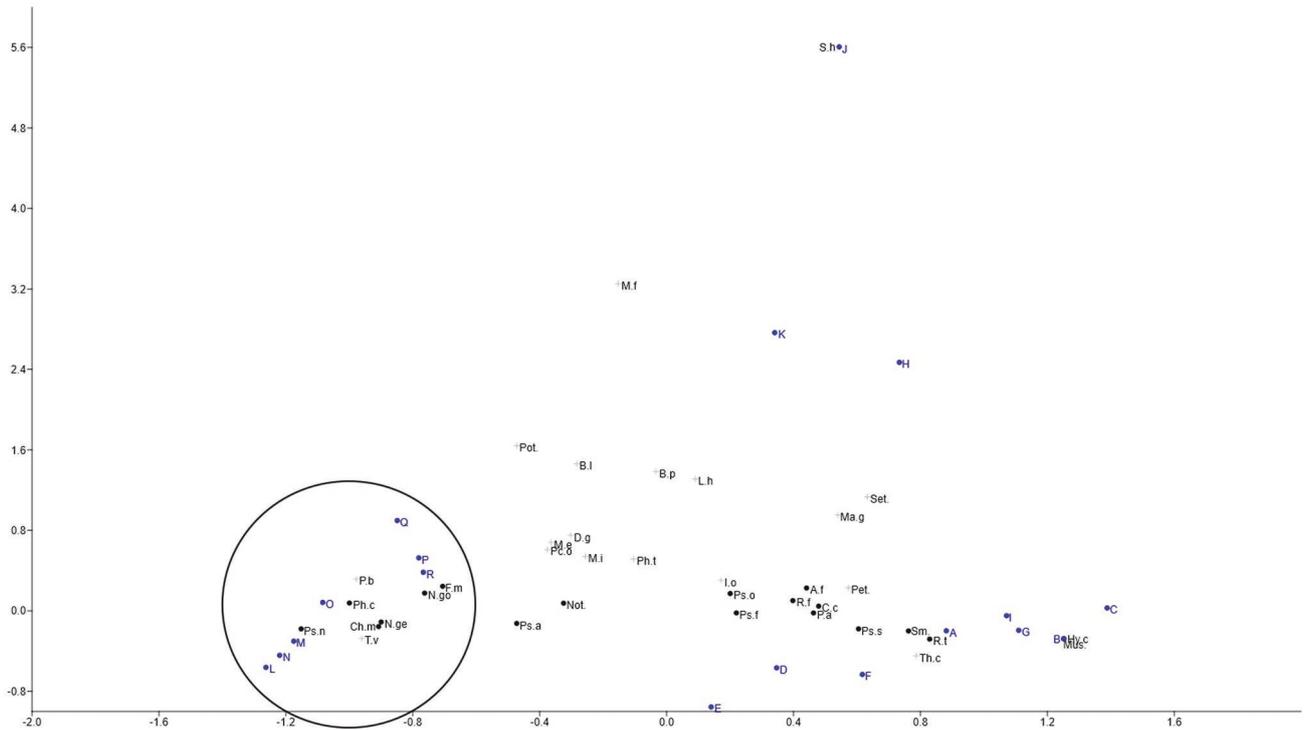
FIGURE 9   Scatter plot of the first two axes of correspondence analysis of the raw Group data from Caladenia Cave. Groups A–K are from the 3 mm sieve and Groups L–R from the 1 mm. Species >250 g are designated with a grey '+'. Clustered Groups correlating with the 1 mm sieve are circled, note that this is not a 95% confidence ellipse. A.f = *Antechinus flavipes*, D.g = *Dasyurus geoffroii*, P.a = *Parantechinus apicalis*, Ph.c = *Phascogale calura*, Ph.t = *Phascogale tapoatafa*, S.h = *Sarcophilus harrisii*, Sm. = *Sminthopsis* sp. indet, I.o = *Isoodon obesulus*, P.b = *Perameles bougainville*, T.v = *Trichosurus vulpecula*, B.l = *Bettongia lesueur*, B.p = *Bettongia penicillata*, Pot. = *Potorous platyops*, M.e = *Macropus eugenii*, M.f = *Macropus fuliginosus*, M.i = *Macropus irma*, Pet. = *Petrogale lateralis*, Set. = *Setonix brachyurus*, C.c = *Cercartetus concinnus*, Pc.o = *Pseudocheirus occidentalis*, Ma.g = *Macroderma gigas*, Ch.m = *Chalinolobus morio*, F.m = *Falsistrellus mackenziei*, N.ge = *Nyctophilus geoffroyi*, N.go = *Nyctophilus gouldi*, Hy.c = *Hydromys chrysogaster*, Mus. = *Mus musculus*, Not. = *Notomys* sp. cf. *N. mitchellii*, Ps.a = *Pseudomys albocinereus*, Ps.f = *Pseudomys fieldi*, Ps.n = *Pseudomys nanus*, Ps.o = *Pseudomys occidentalis*, Ps.s = *Pseudomys shortridgei*, R.f = *Rattus fuscipes*, R.t = *Rattus tunneyi*.

most of the larger species do not obviously cluster with any Group. Notably, *Sarcophilus* sits directly under Group J, and *Hydromys* and *Mus musculus* under Group B, as these species appear only in these Groups. The remaining rodents and dasyurids are generally spread out across the plot, not clustering with any particular Group, possibly due to variation in preservation causing them to be variably retained by both sieves throughout the deposit.

When the different faunal size classes were further examined (Table 4) the relative abundances of the smallest species (<50 g) were significantly higher in Groups where a 1 mm sieve was used (p <0.05).

The Simpson index of diversity was found to be fairly consistent through the upper levels of the deposit until the change in sieve size between Groups K and L (Figure 10). The Groups I–K record a Simpson index of 0.8 or higher, while the same depths sieved with the 1 mm aperture, represented by Groups L–N, drop to

0.5. Despite an increase in sample size the diversity index does not revert again until Group R. This may be explained by an increase in the recovery of smaller specimens resulting from a finer sieve mesh aperture. Relative abundance of 0–50 g species increased from 53.9% to 86.9% of the recovered material (Table 4), but while the sample sizes increased, the number of taxa did not, generating a false impression of a drop in diversity.

Species were grouped into habitat guilds based on current knowledge of ecological preferences, after Adams et al. (2016). Relative abundances of habitat guilds show major fluctuations below Group G (Figure 11). This is most likely to have been caused by differential recovery of the material in those spits that were only sampled by the 3 mm sieve, whereas the same depths covered in Groups L–R, sampled with the 1 mm sieve, from the other 'End' of the trench, show much less fluctuation.

DISCUSSION

The investigation into the fossil vertebrate fauna of Caladenia Cave unearthed a total of 38 native mammal species, consisting of 14 placentals and at least 22 marsupials (*Sminthopsis* and *Dasycercus* were only identified to genus and could each represent two or more species). Current faunal records report only 11 extant native species, the top layer of the deposit alone records 16, and historical records place 28 species in the same area (Wilson et al. 2012). These figures highlight the value of Holocene fossil deposits as records of the original mammalian species richness of the Swan Coastal Plain. The drop in species richness on the northern Swan Coastal Plain can only be attributed to

the impacts of European settlement, as other factors, the changes in rainfall or the arrival of the dingo in the area, have not produced the same dramatic effect anywhere in this long-term data set.

TAPHONOMY

The body mass range, condition and breakage patterns observed in a majority of the fossil mammal assemblage from Caladenia Cave are characteristic of an owl accumulation (Andrews 1990; Lyman 2012a). *Tyto delicatula* Gould, 1837, the Australian barn owl, is the species most likely responsible for the accumulation, as a majority of the postcranial material examined shows little or no digestive erosion of the bone surface and most long bones are intact (see Figures 6–7). *Tyto delicatula* has been recorded on the northern Swan Coastal Plain (Storr et al. 1978; Atlas of Living Australia 2013). The majority of the prey material is composed of rodents and small marsupials, most of which can be swallowed whole by owls (Morton and Martin 1979; Andrews 1990; McDowell and Medlin 2009).
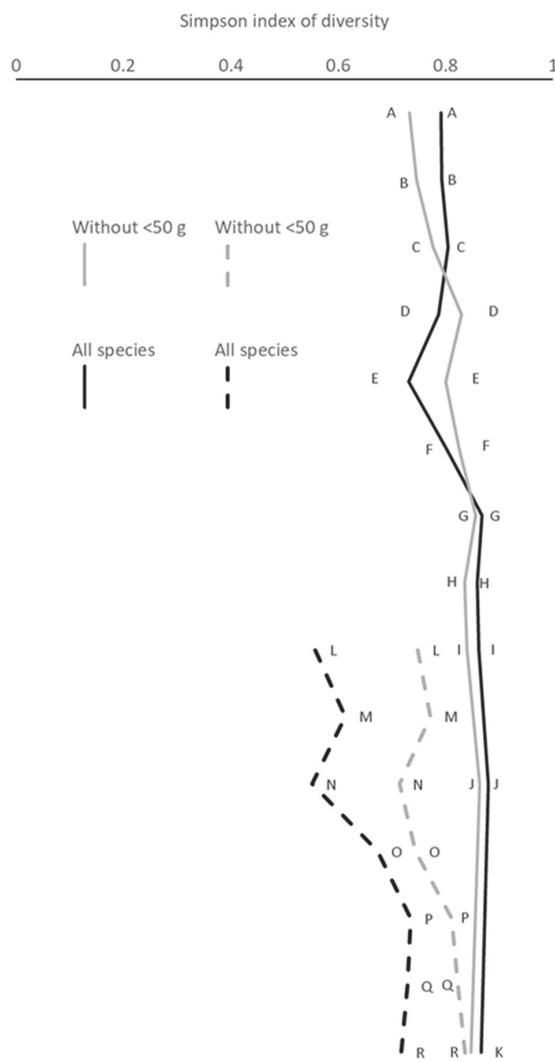
FIGURE 10   Simpson index of diversity of each Group in Caladenia Cave. When all species with a body mass of less than 50 g were removed from the entire dataset, diversity across the deposit appears more even. Solid lines represent the Groups sieved with a 3 mm mesh aperture, dashed lines with a 1 mm aperture.
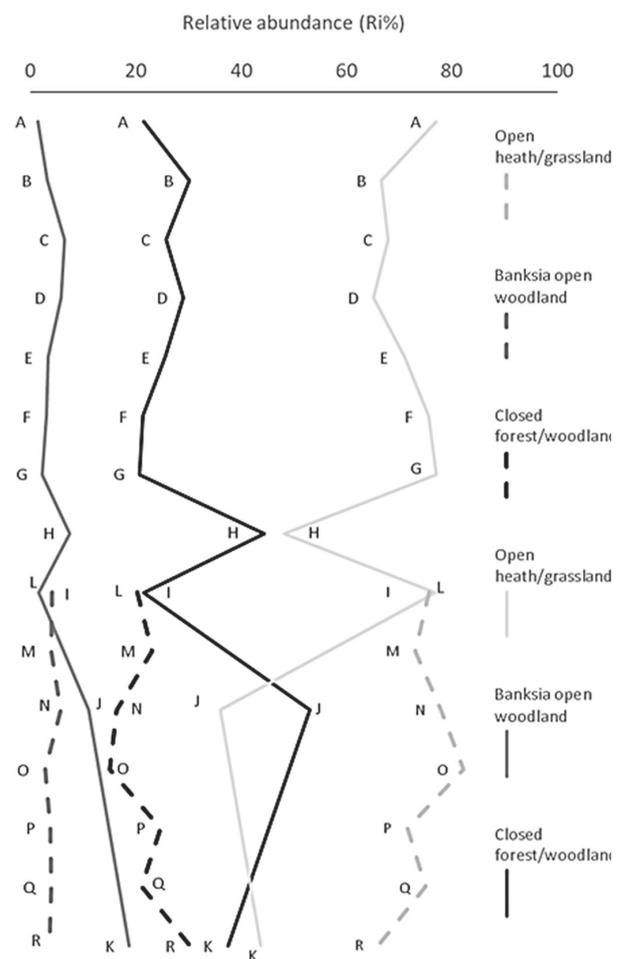
FIGURE 11   Changes in relative abundances of habitat guilds of fossil mammal species >50 g in Caladenia Cave. Species were grouped according to information displayed in Appendix 1.

The use of a sieve of larger mesh aperture for the upper levels of the excavation caused differential recovery of the largest and loss of the smallest mammals, particularly in the deeper layers where the bone was more fragile, creating a bias in the species' relative abundances through time (Lyman 2012b). Where the 3 mm sieve was used, a lower proportion of the smaller species such as *Sminthopsis* sp. indet., *Cercartetus concinnus*, *Chalinolobus morio* and *Pseudomys albocinereus* was recovered, as evident in the correspondence analysis (Figure 9). Isolated molars, canines or even entire maxillae from these species with a minimum dimension of ~2 mm, were less likely to be retained than those of larger species (Lyman 2012b). Although Caladenia Cave was excavated in the 1970s, differential recovery is still not uncommon in palaeontological and archaeological investigations and is often not considered in analyses (Baynes personal observation 2016). The results of the Caladenia Cave analyses demonstrate that sieve bias can overwhelm the palaeoecological signal in relative abundance data. Screen mesh aperture is an important factor that should be considered in planning the methodology of an excavation. Preliminary research into the size of the expected specimens, and how they were accumulated is wanted, as well as the use of an appropriate minimum sieve mesh aperture when small faunal material is present in a deposit.

EVIDENCE FOR CLIMATE CHANGE

Three semi-arid and arid-dwelling species, *Phascogale calura* (Figure 12), *Perameles bougainville* and *Lagorchestes hirsutus*, are present in the deposit below a depth of 1540–1600 mm (Group J, 4868–4569 cal. BP; Table 2), but absent above it. These three species are part of a suite of six which shows the same pattern of change from presence to absence in the mid Holocene levels of the deposit in Hastings Cave, about 120 km north of Caladenia Cave on the Swan Coastal Plain (Baynes 1979). Moreover, there are no specimens of the three species in the Western Australian Museum vertebrate palaeontological collection from cave floor surface faunas (of late Holocene age) from any of the many caves in the northern Swan Coastal Plain represented in that collection; see, for example, the distribution records for *P. calura* in Figure 12. This pattern of faunal change suggests that local winter rainfall increased. The other semi-arid and arid proxy species in this group (*Perameles bougainville* and *Lagorchestes hirsutus*) also have live-caught records from areas of low winter rainfall (Atlas of Living Australia 2013).

Support for this change was previously found south of Caladenia Cave: invertebrate climate proxies relating to the flow of the Swan River indicating an increase in effective rainfall since 4853–4292 cal. BP (Kendrick 1977; Yassini and Kendrick 1988).

PALAEOECOLOGY

The change in sieve mesh aperture size generated a more precise representation of the <50 g mammals in the lower layers of the Caladenia Cave deposit. This action, taken part way through the excavation, means that the bulk of the youngest material collected has been biased such that smaller mammals are underrepresented. Correspondence analysis was initially applied to the relative abundances of each species recovered from each layer. The resulting plot shows that species and layers grouped in accordance with the size of the sieve used (Figure 9). Consequently, an unbiased interpretation of ecological change over time based on relative abundances was not possible (see also Figure 10 for how diversity, calculated with relative abundances, was impacted by differential recovery). The change in sieve size appears to correlate directly with the change in abundance of the smallest species (<50 g), which in turn affects the Simpson diversity index for Groups L–R where sample size increases but species richness does not, creating a downward trend in overall diversity in comparison to Groups I–K (3 mm sieved units). Change

Key
● Records based on remains
▲ Pre-1954 live-caught record
△ Post-1963 live-caught record
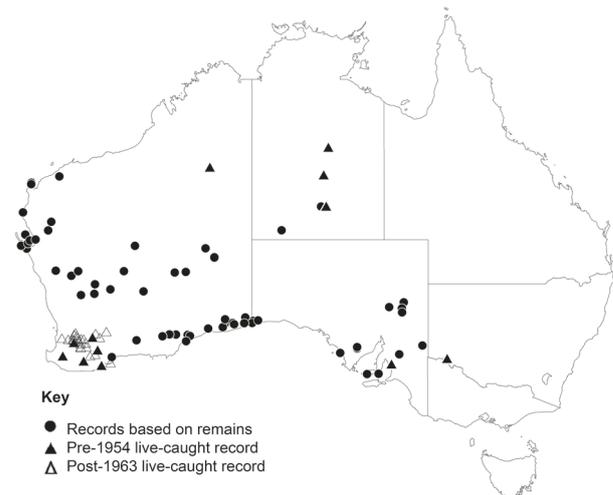
FIGURE 12   The distribution of *Phascogale calura*. The species was restricted to areas characterised by persistently dry hot summers, with semi-arid to arid climates (Kitchener et al. 1980; Australian Bureau of Meteorology 2013). The gap between mid-latitude and southern records in Western Australia reflects a lack of sites containing mammal remains rather than an absence of original populations, except that, being arboreal, *P. calura* did not occur on the treeless Nullarbor Plain. Data from Thomas (1888), Wakefield (1966), Parker (1973), Baynes and Baird (1992), Baynes and Johnson (1996), Baynes and McDowell (2010), the vertebrate palaeontological and mammal collections of the Western Australian Museum and the mammal collection of the South Australian Museum.

in the preservation of material seems to also have disrupted any ecological patterns in the data, evident in the 'noise' shown in Figure 11. A trend of mostly open heath/grassland species appears to be disrupted in units L–G by an increase in larger species' relative abundance. This is most likely due to the taphonomic features of bone breakage and digestion (Figures 6 and 7) decreasing preservation of the bone, leading to differential recovery in the 3 mm sieved Groups.

An important finding uncovered by the excavation of Caladenia Cave, not impacted by differential recovery, is the presence of a specimen of *Thylacinus cynocephalus* with an associated radiocarbon date of 3254–2925 cal. BP. Until now, the youngest mainland Australian specimen of *Thylacinus* is dated to 3379–3060 cal. BP (McDowell 1997). The timing of the mainland thylacine extinction has been directly associated with the arrival of the dingo at 3904–3445 cal. BP (Milham and Thompson 1976). Fillios et al. (2012) described the impact of dingo immigration on the fauna of mainland Australia as a 'trophic cascade', as it interrupted the thylacine's suppressive effect on herbivores and small predators, indirectly impacting smaller herbivores and vegetation. By contrast, the only significant faunal change discovered in Caladenia Cave pre-dates the arrival of the dingo. Similar results were found in an investigation of Hastings Cave (Baynes 1979), demonstrating a lack of evidence for any 'trophic cascade' occurring on the northern Swan Coastal Plain.

Other than the loss of the dry-land species due to increased rainfall, fine scale local changes in the palaeoecology of the northern Swan Coastal Plain cannot be elucidated. The continued presence of most species throughout the assemblage suggests ecological stability during the Holocene, despite apparent changes in rainfall or the arrival of the dingo. This is in contrast to the effects of European settlement in the area which resulted in local extinction of many mammals such as *Parantechinus*, *Pseudocheirus* and five of the seven native rodent species, and a drastic change from all native vegetation to an agricultural mosaic

THE FUTURE

Because of the limitations imposed on the Caladenia Cave data by differential recovery of mammal remains, further research is needed to elucidate the relationships between the original biotic communities of the Swan Coastal Plain. A re-investigation of the vertebrate assemblage in Wedge's Cave (Lundelius 1960), the ongoing investigation of Yellabiddie Cave (Monks et al. 2016) or another excavation of the East Moore caves, may provide the material required for a palaeoecological comparison with both Hastings and Caladenia Cave. This study shows that excavated sediment must be processed using a 1 mm or 0.5 mm sieve mesh aperture for the entire excavation. Unfortunately, future excavation of Caladenia Cave would not be practical as the ideal location and much of the remaining sediment

has already been disturbed. However, 30 other caves have been recorded in the 'Lower South West' region that should be explored for fossil remains (Matthews 1985). Evidence collected from other caves further south could also extend the range of interpretation of the Holocene Swan Coastal Plain and provide more information for restoration ecology.

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APPENDIX 1   Species guild designation references

TABLE A1 Grouping of non-volant mammal species into vegetation guilds according to the references below. These groupings were used for Figure 11.

	Species	Baynes 1979	Dortch 2004	Van Dyck & Strahan 2008	Adams et al. 2016
Closed Forest/Woodland	*Antechinus flavipes*	x		x	x
	Dasyurus geoffroii	x		x	
	Phascogale tapoatafa	x		x	x
	Sarcophilus harrisii	x		x	x
	Isoodon obesulus	x		x	x
	Trichosurus vulpecula	x		x	x
	Potorous platyops			x	x
	Setonix brachyurus	x	x	x	
	Pseudocheirus occidentalis	x		x	
Banksia Open Woodland	*Parantechinus apicalis*	x		x	
	Phascogale calura	x		x	
	Bettongia penicillata	x		x	x
	Cercartetus concinnus	x		x	x
	Pseudomys occidentalis	x		x	x
Heath/Grassland	*Perameles bougainville*	x	x	x	x
	Bettongia lesueur	x	x	x	x
	Lagorchestes hirsutus	x		x	
	Macropus eugenii	x	x	x	x
	Macropus fuliginosus	x		x	x
	Macropus irma	x		x	
	Petrogale lateralis	x	x	x	
	Notomys mitchellii			x	
	Pseudomys albocinereus	x		x	
	Pseudomys fieldi	x		x	
	Pseudomys shortridgei	x		x	x
	Rattus tunneyi	x		x	

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APPENDIX 2 Section of 'Stone heap end' and test pit

FIGURE A2 Section illustration of 'Stone heap end' and the centralised test pit, originally drawn by Duncan Merrilees, traced, digitised and labelled by Thorn. See Table 1 in the paper for details on how the stratigraphy was assigned into spits and units. The test pit shown below was added at the suggestion of Merrilees after review of Roe's notes on the excavation (Roe 1971).
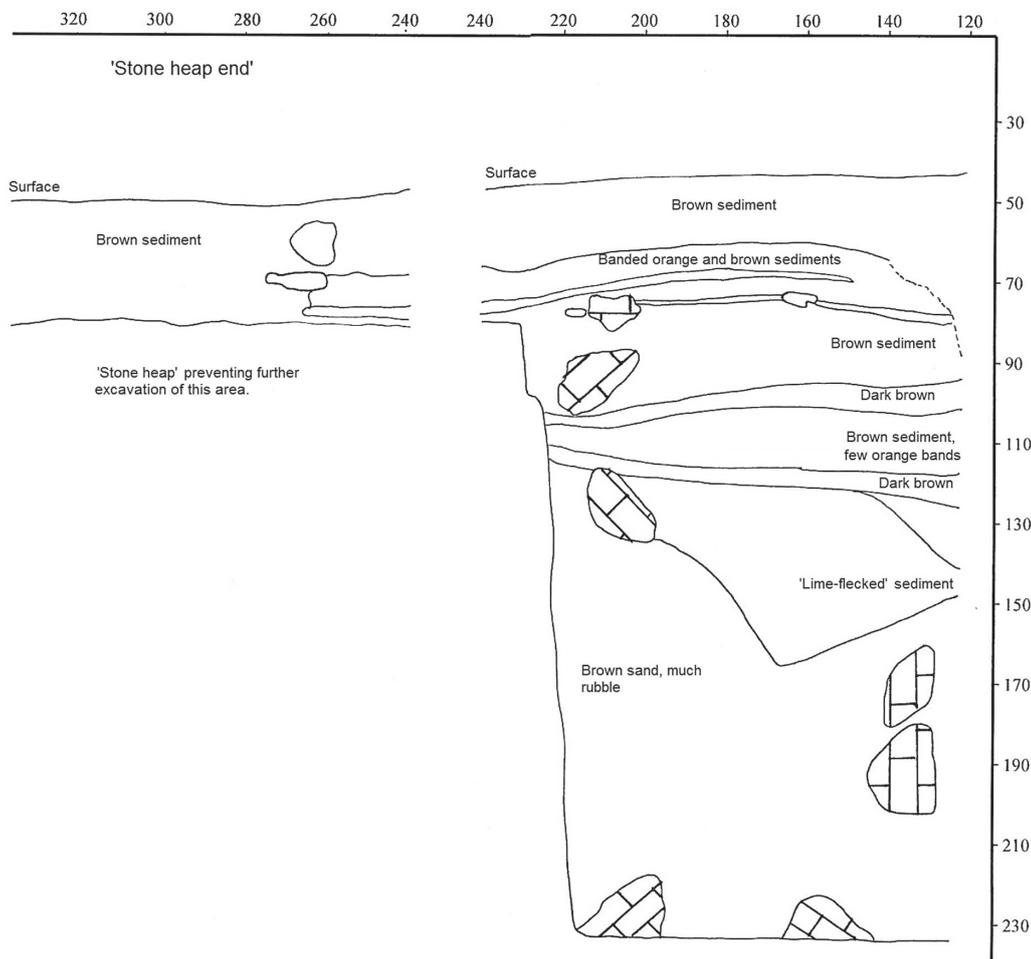
APPENDIX 3 Statistical tests for the taphonomic two size classes

TABLE A3.1 Shapiro-Wilk test for normality in the distribution of the digestion damage data within the two sizes.

	<50 g	>250 g
N	54	54
Shapiro-Wilk W	0.5919	0.9271
p(normal)	5.25E-11	0.002808

TABLE A3.3 Shapiro-Wilk test for normality of the bone breakage data within the two size classes, <50 g and >250 g.

	<50 g	>250 g
N	54	54
Shapiro-Wilk W	0.864	0.8547
p(normal)	2.02E-05	1.08E-05

TABLE A3.2 Paired t-test to see if the <50 g class and the >250 g class show similar rates of digestion damage.

	<50 g		>250 g
N	51		
Mean	0.37255		2.6863
Median	0		3
t-test	-10.99	p(same)	6.06E-15

TABLE A3.4 Paired t-test to see if the <50 g class and the >250 g class show similar rates of bone breakage.

	<50 g		>250 g
N	51		
Mean	86.373		45.98
Median	90		30
t-test	7.848	p(same)	2.86E-10

APPENDIX 4   FIGURES A4A–R Rarefaction graphs to test for sufficient sample size in each of the Groups (A–R) listed in Table 1.

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