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Research Article

Late Pleistocene to Holocene mammal faunal change on a small Landbridge Island in Bass Strait, South-Eastern Australia, and its implications for future reintroductions

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Abstract

We examined a zooarchaeological assemblage from Badger Island, a 12.4 km^2 landbridge island in the Furneaux Group, Bass Strait, south-eastern Australia. The accumulation consisted of Pleistocene and Holocene strata that were rich in mammal remains. Small mammal remains were accumulated by owls, whereas large mammal remains were accumulated by people and/or autochthonous mortality. The Pleistocene fauna was dominated by grassland mammals, particularly *Mastacomys fuscus* (Broad-toothed Rat), but these gradually declined and were largely replaced by forest–woodland dwelling mammals in the Holocene. The same pattern of faunal change has been observed on the large main island of Tasmania (~65,000 km^2), suggesting changes observed at Beeton Rockshelter are representative of the region. Because all of the Furneaux Group Islands were united as one landmass in the past, the fossil fauna observed in Beeton Rockshelter is relevant to conservation-oriented mammal-restoration initiatives, which are being considered throughout the entire Furneaux Group.

Keywords: Late Quaternary; sea-level rise; *Mastacomys fuscus*; conservation; landbridge island

Introduction

Since European colonization, Australia has been losing mammals to extinction more rapidly than any other nation in the world. In 1788, Australia had 441 living mammal species and subspecies, more than 80% of which were endemic. Since then, 46 species and subspecies (10.4%) are known to have become extinct and 86 (19.5%) are currently threatened with extinction (Woinarski et al., 2015; Fusco et al., 2017; Burbidge, 2024). Further, the ongoing recognition of new taxa (e.g., Start et al., 2012; Travouillon and Phillips, 2018) suggests the full extent of Australia's biodiversity loss has been underestimated (Abbott, 2000; Woinarski et al., 2014; Abbott and Wills, 2016; Burbidge and Abbott, 2017; Newman-Martin et al., 2023; Burbidge, 2024). Environmental effects related to the European colonization of Australia continue to pose challenges for the conservation and restoration of Australia's ecosystems.

At least nine species of mammals that were once widespread on the Australian mainland now survive only on landbridge islands (Woinarski et al., 2014; Burbidge et al., 2008). Islands have become important for conservation, as sites from which invasive predators can be eradicated and genetic diversity preserved (Abbott and Wills, 2016). Choosing suitable introduction sites for range-restricted species can be challenging, but Pleistocene–Holocene fossil accumulations can provide concrete evidence of where a species lived prior to European settlement. They can also be used to establish appropriate baselines to measure long-term biodiversity trends, and to evaluate the suitability of islands as refuges for species that are threatened on mainland Australia (McDowell, 2014).

Due to limited immigration and the effects of isolation and species life-history traits, terrestrial vertebrate faunas frequently have higher extinction rates on islands than on adjacent mainlands (Burbidge and Manley, 2002; Loehle and Eschenbach, 2012; Burbidge and Abbott, 2017), prompting Woinarski et al. (2011) to describe islands as both "refuge and death-trap." Therefore, understanding the rates and causes of extinctions on islands, and the minimum island size required to support a viable population of a target species is critical knowledge for the effective conservation of island biodiversity (Hanna and Cardillo, 2014; Burbidge and Abbott, 2017).

During the Pleistocene, sea level was lower than present (Lambeck and Chappell, 2001), and much of the continental shelf was exposed, including the area known as the Bassian Plain, which formed a landbridge between Tasmania and mainland Australia (Figure 1). Around 17 thousand years ago rising seas began to encroach on the Bassian Plain, eventually

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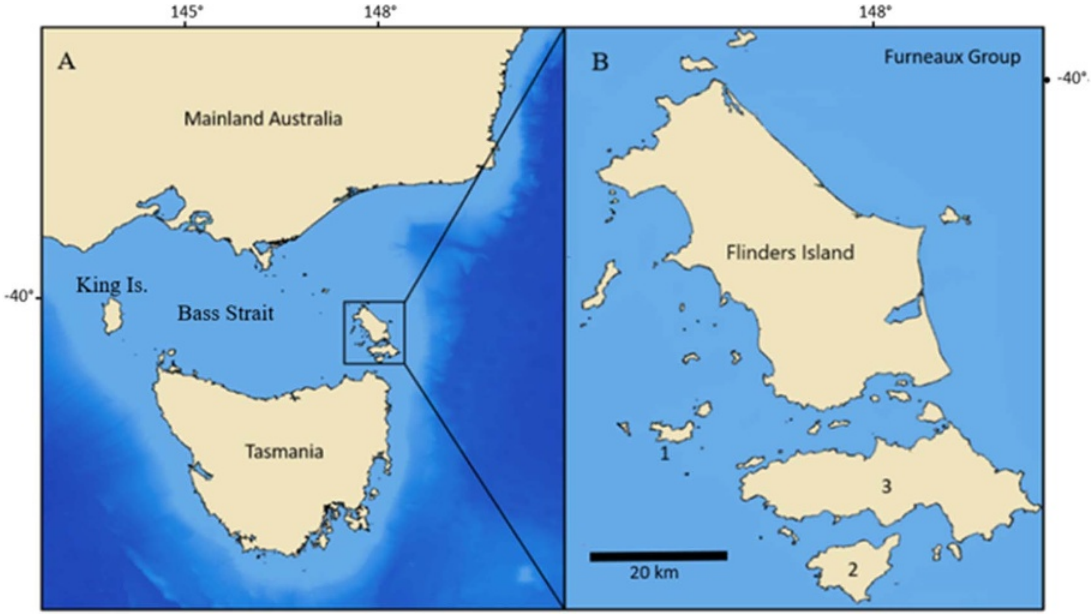

Figure 1. Locations of (A) the Furneaux Group of islands in relation to the main island of Tasmania, Bass Strait, and mainland Australia, and (B) the Furneaux Group of islands; 1 = Badger Island; 2 = lungtalanana/Clarke Island; 3 = truwana/Cape Barren Island in Bass Strait at present day sea level. Light-blue sea indicates extent of the continental shelf, much of which was exposed during the Late Pleistocene forming the Bassian Plain.

severing the landbridge by about 11 ka, re-forming Bass Strait and converting more than 150 former hills and promontories into islands (Hope, 1974; Brothers et al., 2001), including the Furneaux Group (Flinders Island and its near neighbors).

Paleontological and zooarchaeological assemblages that provide archives of past species and ecologies are rarely found on small landbridge islands. Even more rarely do they record long periods of time that encompass the glacial to interglacial transition, potentially recording how island mammal faunas responded to increasing isolation, decreasing land area, and climate-driven habitat change. Beeton Rockshelter, located on Badger Island in Bass Strait (Figure 1), is one of very few known locations where this is possible, making it an exceptionally important site with the potential to reveal how Australian native mammals responded to past climate change and isolation. In this study we undertook a detailed paleontological analysis of the fossil material from this site. The aim was to describe changes in the mammal assemblage of Badger Island from the Pleistocene, when it was a high point or hill on the Bassian Plain, to the Holocene when sea-level rise transformed it into the island we know today, and thereby provide key information for future restoration.

Methods

Site, excavation and stratigraphy

Badger Island may have been named after wombats (*Vombatus ursinus ursinus*), discovered by Matthew Flinders on Clarke Island in 1797 (wombats are still called badgers in the Furneaux Group today). But only two species (*Notamacropus rufogriseus* and *Thylogale billardierii*) were recorded from Badger Island by European explorers (Hope, 1974), providing no definite evidence that wombats were present on Badger Island at the time of colonization. An alternative explanation suggests the island was named after a ship that was wrecked there (https://www.placenames.tas.gov.au/#p1 [accessed 26 December 2024]).

Badger Island is a 12.4 km^2 (1240 ha), low-lying island largely composed of granite, hornfels, and Cenozoic limestone covered by a thin soil. Despite its low relief, most of Badger Island's coast consists of significant cliffs. It is unclear, however, how the Furneaux Group will be affected by future climate change and sea-level rise.

Beeton Rockshelter occurs in a substantial limestone outcrop on the northwest tip of the island. It consists of a 21-m long and 5-m deep wave-cut notch that covers over 60 m^2 of occupiable area (Figure 2), about 5 m above present-day sea level. Beeton Rockshelter was excavated by Sim in 1992 under Aboriginal Heritage Tasmania permits (P87/4, P88/9, P90/3, and P92/2) to excavate, collect, remove and study Tasmanian Aboriginal heritage. All research was carried out with the requisite Australian National University (ANU) Ethics Committee approvals.

Sediments were excavated in 2.5-cm or 5-cm excavation units (XUs) within stratigraphic units (SUs). Ten-liter buckets were used to quantify sediment mass and volume, then sediments were dry sieved using 7-mm and 3-mm mesh. Charcoal, marine mollusks, vertebrate remains and worked or manuport stones from each XU were retained for further analysis (after Sim, 1998).

Fauna

Taxonomic nomenclature in this research follows The Australian Mammal Taxonomy Consortium Australian mammal species list (AMTC, 2023). The Beeton Rockshelter assemblage is curated by the Tasmanian Aboriginal Centre, 198 Elizabeth Street, Hobart, Tasmania, 7001, Australia.

Diagnostic specimens (primarily crania or isolated maxillae, dentaries, and teeth) were identified by McDowell following methods outlined in McDowell et al. (2012). Comparative specimens held by the Tasmanian Museum and Art Gallery and published information (e.g., Green, 1968, 1983; Watts and Aslin, 1981; Baker et al., 2015) were also used to help identify diagnostic material.

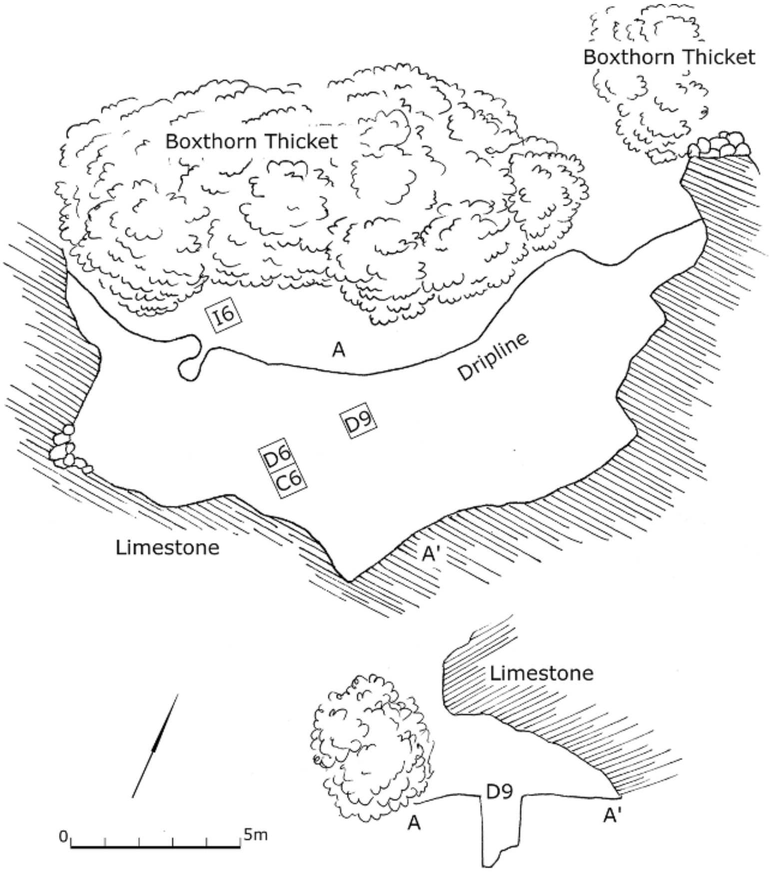

Figure 2. Plan view of Beeton Rockshelter, Badger Island, with a cross section of excavation Square D9 (after Sim, 1998).

Fossils were typically highly fragmented, making it difficult to identify *Antechinus* and Peramelidae specimens to species. Reptile, bird, frog, and fish bones were also recovered from the excavation and have been reported as present in Table 2 but were not included in data analyses because they were extremely rare and could not be identified below family level.

Species richness was derived from the number of species represented in each stratigraphic unit (SU) and excavation unit (XU) of the fossil assemblage (Table 2). Specimens that could not be identified to species were excluded from this calculation unless they were the only representative of a genus. The number of identified specimens (NISP) was recorded for each species in each XU and SU. The NISP was converted to relative abundance (Ri%) to enable comparison to be made between different sized samples, by dividing a sample's species NISP by the sample's total NISP, multiplied by 100. The relative abundances of mammals assigned to Grassland, Forest/Woodland, and Heathland communities (as indicated in Table 2) were aggregated to investigate changes in those communities over time. Specimens identified as species indeterminate (sp. indet.) were excluded from the community aggregates unless their affiliations were unambiguous.

Stratigraphic unit NISP data were used to perform a Diversity Permutation Test (also called a re-randomization test), using PAlaeontological STatistics (PAST) software Version 4.01 (Hammer et al., 2001). This test computes a range of diversity indices for two samples, and then compares the diversity estimates between samples using random permutations, to assess statistical significance of the observed differences, thereby allowing for an objective evaluation of whether statistically meaningful changes in assemblage structure had occurred (Hammer and Harper, 2008). Rarefaction was also used to assess whether sample sizes were large enough to have captured species richness in its entirety in each time interval.

Taphonomy

Before different stratigraphic units can be compared it is important to ensure that they have experienced similar taphonomic processes and accumulating agents (Adams et al., 2016). Therefore, we investigated taphonomic indicators such as body size of prey species, burning, and vegetation community. Most bones showed evidence of fresh, dry bone breaks, which probably occurred during excavation or due to trampling hard-hooved livestock. Therefore, bone breakage was not investigated further.

Radiocarbon dating

Square D9 of Beeton Rockshelter was originally dated in the 1990s using a mixture of gas proportional counting and accelerator mass spectrometry (AMS) radiocarbon dating (Sim, 1998; Table 1). Gas proportional counting is rarely used today because it requires very large samples, takes a long time, and costs almost as much as AMS radiocarbon dating. The accuracy and precision of radiocarbon dating has improved dramatically since the original dates were measured, necessitating reassessment of the site's chronology. We submitted 12 bone samples (6 each from Unit IV and Unit III) from Beeton Rockshelter to the ANU AMS radiocarbon dating laboratory to test the accuracy and precision of the ages obtained by Sim (1998) and better determine the timing of faunal change. All radiocarbon ages are given at 95.4% probability, and were calibrated in

Table 1. Radiocarbon ages obtained from Beeton Rockshelter. Lab codes with ANU prefix were measured in the 1990s using gas proportional counting; Lab codes with AA, OZA/B, and SANU prefix were measured using an Accelerator Mass Spectrometer. All ages were calibrated at a 95.4% confidence interval using SHCal20 or Marine20.

XU	SU	Lab code	Species	Material dated	Conventional age BP	Calibrated age BP
04	III	ANU–8130[1]	*Cellana solida*	Shell	8700 ± 125	9756–8961
06	III	OZB 591[1]	*Puffinus carneipes*	Bone	4540 ± 90	5083–4383
06	III	SANU6810[2]	Peramelidae indet.	Bone	6671 ± 37	7580–7430
06	III	Failed[2]	Peramelidae indet.	Bone	—	—
07	III	OZB593[1]	*Puffinus griseus*	Bone	4950 ± 90	5552–4891
07	III	OZB594[1]	*Puffinus pacificus*	Bone	5080 ± 80	5930–5600
10	III	SANU6882[2]	Peramelidae indet.	Bone	5413 ± 27	6290–6000
10	III	Failed[2]	Peramelidae indet.	Bone	—	—
10	III	AA–15143[1]	*Dromaius* sp. indet.	Eggshell	23,180 ± 1280	30,720–25,170
11	III	SANU6881[2]	Peramelidae indet.	Bone	5365 ± 27	6270–5990
11	III	OZA782[1]	*Puffinus tenuirostris*	Bone	5440 ± 110	6137–5472
11	III	Failed[2]	Peramelidae indet.	Bone	—	—
14	IV	ANU8751[1]	Hearth charcoal	Charcoal	18,180 ± 940	24,500–19,850
14	IV	Failed[2]	*Mastacomys fuscus*	Bone	—	—
14	IV	Failed[2]	*Mastacomys fuscus*	Bone	—	—
17	IV	ANU8752[1]	Charcoal cluster	Charcoal	19,300 ± 730	25,270–21,770
17	IV	Failed[2]	*Mastacomys fuscus*	Bone	—	—
17	IV	Failed[2]	*Mastacomys fuscus*	Bone	—	—
20	IV	ANU8753[1]	Hearth charcoal	Charcoal	16,250 ± 2620	32,900–13,390
20	IV	Failed[2]	*Mastacomys fuscus*	Bone	—	—
20	IV	Failed[2]	*Mastacomys fuscus*	Bone	—	—

[1]Ages reported by Sim (1998); [2]ages reported in this study.

OxCal 4.4 (Bronk Ramsey, 2009) using either the SHCal20 curve for mammal bone, charcoal, and emu eggshell; or Marine20 with a ΔR of −151 ± 79 obtained from the Marine Reservoir Correction Database (http://calib.org/marine/) for *Cellana solida* limpet shell and for mutton bird (*Puffinus* spp.) bone.

Results and discussion

Stratigraphy

Sim (1998) identified four stratigraphic units (Figure 3) but reported that Unit I did not contain diagnostic animal remains. Unit II was absent from the D9 excavation. Consequently, these units are excluded from further discussion. Unit IV (XU14–21) consisted of undisturbed Pleistocene, loosely consolidated medium to coarse calcareous sand that was yellow-orange (10YR7/4) in color (Munsell Color, 2010). Unit III (XU4–13) consisted of Holocene grayish, yellow-brown (10YR5/2), loosely consolidated medium- to coarse-grained calcareous sand (Figure 3) that had experienced bioturbation due to mutton bird burrowing. The boundary between Unit IV and Unit III undulates irregularly. Because Unit IV was in situ, data from XUs 14–21 could be used in the faunal analysis, but because Unit III was bioturbated it was treated as a single depositional unit.

We postulate that the rate of sedimentary deposition in Beeton Rockshelter correlated with past wind strength and vegetation density on the Bass Plain. Sedimentation probably began at 30–25 ka when strong winds transported sand-sized particles from the Bassian Plain into the shelter. The rate of deposition appears to have increased towards the last glacial maximum (LGM), probably correlating with increasing wind strength. This type of sedimentation would have halted when the sea inundated the Bassian Plain, effectively removing the sediment source. Sedimentation probably re-commenced after the sea stabilized at its present level and a beach/dune system developed, creating a new, even more local, source of aeolian sediments.

Radiocarbon dating

Of the 12 bone specimens we submitted for radiocarbon dating only three specimens from Unit III yielded datable collagen (Table 1). The three peramelid (bandicoot) bones that were successfully dated suggest that despite being reworked, at least part of Unit III accumulated during the Holocene between about 6–5 ka.

Sim (1998) radiocarbon dated mutton bird (*Puffinus carneipes*, *P. griseus*, and *P. tenuirostris*) bones from Unit III, which were aged from 5440 ± 110 cal yr BP (6137–5472 cal yr BP) to 4540 ± 90 cal yr BP (5083–4383 cal yr BP). Several radiocarbon ages from Unit III are out of chronological sequence (Table 1), including a fragment of Pleistocene emu eggshell dated at 23,180 ± 1280 cal yr BP (30,736–25,211 cal yr BP) from XU10, and a *Cellana solida*

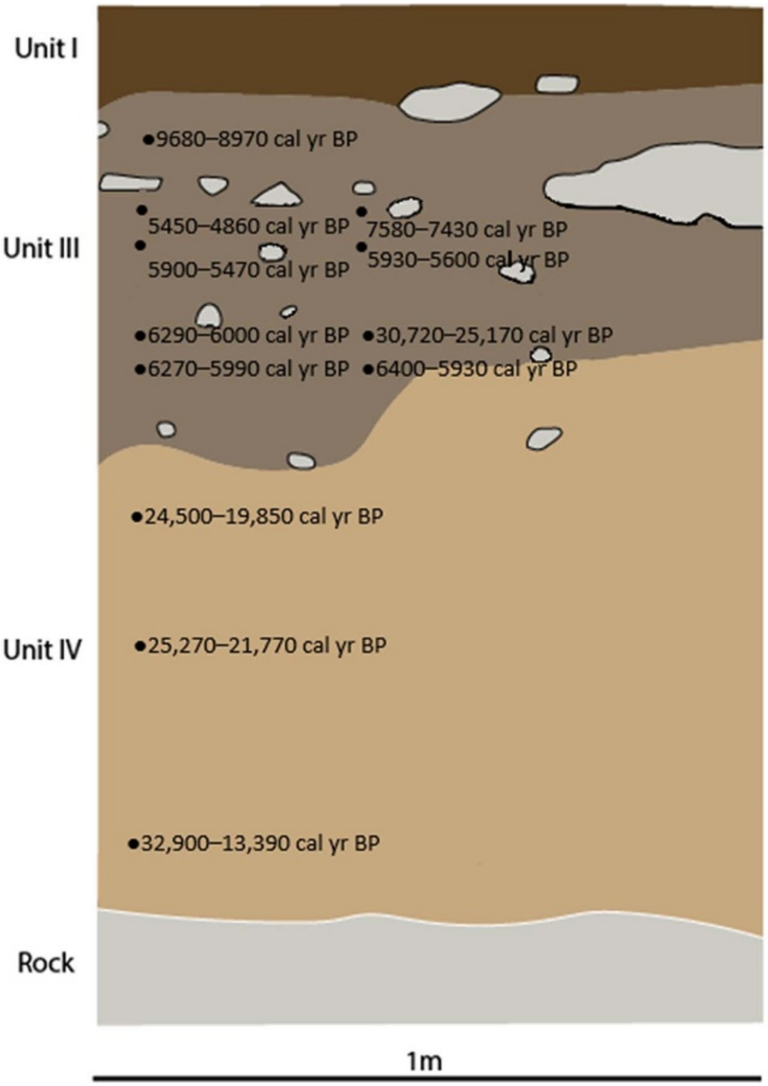

Figure 3. Stratigraphic section of the southeast face of Square D9 (after Sim, 1998). Unit I consists of dark brown (10YR2/3) humus-rich material made up of decomposed sheep and cattle dung. Unit II is absent from square D9, but in other areas consists of sand with no inclusions. Unit III consists of grayish, yellow brown (10YR5/2) medium- to coarse-grained sand that has been bioturbated by mutton bird burrowing. Unit IV consists of yellow orange (10YR7/4) loosely consolidated medium- to coarse-grained calcareous sand. Munsell Color (2010) used for unit colors.

marine mollusk shell from XU04 dated at 8700 ± 125 cal yr BP (9700–8900 cal yr BP).

This suggests that Unit III has been subjected to bioturbation by mutton bird burrowing, which may also have resulted in some mixing between Unit IV and Unit III. Radiocarbon ages from Unit IV indicate that it is otherwise undisturbed and accumulated during the Pleistocene.

Taphonomy

Maximum body mass (MBM) data of mammal species recovered from Beeton Rockshelter are presented in Figure 4. Unit IV and Unit III are both dominated by the remains of mammals with MBM of $<$ 0.5 kg, (Figure 4; Supplemental S1). Mammals with MBM of 1–2 kg (Figure 4; Supplemental S1) are moderately common in both Unit IV and Unit III. Mammals with MBM of $>$ 2 kg are rare in Unit IV but moderately common in Unit III (Figure 4; see Supplemental S1). The Beeton assemblage did not include any mammals with MBM of 0.5–1.0 kg. Mammals with MBM of $<$ 0.5 kg are consistent with prey accumulated by owls, but mammals with MBM of $>$ 1 kg, particularly when burnt, are consistent with prey accumulated by people. Masked Owls (*Tyto novaeholandiae*) and Eastern Barn Owls (*Tyto javanica*) are both known to occur in the Furneaux Group (Atlas of Living Australia; ala.org.au [accessed 12 September 2024]). Both owls hunt at night, catching and consuming adult small-bodied mammals with a maximum body mass of up to approximately 0.5 kg. This includes juveniles of mammals with an adult maximum body mass of 1–2 kg (Young et al., 2020). Owls do not have a gizzard, meaning they are unable to grind up the bones of their prey. Instead, they compress any indigestible material they ingest into a mucous-coated pellet which they regurgitate at their roost. If dropped into cave or rockshelter sites, pellets can accumulate over thousands of years, breaking down over time to leave bones in the sediments.

Large mammal remains can be accumulated by people, other mammalian predators, or as a result of autochthonous mortality (Baird, 1991). Small mammal remains recovered from Beeton Rockshelter are characteristic of owl accumulations whereas large mammal remains (particularly when burnt) are characteristic of bones accumulated by people, or autochthonous mortality.

Occupation

When Europeans first encountered the Furneaux Group of islands in the early nineteenth century, they were uninhabited, despite abundant terrestrial and marine food resources and

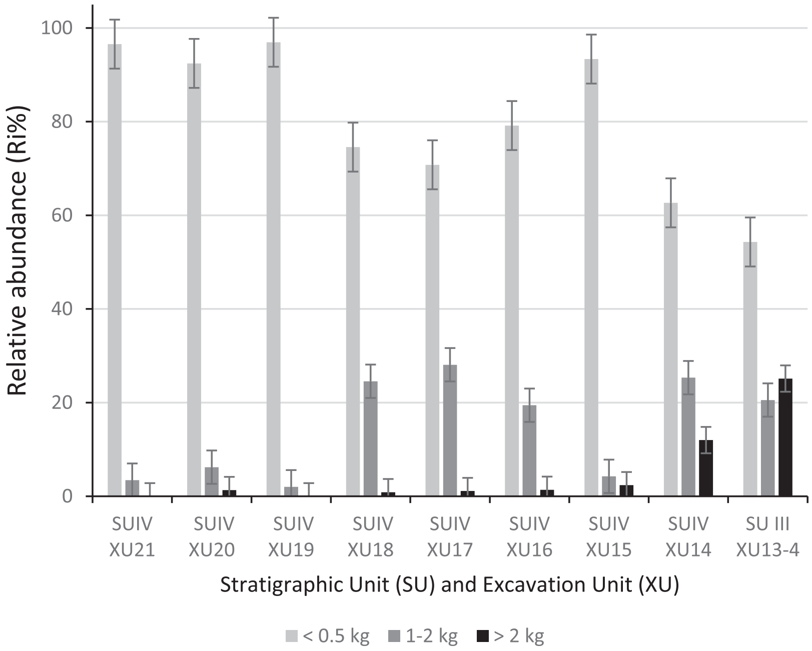

Figure 4. Distribution of mammal maximum body mass (MBM) for each excavation unit of SUIV, and all XUs of SUIII combined, with standard errors indicated for each, from Square D9, Beeton Rockshelter.

permanent fresh water on Flinders Island (Sim, 1994). Evidence that Indigenous people lived on Greater Furneaux Island prior to Holocene sea-level rise (Orchiston and Glenie, 1978; Brown, 1993; Sim, 1998) suggests people disappeared from the Furneaux Group sometime in the Early Holocene. Sim (1998) concluded that people camped at Beeton Rockshelter between 23,180 ± 1280 cal yr BP (30,720–25,170 cal yr BP, AA-15143) and 8700 ± 125 cal yr BP (9756–8961 cal yr BP, ANU-8130) (after Sim, 1998). Sim (1998) also reported 5% of bone mass from Unit IV, and 17% of bone mass from Unit III (Sim, 1998, table 4.23a, p. 156) had been calcined, charred, or blackened.

In rockshelter deposits, burnt or charred bone is recognized as a relatively reliable indicator of human activity (Sim, 1998). The divergent pattern found in burnt bone remains suggests that human predation was responsible for a major portion of this bone, and that people were principally targeting large and medium-sized animals. Sim (1998, pp. 154–155) stated "The majority of the burnt bone identifiable to family from this body size range was wallaby, pademelon and wombat, suggesting these may have been the principal species being exploited for food by people inhabiting the Beeton Rockshelter". Small mammal remains would have continued to be accumulated by owls when people were absent and had abandoned the island for good.

Fauna

The NISP and relative abundance results for the mammal remains excavated from Beeton Rockshelter are presented in Tables 2a and 2b, respectively. Total species richness of Unit IV and Unit III is about equal despite a large difference in specimen yield (Table 2a). Rarefaction curves (Figure 5), however, suggest that the samples from Unit IV and Unit III were both large enough to estimate species richness reliably. The shapes of the two rarefaction curves are similar and both approach an asymptote, suggesting the addition of more specimens would be unlikely to result in the addition of more species (Hammer and Harper, 2008). The diversity permutation test (Table 3) shows that, except for species richness, all diversity and evenness indices are statistically significantly different between Unit IV and Unit III at $p = 0.01$. These differences indicate large changes in the pattern of relative abundance of the species recovered from Units III and IV, despite little faunal turnover or absolute changes in richness.

The mammal fauna from Beeton Rockshelter during the Pleistocene was dominated by grassland species (predominantly *Mastacomys fuscus*; the Broad-toothed Rat) which made up around 80 Ri% of the fauna of XUs 21–19 (base of Unit IV) but fell to 18 Ri% of the fauna in Unit III. The dominant grassland species were replaced by a suite of forest- and woodland-dwelling mammals, which made up the majority of the relative abundance of Unit III (Figure 6). Heath-dwelling species were more common in Late Pleistocene XUs but never made up a substantial proportion of the Beeton fauna. The mammal remains recovered and identified from Beeton Rockshelter showed the same pattern of faunal change over time as the broader fauna of Tasmania based on other main-island sites (see McDowell et al., 2022).

The fauna from Unit III consists mostly of forest- and woodland-dwelling species, including *Pseudomys higginsi* (Long-tailed Mouse), two species of *Antechinus, Isoodon obesulus* (Southern Brown Bandicoot), *Thylogale billardierii* (Tasmanian or Rufous-bellied Pademelon), *Notamacropus rufogriseus* (Red-necked or Bennett's Wallaby), and *Macropus* spp. Several tiny forest-dwelling species are, however, notably absent from the Beeton assemblage (see species marked with * in Supplemental S1). *Pseudomys novaehollandiae* (New Holland Mouse), which was recently found living on Flinders Island (Natural and Cultural Heritage Division, 2014a), is represented by two specimens found only in Unit IV. But *Cercartetus nanus* (Eastern Pygmy Possum), *C. lepidus* (Little Pygmy Possum), and the White-footed Dunnart (*Sminthopsis leucopus*) are not recorded anywhere in the assemblage. *Cercartetus nanus, C. lepidus*, and *S. leucopus* share similar habitat preferences with the larger *P. higginsi* and these species are

Table 2a. Number of Identified Specimens (NISP) of mammal remains recovered from the excavation of Square D9, Beeton Rockshelter. Note that Unit III has been bioturbated and while XU data are presented, the SU is treated as a single depositional unit in the analysis. XUs 08 and 05 did not include any mammal remains. Vegetation community indicates broad species vegetation adaptations: G = Grassland; F/W = Forest/Woodland; H = Heathland.

Stratigraphic Unit (SU)	Unit IV								Total	Unit III								Total	Vegetation
Excavation Unit (XU)	21	20	19	18	17	16	15	14	SUIV	13	12	11	10	09	07	06	04	SUIII	community
Dasyurus viverrinus	—	1	—	—	3	3	3	2	12	3	—	—	—	—	—	—	—	3	G
Dasyurus sp. indet.	1	—	2	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—
Antechinus minimus	—	1	—	2	—	1	—	—	4	—	1	—	—	—	—	—	6	7	F/W
Antechinus swainsonii	—	—	2	—	1	—	2	—	5	—	—	—	—	—	1	1	2	4	F/W
Antechinus sp. indet.	—	—	—	—	—	—	1	1	2	1	1	2	—	1	—	—	9	14	F/W
Isoodon obesulus	—	2	—	—	—	—	3	—	5	1	—	1	—	1	—	—	—	3	F/W
Perameles gunnii	—	—	—	—	2	—	—	—	2	—	—	—	—	—	—	—	—	—	G
Perameles sp. indet.	—	1	—	3	—	—	—	5	9	—	—	—	—	—	—	—	—	—	G
Peramelidae indet.	—	10	4	25	20	11	3	12	85	9	3	6	5	—	2	2	—	27	—
Vombatus ursinus	—	—	—	—	—	—	—	—	—	1	6	1	1	2	6	—	—	17	F/W
Bettongia gaimardi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	2	F/W
Potorous tridactylus	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	F/W
Potoroidae indet.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	2	—
Thylogale billardierii	—	—	—	—	—	—	1	4	5	—	3	1	—	5	1	—	—	10	F/W
Macropus fuliginosus/giganteus	—	3	—	—	—	1	—	—	4	—	3	—	1	3	—	—	—	7	F/W
Notomacropus rufogriseus	—	—	—	1	1	—	4	5	11	—	—	—	—	4	1	—	—	5	F/W
Macropodidae indet.	—	—	—	—	—	—	—	—	—	6	5	—	—	—	10	—	—	21	—
Mastacomys fuscus	23	173	163	61	42	41	139	37	679	18	11	3	2	2	2	1	—	39	G
Pseudomys higginsi	2	16	7	17	15	13	36	3	109	4	5	2	2	7	4	7	4	35	F/W
Pseudomys novaehollandiae	—	1	—	1	—	—	—	—	2	—	—	—	—	—	—	—	—	—	H
Pseudomys sp. indet.	—	—	—	—	—	—	—	—	—	—	—	1	3	—	—	—	13	17	—
Rattus lutreola	3	17	19	4	5	2	19	6	75	2	—	—	—	1	—	—	1	4	H
Agamidae indet.	—	—	—	—	—	—	—	—	—	*	—	*	*	—	—	—	*	*	—
Anura indet.	—	—	—	—	—	—	—	—	—	—	—	—	—	*	—	—	—	*	—
Elapidae indet.	—	—	—	—	—	—	*	—	*	—	*	—	—	—	—	*	—	*	—
Scinidae indet.	—	—	—	—	—	—	—	—	—	—	—	—	*	*	—	—	—	*	—
Varanus sp. indet.	—	*	—	—	—	—	—	—	*	—	—	—	—	—	—	—	—	—	—
Aves indet.	*	*	*	*	—	—	*	*	*	—	—	*	*	*	*	*	*	*	—
Osteichthyes indet.	—	—	—	—	—	—	—	*	—	—	—	—	—	—	*	—	—	*	—
Mammal NISP Totals	29	225	197	114	89	72	211	75	1012	45	39	17	14	26	29	13	35	218	—
Mammal species richness	4	9	6	7	7	7	8	7	12	8	8	6	5	9	8	5	4	15	—

Table 2b. Relative Abundance (Ri%) of mammal remains recovered from the excavation of Square D9, Beeton Rockshelter. Note that Unit III has been bioturbated and while XU data are presented, the SU is treated as a single depositional unit in the analysis. Vegetation community indicates broad species vegetation adaptations: G = Grassland; F/W = Forest/Woodland; H = Heathland.

Stratigraphic Unit (SU)	Unit IV								Total	Unit III								Total	Vegetation
Excavation Unit (XU)	21	20	19	18	17	16	15	14	SUIV	13	12	11	10	09	07	06	04	SUIII	community
Dasyurus viverrinus	—	0.44	—	—	3.37	4.17	1.42	2.67	1.19	6.67	—	—	—	—	—	—	—	1.38	G
Dasyurus sp. indet.	3.45	—	1.02	—	—	—	—	—	0.30	—	—	—	—	—	—	—	—	—	—
Antechinus minimus	—	0.44	—	1.75	—	1.39	—	—	0.40	—	2.56	—	—	—	—	—	17.14	3.21	F/W
Antechinus swainsonii	—	—	1.02	—	1.12	—	0.95	—	0.49	—	—	—	—	—	3.45	7.69	5.71	1.83	F/W
Antechinus sp. indet.	—	—	—	—	—	—	0.47	1.33	0.20	2.22	2.56	11.76	—	3.85	—	—	25.71	6.42	F/W
Isoodon obesulus	—	0.89	—	—	—	—	1.42	—	0.49	2.22	—	5.88	—	3.85	—	—	—	1.38	F/W
Perameles gunnii	—	—	—	—	2.25	—	—	—	0.20	—	—	—	—	—	—	—	—	—	G
Perameles sp. indet.	—	0.44	—	2.63	—	—	—	6.67	0.89	—	—	—	—	—	—	—	—	—	G
Peramelidae indet.	—	4.44	2.03	21.93	22.47	15.28	1.42	16.00	8.40	20.00	7.69	35.29	35.71	—	6.90	15.38	—	12.39	—
Vombatus ursinus	—	—	—	—	—	—	—	—	—	2.22	15.38	5.88	7.14	7.69	20.69	—	—	7.8	F/W
Bettongia gaimardi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15.38	—	0.92	F/W
Potorous tridactylus	—	—	—	—	—	—	—	—	—	—	2.56	—	—	—	—	—	—	0.46	F/W
Potoroidae indet.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.90	—	—	0.92	—
Thylogale billardierii	—	—	—	—	—	—	0.47	5.33	0.49	—	7.69	5.88	—	19.23	3.45	—	—	4.59	F/W
Macropus fuliginosus/giganteus	—	1.33	—	—	—	1.39	—	—	0.40	—	7.69	—	7.14	11.54	—	—	—	3.21	F/W
Notomacropus rufogriseus	—	—	—	0.88	1.12	—	1.90	6.67	1.09	—	—	—	—	15.38	3.45	—	—	2.29	F/W
Macropodidae indet.	—	—	—	—	—	—	—	—	—	13.33	12.82	—	—	—	34.48	—	—	9.63	—
Mastacomys fuscus	79.31	76.89	82.74	53.51	47.19	56.94	65.88	49.33	67.09	40.00	28.21	17.65	14.29	7.69	6.90	7.69	—	17.89	G
Pseudomys higginsi	6.90	7.11	3.55	14.91	16.85	18.06	17.06	4.00	10.77	8.89	12.82	11.76	14.29	26.92	13.79	53.85	11.43	16.06	F/W
Pseudomys novaehollandiae	—	0.44	—	0.88	—	—	—	—	0.20	—	—	—	—	—	—	—	—	—	H
Pseudomys sp. indet.	—	—	—	—	—	—	—	—	—	—	—	5.88	21.43	—	—	—	37.14	7.8	—
Rattus lutreola	10.34	7.56	9.64	3.51	5.62	2.78	9.00	8.00	7.41	4.44	—	—	—	3.85	—	—	2.86	1.83	H
Agamidae indet.	—	—	—	—	—	—	—	—	—	*	—	*	*	—	—	—	*	*	—
Anura indet.	—	—	—	—	—	—	—	—	—	—	—	—	—	*	—	—	—	*	—
Elapidae indet.	—	—	—	—	—	—	*	—	*	—	*	—	—	—	—	*	—	*	—
Scinidae indet.	—	—	—	—	—	—	—	—	—	—	—	—	*	*	—	—	—	*	—
Varanus sp. indet.	—	*	—	—	—	—	—	—	*	—	—	—	—	—	—	—	—	—	—
Aves indet.	*	*	*	*	—	—	*	*	*	—	—	*	*	*	*	*	*	*	—
Osteichthyes indet.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*	—	—	*	—
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	—

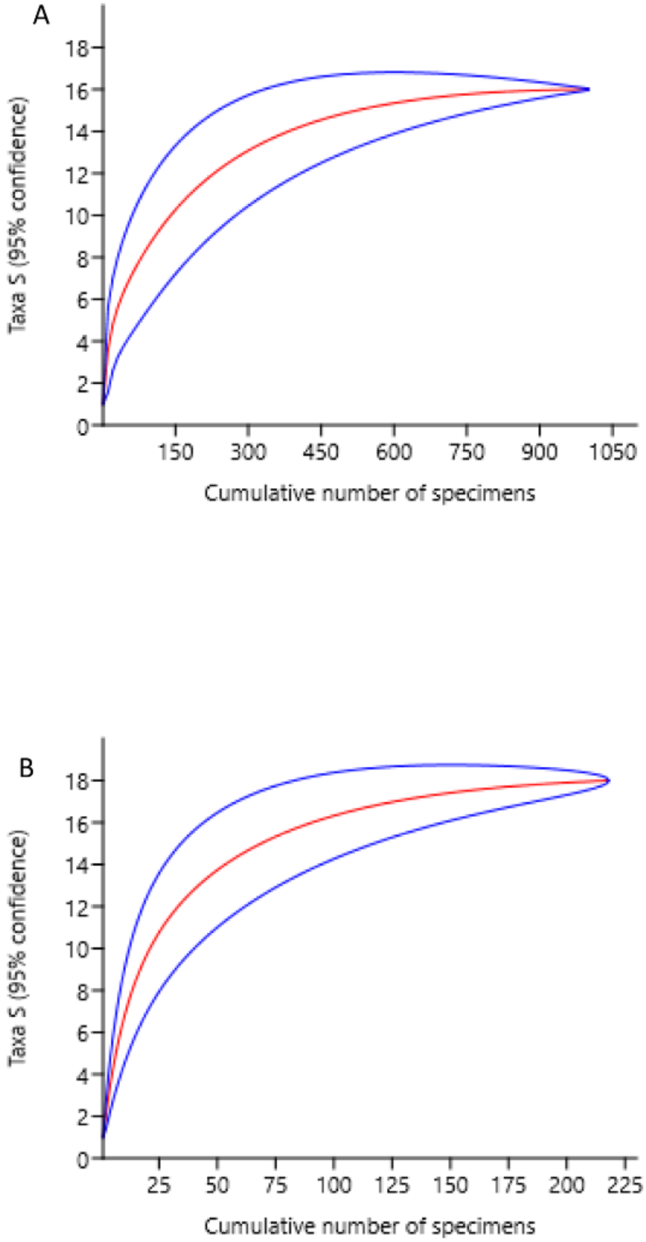

Figure 5. Rarefaction curves for (A) Unit III, and (B) Unit IV. The red line is the central estimate, blue lines are 95% confidence bounds. S = species richness.

frequently found together in fossil assemblages (e.g., McDowell et al., 2022). The nearly total absence of these very small species contrasts with the almost continual occurrence of *P. higginsi*, suggesting that the entire assemblage has been subjected to differential recovery bias (Lyman, 2012; Baynes et al., 2019), probably because Sim (1998) screened the sediment samples using 7-mm and 3-mm sieves, the mesh apertures of which are too large to consistently retain the teeth and jaws of very small mammals such as *Sminthopsis leucopus, P. novaehollandiae*, and, particularly, *Cercartetus* spp., which has probably caused an underestimate of species richness. However, because the biasing process was consistent throughout the assemblage it should not affect the comparisons between Pleistocene and Holocene faunal habitat adaptation, relevant ecology, and current distribution.

Hydromys chrysogaster (Water Rat or rakali) and *S. leucopus* occur on some Furneaux Group Islands today (Harris and Reimer, 1994; Natural and Cultural Heritage Division, 2014b) but are absent from the fossil record. *Hydromys chrysogaster* are large and dangerous prey for Masked and Barn Owls and frequently occupy a marine environment, reducing their exposure to owl predation. In contrast, *S. leucopus* is commonly consumed by owls. Several larger species that frequently co-occur with *S. leucopus* were detected in the Beeton Rockshelter assemblage, suggesting the absence of *S. leucopus* may be related to collection bias, as mentioned above.

The occurrence of *P. novaehollandiae* in Pleistocene Unit IV, albeit at very low relative abundance, suggests heathy vegetation probably occurred on or near (what would become) Badger Island. The relative abundance of *M. fuscus* in the Late Pleistocene Unit IV is consistent with other evidence that the exposed continental shelf and Bassian Plain at that time were vegetated predominantly with grasses, heath, and few trees (Adeleye et al., 2021). In contrast, the Holocene-aged fauna recovered from Unit III is largely made up of forest–woodland species (Table 2a). This is consistent with faunal change observed in Tasmania across the same time period (McDowell et al., 2022). During the Pleistocene the small mammal fauna of Tasmania was dominated by *M. fuscus*, which contributed up to 80% of the fauna recovered from owl roost assemblages dated to that epoch. However, during the Holocene *M. fuscus* was comparatively rare, and a suite of forest dwelling small mammals made up the majority of species recovered from owl roost assemblages (McDowell et al., 2023). The animals identified from Beeton Rockshelter show the same pattern of faunal change over time, suggesting that the fauna of Tasmania and the Bass Strait islands were strongly influenced by vegetation and temperature change associated with the Pleistocene–Holocene transition.

Conservation

Landbridge islands are frequently used as conservation refuges, to which threatened mainland species might be translocated (Peacock et al., 2018). But it is important to consider whether the species to be conserved will thrive in the island environment. Fossil assemblages on islands can provide excellent evidence that an island has provided habitat for a range of species in the past and might therefore do so again and into the future (Burbidge et al., 2008; Peacock et al., 2018; Dietl, 2019; Grealy et al., 2020). Bass Strait and Tasmania have (or had) some of the most (mammal) species-rich islands in Australia (Burbidge et al., 1997), and several small Bass Strait islands have been declared conservation areas (Parks and Wildlife Service, 2000). However, Abbott (2000) recommended several factors, including island area (1 km^2 minimum), degree of isolation, and habitat availability, that should be considered when selecting an island for conservation purposes.

Under private ownership, Badger Island was subjected to overgrazing, vegetation clearing, inappropriate burning regimes, and the introduction of exotic plants and animals. However, since being declared an Indigenous Protected Area in 2000, the island has undergone weed eradication, revegetation, and feral animal control. Following the restoration of its natural vegetation and eradication of feral cats, Badger Island will meet all of Abbott's (2000) criteria and will make an excellent mammal conservation area that could support several of the species identified in Beeton Rockshelter.

Four other Indigenous Protected Areas managed by the Tasmanian Aboriginal Centre (TAC) occur in the Furneaux Group. Babel Island, Great Dog Island, and Mount Chappell Island host

Table 3. Results of a Diversity Permutation Test showing that diversity and evenness indices calculated for Unit IV and Unit III are highly statistically significantly different (at $p = 0.01$), indicating the probability that any dependency in assemblage composition between Unit IV and Unit III can be explained by chance is extremely low, despite the near identical raw species richness figures of the two Units.

Diversity index	Unit IV Late Pleistocene	Unit III Mid Holocene	Permutation *p* (equal)
Richness	12	14	0.9905
Individuals	998	164	—
Dominance	0.4881	0.1503	0.0001
Shannon H	1.16	2.162	0.0001
Evenness	0.2453	0.6204	0.0001
Simpson index	0.5119	0.8497	0.0001
Menhinick	0.4115	1.093	0.0073
Margalef	1.738	2.549	0.0025
Equitability J	0.4522	0.8191	0.0001
Fisher alpha	2.11	3.661	0.0015
Berger–Parker	0.6804	0.2378	0.0001

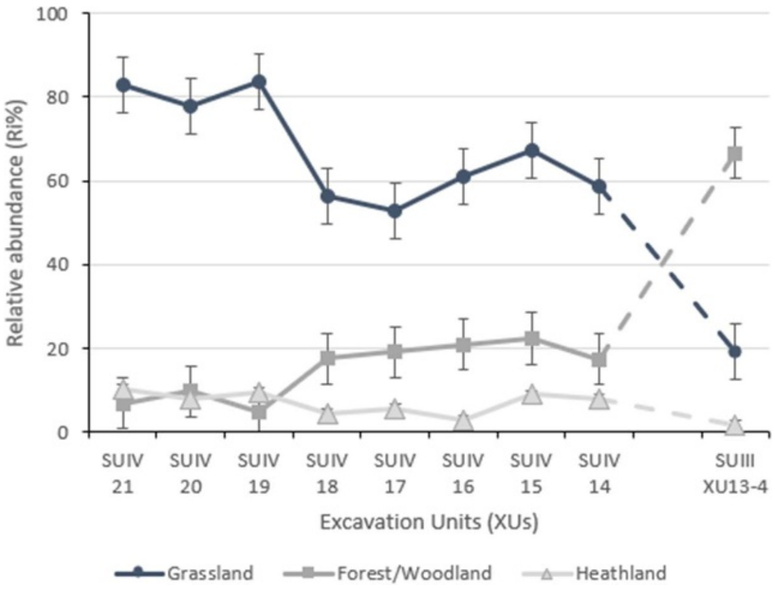

Figure 6. Plot of combined species relative abundances of mammals in the three vegetation communities for each excavation unit of stratigraphic unit IV (SUIV) and the combined excavation units of stratigraphic unit III (SUIII) from Square D9, Beeton Rockshelter. Dashed lines indicate reworked and therefore time averaged strata. Data from Table 2b.

important mutton bird rookeries and lungtalanana. Clarke Island, the third largest island in the Furneaux Group (Brothers et al., 2001), is a valuable conservation area. Unfortunately, little is known of its pre-European mammal fauna. The island is not known to hold zooarchaeological assemblages and its historical fauna was poorly documented. But during glacial periods the Furneaux Group was a single land mass. Therefore, fossil mammals from Beeton Rockshelter should be representative of the mammal fauna that once occurred on the Furneaux Group in general, including lungtalanana.

Lungtalanana appears to provide suitable habitat for *Rattus lutreola*, *P. higginsi*, *V. ursinus*, *Perameles gunnii*, or *I. obesulus*. Even though the Beeton Rockshelter assemblage shows that *M. fuscus* experienced extensive population decline on Badger Island, it still occurred there during the Holocene, and lungtalanana's extensive native grasslands (Natural and Cultural Heritage Division, 2014a) should provide suitable habitat for it to thrive. Assuming threatening processes (predation by feral cats, wildfire, habitat fragmentation, and degradation) caused by domestic- and feral-introduced herbivores and habitat alteration caused by logging and invasive weeds (Green and Osborne, 2003; Green et al., 2008; Woinarski et al., 2014) are controlled or eliminated, and suitable genetic stock is available, any of these species might benefit from translocation to Badger Island and lungtalanana.

Mastacomys fuscus is rarely considered for reintroduction to islands because it is mainly thought of as an alpine species. *Mastacomys fuscus* is a specialist graminivore (grass eater) that lives predominately in wet grassland, sedgeland, and heathland, but has also been occasionally recorded in wet sclerophyll forest with dense grassy undergrowth. While it currently occurs at alpine to subalpine elevations in south-eastern Australia and in button-grass habitats of western Tasmania, it also lives in wet coastal heath and nearby grasslands in Victoria (Warneke, 1960; Seebeck, 1971; Wallis et al., 1982; McDowell et al., 2023). The fossil record shows that *M. fuscus* lived at lower altitudes in the past than in the present day across much of south-eastern Australia, and that it occurred near sea level in the Coorong, Fleurieu Peninsula, and Kangaroo Island of South Australia (McDowell, 2013; Adams et al., 2016; Fusco et al., 2016). In addition, Henderson and Nest (2024) recently recovered *M. fuscus* hair from a Spotted-tailed Quoll (*Dasyurus maculatus*) scat collected approximately 50 km SW of the endangered Barrington Tops *M. fuscus* population in New South Wales. The scat was found in mixed sclerophyll forests and grassy eucalypt woodlands that have been fragmented by mining and farming. This suggests that *M. fuscus* can tolerate warmer and/or drier environments than the alpine areas where it is typically found today (McDowell et al., 2023).

Mastacomys fuscus fuscus (the Tasmanian subspecies) is considered 'near threatened' and decreasing according to the IUCN Red List (IUCN, 2024), while *Mastacomys fuscus mordicus* (the mainland subspecies) is listed as 'endangered' by the Australian Commonwealth (https://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=87617), and occurs in low-elevation habitats. Therefore, we strongly recommend that *M. fuscus, P. novaehollandiae*, and *Dasyurus viverrinus* (Eastern Quoll) be considered for reintroduction to Badger Island and lungtalanana. These islands may be too small to carry a population of *D. viverrinus* but provide highly suitable habitat for the species (Barlow et al., 2021).

Conclusion

The Beeton Rockshelter assemblage provides valuable insights into how mammals responded to Pleistocene–Holocene climate change and sea-level rise. *Mastacomys fuscus* dominated the Pleistocene portion of the fossil assemblage, suggesting extensive grasslands existed in the region at that time. In the Holocene, grassland-dwelling species had declined in relative abundance and were partially replaced by forest/woodland species, particularly *P. higginsi*. However, *M. fuscus* was still the most common species recovered from Holocene strata, showing that despite being thought of as an alpine species, it can prosper at or near sea level, provided suitable habitat exists (a finding reinforced by the long-term species distribution modeling reported in McDowell et al., 2023).

Faunal remains recovered from Beeton Rockshelter demonstrate strong trends of Pleistocene–Holocene faunal change that echo those observed in Tasmania's fossil record over the same time period (McDowell et al., 2022). Therefore, faunal change trends observed in the Beeton Rockshelter assemblage are best explained by vegetation shift rather than effects of isolation and island-area reduction. Given the small sample size, fossil assemblages from other small landbridge islands such as the zooarchaeological assemblage excavated from Prime Seal Island (Brown, 1993) could be studied to corroborate our findings and fill gaps in the Beeton Rockshelter record.

For conservation recovery programs, the Beeton Rockshelter fauna provides a list of mammals that could be reintroduced to a number of islands in the Furneaux Group. However, an in-depth analysis of social, cultural, and environmental values would be essential to ensure the animals recommended for reintroduction are indeed suitable for the islands. As the managing organization, these decisions are the domain of the TAC and the Tasmanian Aboriginal community. As always, the success of any reintroduction program is subject to the eradication or management of exotic predators and competitors and demographic and genetic considerations (Morris et al., 2021).

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