Small game hunting in montane rainforests: Specialised capture and broad spectrum foraging in the Late Pleistocene to Holocene New Guinea Highlands

Dylan Gaffney[1]*, Glenn R. Summerhayes[2, 3] Sindy Luu[2, 4], James Menzies[5], Kristina Douglass[6], Megan Spitzer[7], Susan Bulmer[†]

1. Department of Archaeology
   University of Cambridge
   Cambridge, CB2 3DZ
   United Kingdom

2. Archaeology Program
   School of Social Sciences
   University of Otago
   Dunedin, 9054
   New Zealand

3. Archaeology Program
   School of Social Science
   University of Queensland
   St Lucia, QLD 4072
   Australia

4. Department of Anatomy
   University of Otago
   Dunedin, 9054
   New Zealand

5. School of Biological Sciences
   University of Adelaide
   Adelaide, SA 5005
   Australia

6. Department of Anthropology and Institutes for Energy and the Environment
   The Pennsylvania State University
   University Park, PA16802
   United States of America

7. Bird Division
   National Museum of Natural History
   Smithsonian Institutions
   Washington, DC
   United States of America

[†] Deceased

* Correspondence: dacg2@cam.ac.uk

Abstract

Moving into montane rainforests was a unique behavioural innovation developed by Pleistocene *Homo sapiens* as they expanded out of Africa and through Southeast Asia and Sahul for the first time. However, faunal sequences from these environments that shed light on past hunting practices are rare. In this paper we assess zooarchaeological evidence from Yuku and Kiowa, two sites that span that Pleistocene to Holocene boundary in the New Guinea Highlands. We present new AMS radiocarbon dates and a revision of the stratigraphic sequences for these sites, and examine millennial scale changes to vertebrate faunal composition based on NISP, MNI, and linear morphometric data to shed light on variability in hunting practices, processes of natural cave deposition, and the local palaeoenvironment at the end of the LGM through to the Late Holocene. We show that Yuku was first occupied at least c. 17,500 years ago and that Late Pleistocene–Early Holocene hunters targeted a wide range of small-bodied and agile species from the mid-montane forest, with a particular focus on cuscus (*Phalanger* spp.). At Kiowa, occupied from around 12,000 years ago, a similar range of species were targeted, but with an added emphasis on specialised *Dobsonia magna* fruit bat hunting. We then integrate other zooarchaeological data from the wider Highlands zone to build a model of generalist-specialist hunting dynamics and examine how this more broadly contributes to our understanding of tropical foraging during the Late Pleistocene and Holocene.

Key words: Rainforest hunter-gatherers; LGM, zooarchaeology; marsupials; Sahul; New Guinea

1. Introduction

During the Late Pleistocene and Early Holocene, *Homo sapiens* began to disperse into a wide variety of challenging and marginal ecological zones (Boivin et al., 2013; Rabett, 2018) an adaptive radiation which necessitated novel, innovative behavioural transformations to meet subsistence needs. Moving into dense tropical rainforests was one such example of this diversification, during which hunter-gatherers were confronted with challenges to navigation, raw material acquisition, and, particularly, food procurement under the canopy (Roberts et al., 2016). Movements into high altitudes represent a similar stretching of human adaptive flexibility and were associated with their own challenges for locomotion and thermoregulation, particularly given the sheer terrain and reduced temperatures high above sea level (Moore et al., 2000). However, despite previous work examining adaptation to rainforests and montane zones (e.g. Bailey and Headland, 1991; Pitblado, 2017; Roberts and Petraglia, 2015; Vogelsang et al., 2018), we have a more limited understanding of the evolutionary constraints and opportunities offered by the combination of these environments. It remains unclear whether these combined factors exacerbated difficulties of subsistence maintenance in montane rainforests (Gaffney and Denham, in press), and whether humans moving into these environments organised themselves as broad-spectrum foragers or were prompted to specialise in hunting a limited number of species, targeting ‘sweet spots’ (see Allen and O’Connell, 2008) of high-ranked game and calorie-rich plant foods. Moreover, the dynamics of how hunting practices shifted in response to environmental changes through time, especially as extreme cold conditions during the Last Glacial Maximum (LGM) meliorated at the terminal Pleistocene–Early Holocene, and as megafauna disappeared in many regions, need to be explored in more detail.

Globally, rainforest populations shared commonalities in their environments in terms of abundant vegetation, often scarce large-bodied fauna, stable temperatures, and low visibility, which led to convergent adaptive responses in the form of foraging practices with an emphasis on readily available forest resources such as wild plant foods and small animals (Denham, 2016a). Since the Late Pleistocene, many tropical forest environments including parts of Sahul (the former continent formed of Australia, New

Guinea, and Tasmania), Southeast Asia, and the Neotropics, were actively managed through burning and tree felling to facilitate hunting and settlement amongst the clearances (Gnecco, 2003; Haberle et al., 2001; Hunt et al., 2012; White et al., 2004). However, in each region, historical and ecological contingencies led human groups to respond to these novel environments in a variety of locally specific ways. In South Asia, for instance, foraging groups mitigated ecological challenges by innovating projectile technologies and specialised in hunting small, mobile, and hard-to-catch game from the upper canopy, including monkeys and squirrels (Langley et al., 2020; Wedage et al., 2019), while in Mainland Southeast Asia hunters devised composite technologies and trapping to maintain a broad spectrum subsistence base, particularly targeting mixed resources of mid-sized terrestrial fauna and smaller arboreal species (Piper and Rabett, 2009; Shoocongdej and Wattanapituksakul, 2020). These capacities to maintain broad spectrum, innovative, and sometimes experimental subsistence behaviours, while at the same time intensively monopolising locally abundant resources when they were encountered, seems to have led to our species' long-term perseverance in these environments, at least throughout Marine Isotope Stage (MIS) 3 to MIS-1.

Moving into montane tropical forests was a unique behavioural innovation developed by Pleistocene *Homo sapiens* as they moved out of Africa and through Southeast Asia and Sahul for the first time. Within Africa, human occupation of shelters in the Ethiopian Highlands from 53,000–38,000 years ago may have been associated with tropical forest and savannah mosaics, in which people targeted large mammalian game, but the poorly preserved palaeoenvironmental evidence makes further conclusions difficult (Brandt et al., 2012, 2017). However, these movements occurred contemporaneously with the first forays into montane New Guinea, during MIS-3, suggesting this was part of the broader ecological diversification of our species. Although the first clear evidence for montane rainforest occupation comes from 49,000–43,000 years ago in the Ivane Valley of southeast New Guinea (Summerhayes et al., 2010), preservation issues in such environments mean that faunal sequences documenting the Pleistocene are incredibly rare (Summerhayes et al., 2017). It has therefore been difficult to assess the nature of subsistence in these environments, and how people responded to fluctuations in climate. This paper therefore presents zooarchaeological evidence at the sites of Yuku and Kiowa in the Bismarck Range of the New Guinea Highlands (Fig. 1) to investigate how people in the mountain forests of northern Sahul strategised their hunting practices, including how processes of broad spectrum and specialised hunting were integrated within the wider landscape. Faunal information from these important Pleistocene–Holocene records have remained unpublished (Bulmer, 1979) or have only been reported in summary form (Bulmer, 1982; Sutton et al., 2009). In particular, the paper presents new AMS radiocarbon dates and a revision of the stratigraphic sequences for these sites, and examines millennial scale changes to vertebrate faunal composition to shed light on modifications to hunting practices, processes of natural cave deposition, and the local forest environment at the end of the LGM from c. 17,500 years ago through to the Late Holocene. This was a time of substantial environmental change and social transformation in the montane zone. Did these ecological changes encourage increased hunting specialisation as a mode of risk reduction to cope with these challenging and unpredictable environments?

Figure 1. Yuku and Kiowa rockshelter sites situated within the changing environments of the New Guinea Highlands. Generalised palaeoenvironments of (A) northern Sahul at the LGM and (B) New Guinea in the Holocene (redrawn from van der Kaars, 1991) with colour key to environmental zones shown below; inset (C) shows key Highlands sites mentioned in the text (Photos courtesy of Dylan Gaffney, Anne Ford, and Ben Shaw).

2. Background

2.1. Quaternary faunal distributions in highland New Guinea

The New Guinea Highlands consist of steep valley systems and mountain peaks over 1200 m above sea level (asl), which run west to east through the interior of the island (Fig. 1). The majority of today's settlements are located within a series of wide inter-montane valleys between 1400 m and 2000 m asl (Löffler, 1977), but smaller hamlets and hunting camps are sometimes present above 3500 m asl (Brookfield and Allen, 1989). Although New Guinea's rainforests are consistently warm and humid at sea level, in altitudes above 1500 m asl, and particularly above 2500 m asl, air temperatures can reach freezing point and there are periodic frosts (Brookfield and Allen, 1989). Ecotonal clines between the coast and mountains are reflected by vegetational changes, with nut-bearing beech trees (*Nothofagus, Lithocarpus*, and *Castanopsis*) dominating the lower montane rainforests, but pines (Phyllocladus) and conifers (*Dacrycarpus, Podocarpus* and *Papuacedrus*) more common in cloud forests at higher altitudes (Walker and Flenley, 1979). Today, forest growth does not extend beyond 3000–3600 m asl and above this are open environments with grasslands, fern trees, and ericaceous shrubs, while bare rocky ground, snow, and glaciation occur above 4500 m asl (Flenley, 1984).

In terms of vertebrate fauna, although the New Guinea Highlands is a region of high species richness and endemism (Miller et al., 1994), it is depauperate with regards to the number of mammal families present; that is, the region today lacks many types of placental and marsupial mammals present in adjacent regions, especially larger bodied megafauna (Menzies, 2011: 4). Extant marsupial families include small arboreal varieties such as cuscus (Phalangeridae), ringtail possums (Pseudocheiridae), striped possums and sugar gliders (Petauridae), and tree-kangaroos (Macropodidae), and terrestrial animals such as bandicoots (Peramelidae), quolls (Dasyuridae), wallabies and pademelons (Macropodidae), as well as one family of monotreme echidnas (Tachyglossidae) (Flannery, 1995). Only three species of pteropodid fruit bats currently occur above 1500 m asl: *Dobsonia magna* which commonly roosts in caves, the blossom bat *Syconycteris hobbit,* and the once-thought-extinct *Aproteles bulmerae* which was rediscovered at 2300 m asl in the 1970s (Hyndman and Menzies, 1980). The only non-volant, placental mammals native to the Highlands are rodents (Muridae) which display substantial variability in body size, from the giant *Mallomys* spp. weighing up to 1500 g to smaller varieties growing to less than 50 g (Menzies and Dennis, 1979). A number of ground dwelling brush turkeys (Megapodidae), dwarf cassowaries (*Casuarius benneti*), and quails (Phasianidae), a rich array of parrots (Psittaciformes), a hornbill (*Rhyticeros plicatus*), and birds of paradise (Paradisaeidae), along with monitor lizards (Varanidae), frogs (Anura), and large pythons (Pythonidae) are also found throughout the interior. Alongside this, pigs (*Sus scrofa*), dogs (*Canis familiaris*) and chickens (*Gallus gallus*) were introduced during the Late Holocene and are now important for subsistence, exchange, and social relationships (Sutton et al. 2009). Dogs are particularly used as hunting companions (Bulmer, 1968), while pigs are often left to roam, and feral populations are hunted in the bush (Hide, 2003).

However, throughout the Quaternary, floral and faunal distributions have shifted in response to climatic change and human activities. LGM temperatures in the inter-montane valleys were reduced by on average 7 ^{O}C, meaning that the tree line was compressed down to around 2200 m asl, with expansive sub-alpine grasslands above that (Haberle, 1993; Hope, 2009; Summerhayes et al., 2010), within which now-extinct megafauna such as Diprotodontids and *Protemnodon* roamed until at least the end of MIS-3 (Flannery et al., 1983). Following the LGM, the terminal Pleistocene marked a period of rapid and unstable climatic amelioration that resulted in warmer average temperatures, leading to a retreat of open terrain and the expansion of the montane rainforest upslope (Hope et al., 1983). Although deglaciation began from around 15,000 years ago (Flenley and Morley, 1978), essentially modern conditions only became stable around 8500 years ago (Hope and Haberle, 2005). It is therefore likely that the current distribution of many animal species is in part due to these climatic shifts (Hope et al., 1993), and in part due to clearances by humans (Dwyer, 1978), with resultant forest regrowth and grasslands initially being repopulated by opportunistic and adept coloniser species, and forest fragmentation exacerbating processes of divergence, endemism, and extinction.

2.2. Hunting and settlement in the New Guinea Highlands

Because the availability of game was predominantly restricted by habitat type and altitude, humans passing through different ecotones would have been presented with variable hunting opportunities. These factors, along with the different behaviours of the species being hunted, necessitated a diverse range of tracking, capture, and butchery techniques. Ethnographic surveys from across the New Guinea Highlands draw attention to the importance of bows and arrows, spears, clubs, and throwing stones for hunting (Bulmer, 1968). In the Eastern Highlands, hunters identified areas with signs of recent animal activity during the day and returned to these areas, laying in ambush overnight for nocturnal animals, or patrolled along tracks in the hope of encountering game (Dwyer, 1974). In the Western Highlands, a number of strategies were employed including poking in the undergrowth for terrestrial game, shooting arboreal animals with bow and arrow, and laying snares across branches and vines (Fig. 2). Nocturnal and arboreal mammals were commonly hunted by men, alongside terrestrial marsupials, birds, and large reptiles, while women and children tended to hunt for smaller frogs, rodents, grubs, and insects (Bulmer, 1972). Fruit bats were also easy prey due to their habit of roosting in caves, meaning they could be shot with arrows and slings, or smoked out and then netted (Hyndman and Menzies, 1980). In some accounts, up to 1600 bats were killed at a time from the same cave (Salisbury, 1965), being cooked but not skinned or gutted (Dwyer, 1975).

The by-products of many animals have been especially important to Highlanders as well. For instance, cassowary tibiotarsi were often sharpened into daggers (Zegwaard, 1959) and spatulae (Bulmer and Bulmer, 1964: 55) and their manufacture involved the careful removal of cancellous bone and polishing of the cortical bone (Dominy et al., 2018). The eggshell and feathers of cassowary, along with the plumes of bird-of-paradise were also collected for adornment and trade, as too were marsupial furs (Williams, 1940: 20; Salisbury, 1962: 90; Sillitoe, 1988; Swadling, 1996).

Although the majority of these ethnographic observations indicate hunting practices were diverse, they also imply that hunting contributed little to overall subsistence maintenance. Many scholars have suggested that hunting was more energetically costly than its returns. Dwyer (1974, 1980) for instance, noted that Siane hunters on Mt Elimbari obtained only 1 kg of meat from around 25 human hours invested. Put another way, this means that only about 55 kilocalories of energy were obtained for every 100 kilocalories invested. This has led to the presumption that people were not able to permanently occupy highland rainforests until they could supplement wild animal and plant foods with agricultural crops (e.g. Sillitoe, 2003). It is important to note, however, that although hunting today remains subsidiary to horticulture and pig husbandry in densely populated inter-montane valleys, in sparsely populated areas — simulating lower densities of occupation during the Late Pleistocene and Early Holocene — hunting contributes important animal protein to the diet (Bulmer, 1972).

Moreover, as Ralph Bulmer (1976) has demonstrated through ethnozoological studies around the Kaironk Valley, the bones that have survived to be studied by archaeologists do not only vary according to the availability of game in the local area, but also the hunters' interest in different animals for ritual or ceremonial purposes, social and dietary restrictions on eating certain species, the prestige produced by hunting specific prey, and a multitude of other factors. Amongst the Siane, hunting was not usually motivated by individual subsistence requirements but by reciprocal obligations to provide bushmeat to others in the community, as marriage gifts, as a method for easing tensions between feuding kin, and as a way to provide for injured, young, or elderly members of the group (Dwyer, 1985). In this sense, hunting practices and food getting cannot be separated from practices of socio-political maintenance and reorganisation. Additionally, apart from a few venomous snakes, and cassowaries which have a deadly kick, today's native Highlands fauna presents very little risk for humans — the largest native mammalian carnivore being a quoll weighing about 600 g — and hunting could be undertaken with little attention to risk-reduction strategies.

Figure 2. Common hunting methods in the New Guinea Highlands: a) Maring man pokes forest undergrowth with bush knife in search of marsupials and other game; b) Maring man shoots into the canopy with bow and arrow; c) Maring snare laid across branch; d) Kalam men with possum after successful hunt; e) juvenile bandicoot caught by hand amongst grassland and scrub in Kaironk Valley (Photographs: a-d Roy Rappaport 1962-1963, University of California San Diego, Special Collections and Archives, MSS 0516; e) Dylan Gaffney 2015).

3. Archaeological context

The archaeological sequences from Yuku and Kiowa document crucial periods of climatic change from the Pleistocene to the Holocene and shed light on how human hunting and gathering strategies were transformed during this period. The sites were originally excavated in 1959-1960 by Susan Bulmer, who recovered large lithic and faunal assemblages that were used to construct the first tentative culture history for the Highlands (Bulmer, 1966a; Bulmer and Bulmer, 1964).

3.1. Excavations at Kiowa, 1960

Kiowa (1500 m asl) is a small limestone rockshelter that connects with larger caverns containing bat colonies on the slopes of Mt Elimbari, Chimbu Province (Bulmer, 1960). On-site isotopic evidence from bat, rodent, and marsupial teeth suggests that throughout the terminal Pleistocene and Holocene Kiowa was located under the forest canopy (Roberts et al., 2017). A small tributary to the Mae River is located about 20 m from the site, which provided most of the lithic raw material for on-site tool making and use (Gaffney et al., 2015a). The presence of marine shell and pottery suggests trade connections with the coast and other parts of the Highlands were operating by the Late Holocene (Gaffney et al., 2016, 2019).

The stratigraphy was well differentiated with layers of mixed ash and orange clay interleaved with defined ash lenses (refer to Table S1 for a full description). Conventional radiocarbon dating established that Kiowa was first occupied during the terminal Pleistocene, with regular occupations continuing until the Mid-Late Holocene (Bulmer, 1966b). A thick surface soil (Level 1) initially suggested that the site had not been regularly occupied during the Late Holocene (Bulmer, 1964: 260); however, AMS dating has demonstrated that sporadic visitation in fact continued until the recent past (Denham, 2016b). Level 2 was compact and implied that after abandonment, grass grew over the site and subsequent organic processes altered and mixed the upper habitation horizons. Below that, the top of Level 3 represented the most recent undisturbed habitation deposit, and ash from the uppermost *in situ* hearth returned a date of 4,840±140 BP (Y-1371). All underlying levels down to base of excavations were characterised by radiating ash lenses, denoting short-duration hearths. Many of these lenses distinctly separated the strata implying the deposit was relatively undisturbed, especially in the southwest corner of the East Extension. However, in Level 8 thin laminations suggested that the former ground surface sloped towards the cave entrance and interior rock face, while depressions in the centre of excavations were interpreted as shallow fireplaces dug into the ground with ash radiating from them. The Level 10 date of 9,300±200 BP (Y-1367) obtained by Bulmer represents ash from the deepest *in situ* hearth at 12 ft (3.7 m) below surface. From Level 9–10, limestone boulders began to inhibit excavations and digging ceased at 15 ft (4.6 m) deep in Level 12C. Bulmer's basal date from Level 12A dating to 10,350±140 BP (Y-1366) represents scattered charcoal atop loose scree at 14.5 ft (4.4 m) below surface, and no evidence for fires was identified below this. It is possible that all Level 12A–12C artefactual material derived initially from 12A, the base of which was loose water-lain scree allowing heavier lithics to work downwards through the deposit. This scree was also present at the base of excavations, indicating that a stream had originally flowed through the caves, and that this stream had periodically reappeared throughout Level 12.

3.3. Excavations at Yuku, 1959

Yuku (1280 m asl) is a limestone rockshelter that lies in the Lanim gorge near the junction of the Yuem and Lanim Rivers on the northwestern slopes of Mt Hagen (Bulmer, 1960). Bulmer (1966a) suggested that the cave was first occupied as a hunting camp when it was on the bank of the river, but that the water has subsequently changed its course. At the time of excavation, the site lay within horticultural land and was occasionally used as a place for cooking game, including marsupials, pythons, and eels. Unlike Kiowa, the site did not have immediate access to bat roosts, but other caves in the vicinity did (Bulmer, 1960).

The two excavation squares (Sq 1 and Sq 2) were initially laid out at right angles to the rock face to avoid disturbance from cooking pits visible on the surface. The baulks between these squares (Baulk 1-2) and between Sq. 1 and the shelter wall (South Baulk) were later excavated, completing a 14 ft (4.3 m) long trench (TR). Finally, an adjacent unit to the east (Sq 1A) was excavated, removing the last of the undisturbed deposit at the site.

The stratigraphy, composed of mixed ash lenses and clay horizons, was divided into levels based on changes to sediment colour and texture (see Table S2 for a full description). Thick levels with no clear changes to the stratigraphy were subdivided in order to constrain the depth of excavation. Level 1 comprised soft grey sediment and there is evidence that cooking pits and post holes were dug down from Level 1 into Level 2. Disarticulated and fragmentary skeletal material was found in Sq. 2 Level 1, associated with a large spherical stone of a type commonly buried on the abdomen of dead Kyaka Enga people who inhabit the area today and claim to have inhabited the area for at least six or seven generations (Bulmer, 1960). In Sq. 1 Level 3, a second badly disturbed human burial was capped by Level 2 indicating that the bones had been placed already-disarticulated in a small hole from Level 2 or 3. In Sq. 1A, a third burial lay within Layer 3A, with articulated vertebrae showing the individual was lying on their left side. A Crevice (CR1), present behind surface boulders, was filled with uncemented deposit and was excavated separately and assigned stratigraphic levels relative to the deposit in the main Trench. As such, the Yuku deposit can be considered visibly disturbed at least down into Level 3. Disturbed ash lenses extended throughout Sq 1, Baulk 1-2, and Sq 2 but ended around 1.5 m before the drip line.

Level 3 to Level 5 represented progressively undifferentiated clays along with patches of calcified and cemented limestone rubble. In the lower parts of Level 5, a series of clay and ashy clay lenses separated the upper deposits from Level 6–7, which again were composed of cemented rubble fragments. These calcified layers likely formed over long periods due to roof fall creating rubble as well as periodic rainwater running down the limestone shelter roof and pooling on the shelter floor. Bulmer (Bulmer, 1975) suggested that the absence of ash, and the small number of lithics, bones, and eggshell in Level 6 denotes abandonment or infrequent habitation. Below, Level 7 contained ash lenses interleaved with heavily cemented red clay and rubble. Excavations ceased at a depth of 9 ft (2.7 m) when large water-rolled boulders were reached and could not be removed. However, a small crevice (Crevice 2) was present in Sq. 1A Level 7, which extended down at least to 12 ft (3.6 m) and could not be fully excavated due to its narrowness; it contained loose red clay, limestone rubble, and ash, alongside non-diagnostic bone and snail shell.

Initial dating targeted the middle of the deposit (Level 3A, 4C, and 5B) and suggested the shelter was occupied by at least the Early Holocene or terminal Pleistocene (Bulmer, 1975). This dating primarily derived from animal bone, which generated substantial inconsistencies between the collagen and apatite components (Table S2). A single more reliable date was obtained on wood charcoal and demonstrated that the middle of the deposit likely corresponded with the Early Holocene at 9,780±150 BP (ANU-358). However, the archaeological sequence extended 1.5 m below the deepest material able to be dated with conventional techniques in the 1970s. Bulmer (2005) therefore extrapolated rates of deposition to conclude that the site was first occupied by about 15,000 BP. Recent AMS analysis subsequently directly dated macrobotanical remains from Levels 2–5C and all but one of these returned dates within the last millennium BP (Denham, 2016b). This drew into question the Yuku sequence, suggesting that the deposit was heavily disturbed, but that this had not been identified during excavation due to poor visibility and a complex stratigraphy impacted by natural and human processes. It also implied that previous analyses of lithic technological change (Bulmer, 1977, 1964a), plant micro-fossil distributions (Horrocks et al., 2008), and faunal turnover (Bulmer, 1982; Sutton et al., 2009) at the site were unreliable.

4. Methodology

To examine changes to hunting practices over time, and to evaluate the integrity of Kiowa and Yuku, we undertook AMS radiocarbon dating and critically re-examined the stratigraphy to provide a new appraisal of the temporal sequences at both sites. We then generated zooarchaeological data from the available faunal assemblages at Kiowa and Yuku and contextualised these results within our revised chronostratigraphic sequences.

4.1. Radiocarbon dating and stratigraphic reassessment

A new AMS dating programme was undertaken at the Energy and Environmental Sustainability Laboratories, Pennsylvania State University, to assess the stratigraphic integrity at both sites. At Kiowa, the intention was to refine the established sequence and to evaluate the rate of deposition and any potential disturbance. At Yuku, the aim was to clarify the initial timing of occupation, and how deeply the aforementioned disturbance reached. We selectively targeted cassowary (*Casuarius sp.*) and other bird spp. eggshell from key levels at both sites, which were identified under optical microscopy and scanning electron microscope. Targeting these remains with no inbuilt age improves on previous attempts at chronometric hygiene (see Higham, 1994). By directly dating eggshells it also provides secure and well-dated evidence for bird exploitation throughout the Late Pleistocene and Holocene.

4.2. Zooarchaeological analysis

During the 1960 excavations at Kiowa sieves were not used and specimens were collected by hand. Following excavation, all cranial and mandibular material along with worked bone, eggshell, and large bones were kept for later analysis. However, due to transportation difficulties only a small subsample of post-cranial material filling two c. 30 x 30 cm bags from each level was retained (Bulmer, 1966b: 94). As such, the assemblage is likely to be biased towards larger animals, and robust quantitative analysis is not possible with the post-cranial material (Sutton et al., 2009). Similarly, during the 1959 excavations at Yuku sieves were not used and material was collected by hand, but all excavated bone was retained for further analysis. Due to disturbance identified in the stratigraphy at Yuku (see section 5.3), temporal trends in the assemblage cannot be examined on the millennial scale like at Kiowa, instead being divided into three analytical units: Analytical Unit I (Levels 1-3C), Analytical Unit II (Levels 4A-5C), and Analytical Unit III (Levels 6-7B).

Initial zooarchaeological identifications were produced by J. Menzies and G. Fenner using reference collections at the Department of Biology, University of Papua New Guinea. Linear morphometric analysis was undertaken on cuscus teeth (*Phalanger* spp.) using Vernier callipers in order to demonstrate species attributions. David and Susan Bulmer later undertook quantitative analysis of the total cranial assemblage in Auckland, New Zealand. The full details of this analysis have remained unpublished and this paper is the first attempt to compile a thorough account of the Kiowa and Yuku faunal sequences. We emphasise that these data derive only from the identification of cranial, mandibular, and dental elements, except for cassowary which includes post-cranial elements, primarily because complete skeletal reference collections for small mammals were unavailable to the analysts. A wider range of prey may have been hunted at the sites, especially those whose skulls do not preserve well. As such, the present data must be considered to provide a good indication of hunting breadth but may not reflect the total range of species deposited at the sites.

Given the fragmentary nature of cuscus (*Phalanger* spp.) remains, it was not possible to confidently differentiate between *Phalanger carmelitae* and *Phalanger vestitus,* which are morphologically similar and overlap in their altitudinal ranges. In this paper they are grouped as *Phalanger carmelitae/vestitus.* Moreover, the *P. orientalis* species complex is morphologically diverse (see Menzies and Pernetta, 1986; Flannery, Archer and Maynes, 1987; George, 1987; Groves, 1987; Norris and Musser, 2001; Helgen and Jackson, 2015) and the fragmentary crania and mandibles were considered insufficient to further delineate the specimens to the sub-species or population level.

High altitude varieties, living up to around 1400 m asl on mainland New Guinea, or sometimes to 1800 m asl on offshore islands, can usually only be differentiated by their darker colouring and woolly fur (Menzies and Pernetta, 1986). Although protein analysis suggests the variety present today between 1150-1200 m asl around Chimbu may be assignable to *Phalanger intercastellanus* (Colgan et al., 1993), the zoological specimens have since been revised to *Phalanger mimicus.* The small sample size of Colgan and colleagues' analysis (n=2) restricts further comment. More comprehensive mitochondrial DNA analysis suggests that within the *P. orientalis* morphotype, *P. mimicus* may represent a monophyletic clade, and one of the Chimbu samples initially analysed by Colgan and colleagues (1993) groups within this clade, alongside specimens morphologically identified as *P. orientalis, P. intercastellanus,* and *P. mimicus* from the Southern Highlands (Kealy et al., 2019). Based purely on the zooarchaeological analysis of cranial morphology, it is unclear where the Kiowa and Yuku remains should be assigned, and so the broad grouping of *Phalanger orientalis* sensu lato is retained, in accordance with summary data presented by Sutton and colleagues (Sutton et al., 2009), pending further taxonomic and archaeogenetic clarification.

The cranial, mandibular, and dental remains were quantified by number of identified specimens (NISP) and assigned to the lowest possible level of taxonomic classification. Minimum number of individuals (MNI) were quantified by tallying the most abundant skeletal elements represented for each taxon per layer, which usually consisted of either the right or left side of broken mandibles. Both NISP and MNI produce values that do not totally represent the target variable, which in this case is the number of different animals being hunted (see Lyman, 2008: 26). For instance, NISP can vary between species due to different taxa having different birth and death rates, especially amongst small mammals, and being subject to different butchery practices (Grayson, 1984). MNI represents only the minimum number of animals needed to account for the skeletal evidence and does not necessarily provide an accurate assessment of how many animals could have contributed to the sample (Allen and Guy, 1984). However, by presenting both NISP and MNI data it allows for the evaluation of consistency in frequency changes through time, as well as an assessment of fragmentation. The mean weight (g) of animals hunted at each site was estimated by multiplying MNI by body mass calculations reported in Dwyer (1983) and Flannery

(1995). Edible meat weights (g) were estimated for a selection of key game by multiplying MNI values with body mass and edible meat ratios. Edible meat ratios for a number of marsupial and rodent species are reported in Dwyer (1980).

5. Results

5.1. The revised chronostratigraphy at Kiowa

The AMS dating results presented in Table 1 and Figure 3 confirm that the sequence of Kiowa's East Extension, from which most archaeological material derives, is relatively undisturbed throughout the deposit. The deepest eggshell carbonate determinations from Level 12A closely corresponds with existing wood charcoal and bulk fire-ash dates, which suggest that the first human occupation began sometime between 12,000-12,400 years ago. Additionally, we confirm a Mid-Holocene date for the most recent undisturbed occupation in Level 3, with the overlying Level 2 being affected by bioturbation and probably representing a combined Mid-Late Holocene context. The new dates do suggest that there was minor mixing between levels due to slight movements of material down the deposit, or redeposition of older material in the middle of the sequence between Level 4 and Level 6, and between Level 7 and Level 8A which are inverted (Fig. 3B). It is also important to note that although the deposit was systematically excavated, the levels represent complex aggregations of clays, ash lenses and fire features such that the subtle geoarchaeological relationships between the deposits cannot be assessed without re-excavation. Despite this, depositional rates and sediment build up were relatively steady throughout the 4.6 m sequence, with very little evidence for disturbance.

Table 1. PSU radiocarbon dates on cassowary and other bird spp. eggshell carbonate from Kiowa. Calibrated dates given to two standard deviations using IntCal13 curve with Calib 7.1 (Southern Hemisphere curve not used due to site being only a few degrees south of the equator).

Code	*Site*	*XU*	*Level*	*Material*	*%Mod*	*±*	*$D^{14}C$ %*	*±*	*^{14}C age BP*	*±*	*Calibrated date BP (2σ probability)*
PSU-4370	Kiowa	EE	3	Eggshell carbonate (*Casuarius* sp.)	0.4820	0.0017	-518.0	1.7	5,860	30	6585–6567 (0.023) 6623–6619 (0.003) 6749–6626 (0.974) 6771–6769 (0.001)

PSU-4368	Kiowa	EE	4	Eggshell carbonate (Aves sp.)	0.4625	0.0018	-537.5	1.8	6,195	35	7179–6991 (0.954) 7238–7198 (0.046)
PSU-4369	Kiowa	EE	6	Eggshell carbonate (*Casuarius* sp.)	0.4719	0.0018	-528.1	1.8	6,035	30	6956–6790 (1.000)
PSU-4371	Kiowa	EE	8	Eggshell carbonate (*Casuarius* sp.)	0.3649	0.0018	-635.1	1.8	8,100	40	8826–8796 (0.017) 8880–8869 (0.005) 9135–8976 (0.963) 9179–9199 (0.008) 9238–9222 (0.007)
PSU-4367	Kiowa	EE	12	Eggshell carbonate (Aves sp.)	0.2737	0.0019	-726.3	1.9	10,410	60	12444–12061 (0.904) 12529–12453 (0.096)

Figure 3. Plan of Kiowa excavations and radiocarbon determinations relative to stratigraphic level. A: plan of Kiowa rockshelter site and excavated units, along with entrance to main cave system in the south. TR=Trench; MS= Main Square; EE= East Extension; EB= End Baulk; SE= South Extension. Red lines bordering EE denote stratigraphic profiles drawn in B and C (adapted from Bulmer, 1966b); B: the north face of the East Extension and End Baulk; C: the south face of the East Extension prior to excavation of the South Extension (adapted from Bulmer, 1966b). Dates include those previously reported by (Bulmer, 1964b) and Denham (2016a) alongside new PSU dates.

5.2. Kiowa faunal remains

At Kiowa, the faunal assemblage is dominated by Pteropodid fruit bats alongside arboreal marsupials, specifically several species of cuscus (*Phalanger* spp.), and, particularly in Mid-Late Holocene levels, terrestrial pademelons of the genus *Thylogale* and giant rats (Table 2). Minor components of the assemblage include arboreal ringtail possums (*Pseudochirops corrinae*, *Pseudochirops cupreus,* and *Pseudochirulus forbesi*), striped possums (*Dactylopsila trivigata*), trioks (*Dactylopsila palpator*), pygmy possums (*Carcatetus* sp.), sugar gliders (*Petaurus* sp.), and tree kangaroos (*Dendrologus goodfellowi*), along with terrestrial game ranging from *Dorcopsis* and *Dorcopsulus* wallabies, to echidnas (*Zaglossus* sp.), quolls (*Dasyurus albopunctatus* and *Phascolosorex dorsalis*), bandicoots (*Echimipera* sp. and *Peroryctes* sp.), and a wide range of rodents (Table 2). The largest animals occasionally hunted were the marsupial wolf (thylacine), dwarf cassowary (*Casuarius bennetti*), and pythons, which can all grow to over 20 kg. Although dwarf cassowary and python populations remain relatively stable in the Highlands, marsupial wolves are now extinct and extremely rare archaeologically, with only one confirmed mandible deriving from Level 9, dating to the Early Holocene (originally reported by Van Deusen, 1963). This is the most northern evidence of the thylacine known from Sahul.

Arboreal and terrestrial mammals held secondary importance to fruit bats (*Dobsonia magna* and *Aproteles bulmerae*) throughout most of the sequence, but cuscus became dominant in Level 2B (both in NISP and MNI counts), immediately following the most recent period of sustained occupation at the site (Fig. 4). This suggests that the site's more regular inhabitation throughout the Early to Mid-Holocene was facilitated by the immediately available bat colonies present inside the Kiowa cave systems, and that, during the Late Holocene, site function shifted to temporary use facilitating hunting in the forests. *Aproteles bulmerae* (Fig. 5), now locally extinct, was initially targeted in large numbers in Level 12A-10B, between 12-10,000 years ago, after which the population seems to have dwindled and there is only fleeting presence of this species in Early to Mid-Holocene levels. *Dobsonia magna* came to replace *A. bulmerae,* as the target of choice by Level 10A at the start of the Holocene. Here we use the term *D. magna* for the Sahullian variety of large *Dobsonia*, following Bergmans and Sarbini (1985); however, there is yet to be a clear taxonomic distinction made between *D. moluccensis* [Quoy and Gaimard 1830] or *D. molluccensis magna* [Thomas 1905].

Table 2. Kiowa NISP and (MNI) counts based on crania and mandibles.

Figure 4. NISP of two key families represented at Kiowa, showing changing emphasis from hunting large fruit bats (Pteropodidae) with a peak in Early-Mid Holocene levels, followed by an increasing uptake in hunting cuscus (Phalangeridae) in the Mid-Late Holocene.

Although fruit bats can roost socially at rockshelter and cave sites, if the *D. magna* remains were primarily resultant from natural deaths we would expect a more regular distribution throughout the sequence given the relatively steady rate of sediment deposition at the site. Anthropogenic accumulation is supported by burning on many specimens, and the fact that today *D. magna* roost inside the Kiowa cave system but not above the rockshelter site itself. However, many of the smaller bats present in comparatively large numbers in the middle of the sequence, particularly *Hipposideros diadema*, are likely to represent natural deaths or the incidental capture of these animals while netting *Dobsonia magna*, given the species are sympatric and known to roost in the same caves (Meinig, 2002). The presence of the intermediate-sized *Rousettus amplexicaudatus* is less clear and plausibly reflects incidental capture given this species is hunted in parts of Wallacea and Melanesia today (Hawkins, O'Connor and Kealy, 2016: 10).

Figure 5. Holotype specimen K-EE-12-31 for *Aproteles bulmerae*. Right cranial fragment with M^1-M^3 *in situ*.

The rodent assemblage at Kiowa is essentially modern in its composition, except for in Level 12C (Fig. 6). In this level, two rats cannot be assigned to species due to their fragmentary nature, but do not exist in the Highlands today; these include one individual with a very short face that is likely an arboreal *Melomys*, along with a large rat with massive molar alveoli and narrow incisors (unfortunately the molars are missing). Another group, the *Macruromys*, were common in this early level but are now very rare in the Highlands and absent from Mt Elimbari (see Table S3 for a comparison between present day fauna on Mt Elimbari and those present at Kiowa). Importantly, the small rats in this deposit also exhibit etching consistent with digestion and undoubtably derive from predator pellets, either a raptor (see Bochenski et al., 2018; Hawkins et al., 2018, 2019), or a quoll (see Miscamble and Manne, 2016). Birds of prey in the area are able to take down animals up to around 1 kg when they are on the ground, the size of small possums such as *Pseudochirulus forbesi* (Dwyer, 1983). However, the larger macropods in Level 12C suggest that, either there has been a post-depositional movement of bones down the deposit from Level 12A, or that humans and birds of prey fleetingly overlapped during initial shelter occupation, with the raptors later being dispossessed during the Holocene. Gnawing marks on mammal long bone from East Extension Level 10B and Level 12 suggest that rats were living commensally around the caves while humans were processing food there. In Holocene levels, the presence of giant rats like *Mallomys rothschildi* (Fig. 7), *Uromys caudimaculatus, Uromys anak,* and *Hyomys goliath* demonstrate people were collecting these animals particularly from the forest floor in primary rainforests, while water rats such as *Hydromys sp.* indicate animals were also taken from nearby streams and riverbanks.

Figure 6. Rodents present at Kiowa: a) *Anisomys imitator*; b) *Parahydomys asper*; c) *Macruromys major*; d) *Macruromys major*; e) *Uromys anak*; f) *Uromys anak*; g) *Hyomys goliath*; h) *Rattus niobe*; i) *Hyomys goliath*; j) *Pogonomys* sp.

Figure 7. Giant rat *Mallomys rothschildi* from Kiowa: a) K-EE-4-220 cranium fragment with *in situ* molars; b) K-EE-4-204 right mandible.

There is no clear evidence for volant birds being hunted at Kiowa, although two direct dates on eggshell attest to the possible exploitation of brush turkeys throughout the terminal Pleistocene to Mid-Holocene. All identifiable avian bone remains (NISP=28) are referable to the genus *Casuarius* (Table 3). Of these, fifteen specimens could be identified to dwarf cassowary (*Casuarius bennetti*), which is the only species present in the Highlands today. Hundreds of eggshell fragments, predominantly identified to the genus *Casuarius*, were also recovered and present some of the earliest recorded evidence of human exploitation of cassowary nests. The first positive instance of cassowary hunting comes from Level 12B, where two fragments of pelvis, one right distal femur, and three shaft fragments most likely derive from one individual. Cassowary remained intermittently present from Level 9 to Level 2A, with a substantial number found in excavation EE, Level 4 (29% of EE, NISP=8). All of the elements, with the exception of the two pelves from Level 12B, derive from hind limbs. The vast majority of specimens are tibiotarsi (57%), femurs (14%) and tarsometatarsi (14%), although one fibula and an ungual phalanx (claw) are also present. The absence of wing and cranial elements could be explained by their lower density making them susceptible to being crushed, but this does not account for the lack of the sternum, which is quite large and dense. More likely, because *Casuarius bennetti* are quite heavy birds weighing on average about 18 kg (Hutchins *et al.*, 2002: 80), carcasses were processed where they were caught and only the high value hind limbs were brought back to Kiowa. Being a flightless bird with extremely reduced wings, the femur and tibiotarsus of a cassowary would provide the most meat. This practice may also explain the near absence of other medium sized game such as Thylacine at the site.

Table 3. Cassowary NISP and (MNI) counts at Kiowa based on post-cranial remains.

	Excavation level																	
	Term. Pleistocene			Early Holocene							Mid-Holocene				Late Holocene			
Taxon	*12C*	*12B*	*12A*	*11*	*10B*	*10A*	*9*	*8B*	*8A*	*7*	*6*	*5*	*4*	*3*	*2B*	*2A*	*1*	*Total*

Casuarius bennetti		3(1)					1(1)			1(1)			8(1)	1(1)		1(1)		15 (6)
Casuarius sp.		3(1)							2(1)	1(1)			3(1)		2(1)	2(1)		13 (6)

Like the marsupial wolf (*Thylacinus* sp.), dog (*Canis* sp.) remains are rare at the site. One individual was identified from a fragmentary mandible on the ground surface of Level 1, which may be a trophy related to secondary burials on the cliff abutting the southern side of the shelter. Two other fragments of crania were identified in Level 3 and Level 7, assigned to either Thylacine or dog (see Letnic et al., 2012 for similarities in cranial morphology). Given that Level 7 is Early Holocene in age, it is worth emphasising that it is very unlikely that this material represents *Canis* sp. and is almost certainly assignable to *Thylacinus* sp. Seven specimens of pig were identified in Late Holocene levels (SE=2 and MS=5), including a mandible with one *in situ* tooth, a cranial fragment from a female individual, and disarticulated P_2, P_3 and P_4 from Level 2A, while a small fragment of maxilla was present at the base of Level 2B/top of Level 3 (here, conservatively assigned to Level 2B). Original faunal lists produced in the 1960s and 1970s also note that a single pig incisor and an *in situ* M^1 associated with a maxillary fragment were present from EE, Level 12A. The 12A material has subsequently been separated from the Bulmer Collection and as such morphological analyses and direct dating attempts cannot be made at this time.

The majority of remains deposited at Kiowa derived from animals below 500 g in size (median = c.436 g, mean = c.1233 g). In particular, the animals present in Level 12C were somewhat smaller than most of those from Levels 1-11, which is likely because both animal predators and human hunters contributed to the discard of bone (Fig. 8A). The species hunted during Level 12A-10B were of a comparable size to those targeted in Level 4-2B, however there was a marked reduction in the size of animals captured from Level 10A to Level 5. This is due to an intensive focus on *D. magna* bats during the Early to Mid-Holocene compared to the larger bodied *Aproteles bulmerae* hunted in the terminal Pleistocene and increasing reliance on cuscus and macropods in the Mid-Late Holocene.

Throughout the sequence, most animals derived from primary montane rainforest, although some species were capable of inhabiting more open secondary forest, meaning that it is possible that processes of clearance and regrowth were occurring nearby (Fig. 8B). Grassland species became increasingly common after Level

11-12A, but never formed a major contribution to the assemblage. The presence of grassland pademelons (*Thylogale* sp.) and bandicoots (*Echymipera* sp.) in almost every level suggests people were also hunting in grasslands at the edge of the treeline, several kilometres upslope, or in more open secondary bush, perhaps characteristic of the Mt Elimbari karst itself.

Figure 8. Size and habitat data at Kiowa by stratigraphic level. A: Average mass (g) of animals identified from MNI data (mean weight of species derives from Flannery 1995); B: Preferred habitat of animals identified from MNI data (this excludes bats; habitat data from Dwyer, 1983 and Flannery, 1995).

5.3. The revised chronostratigraphy at Yuku

The new radiocarbon dates for Yuku are presented in Table 4 and Figure 9. Two new dates from Yuku Level 6 allow us to push back initial occupation to at least 14,330±100 BP (PSU-4303), calibrated to around 17,000–17,800 years ago (very close to estimations that Bulmer (2005) made). The samples derive from Sq. 1 and Sq. 2 indicating that, at this depth, archaeological material is spatially consistent, with no evidence for disturbance. These new peri-basal dates also imply that occupation likely began 18,000 or more years ago, immediately following the LGM, and during a period of substantially colder temperatures.

Eggshell dates of 8,825±45 BP (PSU-4365) in Level 2, 8,705±45 BP (PSU-4366) in Level 3A, and 11,930±70 BP (PSU-4301) in Level 5C, are in association with charcoal and Pandanus dating to the last few hundred years. This suggests that processes of disturbance identified in Level 1–3 extended into Early Holocene and terminal Pleistocene Levels 4–5. We can therefore assume that there has been substantial mixing of archaeological material, particularly smaller objects, throughout the Holocene sequence. Loose limestone rubble, partially calcified and cemented together from Level 3 to Level 5, would have allowed small macrobotanicals and charcoal turned over through digging activities in Level 1–3 to work their way down the deposit. As noted above, the sequence can now be divided into three units of analysis based on post-depositional taphonomy: I) Levels 1–3 represent Mid-Late Holocene deposits heavily disturbed by burial and cooking activities, with Early Holocene material from below having been redeposited in secondary context; II) Levels 4–5 representing Early

Holocene and terminal Pleistocene deposits with potential contamination of small Late Holocene objects down the deposit; and III) Levels 6–7 representing LGM or immediately post-LGM deposits with no evidence of disturbance.

This disturbance particularly has implications for past analyses of plant microfossils at the site, which found high levels of *Elaeocarpus* (or possibly *Maesa* or *Sericolea*) pollen, alongside starches from lesser yam (*Dioscorea esculenta*) and another unidentified yam (*Dioscorea* sp.) throughout the sequence, as well as banana (*Musa* sp.) occurring from Level 3A and grasses (Poaceae) from Level 2 (Horrocks et al., 2008). As such, samples from Level 2 down to 5A represent the presence of these species at *some time* during the Holocene. However, the microbotanical identifications from Levels 6 and 7 should still stand and provide evidence for *Elaeocarpus* sp. or similar trees and tree ferns in the local area in the Late Pleistocene, immediately following the LGM.

Unfortunately, this disturbance also has implications for the archaeological phases put forward by Bulmer (1975; later revised in Bulmer 2005), based on changes to large stone tools, including distinctive waisted axes and pebble core tools. These remain the only well-studied component of the lithic assemblage (Bulmer, 1977; a more detailed analysis of the flake-core assemblage including refitting artefacts from different levels will be required to fully evaluate the disturbance to the lithic material). Moreover, the new interpretation of chronostratigraphy at Yuku has implications for previous studies of faunal turnover at the site (Sutton et al., 2009). The zooarchaeological data from Yuku will now be presented with reference to this revised chronostratigraphic interpretation and the three broad units of analysis.

Table 4. PSU radiocarbon dates on cassowary eggshell from Yuku. Calibrated dates given to two standard deviations using IntCal13 curve with Calib 7.1 (Southern Hemisphere curve not used due to site being only a few degrees south of the equator).

Code	*Site*	*XU*	*Level*	*Material*	*%Mod*	±	*D^{14}C %*	±	*^{14}C age BP*	±	*Calibrated date BP (2σ probability)*
PSU-4365	Yuku	Sq 1	2	Eggshell carbonate (Casuarius sp.)	0.3333	0.0018	-666.7	1.8	8,825	45	9964–9697 (0.700) 10045–9984 (0.089) 10153–10050 (0.211)
PSU-4366	Yuku	Sq 1A	3A	Eggshell carbonate (Casuarius sp.)	0.3384	0.0018	-661.6	1.8	8,705	45	9796–9545 (0.965) 9817–9804 (0.011) 9865–9876 (0.016) 9885–9876 (0.008)

PSU-4301	Yuku	Sq 1	5C	Eggshell carbonate (Casuarius sp.)	0.2264	0.0019	-773.6	1.9	11,930	70	13975–13569 (1.000)
PSU-4302	Yuku	Sq 1	6	Eggshell carbonate (Casuarius sp.)	0.1764	0.0019	-823.6	1.9	13,940	90	17212–16550 (1.000)
PSU-4303	Yuku	Sq 2	6	Eggshell carbonate (Casuarius sp.)	0.1680	0.0019	-832.0	1.9	14,330	100	17747–17127 (1.000)

Figure 9. Above: plan of Yuku rockshelter showing sequence of radiocarbon dates for each excavation unit. Below: stratigraphic profile of Yuku Trench (South Baulk, Sq. 1, Baulk 1-2, and Sq. 2) (adapted from Bulmer, 1966b).

5.4. Yuku faunal remains (2000 words)

Much of the Yuku faunal remains were highly fragmented and calcified, reducing the number of identifications. Throughout the sequence, cuscus (*Phalanger* spp.) formed the dominant component (Table 5). In particular *P. carmelitae/vestitus*, was almost always dominant, although crania and mandibles comparable to *P. orientalis* sensu lato reference specimens were also common. The basal cuscus remains from Yuku, Square 1A, Level 7B have been designated '*Phalanger* A' and appear to be a now extinct species. The remains most closely resemble *Phalanger carmelitae* in dental metrics (Fig 10A), although mandibular depth at the mid-point of the mandibular body is substantially greater than extant *P. carmelitae* (Fig 10B). This indicates Phalanger A was either an LGM Highlands population of *P. carmelitae* with a more robust than average jaw, or a large variety of *P orientalis*, some of which typically have a deeper jaw than other cuscus.

Secondary components of the assemblage include ringtail possums (Pseudocheiridae spp.) particularly in Analytical Units II–III, forest wallabies (*Dorcopsulus* sp.) and grassland pedemelons (*Thylogale* sp.), predominantly in Analytical Units I–II, and *D. magna* fruit bats throughout the sequence. Minor contributions include striped possums (*Dactylopsila trivirgata* and *Dactylonax palpator*), bandicoots (*Echimipera* sp. and *Perorhyctes* sp.), quolls (*Dasyurus albopunctatus*), rodents (Muridae), a small bat (Microchiroptera), pythons (Pythonidae), monitor lizards (*Varanus* sp.), forest dragons (*Goneocephalus* sp.), and freshwater eels (*Anguilla* sp.) (Table 5). Fragmentary terrestrial snail shell found particularly in Level 6 suggests they formed an important part of the diet during the initial period of occupation following the LGM. There is little evidence for medium sized game, although large pythons can grow to over 20 kg.

Table 5. Yuku NISP and (MNI) counts based on crania and mandibles.

Figure 10. Yuku *Phalanger* 'A' mandible measurements showing its close grouping with *Phalanger carmelitae* and *Phalanger sericeus* in its tooth row and premolar length, but separation based on mandibular depth.

Dobsonia magna contributed substantially less to the diet than at Kiowa, due to the fact that Yuku is not immediately connected to caves housing bat colonies. There is no evidence for bat hunting in Analytical Unit III, following the LGM, and the first evidence derives from Level 5C, which is likely to be contemporaneous with Kiowa at the terminal Pleistocene and Early Holocene. Later in time, *D. magna* appear to have contributed important raw materials to the tool assemblage, with bat long bones being used as 50 mm long needle points in Level 2. Other bone tools from unidentified species include a 22 mm long bone point in Level 3A-B, three broken bone points in Level 4B, a single broken point or arrow tip in Level 4C, and a broken mid-section from a small spatula or point in Level 5A.

Rodent remains include a variety of giant terrestrial rats from primary montane rainforest (*Xenuromys sp., Hyomys goliath, Mallomys rothschilde, Uromys caudimaculatus,* and *Uromys anak*), which were likely hunted as small game throughout the Late Pleistocene and Holocene. The presence of the much smaller *Melomys leucogaster, Melomys rubex, Rattus praetor* and *Rattus verecundus* may be natural inclusions given some of these species are proficient burrowers. The relationship between Late Holocene *R. praetor* in the Highlands and those on the coast remains to be fully understood; however, these animals become smaller and less spiny with increasing altitude (Taylor et al., 1982). Hulme-Beaman and colleagues (2018) suggest *R. praetor* constitutes a species complex and those from the New Guinea mainland belong to the subspecies *R. praetor coenorum,* which can be distinguished based on dental morphology.

Non-native animal remains were evident at the site including a number of pig teeth and cranial fragments (NISP= 36) and dog crania (NISP=2). The distribution of these remains is consistent with primary deposition in Analytical Unit I followed by disturbance and downwards movement into Analytical Unit II. Of the *Sus* sp. remains, 17% (NISP=6) were excavated from Level 3A-C, 53% (NISP=19) from Level 2, and 28% (NISP=10) from Level 1, however only a single element was recovered from Level 5A. Half of the pig remains derived from juvenile and even infant individuals, with burning marks suggesting the capture of feral pigs in the surrounding forest, and cooking on site (ethnographically, domestic pigs tend to be allowed to grow to maturity before they are eaten). *Canis* sp. remains were recovered from Level 1 and Level 5, with the deeper specimen most likely representing disturbance from above.

The size of most game hunted at Yuku was under 1700 g (mean= 3519 g, median= 1697 g), meaning the majority of animals, particularly cuscus and macropods, were larger than the species collected around Kiowa. Figure 11A shows that in Analytical Unit I, animals were larger in size than those in Analytical Units II-III, primarily due to the presence of large pythons and introduced mammals such as pigs and dogs, reflective of the site functioning as a specialised cooking area for ritually hunted game (as per local oral traditions described to Bulmer 1960). Analytical Unit II represents primarily small arboreal game identical to that in Analytical Unit III but with the intrusion of pig and dog remains from Analytical Unit I. Analytical Unit III shows that at the tail-end of the LGM, small game was exclusively targeted and there is no evidence for any animals over about 3000 g being hunted. Most of these species provided edible meat between 50-80% of their total body weight (Table S4), necessitating frequent capture (Dwyer, 1980).

The habitats exploited by hunters seem to have remained stable from the Late Pleistocene to the Holocene (Fig. 11B). People at Yuku were predominantly taking prey from the lower montane, closed canopy rainforest. This is attested to by the presence of arboreal cuscus, ring-tail possums, and tree kangaroos, which subsist on fruits and foliage in the mixed beech forests, and terrestrial *Dorcopsulus* wallabies and giant rats (*Xenuromys sp., Hyomys goliath, Mallomys rothschilde*), which have primarily been observed inhabiting the forest floor. A smaller number of species which can subsist in both primary and secondary forest are present throughout the deposits and there is a slight increase in the number of grassland species later in time (Analytical Unit I), perhaps indicative of forest clearances around Mt Hagen in the Mid-Late Holocene. Because the upper units are disturbed, it is currently impossible to provide finer resolution information about environmental change around Yuku.

Figure 11. Size and habitat data at Yuku by analytical unit. A: Average mass (g) of animals identified from MNI data (mean weight of species derives from Flannery 1995); B: Preferred habitat of animals identified from MNI data (this excludes bats and eels; habitat data from Dwyer, 1983 and Flannery 1995).

6. Discussion

Having presented the chronostratigraphical and zooarchaeological evidence from Kiowa and Yuku in detail, we now 1) elaborate on the nature of faunal turnover and hunting strategies employed at the two sites, then 2) build a model of generalist–specialist hunting dynamics in the New Guinea Highlands, and 3) conclude by exploring how this helps us to more broadly understand tropical high-altitude human foraging behaviours during the Quaternary. We show that early Highlanders shifted flexibly between broad spectrum foraging, hunting a wide range of locally available game, and specialised hunting, intensively targeting species that occupied 'sweet spots' and provided reliable protein in a terrain otherwise unpredictable with regards to prey availability. This interplay allowed mobile rainforest hunter-gatherers to maintain a viable protein supplement to what was likely a plant-rich diet, as attested to at a handful of key archaeological sites (Denham, 2019; Summerhayes et al., 2010).

6.1. Hunting strategies and faunal turnover at Kiowa and Yuku

The revised chronostratigraphy demonstrates that hunting at the two shelters initially began during cold periods — at the end of the LGM at Yuku (c. 18,000 years ago), and during the Younger Dryas at Kiowa (c. 12,000 years ago) — but continued regularly as climates warmed in the Holocene. Throughout this transition, the composition of fauna indicates both sites were situated within the mid-montane rainforest, with patches of more open forest and grasslands present nearby. These results support pollen and phytolith studies that suggest the area above Kiowa on Mt Elimbari was covered in

Nothofagus sp. beech trees and ferns (Gillieson et al., 1986), while the Lanim Gorge around Yuku was dominated by *Elaeocarpus* sp. trees and ferns (Horrocks et al., 2008).

During this time, people at Kiowa and Yuku focussed their hunting efforts on a wide variety of small to mid-sized game. From Kiowa, at least 1965 individuals representing 38 species of mammals, one bird species, and two reptiles were recovered, with an average of one individual animal deposited every six years based on the depth of the deposit. As shown in Table S3, this represents a substantial proportion of the 46 species of mammals available from the upper slopes of Mt Elimbari today (Dwyer, 1983). It is also closely comparable to the 43 mammal species hunted today in the Kaironk valley (Bulmer and Menzies, 1972: 488). Similarly, from Yuku at least 694 individual animals representing 29 mammal species, five reptiles, and one fish were identified (with an average of one identifiable individual deposited every 30 years based on the depth of the deposit). Most of this deposition appears to have been the direct result of human predation and suggest that hunters were targeting almost all locally available mammalian game, predominantly those under 2 kg in size at Yuku and under 0.5 kg at Kiowa. In addition to meat, people at both sites exploited animal by-products, including bird eggs and bone (for tool production). Although the two sites have similar faunal sequences, attesting to broad-spectrum foraging, there was a particular preference for arboreal cuscuses (*Phalanger* spp.), and an additional component at Kiowa documents the specialised and repeated capture of large quantities of locally abundant fruit bats (Pteropodidae). This array of prey species would have been captured using a variety of methods given they occupy different layers in the canopy, are active both at night and during the day, and range from being very agile to slow moving.

Many cuscuses would have been targeted in the forest understory or canopy. In Karamui at 1400m asl, *Phalanger orientalis* are known to aggregate with *Phalanger gymnotis* at fruiting *Lithocarpus* trees during August and September allowing hunters to lie in wait and shoot the animals with bow and arrow (Hide et al., 1984). Similarly, in Kaironk *Phalanger gymnotis* have been observed gathering to feed from *Elaeocarpus, Ficus, Pipturus* and *Pandanus* trees, while *Phalanger carmelitae* feeds on *Pandanus* fruits and young shoots (Bulmer and Menzies, 1972). As such, any seasonal movement into the Highlands by humans, especially during glacials and stadials, would have likely involved not simply the procurement of carbohydrate-filled *Pandanus* and other fruiting tree nuts from specific stands, but the reliable hunting of arboreal game. Moreover, today cuscus are ritually important animals and their fur is highly valued for personal ornamentation — during the LGM, these furs may have played an important role in thermoregulation for mobile hunters (see similar arguments for the use of marsupial furs for the LGM occupation of Tasmania in Gilligan, 2014). Although some of the cuscuses present in early deposits at Yuku (*Phalanger* 'A') were somewhat larger than their Holocene iterations, the absence of megafauna may also lend further support to the disappearance of these animals sometime during MIS-3 or the start of MIS-2.

As well as these 'sweet spots' within the forest, the Kiowa cave system itself seems to have been a locational focus of specialised fruit bat hunting from the outset. *Aproteles bulmerae* and *D. magna* — the former substantially larger than the latter — represent over half of all animals deposited at the site and would have been an important contribution to the diet (Table 6). Given *A. bulmerae* and *D. magna* are not known to roost together, the cooccurrence of these species may suggest hunters were procuring the animals from a number of different chambers in the cave systems, or that the caves went through alternating phases of occupation by each species, perhaps triggered by human disturbance causing recurring desertion of the colonies. *Aproteles bulmerae* in particular tend to establish large, isolated colonies, which made them sensitive to overhunting by humans, hence their decimation and likely local extinction by about 11,200–10,100 years ago, with only small numbers represented at Kiowa thereafter. An increase in small bat species in the upper half of the Kiowa deposit, beginning around 10,200–9,700 years ago, may reflect more intensive procurement techniques, perhaps involving netting rather than use of projectiles for selective capture of larger fruit bats. This rapid impact is coterminous with the rise in fruit bat hunting upslope at Nombe rockshelter (1750 m asl). Nombe had been occupied since MIS-3 when 15% of all individual animals deposited were fruit bats, but there was a massive increase in hunting during the Early-mid Holocene when the proportion of fruit bats represented 78% of the assemblage (Evans and Mountain, 2005; Mountain, 1991a). This likely suggests that earlier hunting trips to Mt Elimbari were small-scale and focussed on larger game above the treeline. It does not appear that warming temperatures in the Holocene caused a shift in the preferred habitat of *A. bulmerae* further upslope to

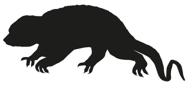
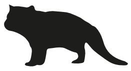
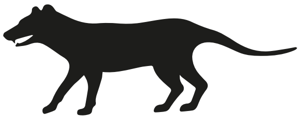
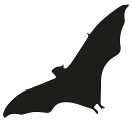
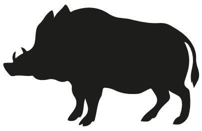
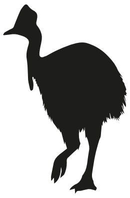
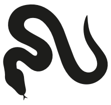
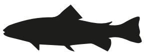
Nombe. Although the Kiowa specimens roosted at 1500 m asl, today the animals are found variably between 500–2000 m asl (Aplin et al., 2016; Flannery and Seri, 1993; Hyndman and Menzies, 1980; Wright et al., 1995).

In addition to the specialised capture of game from fixed locations, hunters also opportunistically hunted arboreal game in *ad hoc* hunting forays. The proportion of approximately 50% *Phalanger* spp. individuals at Yuku and 30% individuals (excluding the fruit bat component) at Kiowa, closely corresponds with collections from modern hunting groups (Table 6; see Menzies cited in Bulmer, 1979). Although arboreal while feeding in the canopy at night, many species such as *Phalanger carmelitae* and *Pseudochirops corrinae* sleep beneath *Pandanus* fronds, in tangles of epiphytes, and within tree hollows during the day, making them easy targets for hunters (Dwyer, 1983; Hide et al., 1984). Some animals like *Petaurus* rest by day in tree hollows (Dwyer, 1983), or, in the case of *Pseudochirulus forbesi,* in distinctive dreys. *Pseudochirops corrinae* sleep exposed on branches during the day making them susceptible to direct capture or arrows. Other animals such as *Dactylopsila*, often prized for their decorative tails, are more difficult to capture even using bow and arrow due to their small size and agility (Dwyer, 1983). Moreover, *Phalanger gymnotis* and *Pseudochirops cupreus* often rest by day in caves (Dwyer, 1983), while some giant rats like *Uromys caudimaculatus* make nests in caves (Flannery, 1995: 217). Therefore hunters approaching shelters would have sometimes come across immediately available game.

A range of swift, terrestrial forest animals were also captured at both sites, including bandicoots, rodents, quolls, and wallabies. Bandicoots are primarily active in rainforest at night (Anderson et al., 1988), and hunters often capture them by lying in ambush close to fruits, which these animals forage for (Flannery, 1995: 78). Some larger omnivorous rodents and quolls are both hard-to-catch and relatively vicious if caught by hand and would likely have been quickly dispatched. However, the presence of *Parahydromys asper* intermittently throughout the Kiowa sequence may indicate that raptors continued to occupy the site when humans were absent, given live and freshly killed animals emanate a repulsive, putrescent odour (Aplin cited in Flannery, 1995). Mid-sized terrestrial mammals like wallabies (*Dorcopsis, Dorcopsulus* and *Thylogale*) could be hunted by ambush, trapping, or by burning forests and grasslands during droughts and funnelling the animals into the flames (Flannery, 1995: 92). The growing presence of these animals in Mid-Holocene levels 5–2A at Kiowa, and in Yuku Analytical Unit I, may suggest that wallabies were increasingly targeted during forest burning activities.

It is unclear if the presence of small game such as rodents, pythons, forest dragons, as well as cassowary and other birds' eggs at both shelters, and fish and terrestrial snails at Yuku, could provide evidence for women and children collecting around the site, as observed ethnographically (see Bulmer, 1972; note also Gaffney, Ford and Summerhayes, 2015: 236 suggest that some lithics may have been produced as practice objects around 7000 years ago at Kiowa). Caves and shelters with reliable water sources nearby would certainly have been important for maintaining hydration and thermoregulation in hot-humid conditions, especially amongst lactating mothers (Bethancourt et al., 2020; Rosinger, 2015). The relative absence of other small animals like birds, amphibians, and lizards at the sites may relate to the consumption of the bones alongside the meat. Alternatively, their absence may be due to sampling error, smaller bones having been overlooked without the use of sieves, given frog remains were recovered nearby at Nombe where the deposit was screened (Menzies et al., 2002). Although this point has important implications for the nature of group organisation and mobility, based on the available data we are cautious not to over-extend these ethnographic scenarios back into deep time without more convincing data.

Table 6. Comparison of MNI values from Kiowa and Yuku (all Levels), including and excluding the fruit bat component at each site.

		Kiowa			*Yuku*		
Taxon		*n*	*%*	*% (excl. fruit bats)*	*n*	*%*	*% (excl. fruit bats)*
Macropodids		126	6.4	12.7	122	17.6	18.6
Cuscus		357	18.1	36.1	358	51.6	54.5
Ringtail possums		120	6.1	12.1	36	5.2	5.5
Striped possums		19	1.0	1.9	7	1.0	1.1
Bandicoots		79	4.0	8.0	25	3.6	3.8
Quolls		22	1.1	2.2	5	0.7	0.8
Echidnas		5	0.3	0.5	0	0	0
Thylacines		1	0.1	0.1	0	0	0
Rodents		159	8.0	16.1	47	6.8	7.2
Fruit bats		987	49.9	–	37	5.3	–
Small bats		78	3.9	7.9	1	0.1	0.2
Introduced mammals		6	0.3	0.6	11	1.6	1.7
Cassowaries		12	0.6	1.2	0	0	0
Reptiles		6	0.3	0.6	38	5.5	5.8
Fish		0	0	0	7	1.0	1.1
Total		*1977*	*100*	*100*	*694*	*100*	*100*

By the Late Holocene, pigs (*Sus* sp.) had been introduced around Kiowa and Yuku, becoming the largest available prey in the Highlands. About half of the pig remains identified at Yuku were juveniles; the hunting of young pigs could have been achieved by trapping, or via opportunistic capture when hunting adult pigs, which escape faster than their offspring. Both juvenile and mature pigs have been observed in Late Holocene levels at other New Guinea Highlands sites including Aibura and Batari (White, 1972). The introduction of dogs (*Canis* sp.) during a similar timeframe would have dramatically reconfigured hunting practices and labour requirements, in some cases quadrupling the number of animals that could be captured, by chasing down fast terrestrial game, and trapping arboreal animals in trees (Bulmer, 2001). The scarcity of dog specimens at both Yuku and Kiowa may indicate that contemporary taboos surrounding eating dogs in the Highlands (Majnep and Bulmer, 2007) extend back several centuries, but this postulation requires further clarification from the post-cranial assemblage.

Based on the revised chronostratigraphy, the earliest secure evidence for dogs at Kiowa comes from within the last few centuries (Level 1), and one specimen dating by association to 5290 years ago at the latest (Level 3) is more likely assignable to *Thylacinus* sp. given that genetic and archaeological evidence for the introduction of the Pacific village dog, the New Guinea singing dog, and the dingo to the Australasian region stands at about 3500 years ago (Greig et al., 2016). At Yuku, dog remains are present in Level 1 (Analytical Unit I) and 5A (Analytical Unit II) and it is likely that the latter is intrusive. Pigs are certainly present by 1060–930 years ago at Kiowa (Level 2B) and although there have been claims that wild suids were present by 12,200-11,700 years ago (Level 12A) (see Bulmer, 1975), this material cannot be further discussed (see Section 5.2). At Yuku, the pig specimen present in Level 5A is again likely to be intrusive, while the majority of pig remains, present in Analytical Unit I, suggest a Late Holocene introduction. We note the presence of early pigs does not align with genetic evidence and linguistic reconstructions that suggest Proto-Oceanic speakers introduced the domesticates in the Late Holocene (Allen et al., 2001; Blust, 1976; Hide, 2003; Larson et al., 2005), and whose influence was being felt in the fringe Highlands by about 3000 years ago (Gaffney et al., 2015b). As Allen and colleagues (2001) noted, we require further taxonomic clarification about the purported early pig specimens alongside direct dating, and Sutton and colleagues (2009) concluded that the evidence remains inadequate to answer whether pigs were present in the Highlands prior to the Late Holocene.

6.2. Generalist-specialist hunting dynamics in the New Guinea highlands

We now integrate the Kiowa and Yuku findings with regional archaeological data and put forward a model for generalist-specialist hunting dynamics in the New Guinea Highlands. This model emphasises that hunters flexibly shifted between periods of broad-spectrum foraging as they moved through the landscape, to more intensive and specialised capture focused on a narrow range of species at specific locations. This dynamic was key to the adaptive success of *Homo sapiens* as they mitigated calorific challenges posed by living at high altitudes under the canopy.

Only five other zooarchaeological sequences from the Highlands have been published: Nombe (Mountain, 1991a), Kamapuk (Aplin, 1981), Aibura (White, 1972: 57–61), Batari (White, 1972: 16–20), and Kafiavana (White, 1972: 91–94) (refer to Fig. 1). These sequences suggest people were primarily occupying mid-montane forests below the treeline, and exploiting a range of environments, including primary montane rainforest, disturbed or more open forest, grasslands, and cave systems (Table S5). During the Late Pleistocene (MIS-3) movements from the coast into the interior were likely spurred on by the presence of megafauna in the sub-alpine grasslands and the abundance of fruiting *Pandanus* and nut-bearing *Lithocarpus* and *Castonopsis* (Fig. 12). Although initial evidence for human occupation in highland New Guinea comes from the Ivane Valley, dated from 49,000–43,000 years ago, where palaeoecological evidence indicates the valley was burned extensively perhaps to facilitate hunting, only three highly fragmented and non-diagnostic faunal remains have preserved archaeologically from Kosipe (AER) with no collagen preservation (Fairbairn et al., 2006; Hope, 2009; Summerhayes et al., 2010). During this early period, humans provisioned themselves with lowland yams and rapidly exploited local *Pandanus* and lithic sources (Summerhayes and Ford, 2014). They may have also overlapped chronologically with diprotodontids and large protemnodons (Hope et al., 1993; Menzies and Ballard, 1994). A small quantity of zooarchaeological material dating from the beginning of the LGM

(MIS-2), around 25,000–20,000 years ago, was excavated at Nombe on the slopes of Mt Elimbari (Denham and Mountain, 2016), including now-extinct megafauna such as a pig-sized diprotodontid, giant kangaroos (*Protemnodon nombe, Protemnodon tumbuna*), tree kangaroos (*Dendrolagus noibano*), and the marsupial wolf (*Thylacinus cynocephalus*) (Flannery et al., 1983; Mountain, 1991a). This tentatively suggests that hunters periodically specialised in the capture of large mammals (although see cautions in Field, Fillios and Wroe, 2008). However, even during this time, a broad-spectrum of small to mid-sized forest game including bandicoots, quolls, cuscus, tree kangaroos, ringtail and striped possums, rodents, echidnas, fruit bats, and lizards formed a substantial part of the hunting focus (Mountain, 1991a, 1991b)

Figure 12. Diagrammatic illustration of changes to movement and hunting ranges in the New Guinea Highlands. As indicated by the model, changes to mobility and hunting may have varied in different areas of the Highlands at different times.

As climates warmed following the LGM (in MIS-1), hunters were confronted with a major change to the available fauna with all large species over about 18 kg becoming extinct (Flannery et al., 1983), leaving exclusively small and mid-sized volant, arboreal, and terrestrial game, many of which were hard to catch. Despite this, forest hunting activities at sites such as Yuku, Manim, and Nombe increased (Christensen, 1975; Denham, 2019; Mountain, 1991b), while a number of other foraging camps such as Kiowa, Kafiavana, and Batari were occupied for the first time in the terminal Pleistocene and Early Holocene (White, 1972). This period of increased hunting activity corresponds to genetic analyses that suggest Highland populations began to dramatically expand in the terminal Pleistocene and Early Holocene (Pedro et al., 2020). Further genetic analyses suggest that Highlanders also became increasingly disconnected from coastal populations (Bergström et al., 2017), and during this time it is likely that many hunters increasingly focussed their efforts within the Highland ranges, rather than moving between the mountains and the coast, perhaps due to the emergence of social boundaries and territoriality. Residential mobility in some areas may have operated laterally between ranges within an altitudinal band of optimal conditions (above the malaria zone and below the zone of harsh frosts; see Groube, 1993), which allowed for temporary base camps to be established along ridge lines, within intermontane valleys, and in large shelters (Gaffney et al., 2015a). While moving between these camps, people would have opportunistically maintained a broad-spectrum diet by collecting plant foods, hunting, trapping, grubbing, and fishing in streams. Logistical hunting forays from these camps then pushed into higher and lower altitudes to exploit a range of plants and animals occupying different ecotones (Christensen, 1975).

At the Highlands sites, a wide range of smaller forest species came to be hunted, and there is evidence for increasing specialisation in the capture of *Dobsonia magna* fruit bats, perhaps by the netting, at sites adjacent to cave systems (Nombe and Kiowa), and *Phalanger* spp. cuscus, possums, macropods, and rodents at shelters within montane rainforest (Yuku) and mosaic environments (Batari and Kafiavana). In the case of Kiowa, bat hunting was undertaken intensively enough to extirpate or displace *Aproteles bulmerae*, although the long-term persistence of forest species such as cuscus and particularly echidnas at many sites attest to the low impact of rainforest hunting and perhaps the low population sizes of these hunting and gathering groups. At the same time, at Nombe there was also a shift to increased cassowary hunting following the extinction of large marsupial game, until the arrival of pigs in the last few millennia. In this way, cassowary traps became fixed points in the landscape encouraging regular logistical mobility from camps (Evans, 2000), and the new findings at Kiowa suggest these animals were butchered offsite with legs being carried back to the shelter for consumption. As Mountain (1991b) notes, in the terminal Pleistocene and Early Holocene the shift from hunting unpredictable and uncommon megafauna to netting and trapping smaller animals at fixed sources reduced risk to subsistence systems. Parallel signs of risk reduction strategies come from the Nombe lithic assemblage, where river cobbles appear to have been stockpiled in the cave to equip the site itself; not only was Nombe then provisioned with locally available fruit bats, but also flakable stone, ready for when hunters revisited sites (Evans and Mountain, 2005). Similarly, at Kiowa the site was selected partly for its abundance in fruit bats, and partly due to its close proximity to a freshwater stream replete with argillite cobbles (Gaffney et al., 2015a). In this way, complex landscape learning processes — perhaps a particularly sapient capacity to rapidly explore nearby terrain and project future requirements ahead of time — allowed humans to provision *in* the landscape, revisiting fixed, reliable nodes of protein as they moved throughout montane rainforests and grasslands between shelters within a known network of sites (Fig. 12). Lithic landscape learning (see Ford, 2011, 2012, 2017; Gaffney et al., 2015a; Gaffney and Summerhayes, 2019) which allowed people to develop an understanding of the underlying geology would not only have been essential to creating cognitive maps of lithic raw material, but would also have helped foragers scouting for new limestone outcrops with likely cave systems and bat colonies. Moreover, logistical forays from these shelters were not necessarily solely focussed around game hunting, and even if unsuccessful in procuring animals, foragers would often return with plant foods, wood or stone raw material, and so forth.

During the Mid-Late Holocene, hunting dynamics in some valley systems was reconfigured by anthropogenic forest clearance and the expansion of gardens. Although early clearances had occurred since the Late Pleistocene (Haberle et al., 2001), and cultivation was taking place in the Wahgi Valley at the start of the Holocene (Denham, 2018; Golson, 1977; Haberle et al., 2012), this became more prevalent throughout several ranges as agricultural practices intensified and expanded (Field et al., 2020; Haberle, 2007, 2003; Hope and Haberle, 2005; Shaw et al., 2020). In the Eastern Highlands, at Aibura, the hunting of forest species, gave way to increasingly hunting grassland *Thylogale browni* during the last millennium (White, 1972). Similarly, at Kamapuk, occupied since the Mid-Holocene, there is evidence for hunting within mosaic environments including primary forest, secondary regrowth, and alpine grasslands, likely indicating active landscape modification in the area (Aplin, 1981).

At many sites, the importance of hunting seems to have only declined within the last few millennia, or even the last few centuries. This likely occurred as gardening and the rearing of domestic animals came to occupy many communities' daily routines and, as such, hunting became less frequent, more opportunistic, and less specialised. Additionally, as populations grew alongside agricultural production, trade networks linked many valley systems together and allowed people to acquire meat and other valuables through exchange rather than direct procurement. Pigs in particular became a major stimulus for political reorganisation in some valley systems (Modjeska, 1982; Rappaport, 1968; Strathern, 1971). It is possible that this species, along with dogs and chickens, were deliberately imported by Highland communities as the attempted translocation of mammals into higher altitudes is attested to ethnographically (Dwyer, 1983). Recent hunters would move from mid montane valleys into lower montane and lowland rainforest to access forest game and trade connections with the coast, and pulses of these connections are observable throughout the Holocene (Gaffney et al., 2019), and particularly since the about 5050–4200 years ago (Gaffney et al., 2016; Shaw et al., 2020; Watson, 1986).

7. Conclusions

7.1. High altitude rainforest hunting in global perspective

We now conclude by exploring how this model of montane New Guinea hunting dynamics helps us to understand tropical and high-altitude human foraging behaviours during the Late Pleistocene and Holocene. Globally, there is little evidence for the wholesale use of montane rainforests during MIS-3 (Summerhayes et al., 2017), but immediately following the LGM humans in a number of regions began to move more decisively throughout these environments. This occurred in Thailand (Higham, 1977), Borneo (Kusmartono et al., 2017), and Sumatra (Bonatz, 2012) during the terminal Pleistocene, and in the sub-Andean forests of Columbia at the start of the Holocene (Mora and Gnecco, 2003). For instance, in the tropical monsoon forests of northwest Thailand, faunal collections from Spirit Cave suggest sporadic periods of hunting occurred from around 14,000-11,000 years ago until around 3000 years ago (Conrad et al., 2016; Gorman, 1970). Foragers targeted a diverse range of terrestrial, arboreal, and aquatic fauna including deer, wild boars, macaques, gibbons, langurs, civet cats, along with smaller game such as flying squirrels, lizards, bats, and rodents (Higham, 1971). Many of these species, being swift and difficult to capture, required specialised procurement techniques, perhaps involving projectiles, trapping, and ambush, on par with those described from New Guinea.

However, the specialised capture of rainforest fauna as a complement to broad-spectrum foraging was not restricted to high elevations and can be seen in a number of other tropical regions. The intensive focus on small and hard-to-catch game, in particular, seems to have been adaptively beneficial for hunters without reliable access to larger sources of protein under the canopy (and particularly on depauperate islands). Similar hunting dynamics emerged in the monopolisation on fruit bats in the small islands of Wallacea (Hawkins et al., 2017, 2016), and in the Bismarck Archipelago (Leavesley and Allen, 1998), the mass capture of forest wallabies in the hills of northwest New Guinea (Pasveer, 2004), the projectile hunting of monkeys from the canopy in Sri Lanka (Wedage et al., 2020, 2019) and Java (Amano et al., 2016; Ingicco et al., 2020), and the focus on juvenile wild pigs in Borneo (Rabett et al., 2013) and Malaysia (Sieveking, 1954; Taha, 1985). This is reflective of what has been called the *Homo sapiens* 'generalist-specialist' niche (Roberts and Stewart, 2018), which refers to the dual capacities for humans to inhabit a wide array of ecological zones, and to then specialise their adaptive strategies to those environments. However, it is important to note that humans maintained their adaptive capacities for experimentation even as they specialised in the local environment. In this way, montane rainforest communities during the Late Pleistocene and much of the Holocene moved dynamically between practicing extremely broad-spectrum foraging as a subsistence base (Denham, 2016b; Gaffney and Denham, in press), as they increasingly attuned their adaptive strategies to their ecology and often specialised in hunting a handful of prey species in unreliable environments, which particularly drove people to revisit key areas known to provide reliable sources of protein.

Acknowledgments

We thank the Bulmer family for making the collection available for study, along with the National Museum and Art Gallery of Papua New Guinea for ongoing loan of the material. We are indebted to David Bulmer for initial bulk faunal identifications and bagging undertaken in the 1980s. Many thanks go to Tim Denham and two anonymous reviewers for their helpful comments on the draft manuscript. We particularly thank Jasmijn Ouwendijk for bibliographic assistance and Les O'Neil for photographing the faunal material.

References

Allen, J., Guy, J.B.M., 1984. Optimal estimations of individuals in archaeological faunal assemblages: How minimal is the MNI? Archaeology in Oceania 19, 41–47.

Allen, J., O'Connell, J.F., 2008. Getting from Sunda to Sahul, in: Clark, G., Leach, F., O'Connor, S.

(Eds.), Islands of Inquiry: Colonisation, Seafaring and the Archaeology of Maritime Landscapes. ANU E Press, Canberra, pp. 31–46.

Allen, M.S., Matisoo-Smith, E., Horsburgh, A., 2001. Pacific "Babes": Issues in the origins and dispersal of Pacific pigs and the potential of mitochondrial DNA analysis. International Journal of Osteoarchaeology 11, 4–13.

Amano, N., Moigne, A.M., Ingicco, T., Sémah, F., Awe, R.D., Simanjuntak, T., 2016. Subsistence strategies and environment in Late Pleistocene–Early Holocene Eastern Java: Evidence from Braholo Cave. Quaternary International 416, 46–63.

Anderson, T.J.C., Berry, A.J., Amos, J.N., Cook, J.M., Anderson, T.I.M.J.C., Berry, A.J., Amos, J.N., Cook, J.M., 1988. Spool-and-Line Tracking of the New Guinea Spiny Bandicoot, Echymipera kalubu (Marsupialia, Peramelidae). Journal of Mammalogy 69, 114–120.

Aplin, K.P., 1981. Kamapuk fauna: A late Holocene vertebrate faunal sequence from the Western Highlands District, Papua New Guinea with implications for palaeoecology and archaeology. Unpublished BA Hons thesis, Department of Prehistory, Australian National University.

Aplin, K., Armstrong, K., Wright, D., 2016. Aproteles bulmerae. The IUCN Red List of Threatened Species e.T1933A22.

Bailey, R.C., Headland, T.N., 1991. The tropical rain forest: Is it a productive environment for human foragers? Human Ecology 19, 261–285.

Bergmans, W., Sarbini, S., 1985. Fruit Bats of the genus Dobsonia Palmer, 1898 from the Islands of Biak, Owii, Numfoor and Yapen, Irian Java (Mammalia, Megachiroptera). Beaufortia 34, 181–189.

Bergström, A., Oppenheimer, S.J., Mentzer, A.J., Auckland, K., Robson, K., Attenborough, R., Alpers, M.P., Koki, G., Pomat, W., Siba, P., Xue, Y., Sandhu, M.S., Tyler-Smith, C., 2017. A Neolithic expansion, but strong genetic structure, in the independent history of New Guinea. Science 357, 1160–1163.

Bethancourt, H.J., Swanson, Z.S., Nzunza, R., Huanca, T., Conde, E., Kenney, W.L., Young, S.L., Ndiema, E., Braun, D., Pontzer, H., Rosinger, A.Y., 2020. Hydration in relation to water insecurity, heat index, and lactation status in two small-scale populations in hot-humid and hot-arid environments. American Journal of Human Biology. https://doi.org/10.1002/ajhb.23447

Blust, R., 1976. Austronesian culture history: Some linguistic inferences and their relations to the archaeological record. World Archaeology 8, 19–43.

Bochenski, Z.M., Tomek, T., Wertz, K., Kaczanowska, M., Kozłowski, J.K., Sampson, A., 2018. Who ate the birds: the taphonomy of Sarakenos Cave, Greece. Archaeological and Anthropological Sciences 10, 1603–1615.

Boivin, N., Fuller, D.Q., Dennell, R., Allaby, R., Petraglia, M.D., 2013. Human dispersal across diverse environments of Asia during the Upper Pleistocene. Quaternary International 300, 32–47.

Bonatz, D., 2012. A Highland Perspective on the Archaeology and Settlement History of Sumatra. Archipel 84, 35–81.

Brandt, S.A., Fisher, E.C., Hildebrand, E.A., Vogelsang, R., Ambrose, S.H., Lesur, J., Wang, H., 2012.

Early MIS 3 occupation of Mochena Borago Rockshelter, Southwest Ethiopian Highlands: Implications for Late Pleistocene archaeology, paleoenvironments and modern human dispersals. Quaternary International 274, 38–54.

Brandt, S., Hildebrand, E., Vogelsang, R., Wolfhagen, J., Wang, H., 2017. A new MIS 3 radiocarbon chronology for Mochena Borago Rockshelter, SW Ethiopia: Implications for the interpretation of Late Pleistocene chronostratigraphy and human behavior. Journal of Archaeological Science: Reports 11, 352–369.

Brookfield, H., Allen, B., 1989. High-altitude occupation and environment. Mountain Research and Development 9, 201–209.

Bulmer, R., 1968. The strategies of hunting in New Guinea. Oceania 38, 302–318.

Bulmer, R., 1972. Hunting, Encyclopaedia of Papua and New Guinea. Melbourne Univeristy Press, Melbourne.

Bulmer, R., 1976. Selectivity in hunting and in disposal of animal bone by the Kalam of the New Guinea Highlands, in: Sieveking, G., Longworth, I., Wilson, K.E. (Eds.), Problems in Economic and Social Archaeology. Duckworth, London, pp. 169–86.

Bulmer, R., Menzies, J.I., 1972. Karam classification of marsupials and rodents. Journal of The Polynesian Society 81, 472–499.

Bulmer, S., 1960. Report on archeological field work in the New Guinea Highlands (October 1959 to May 1960). Unpublished report, Department of Anthroplogy, University of Auckland.

Bulmer, S., 1964a. Prehistoric Stone Implements from the New Guinea Highlands. Oceania 34, 246–268.

Bulmer, S., 1964b. Radiocarbon dates from New Guinea. Journal of The Polynesian Society 73, 327–328.

Bulmer, S., 1966a. The prehistory of the Australian New Guinea Highlands. Unpublished MA thesis, Department of Anthroplogy, University of Auckland.

Bulmer, S., 1966b. Pig bone from two archaeological sites in the New Guinea Highlands. The Journal of the Polynesian Society 75, 504–505.

Bulmer, S., 1975. Settlement and economy in prehistoric Papua New Guinea: a review of the archeological evidence. Journal de la Société des océanistes 31, 7–75.

Bulmer, S., 1979. Archaeological evidence of prehistoric fauna change in Highland Papua New Guinea. Unpublished report, Department of Anthroplogy, University of Auckland.

Bulmer, S., 1982. Human ecology and cultural variation in prehistoric New Guinea, in: Gressitt, J.L. (Ed.), Biogeography and Ecology of New Guinea. Dr W. Junk Publishers, The Hague, pp. 169–206.

Bulmer, S., 2001. Lapita dogs and singing dogs and the history of the dog in New Guinea, in: The Archaeology of Lapita Dispersal in Oceania. Pandanus Books, Canberra, pp. 183–201.

Bulmer, S., 2005. Reflections in stone: axes and the beginnings of agriculture in the Central Highlands of New Guinea, in: Pawley, A. (Ed.), Papuan Pasts: Cultural, Linguistic and Biological Histories of Papuan-Speaking Peoples. Pacific Linguistics, Research School of Pacific and Asian Studies, The

Australian National University, pp. 378–450.

Bulmer, S., Bulmer, R., 1964. The prehistory of the Australian New Guinea Highlands. American Anthropologist 66, 39–76.

Bulmer, S., 1977. Waisted blades and axes: A functional interpretation of some early stone tools from Papua New Guinea, in: Wright, R.V.S. (Ed.), Stone Tools as Cultural Markers: Change, Evolution and Complexity. Australian Institute of Aboriginal Studies, Canberra, pp. 40–59.

Christensen, O.A., 1975. Hunters and Horticulturalists: A Preliminary Report of the 1972-4 Excavations in the Manim Valley, Papua New Guinea. Mankind 10, 24–36.

Colgan, D., Flannery, T.F., Trimble, J., 1993. Electrophoretic and morphological analysis of the systematics of the phalanger orientalis (Marsupialia) species complex in papua new guinea and the Solomon Islands. Australian Journal of Zoology 41, 317–323.

Conrad, C., Higham, C., Eda, M., Marwick, B., 2016. Palaeoecology and forager subsistence strategies during the Pleistocene–Holocene transition: A Reinvestigation of the zooarchaeological assemblage from Spirit Cave, Mae Hong Son Province, Thailand. Asian Perspectives 55, 2–27.

Denham, T., 2016a. Socio-environmental adaption to the montane rainforests of new guinea, in: The Routledge Handbook of Bioarchaeology in Southeast Asia and the Pacific Islands. Routledge, London, pp. 409–426.

Denham, T., 2016b. Revisiting the past: Sue Bulmer’s contribution to the archaeology of Papua New Guinea. Archaeology in Oceania 51, 5–10.

Denham, T., 2018. Tracing Early Agriculture in the Highlands of New Guinea, Tracing Early Agriculture in the Highlands of New Guinea: Plot, Mounds and Ditch. Routledge, London.

Denham, T., 2019. Reconsidering the ‘Neolithic’ at Manim rock shelter, Wurup Valley, Papua New Guinea, in: Leclerc, M., Flexner, J. (Eds.), Archaeologies of Island Melanesia: Current Approaches to Landscapes, Exchange and Practice. Australian National University, pp. 81–99.

Denham, T., Mountain, M.-J., 2016. Resolving some chronological problems at Nombe rock shelter in the highlands of Papua New Guinea. Archaeology in Oceania 51, 73–83.

Dominy, N.J., Mills, S.T., Yakacki, C.M., Roscoe, P.B., Carpenter, R.D., 2018. New Guinea bone daggers were engineered to preserve social prestige. Royal Society Open Science 5, 172067.

Dwyer, P.D., 1974. The price of protein: Five hundred hours of hunting in the New Guinea Highlands. Oceania 44, 278–293.

Dwyer, P.D., 1975. Notes on Dobsonia moluccensis (Chiroptera) in the New Guinea Highlands. Mammalia 39, 113–118.

Dwyer, P.D., 1978. Rats, pigs and men: disturbance and diversity in the New Guinea highlands. Australian Journal of Ecology 3, 213–232.

Dwyer, P. D., 1980. Edible waste ratios for some New Guinea mammals. Science in New Guinea 7, 109–117.

Dwyer, P.D., 1983. An Annotated list of mammals from Mt. Erimbari Eastern highlands Province, Papua New Guinea. Science in New Guinea 10, 28–38.

Dwyer, P.D., 1985. A hunt in New Guinea: Some difficulties for optimal foraging theory. Man 20, 243–

253.

Evans, B., Mountain, M.-J., 2005. Pasin bilong tumbuna: archaeological evidence for early human activity in the highlands of Papua New Guinea, in: Pawley, A. (Ed.), Papuan Pasts: Cultural, Linguistic and Biological Histories of Papuan-Speaking Peoples. Pacific Linguistics, Research School of Pacific and Asian Studies, The Australian National University, pp. 363–386.

Evans, W., 2000. The role of the cassowary in adaptive subsistence in prehistoric Highlands New Guinea. Unpublished BA Honours thesis, Department of Prehistory, Australian National University.

Fairbairn, A.S., Hope, G.S., Summerhayes, G.R., 2006. Pleistocene occupation of New Guinea's highland and subalpine environments. World Archaeology 38, 371–386.

Field, J., Fillios, M., Wroe, S., 2008. Chronological overlap between humans and megafauna in Sahul (Pleistocene Australia-New Guinea): A review of the evidence. Earth-Science Reviews 89, 97–115.

Field, J.H., Summerhayes, G.R., Luu, S., Coster, A.C.F., Ford, A., Mandui, H., Fullagar, R., Hayes, E., Leavesley, M., Lovave, M., Kealhofer, L., 2020. Functional studies of flaked and ground stone artefacts reveal starchy tree nut and root exploitation in mid-Holocene highland New Guinea. Holocene 9, 1360–1374.

Flannery, T.F., 1995. Mammals of New Guinea. Cornell University Press, Ithica, NY.

Flannery, T.F., Seri, L., 1993. Rediscovery of Aproteles bulmerae (Chiroptera : Pteropodidae). Morphology, ecology and conservation. Mammalia 57, 19–26.

Flannery, T.F., Mountain, M.-J., Aplin, K., 1983. Quaternary kangaroos (Macropodidae: Marsupialia) from Nombe Rock Shelter, Papua New Guinea, with comments on the nature of megafaunal extinction in the New Guinea highlands. Proceedings of the Linnean Society of New South Wales 107, 75–98.

Flannery, T.F., Archer, M., Maynes, G., 1987. The phylogenetic relationships of living phalangerids (Phalangeroidea: Marsupialia) with a suggested new taxonomy, in: Archer, M. (Ed.), Possums and Opossums: Studies in Evolution. Surrey Beatty & Sons, Norton, NSW, pp. 477–506.

Flenley, J.R., 1984. Late Quaternary changes of vegetation and climate in the Malesian mountains. Erdwissenschaftliche Forschung 18, 261–267.

Flenley, J.R., Morley, R.J., 1978. A minimum age for the deglaciation of Mt. Kinabalu, East Malaysia, in: Bartstra, G.J., Casparie, W.A. (Eds.), Modern Quaternary Research in Southeast Asia. A.A. Balkema, Rotterdam, pp. 57–61.

Ford, A., 2011. Learning the lithic landscape: Using raw material sources to investigate Pleistocene colonisation in the Ivane Valley, Papua New Guinea. Archaeology in Oceania 46, 42–53.

Ford, A., 2012. Learning the Lithic Landscape in the Ivane Valley, Papua New Guinea: modelling colonisation and occupation using lithic sources and stone tool technology. Unpublished PhD thesis, Department of Anthropology and Archaeology, University of Otago.

Ford, A., 2017. Late Pleistocene lithic technology in the Ivane valley: A view from the rainforest. Quaternary International 448, 31–43.

Gaffney, D., Denham, T.P., in press. The archaeology of social transformation in the New Guinea

Highlands, in: McNiven, I., David, B. (Eds.), Oxford Handbook of the Archaeology of Indigenous Australia and New Guinea. Oxford University Press, Oxford.

Gaffney, D., Summerhayes, G.R., 2019. Coastal mobility and lithic supply lines in northeast New Guinea. Archaeological and Anthropological Sciences 11, 2849–2878.

Gaffney, D., Ford, A., Summerhayes, G., 2015a. Crossing the Pleistocene-Holocene transition in the New Guinea Highlands: Evidence from the lithic assemblage of Kiowa rockshelter. Journal of Anthropological Archaeology 39, 223–246.

Gaffney, D., Summerhayes, G.R., Ford, A., Scott, J.M., Denham, T., Field, J., Dickinson, W.R., 2015b. Earliest pottery on New Guinea mainland reveals austronesian influences in highland environments 3000 years ago. PLoS ONE 10, e0134497.

Gaffney, D., Ford, A., Summerhayes, G.R., 2016. Sue Bulmer's legacy in highland New Guinea: A re-examination of the Bulmer Collection and future directions. Archaeology in Oceania 51, 23–32.

Gaffney, D., Summerhayes, G.R., Szabo, K., Koppel, B., 2019. The Emergence of Shell Valuable Exchange in the New Guinea Highlands. American Anthropologist 121, 30-47.

George, G.G., 1987. Characterisation of the living species of cuscus (Marsupialia: Phalangeridae), in: Archer, M. (Ed.), Possums and Opossums: Studies in Evolution. Surrey Beatty & Sons, Norton, NSW, pp. 507–526.

Gillieson, D., Oldfield, F., Krawiecki, A., 1986. Records of prehistoric soil erosion from rock-shelter sites in Papua New Guinea. Mountain Research & Development 6, 315–324.

Gilligan, I., 2014. Clothing and modern human behaviour the challenge from Tasmania, in: Dennell, R., Porr, M. (Eds.), Southern Asia, Australia and the Search for Human Origins. Cambridge University Press, Cambridge, pp. 189–199.

Gnecco, C., 2003. Against ecological reductionism: Late Pleistocene hunter-gatherers in the tropical forests of northern South America. Quaternary International 109–110, 13–21.

Golson, J., 1977. No room at the top: agricultural intensification in the New Guinea Highlands, in: Allen, J., Golson, J., Jones, R. (Eds.), Sunda and Sahul: Prehistoric Studies in Southeast Asia, Melanesia and Australia. Academic Press, London, pp. 601–638.

Gorman, C.F., 1970. Excavations at Spirit Cave, North Thailand: Some interim observations. Asian Perspectives 13, 79–107.

Grayson, D.K., 1984. Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas. Academic Press, Orlando, Florida.

Greig, K., Walter, R., Matisoo-Smith, E.A., 2016. Dogs and people in southeast Asia and the pacific. The Routledge Handbook of Bioarchaeology in Southeast Asia and the Pacific Islands 462–482.

Groube, L., 1993. Contradictions and malaria in Austrlian and Melanesian prehistory, in: Spriggs, M. (Ed.), A Community of Culture: The People and Prehistory of the Pacific. Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra, pp. 164–186.

Groves, C.P., 1987. On the cuscuses (Marsupialia: Phalangeridae) of the Phalanger orientalis group from Indonesian territory, in: Archer, M. (Ed.), Possums and Opossums: Studies in Evolution.

Surrey Beatty & Sons, Norton, NSW, pp. 569–579.

Haberle, S.G., 1993. Pleistocene vegetation change and early human occupation of a tropical moutainous environment, in: Smith, M.A., Spriggs, M., Fankhauser, B. (Eds.), Sahul in Review: Pleistocene Archaeology in Australia, New Guinea and Island Melanesia. Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra, pp. 109–122.

Haberle, S.G., 2003. The emergence of an agricultural landscape in the highlands of New Guinea. Archaeology in Oceania 38, 149–158.

Haberle, S.G., 2007. Prehistoric human impact on rainforest biodiversity in highland New Guinea. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 219–228.

Haberle, S.G., Hope, G.S., Van Der Kaars, S., 2001. Biomass burning in Indonesia and Papua New Guinea: Natural and human induced fire events in the fossil record. Palaeogeography, Palaeoclimatology, Palaeoecology 171, 259–268.

Haberle, S.G., Lentfer, C., O'Donnell, S., Denham, T., 2012. The palaeoenvironments of Kuk Swamp from the beginnings of agriculture in the highlands of Papua New Guinea. Quaternary International 249, 129–139.

Hawkins, S., O'Connor, S., Kealy, S., 2016. Late Quaternary hominin-bat (Chiroptera) interactions in the Asia-Pacific. Archaeology in Oceania 51, 7–17.

Hawkins, S., O'Connor, S., Maloney, T.R., Litster, M., Kealy, S., Fenner, J.N., Aplin, K., Boulanger, C., Brockwell, S., Willan, R., Piotto, E., Louys, J., 2017. Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. Quaternary Science Reviews 171, 58–72.

Hawkins, S., Samper Carro, S.C., Louys, J., Aplin, K., O'Connor, S., Mahirta, 2018. Human Palaeoecological Interactions and Owl Roosting at Tron Bon Lei, Alor Island, Eastern Indonesia. Journal of Island and Coastal Archaeology 13, 371–387.

Hawkins, S., O'Connor, S., Louys, J., 2019. Taphonomy of bird (Aves) remains at Laili Cave, Timor-Leste, and implications for human-bird interactions during the Pleistocene. Archaeological and Anthropological Sciences 11, 6325–6337.

Helgen, K.M., Jackson, S.M., 2015. Family Phalangeridae (cuscuses, brush-tailed possums and scaly-tailed possum). Handbook of the Mammals of the World 5, 456–497.

Hide, R., 2003. Pig Husbandry in New Guinea: A Literature Review and Bibliography, ACIAR Monograph 108. Australian Centre for International Agricultural Research, Canberra.

Hide, R.L., Pernetta, J.C., Senabe, T., 1984. Exploitation of wild animals, in: Hide, R.L. (Ed.), South Simbu: Studies in Demongraphy, Nutrition and Subsistence. Institute of Applied Social and Economic Research, Boroko, pp. 291–380.

Higham, C., 1971. Appendix 1: Spirit Cave, The Faunal Remains, in: Gorman, C.F. (Ed.), Prehistoric Research in Northern Thailand: A Cultural-Chronographic Sequence from the Late Pleistocene through to the Early Recent Period. University of Hawai'i, pp. 133–136.

Higham, C.F.W., 1977. Economic change in prehistoric thailand, in: Reed, C.A. (Ed.), Origins of

Agriculture. De Gruyter, Berlin, pp. 385–416.

Higham, T., 1994. Radiocarbon dating New Zealand prehistory with moa eggshell: Some preliminary results. Quaternary Science Reviews 13, 163–169.

Hope, G., 2009. Environmental change and fire in the Owen Stanley Ranges, Papua New Guinea. Quaternary Science Reviews 28, 2261–2276.

Hope, G.S., Golson, J., Allen, J., 1983. Palaeoecology and prehistory in New Guinea. Journal of Human Evolution 12, 37–60.

Hope, G., Flannery, T., Boeardi, 1993. A preliminary report of changing quaternary mammal faunas in subalpine new guinea. Quaternary Research 40, 117–126.

Hope, G.S., Haberle, S.G., 2005. The history of the human landscapes of New Guinea, in: Pawley, A., Attenborough, R., Golson, J., Hide, R. (Eds.), Papuan Pasts: Cultural, Linguistic and Biological Histories of Papuan-Speaking Peoples. Pacific Linguistics, Research School of Pacific and Asian Studies, The Australian National University, Canberra, pp. 541–554.

Horrocks, M., Bulmer, S., Gardner, R.O., 2008. Plant microfossils in prehistoric archaeological deposits from Yuku rock shelter, Western Highlands, Papua New Guinea. Journal of Archaeological Science 35, 290–301.

Hulme-Beaman, A., Cucchi, T., Evin, A., Searle, J.B., Dobney, K., 2018. Exploring Rattus praetor (Rodentia, Muridae) as a possible species complex using geometric morphometrics on dental morphology. Mammalian Biology 92, 62–67.

Hunt, C.O., Gilbertson, D.D., Rushworth, G., 2012. A 50,000-year record of late Pleistocene tropical vegetation and human impact in lowland Borneo. Quaternary Science Reviews 37, 61–80.

Hutchins, M., Jackson, J.A., Bock, W.J., Olendorf, D., 2002. Grzimek's Animal Life Encyclopedia, Volume 8, Birds I, 2nd ed. Gale Group, Farmington Hills, MI.

Hyndman, D., Menzies, J.I., 1980. Aproteles bulmerae (Chiroptera: Pteropodidae) of New Guinea is not extinct. Journal of Mammalogy 61, 159–160.

Ingicco, T., Amano, N., Setiagama, K., Moigne, A.M., Budiman, Sémah, A.M., Simanjuntak, T., Sémah, F., 2020. From Food to Grave Good. Current Anthropology 61, 264–277.

Kealy, S., Donnellan, S.C., Mitchell, K.J., Herrera, M., Aplin, K., O'Connor, S., Louys, J., 2019. Phylogenetic relationships of the cuscuses (Diprotodontia:Phalangeridae) of island Southeast Asia and Melanesia based on the mitochondrial ND2 gene. Australian Mammalogy 42, 266–276.

Kusmartono, V.P.R., Hindarto, I., Herwanto, E., 2017. Late Pleistocene to recent: Human activities in the deep interior equatorial rainforest of Kalimantan, Indonesian Borneo. Quaternary International 448, 82–94.

Langley, M.C., Amano, N., Wedage, O., Wedage, O., Deraniyagala, S., Pathmalal, M.M., Perera, N., Boivin, N., Boivin, N., Boivin, N., Boivin, N., Petraglia, M.D., Petraglia, M.D., Petraglia, M.D., Roberts, P., Roberts, P., 2020. Bows and arrows and complex symbolic displays 48,000 years ago in the South Asian tropics. Science Advances 6, 3831–3843.

Larson, G., Dobney, K., Albarelle, U., Matisoo-Smith, E., Robins, J., Lowden, S., Rowley-Conwy, P., Andersson, L., Cooper, A., 2005. Domesticated Pigs in Eastern Indonesia. Science 309, 381.

Leavesley, M.G., Allen, J., 1998. Dates, distrubance and artefact distributions: Another analysis of Buang Merabak, a Pleistocene site on New Ireland, Papua New Guinea. Archaeology in Oceania 33, 63–82.

Letnic, M., Fillios, M., Crowther, M.S., 2012. Could Direct Killing by Larger Dingoes Have Caused the Extinction of the Thylacine from Mainland Australia? PLoS ONE 7, e34877.

Löffler, E., 1977. Geomorphology of Papua New Guinea. ANU Press, Canberra.

Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge University Press, Cambridge.

Majnep, I.S., Bulmer, R., 2007. Animals the Ancestors Hunted: An Account of the Wild Mammals of the Kalam Area, Papua New Guinea. Crawford House, Adelaide.

Meinig, H., 2002. New records of bats (Chiroptera) from Indonesian islands. Myotis 40, 59–79.

Menzies, J., 2011. A Handbook of New Guinea's Marsupials and Monotremes, 2nd ed. University of Papua New Guinea Press, Port Moresby.

Menzies, J.I., Ballard, C., 1994. Some new records of Pleistocene megafauna from New Guinea. Science in New Guinea 20, 113–139.

Menzies, J.I., Dennis, E., 1979. Handbook of New Guinea Rodents. Wau Ecology Institute, Wau, PNG.

Menzies, J.I., Pernetta, J.C., 1986. A taxonomic revision of cuscuses allied to Phalanger orientalis (Marsupialia: Phalangeridae). Journal of Zoology 1, 551–618.

Menzies, J.I., Russell, L., Tyler, M.J., Mountain, M.-J., 2002. Fossil frogs from the central highlands of Papua New Guinea. Alcheringa 26, 341–351.

Miller, S., Hyslop, E., Kula, G., Burrows, I., 1994. Status of biodiversity, in: Sekhran, N., Miller, S. (Eds.), Papua New Guinea Country Study on Biological Diversity. The Department of Environment and Conservation, Waigani, PNG, pp. 67–96.

Miscamble, T., Manne, T., 2016. A taphonomic signature for quolls in the Australian archaeological record. Journal of Archaeological Science: Reports 7, 689–699.

Modjeska, N., 1982. Production and inequality: perspectives from central New Guinea, in: Modjeska, N., A., S. (Eds.), Inequality in New Guinea Highlands Societies. Cambridge University Press, Cambridge, pp. 50–108.

Moore, L.G., Armaza, F. V., Villena, M., Vargas, E., 2000. Comparative aspects of high-altitude adaptation in human populations. Advances in Experimental Medicine and Biology 475, 45–62.

Mora, S., Gnecco, C., 2003. Archaeological hunter-gatherers in tropical forests: a view from Colombia, in: Mercader, J. (Ed.), Under the Canopy: The Archaeology of Tropical Rainforests. Rutgers University Press, New Brunswick, pp. 271–290.

Mountain, M.-J., 1991a. Highland New Guinea Hunter-Gatherers: The Evidence of Nombe Rockshelter, Simbu, with Emphasis on the Pleistocene. Unpublished PhD thesis, Department of Prehistory, Australian National University.

Mountain, M.-J., 1991b. Landscape use and environmental management of tropical rainforest by pre-agricultural hunter-gatherers in northern Sahulland. Bulletin of the Indo-Pacific Prehistory Association 11, 54–68.

Norris, C.A., Musser, G.G., 2001. Systematic Revision Within the Phalanger orientalis Complex (Diprotodontia, Phalangeridae): A Third Species of Lowland Gray Cuscus from New Guinea and Australia. American Museum Novitates 3356, 1–20.

Pasveer, J.M., 2004. The Djief Hunters: 26,000 Years of Rainforest Exploitation on the Bird's Head of Papua, Indonesia. A.A. Balkema, Leiden.

Pedro, N., Brucato, N., Fernandes, V., André, M., Saag, L., Pomat, W., Besse, C., Boland, A., Deleuze, J.-F., Clarkson, C., Sudoyo, H., Metspalu, M., Stoneking, M., Cox, M.P., Leavesley, M., Pereira, L., Ricaut, F.-X., 2020. Papuan mitochondrial genomes and the settlement of Sahul. Journal of Human Genetics 1–13. https://doi.org/10.1038/s10038-020-0781-3

Piper, P.J., Rabett, R.J., 2009. Hunting in a tropical rainforest: evidence from the Terminal Pleistocene at Lobang Hangus, Niah Caves, Sarawak. International Journal of Osteoarchaeology 19, 551–565.

Pitblado, B.L., 2017. The role of the Rocky Mountains in the peopling of North America. Quaternary International 461, 54–79.

Rabett, R.J., 2018. The success of failed Homo sapiens dispersals out of Africa and into Asia. Nature Ecology and Evolution 2, 212–219.

Rabett, R.J., Barker, G., Barton, H., Hunt, C., Lloyd-Smith, L., Paz, V., Piper, P., Premathilake, R., Rushworth, G., Stephens, M., Szabó, K., 2013. Rainforest, in: Barker, G. (Ed.), Rainforest Foraging and Farming in Island Southeast Asia. McDonald Institute of Archaeological Research, Cambridge, pp. 217–254.

Rappaport, R.., 1968. Pigs for the Ancestors: Ritual in the Ecology of a New Guinea People. Yale University Press, New Haven.

Roberts, P., Petraglia, M., 2015. Pleistocene rainforests: barriers or attractive environments for early human foragers? World Archaeology 47, 718–739.

Roberts, P., Stewart, B.A., 2018. Defining the 'generalist specialist' niche for Pleistocene Homo sapiens. Nature Human Behaviour 2, 542–550.

Roberts, P., Boivin, N., Lee-Thorp, J., Petraglia, M., Stock, J., 2016. Tropical forests and the genus Homo. Evolutionary Anthropology 25, 306–317.

Roberts, P., Gaffney, D., Lee-Thorp, J., Summerhayes, G., 2017. Persistent tropical foraging in the highlands of terminal Pleistocene/Holocene New Guinea. Nature Ecology and Evolution 1, 0044.

Rosinger, A., 2015. Dehydration among lactating mothers in the Amazon: A neglected problem. American Journal of Human Biology 27, 576–578.

Salisbury, R.F., 1962. Early stages of economic development in New Guinea. Journal of the Polynesian Society 71, 328–339.

Salisbury, R.F., 1965. The Siane of the Eastern Highlands, in: Lawrence, P. (Ed.), Gods, Ghosts and Men in Melanesia: Some Religions of Australian New Guinea and the New Hebrides. Oxford University Press, Melbourne, pp. 50–77.

Shaw, B., Field, J.H., Summerhayes, G.R., Coxe, S., Coster, A.C.F., Ford, A., Haro, J., Arifeae, H., Hull, E., Jacobsen, G., Fullagar, R., Hayes, E., Kealhofer, L., 2020. Emergence of a Neolithic in highland New Guinea by 5000 to 4000 years ago. Science Advances 6, eaay4573.

Shoocongdej, R., Wattanapituksakul, A., 2020. Faunal assemblages and demography during the Late Pleistocene (MIS 2-1) to Early Holocene in Highland Pang Mapha, Northwest Thailand. Quaternary International. https://doi.org/10.1016/j.quaint.2020.01.022

Sieveking, G.G., 1954. Excavations at Gua Cha, Kelantan 1954. Federation Museums Journal 1, 75–143.

Sillitoe, P., 1988. From Head-Dresses to Head-Messages : The Art of Self-Decoration in the Highlands of Papua New Guinea. Man 23, 298–318.

Sillitoe, P., 2003. Managing Animals in New Guinea: Preying the Game in the Highlands. Routledge, London.

Strathern, A., 1971. The Rope of Moka: Big-men and Ceremonial Exchange in Mount Hagen New Guinea. Cambridge University Press, Cambridge.

Summerhayes, G.R., Ford, A., 2014. Late pleistocene colonisation and adaptation in New Guinea: implications for modelling modern human behaviour, in: Dennell, R., Porr, M. (Eds.), Southern Asia, Australia and the Search for Human Origins. Cambridge University Press, Cambridge, pp. 213–227.

Summerhayes, G.R., Leavesley, M., Fairbairn, A., Mandui, H., Field, J., Ford, A., Fullagar, R., 2010. Human adaptation and plant use in Highland New Guinea 49,000 to 44,000 years ago. Science 330, 78–81.

Summerhayes, G.R., Field, J.H., Shaw, B., Gaffney, D., 2017. The archaeology of forest exploitation and change in the tropics during the Pleistocene: The case of Northern Sahul (Pleistocene New Guinea). Quaternary International 448, 14–30.

Sutton, A., Mountain, M.-J., Aplin, K., Bulmer, S., Denham, T., 2009. Archaeozoological records for the Highlands of New Guinea: A review of current evidence. Australian Archaeology 69, 41–58.

Swadling, P., 1996. Plumes from Paradise: Trade Cycles in Outer Southeast Asia and Their Impact on New Guinea and Nearby Islands until 1920. Papua New Guinea National Museum, Boroko.

Taha, A.H., 1985. Archaeological investigations in Ulu Kelantan, Peninsular Malaysia. Unpublished PhD thesis, Department of Prehistory, Australian National University.

Taylor, J.M., Calaby, J.H., Van Deusen, H.M., 1982. A revision of the genus Rattus (Rodentia, Muridae) in the New Guinean region. Bulletin of the American Museum of Natural History 173, 178–336.

van der Kaars, W.A., 1991. Palynology of eastern Indonesian marine piston-cores: a Late Quaternary vegetational and climatic record for Australasia. Palaeogeography, Palaeoclimatology, Palaeoecology 85, 239-302.

Van Deusen, H.M., 1963. First New Guinea record of Thylacinus. Journal of Mammalogy 44, 279–280.

Vogelsang, R., Bubenzer, O., Kehl, M., Meyer, S., Richter, J., Zinaye, B., 2018. When hominins conquered highlands—an AcheuleansSite at 3000 m a.s.l. on Mount Dendi/Ethiopia. Journal of Paleolithic Archaeology 1, 302–313.

Walker, D., Flenley, J.R., 1979. Late Quaternary vegetational history of the Enga province of Upland Papua New Guinea. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 286, 265–344.

Watson, V.D., 1986. Obsidian as Tool and Trade: A Papua New Guinea Case, Burke Museum

Contributions in Anthropology and Natural History. Thomas Burke Memorial Washington State Museum, Seattle.

Wedage, O., Amano, N., Langley, M.C., Douka, K., Blinkhorn, J., Crowther, A., Deraniyagala, S., Kourampas, N., Simpson, I., Perera, N., Picin, A., Boivin, N., Petraglia, M., Roberts, P., 2019. Specialized rainforest hunting by Homo sapiens ~45,000 years ago. Nature Communications 10, 739.

Wedage, O., Roberts, P., Faulkner, P., Crowther, A., Douka, K., Picin, A., Blinkhorn, J., Deraniyagala, S., Boivin, N., Petraglia, M., Amano, N., 2020. Late Pleistocene to early-Holocene rainforest foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-lena. Quaternary Science Reviews 231, 106200.

White, J.C., Penny, D., Kealhofer, L., Maloney, B., 2004. Vegetation changes from the late Pleistocene through the Holocene from three areas of archaeological significance in Thailand. Quaternary International 113, 111–132.

White, P.J., 1972. Ol Tumbuna: Archaeological Excavations in the Eastern Central highlands, Papua New Guinea, Terra Australis. Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra.

Williams, F.E., 1940. Natives of Lake Kutubu, Papua. Oceania 11, 121–157.

Wright, D.D., Mack, A.L., Paxton, E.H., Menzies, J.I., 1995. Recent Aproteles bulmerae (Megachiroptera: Pteropodidae) bones found in Eastern Highlands Province, Papua New Guinea. Mammalia 59, 163–164.

Zegwaard, G.A., 1959. Headhunting practices of the Asmat of Netherlands New Guinea. American Anthropologist 61, 1020–1041.