



A different paradigm for the colonisation of Sahul

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ABSTRACT

Allen and O'Connell published "A different paradigm for the initial colonisation of Sahul" in the first number of Archaeology in Oceania this year (55: 1–14). We invited comments from several scholars and a riposte from the authors.

Keywords: initial colonisation, Sahul, different paradigm

RÉSUMÉ

Allen et O'Connell ont publié «Un paradigme différent pour la colonisation initiale de Sahul» dans le premier numéro d'Archéologie en Océanie cette année (55: 1–14). Nous avons invité les commentaires de plusieurs chercheurs et une réponse des auteurs.

Mots-clés: Colonisation initiale, Sahul, paradigme différent

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ORIGINAL ABSTRACT

Jim Allen and James F O'Connell

The questions of when and how humans reached Sahul, the Pleistocene continent of Australia and New Guinea, has remained a central issue of Australian archaeology since its development as an academic discipline in the mid-twentieth century. Modelling this event has persistently appealed to minimal assumptions – the simplest watercraft, the shortest routes, the smallest viable colonising groups. This paper argues that Australian archaeology can no longer ignore the way our understanding of this initial colonisation is being reshaped by current genomic research. It reviews this evidence and correct, it suggests that we need to rethink our models, modify or discard the minimalist assumptions that have so far driven them and consider how this different paradigm affects our understanding of early settlement in Sahul.

COMMENTS

Chris Clarkson and Kasih Norman

O'Connell and Allen make three important points in their paper: (1) recent modelling of the dispersal to Sahul makes use of unnecessary minimalist assumptions; (2) genetic estimates suggest large planned voyages to Sahul; and (3) crossings to Sahul were more likely during high sea stands when marine resources were more abundant and facilitated seafaring. While we do not disagree with any of these points in principle, and indeed agree wholeheartedly with their “next steps”, we nevertheless make three observations about recent models and their overly negative portrayal of these.

First, modelling always makes minimalist assumptions. Quantitative models largely adhere to environmental and ecological principles of the kind that underpin human behavioural ecology. These include such variables as

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carrying capacity and patch use, survivorship and fertility, resource competition and least cost, as well as physical variables such as ocean currents, travelling distance, terrain, and intervisibility. Such models seek to create simple explanations from complex variables and act as hypothesis generation tools rather than empirical tests. Their value to the Wallacean human expansion debate lies in their ability to translate complex ecological, demographic and physical variables into a set of testable predictions about expansion pathways, timings and rates of movement. The diet breadth model developed by Allen and O'Connell for the settlement of Wallacea is a case in point (O'Connell & Allen 2012). Many of the recent models of voyaging through Wallacea and settlement of Sahul are sophisticated and multidimensional and employ high powered computational simulations of social, ecological and physical variables that were not possible until recently. The results of these models generally support the conclusions reached by Allen and O'Connell here: that both northern and southern routes were possible, that crossing at various sea levels were also possible and that large populations were involved, implying construction of substantial sea craft, planning and provisioning. Few if any models suggest dispersing *Homo sapiens* lacked complexity or only followed the simplest paths.

Second, there is no mismatch between genomic and modelling results regarding the size of founding populations. On the contrary, as O'Connell and Allen point out, Bird *et al.* (2018) and Bradshaw *et al.*'s (2019) models found large founding populations were required to settle Sahul. Norman *et al.* (2018) also employed realistic demographic parameters based on modern hunter-gatherer survivorship, population growth, fissioning and carrying capacity. Their agent-based simulations imply large populations and explicitly modelled the very push-pull factors O'Connell and Allen suggest. Thus, we do not feel that most recent models have over-simplified or downplayed founding population sizes or complex factors driving migrations.

Third, it is no secret that O'Connell and Allen discount early ages for Sahul and thus settlement during low sea stands of MIS4. Such early ages stand in opposition to their favoured "short" (though steadily increasing) chronology. Allen's accepted ages went from 35 to 40 ka in 1995 (Allen & Holdaway 1995) shortly after the publication of Malakunanja II and Nauwalabila ages of 50–60 ka, to c.50 ka in 2018 shortly after the publication of 65 ka for Madjedbebe (O'Connell *et al.* 2018). We see that O'Connell and Allen update their accepted chronology for Sahul at a moving wall roughly 10–15 ka behind recent developments. Such a conservative approach clearly underpins their dislike of models that demonstrate the feasibility of early settlement of Sahul during MIS4, despite the feasibility of such a crossing (speculations about marine ecosystem fecundity aside). Fossil evidence indicates *Homo sapiens* had left Africa by 200 ka, possibly multiple times (Lahr & Foley 1994) and were present in Asia by 80–60 ka (Groucutt *et al.* 2018; Grün *et al.* 2005; Harvati *et al.* 2019;

Hershkovitz *et al.* 2018; Liu *et al.* 2015; Schwarcz *et al.* 1988; Shackelford *et al.* 2018; Stringer *et al.* 1989; Westaway *et al.* 2017). Simply dismissing inconveniently old sites in Australia is unhelpful and unscientific. Any fall back on genetic estimates of c.50 ka for the occupation of Sahul is overturned by the most recent genetic estimates indicating settlement by at least ~55 ka (95% CI: 42–67 ka) (Pedro *et al.* 2020), with peopling taking place via both the northern and southern routes. Evidence also exists for an earlier Out of Africa remnant contribution (albeit small) to Sahul genomes (Pagani *et al.* 2016). The latest genetic results therefore support both earlier settlement and multiple dispersal routes as predicted by Norman *et al.*'s model and earlier genetic analyses (Nagle *et al.* 2017a, 2017b; Yuen *et al.* 2019).

Rigorous appraisal of ages, artefact associations, model results and hypotheses is important, but so too is an open mind and explanations that accommodate the evidence as it currently stands. Discovering how and when Sahul was settled ultimately requires new models, hypotheses and, most importantly, new archaeological and genetic data. The work is only just beginning.

Murray Cox

Allen and O'Connell (2020) present a critique of minimalist assumptions, such as the favouring of shortest water crossings, in early human settlement models of Australia and New Guinea. While criticism of these assumptions is hardly new (Jones 1968), they nonetheless lie at the heart of most current discussion.

So what has changed? In short, genetics. DNA now suggests that the initial settlement of Sahul was made by hundreds to thousands of people (Bradshaw *et al.* 2019). Allen and O'Connell provide a review of the mitochondrial DNA and Y chromosome evidence, showing that the first settlers to reach Sahul were diverse. While some of this diversity may reflect later movements, multiple maternal (Pedro *et al.* 2020) and paternal (Bergström *et al.* 2016) lineages date back before 50 ka. In contrast to the much later settlement of islands like Madagascar (Cox *et al.*) and New Zealand (Penny *et al.* 2002), genetic data increasingly indicate that continental Sahul was settled by sizable founding populations.

Much debate has turned on two proposed routes of entry into Sahul via Timor and the Bird's Head of New Guinea. In contrast to Allen and O'Connell's optimism, genetics may always struggle to distinguish between them. Southeast Asia in general, and Wallacea in particular, saw extraordinary levels of mobility in the late Pleistocene and early Holocene. Modelling (Vallée *et al.* 2016) and what little ancient DNA is available (Lipson *et al.* 2018; McColl *et al.* 2018) are shaking up past assumptions. Interactions within and between Southeast Asia and Sahul during the late Pleistocene were complex and are still largely unresolved (Hudjashov *et al.* 2017; Jacobs *et al.* 2019). Genetic connections to both Australia and New Guinea are found right across Wallacea (Hudjashov *et al.* 2019), and despite considerable effort (mostly unpublished) no

distinguishing traces of those early routes clearly remain in the genetic data.

Beyond pathways of settlement, Allen and O'Connell touch on three points that may however benefit from further attention.

First, the timing of modern human arrival in Sahul. Madjedbebe is clearly at the sharp end of this discussion, but if the dates hold genetics raises two possible interpretations. Early populations may have gone extinct. This argument has support elsewhere: ancient DNA from the 45-ka Ust'-Ishim individual shows that his community did not contribute to humans alive today (Fu *et al.* 2014). Alternately, Pagani *et al.* (2016) suggest that modern Sahul populations carry a small genomic signal of an early out-of-Africa movement, although this idea has been contested (Wall 2017).

Second, the role of archaic hominins. Current thinking holds that archaic hominins never reached Sahul, but genetically, the modern populations that occupy the ancient continent of Sahul have inherited more DNA from Neanderthals and particularly Denisovans than anyone else. With archaic hominins unambiguously present across major water crossings in Flores (Morwood *et al.* 2004) and the Philippines (Détroit *et al.* 2019), the presumed inability of archaic hominins to reach Sahul is increasingly on shaky ground. Suspicious genetic signals of localized Denisovans have been detected in New Guinea (Jacobs *et al.* 2019).

Third, Australia and New Guinea form a natural whole. Papua New Guinean genetic data are increasingly available and notable globally for its diversity. Although genetic information is more limited for Indigenous Australians, levels of Australian diversity (Malaspinas *et al.* 2016) largely mirror that of Papua New Guineans (Bergström *et al.* 2017). The settlement, archaeology and culture of northern and southern Sahul are often considered separately, but the early history of Australia cannot meaningfully be studied in isolation from the early history of New Guinea. At some point, this artificial divide will need to be bridged.

Where to from here? Allen and O'Connell are mostly silent on genome-scale data for the prosaic reason that there is relatively little available. With minor exceptions (Malaspinas *et al.* 2016), Australia is a notable blank, but even the first genome survey of Indonesia, the world's fourth most populous country, was only published last year (Jacobs *et al.* 2019). Regional genomic data are, however, on its way (Wall *et al.* 2019).

Evidence from across the anthropological sciences, including genetics, increasingly runs counter to the minimalist narrative. The first settlers of Sahul were far more numerous and diverse than we have traditionally thought, and understanding how they entered and engaged with their new environments will require better models and different thinking. Thankfully, Allen and O'Connell open up new intellectual routes for us to explore.

Shimona Kealy

This paper offers another helpful summary by the Allen and O'Connell team on the current status of research investigating initial human arrival on Sahul. Perhaps of greatest use for the archaeological community is their insightful review of various genetic studies and their admirable goal of bringing this key line of enquiry to the full attention and consideration of archaeologists. I would offer, however, a word of caution regarding the way in which molecular dates are obtained and how we as archaeologists interpret their results. Allen and O'Connell also propose in their paper an interesting hypothesis regarding occupation patterns in Wallacea during the last glacial maximum (LGM) which, despite not being quite as clear-cut in the archaeological record as suggested, is still an interesting scenario worthy of future analysis.

Modern molecular dating relies on a wide range of assumptions, many of which have substantial impacts on the divergence estimates obtained (Bromham 2019). Recent mutation rate studies have also suggested significantly slower annual rates than previously estimated (Besenbacher *et al.* 2018; Scally 2016) which would consequently push back divergence dates such as those discussed by Allen and O'Connell (2020). While these rate studies are based on genome-wide calculations, and not focused on mitochondrial DNA (Tobler *et al.* 2017) or Y chromosomes (Bergström *et al.* 2016), continued changes in our understanding of mutation rates have substantial implications for studies relying on molecular clocks and the divergence estimate(s) which they produce (Moorjani *et al.* 2016; Sikora 2017).

One method to alleviate some of these assumptions is to apply fossil calibrations; however, these come with their own baggage of inherent assumptions (Bromham 2019). When asking questions about specific node divergence estimates, it is important to recognise which nodes or tips in a tree were calibrated and what calibration was used. For the question of Sahul arrival, it is important to recognise the two-tailed nature of the Signor-Lipps effect (Raup 1986; Signor & Lipps 1982), which in addition to the now proven existence of sites on Sahul's submerged continental shelf (Benjamin *et al.* 2020), strongly suggests that dates obtained from these [then] "inland" sites represent a period sometime *after* initial human arrival in Sahul. Thus, while I strongly support Allen and O'Connell's directive for archaeologists to be more inclusive in their consideration of genetic data, I also caution the use of divergence estimates to "prove" or "disprove" particular aspects of the archaeological record without due consideration to what (if any) archaeological data were used for calibration, and where those calibrations are located. As with changes to mutation rates, different applications of tip/node calibrations can also significantly impact estimates of divergence (Bromham 2019).

Regarding Allen and O'Connell's hypothesis for "reduced mobility and site occupation during the LGM

sea-level decline”, while probable, some of the site interpretations used to support the hypothesis appear to be missing key dates or are perhaps over-simplified. In particular, Allen and O’Connell suggest site abandonment on Gebe Island between ~26 ka and the terminal Pleistocene/Holocene (i.e. ~11.7 ka). However, despite some evidence for stratigraphic disturbance and inversions in the dates, the Golo record nevertheless recovers dates for occupation of ~25 ka, ~22 ka, ~21 ka, and ~19 ka calBP (Bellwood 2019). These dates fall within Bellwood *et al.*’s (2019) “Phase 2” (25–11 ka) which, while notable for its “intermittent ... [and] diminished density of occupation” (Bellwood *et al.*, 2019) is certainly not suggestive of site abandonment during the LGM.

Regarding the Timor record, while Asitau Kuru (previously Jerimalai) does appear to have a hiatus in the record over the LGM period as Allen and O’Connell discuss, I draw their attention to O’Connor *et al.* (2010) which published the results of excavations at Lene Hara, additional to those presented by O’Connor *et al.* (2002). The later Lene Hara paper included additional dates which extend the early record at this site to ~21 ka, and through the LGM. A third Timor site, Laili, also records dates for occupation across the LGM period (Hawkins *et al.* 2017). These records suggest that the scenario of a negative correlation between Wallacean occupation and LGM sea-level decline was perhaps not as extreme as Allen and O’Connell present. However, as demonstrated by the Golo record (Bellwood *et al.* 2019), I think further investigations regarding the *intensity* of occupation across the region during this time would certainly be worthwhile. Additionally, Allen and O’Connell’s hypothesis that people were forced to become less reliant on reef resources and broadened their diets in response to the lowering sea levels of the LGM is further supported by the recent isotope work of Roberts *et al.* (2020).

Craig Millar and Dave Lambert

Allen and O’Connell (2020) not only offer a different paradigm for the colonisation of Sahul but also analyse the underlying rationale that has dominated this field for many years. They argue that explanations for the settlement of Sahul have generally invoked a minimalist view. This approach suggests that simple explanations are more likely to be correct than are complex ones based on a relatively large number of assumptions. Hence, theirs is a thoughtful and important contribution. The minimalist approach is more generally known as Occam’s Razor. Since the Middle Ages this touchstone principle has been used to evaluate and formulate many scientific hypotheses. For example, in contemporary phylogenetics, the “law of parsimony” is used to evaluate different evolutionary hypotheses. However, Francis Crick warned against this general idea suggesting that it might not be well suited to the “messy world of biology”. Allen and O’Connell suggest that “... Australian archaeologists can no longer ignore the way our understanding of this initial colonisation [of Sahul] is being reshaped by current genomic research”. We agree. They go

on to review the use of mitochondrial DNA to reconstruct relationships among maternal lineages and to use mutation rates to determine the Time to the Most Recent Common Ancestor (TMRCA) of those lineages. Finally, they use their results to support particular hypotheses about the pattern and timing of the colonisation of Sahul. The authors review only the mitochondrial data and briefly refer to Y chromosome variation. They justify this approach by pointing out that mitochondrial genetics is well understood and because there is a large amount of data reported for this genome. This includes substantial datasets of modern Aboriginal Australian populations. Population and demographic modelling are needed to estimate the timing of past founding or bottle neck events. Unfortunately, such modelling is associated with large confidence intervals when based on a single non-recombining locus such as the mitochondrial genome (e.g. Stoneking 2017: 179). It is therefore surprising that the authors put so much faith in the power of mitochondrial sequences to estimate arrival times in Sahul. Another difficulty with estimations of TMRCA using mitochondrial data is that their reliability is difficult to assess, particularly as researchers attempt to make estimations for older and older time periods. In addition, mitochondrial DNA has some more general limitations. For example, it does not show any sign of the admixture between anatomically modern humans and archaic hominins. This illustrates that it does not fully reflect past demography. However, some of these limitations can be overcome. For example, it is possible to improve estimates of TMRCA by incorporating ancient mitogenomes of known age material into models. Unfortunately, Allen and O’Connell do not use this approach. They acknowledge that estimates of the size and frequency of colonisation events are dependent on a critical assumption. This is that observed diversity of major mitochondrial haplogroups had its origins outside Sahul. If this is not correct their argument is substantially weakened. Again, this issue could be resolved by using analyses of ancient material. A substantial advance on Allen and O’Connell’s reliance on mitochondrial data would be to use nuclear genomes. This is because such data provide millions of loci for demographic modelling. This leads to much reduced confidence intervals that are more accurate and robust in comparison to those resulting from single locus mitochondrial data. Furthermore, nuclear data are comprised of maternally and paternally inherited genetic markers that allow a clearer picture of past demographic patterns. Unfortunately, in the beginning of their paper, Allen and O’Connell dismiss this possibility and suggest that there are too few nuclear genomes available at this time. We would argue against this and point to the ever-increasing number of modern and ancient nuclear genomes that have now been sequenced (e.g. Rasmussen *et al.* 2011; Malaspina *et al.* 2016; Wright *et al.* 2018). In summary, although arguing convincingly against the minimalist approach, Allen and O’Connell (2020) appear to have fallen into their own trap when analysing the genetic data. Notwithstanding the widespread popularity of mitochondria data, their analyses are subject

to a range of problems and inaccuracies that stem from the analysis of a single haploid genetic marker.

Nicola Stern

Relentless advances in the recovery, analysis and interpretation of genetic data over the past 30 years mean that questions which were once the purview of archaeologists and palaeontologists are now routinely addressed by geneticists (Llamas *et al.* 2017; Nielsen *et al.* 2017; Pääbo 2014). This includes discussions about the origin and dispersal of our species (e.g. Ingam *et al.* 2000), and recent demographic history (e.g. Gosling & Matisoo-Smith 2018). Allen and O'Connell (2020: 5, 10) exhort archaeologists to engage with these data and the narratives written from them because of the bearing they have on long-standing ideas about the settlement of Sahul. This exhortation presents archaeologists with a number of challenges, not the least of which is identifying the unique contribution they can make to the narratives of recent human history.

It is widely argued that information generated from studies of mtDNA, Y-chromosome and whole genome data has much greater potential than archaeological data for answering questions about when and by whom the continent was colonised, as well as the pattern of dispersal and the adaptive shifts this process entailed. This is because the material record is fragmentary as well as an indirect source of information about past adaptations (e.g. Nielsen *et al.* 2017). Archaeologists do need to acknowledge that traces of past human activity can only be preserved in landforms or depositional traps that were accumulating sediment during the relevant time frame, with the result that even an exceptionally dense record, dated with high precision, is unlikely to solve the problem of "first appearance data" always being provisional and incomplete, and not especially useful for identifying routes, landfall or dispersal patterns (e.g. Dennell 2017: 383).

However, estimates for the timing of initial settlement based on archaeological data will always invite comparisons with estimates based on genetic data (e.g. Bergström 2017: 35; Clarkson *et al.* 2017: 309; Dortch & Malaspinas 2017) and, of course, resolving mismatches has the potential to enhance methods and data quality. Concordance in the inferences drawn from studies of these substantively different datasets can be seductive but does not obviate the need to assess those inferences in terms of the data and analytical and interpretive approaches that generated them.

Caveats and error margins are integral to the genetic data pertaining to the settlement of Sahul, and they arise from the processing and analytical techniques employed, as well as the use of different data bases, drawn from different samples. Some types of studies generate data that are more robust for addressing some questions than others, but despite this, there is a measure of consensus that the continent was colonised ~45–65 ka, that populations from Papua New Guinea and Australia diverged long before the post-glacial sea level rise that separated the two land masses (Bergström 2017: 32–33), and that population structure in

Australia pre-dates the last glacial maximum (Bergström 2017: 34) and may in fact have originated with the initial settlement of the continent (Tobler *et al.* 2017). As Allen and O'Connell (2020: 6–7) discuss, there is less consensus about the number of mtDNA haplogroups represented in Sahul's founding population, how recently each last shared a common ancestor and whether the haplogroups diversified before or after arriving in Sahul.

The argument that haplogroups diversified prior to their arrival in Sahul is predicated on the estimates of divergence times (Table 1) and initial colonisation of Sahul at ~50 ka (as this allows time for the haplogroups to diversify and for anatomically modern humans (AMH)-Denisovan introgression). Both points are the subject of debate but are fundamental to the argument that during a limited time interval, different genetic populations arrived along different parts of the coastline. The number of haplogroups that might have been lost since then is, of course, unknown. Less controversial is the suggestion that those founding groups were large and, at any given locality, in close proximity, given the importance of social networks to the long-term viability of foraging communities (Migliano *et al.* 2017; Moore 2001).

The argument that people arrived in different parts of the continent repeatedly during a constrained time interval, together with Kealy *et al.*'s (2016) suggestion that people moved through the islands of Wallacea in a radiating pattern that resulted in an easterly extension of the biogeographic range, renders the search for a single route through Wallacea redundant. Archaeological effort is thus more productively focused on establishing the diet and foraging strategies, technologies and social networks that solved the ecological challenges presented by this island landscape as well as the palaeolandscape and palaeoenvironmental triggers that may have destabilized those adaptations and encouraged people to push at the boundaries of existing foraging ranges (e.g. O'Connor *et al.* 2017; Roberts *et al.* 2020).

Given the issues involved in establishing the age of the oldest archaeological or palaeontological occurrences in any given region, for now, information about dispersal within Sahul will be generated primarily from genetic evidence for the distribution of mtDNA or Y-chromosome haplogroups. This provides an opportunity for archaeologists to pursue a range of questions about how people in a tropical environment with a predominantly marine subsistence base settled into the unpeopled and unfamiliar landscapes of a vast, semi-arid and arid landmass. This includes questions about the changes in diet and foraging strategies, and technologies, that were made as people extended their ranges into terrestrial habitats that offered more abundant and predictable prey. It also includes questions about the circumstances in which social groups on the edges of a range split from their parent populations (the terrestrial equivalent of whether rising or falling sea levels are a trigger to movement) as well as the types of social networks that facilitated this through the exchange of information as well as marriage partners. Maintaining those

social networks may have been particularly challenging when social groups were small and scattered (e.g. Veth *et al.* 2011: 219).

Allen and O'Connell's (2020: 10) call for the integration of multiple datasets to define future research directions needs to be followed by sustained, inter-disciplinary research programs that will generate the information needed to address those questions. Few researchers have sufficient knowledge of the theoretical, methodological and analytical techniques fundamental to the practice of archaeology as well as the quaternary sciences and genetics, which emphasises the importance of both inter-disciplinary research teams and frequent inter-disciplinary dialogue (e.g. Sykes *et al.* 2019).

Peter Veth

Allen and O'Connell have pitched a "different paradigm" for the settlement of Sahul. Their assumptions include (a) larger founding populations based on genomics, (b) longer crossings between islands, (c) presence of a "marine highway" ceasing during lower sea levels, (d) radiation allowing multiple entry points into Sahul and (e) depletion of higher ranked coastal resources during lower sea levels. Many ideas appear in other papers (e.g. Bird *et al.* 2018, 2019; Bradshaw *et al.* 2019; Kealy *et al.* 2017; Veth *et al.* 2017).

Potentially innovative elements of this paper include (i) >1000 people in founding groups, (ii) diversification of haplogroups before arrival in Sahul, (iii) discontinuity of genetic flow through Wallacea and Sahul by 35 ka and (iv) adoption of a *strandlooper* foraging strategy due to falling sea levels with a reduction in both reef area and high-ranked resources.

Recent mtDNA analyses show that two groups of settlers arrived between 50 and 65 ka settling Northern (Papuan) and Southern Sahul (Pedro *et al.* 2020). Lineages became geographically structured between 10 and 32 ka (Tobler *et al.* 2017) due to environmental changes. Bradshaw *et al.* (2019) also estimated the size of founding populations based on demographic rates from hunter-gatherers and a carrying capacity model for northern Sahul. Similar to the current estimates of Allen and O'Connell, they conclude a founding population of 1300 and 1550 individuals. Voyaging simulation models show that passage to Sahul was not accidental (Bird *et al.* 2018, 2019). Greater AMH mobility before 50 ka is supported, as is restriction during the terminal Pleistocene; however, the link with depleted coastal resources is not established.

There is increasing evidence from the NW Shelf, East Timor and Borneo for early maritime technologies and diets reflecting peoples' ability to purposefully voyage over large tracts of ocean and systematically harvest resources from it. The presence of burnt fragments of dietary shellfish from the earliest occupation units (SU9) of Boodie Cave (Veth *et al.* 2017) are dated to 53 ka, and when combined with sites in East Timor and Borneo provide evidence for maritime competencies on the Southern Dispersal Route (Kealy *et al.* 2017). Veth *et al.* (2017: 27) note "Remarkably

the early colonists of the now-submerged shelf of Greater Australia did not turn their back on the sea or remain coastally tethered, but instead rapidly adapted to the new marsupial animals and arid zone plants of the extensive maritime deserts of North West Australia". An early and hybrid economy including marine animals and molluscs existed with (sub) coastal terrestrial fauna and flora. This could have existed at other landing points and does not require the depletion of higher ranked reef flat molluscs, such as the Giant Clam (*Tridacna*). Pleistocene shellfish assemblages of East Timor do not show depression of species.

The authors accept settlement at 50 ka consistent with an increasing number of sites dated to 45–55 ka (Boodie Cave, Minjiwarra, Carpenter's Gap 1, Karnatukul, Nawarla Gabarnmang, Watari Jurnti, Yurlu Kankala, Devil's Lair, Warratayi, Willandra Lakes and the Ivan Valley (Veth *et al.* 2019). However, 50 ka clearly falls short of the new optically-stimulated luminescence chronology of c.60 ka for Nauwalabila and c.65 ka for Madjedbebe (Clarkson *et al.* 2017). Given multiple desert sites are now pegged to c.50 ka, it is time to recast occupation and genomics models to an earlier 50–60 ka bracket for arrivals (Veth 2017).

This latest offering prompts archaeologists to embrace new complexities in settlement models based on genomics, demography and a recasting of maritime skills. Purposeful, radiating groups of maritime voyagers entered Sahul in at least two major areas with genetic diversification likely occurring before 55 ka. Changes in gene flow associated with the Last Glacial Maximum occurred along Wallacea and within Sahul. Regionally distinct populations from 30 ka would likely have resulted in new technological and symbolic systems due to selective pressures and divergence.

RIPOSTE

James F. O'Connell and Jim Allen

We wrote this paper as a conversation piece, to provoke broader integration of archaeological data with other sources of information. Commentators have remarked on ways of meeting that goal. Four issues merit reply.

Dating

Establishing the time of human arrival in Sahul is central to any argument about the colonisation process. Archaeological evidence is key to resolving this issue. Several commentators (Veth, Clarkson and Norman) cite the purported 65 ka date for Madjedbebe but fail to reference detailed critiques of this proposition presented since the 2017 *Nature* paper was published (O'Connell *et al.* 2018; Williams 2019). In particular, Clarkson offered no response to our comprehensive 2018 review in *PNAS* – a journal that would have allowed a fulsome (text plus SI) reply, published within a few weeks of submission. Clarkson and Norman portray us as unhelpful and unscientific because we do not uncritically accept their questionable data. Apart from exposing themselves and colleagues to greater opprobrium

for their unargued dismissal of counter arguments, they overlook a basic tenet of science: the reproducibility of results, in this case away from the Arnhem Land sand sheet. It is 30 years since Jones and Roberts began that unfulfilled quest. People might have been in Sahul 65 ka but that is not established at Madjedbebe nor yet anywhere else in Sahul.

Clarkson and Norman take solace in the fact that over the past 30 years our estimate for first colonisation has increased from c.40 ka to c.47–50 ka. As previously observed (Allen & O’Connell 2014), this is a product of improved dating methods, not the discovery of older sites. That improvement continues: witness the IntCal20 radiocarbon calibration curve (Reimer *et al.* 2020) which when adjusted for the Southern Hemisphere will require reconsideration of all Sahul ¹⁴C dates currently pegged >40 ka. Initial applications (e.g. Bard *et al.* 2020) suggest that dates now cited >45 ka will be shortened by several centuries, contracting – not expanding – the best-supported time frame for Sahul colonisation.

Genetics

Millar and Lambert criticise our reliance on uniparental markers, asserting that nuclear genome data would be more informative. We agree, but as Cox notes, where are the data? At present, none of the sources Millar and Lambert cite offer as much insight on the identities, numbers and arrival times of early colonists as do published haploid data. They also advocate reliance on aDNA rather than information from living populations in discussions of coloniser identities. Again, such data are essentially unavailable at present and given conditions governing contamination-free tissue preservation across the tropics and Sahul are unlikely ever to be common enough to significantly offset what can be learned from modern sources.

Kealy raises an important point concerning uncertainty about mutation rates as a basis for estimating lineage ages and related inferences about colonisation dates. We share her concern. On the other hand, the fact that two widely referenced rates (Soares *et al.* 2009; Fu *et al.* 2013) based on different lines of evidence yield similar estimates for mtDNA is sufficient to warrant constructive speculation of the sort we and others are pursuing.

Millar and Lambert reckon our estimate of as many as a dozen mitochondrial lineages among Sahul founders is too high. They invite the inference that the number may have been as low as three, including only macro-haplogroups M, N, and R^N. If that were so, then the mutations that define all “daughter” lineages found in modern indigenous Sahul populations must have occurred *after* those macro-haplogroups arrived in the continent. Veth, Clarkson and Norman endorse low haplogroup diversity among founders, citing Pedro and colleagues’ (2020) recent TMRCA estimates >> 50 ka for some of those lineages. They confuse these TMRCA estimates with dates for their presence in Sahul. These are not the same thing: diversification could have occurred *prior* to arrival in Sahul. For reasons argued in our paper we think this more likely.

Pedro *et al.* (2020) agree:

The scenario we might postulate from these results suggests (1) the diversification of ancestral Sahul lineages in a population located in Sunda, (2) two (or more) dispersal events to Sahul within the same narrow time frame around 45–55 ka, (3) a dispersal to Sahul of a group of settlers carrying lineages observed today in Northern Sahul (M27, M28, M29’Q, P1, P2, P4a, P10, P13b), (4) another dispersal to Sahul of a group of settlers carrying the lineages observed today in Southern Sahul (O, S, N13, M42a’c, P5, P6, P7, P8, and other P) ...

This summary makes Millar and Lambert’s caution look too conservative. It also shows that Veth, Clarkson and Norman have misunderstood Pedro and colleagues’ argument.

Colonisation process

Pedro and colleagues’ reference to two “dispersal events” underplays what must have been a very complex diaspora, since it involved at least 17 mitochondrial lineages and perhaps as many or more separate colonising voyages.

Our argument, developed in detail elsewhere (O’Connell & Allen 2012), posits rapid coloniser movement through Wallacea and across Sahul driven by serial depletion of high-ranked prey. Stern rightly notes that archaeological assessment of that argument will not be easy. Archaeologists must broaden their inquiry to include information on the relative costs and benefits of exploiting various resources and on the ecological and archaeological consequences of doing so. Investigations of shellfish use by modern Torres Strait foragers (Bird & Bliege Bird 1997; Codding *et al.* 2014) offer important leads for this effort.

Veth implies that our argument is refuted by the absence of high-ranked shellfish remains, specifically tridacnids, in early coastal middens. Ethnographic data and formal models of prey handling show that among pedestrian foragers certain resources will be processed, and the resulting waste abandoned at or near the collection point, consistent with the goal of increasing the nutritional utility of loads returned to a residential base. Tridacnids are such a resource. Giant clams are unlikely to be represented in coastal middens in proportion to their use as food. Additionally, they become attractive to collectors before reaching reproductive age. Under predation pressure local populations will often be reduced in abundance to the point that coastal foragers either broaden their diets or move to habitats where tridacnids are still common. Veth misunderstands the complexity of the archaeological test. On a similar theme, his claim for shellfish exploitation at 53 ka is contradicted by his cited source (Veth *et al.* 2017) which places this event no earlier than 51.1 or 42.5 ka.

Kealy suggests the possibility of a significant time lag between the initial spread of foragers along Sahul coast lines and movement into the interior. Our reading of the early continental chronology indicates near-simultaneous movement into a wide range of terrestrial habitats based on cost/benefit foraging trade-offs. We expect movement

inland off coastlines to have been archaeologically instantaneous. Wherever we have insights (Boodie Cave, Huon Peninsula, New Ireland, Timor) we are not seeing “coastal” dates older than the earliest from the continental interior.

We thank Kealy for drawing attention to additional Wallacean dates at and around the LGM. As we noted, gaps in the chronological record roughly 35–25 ka might be explained by tight coastal occupation with the evidence now underwater. The flurry of LGM dates implies a period of more mobile, broad-spectrum food collection, perhaps by reduced populations, best explained by the catastrophic sea level fall from c. –60 m to c. –130 m in 2000–3000 years.

Clarkson and Norman claim we dislike models that promote the feasibility of early settlement of Sahul during MIS4, “speculations about marine ecosystem fecundity aside”. This misses the point: “ecosystem fecundity” is critical to the argument. It cannot be set aside. The same factors that likely inhibited trans-Wallacean movement during the LGM also applied during similar MIS4 sea level lows.

Back to genetics

Finally, and perhaps most provocatively, Cox flags recently published whole genome data indicating an unexpected component of archaic human DNA among modern Sahul indigenes (Jacobs *et al.* 2019). Combined with increasing fossil and archaeological evidence of an ancient human presence in Wallacea (O’Connell *et al.* 2018), this could mean that *sapiens*-archaic introgression took place there as well as in Sunda to the west as *sapiens* populations passed through the region. But Jacobs *et al.* also raise the possibility of a Denisovan presence in northern Sahul, one that might have been established well before 50 ka and where at least some *sapiens*-archaic introgression may also have occurred. If the purported 65 ka date for Madjedbebe’s archaeology were ever supported by evidence from other Sahul sites, one would need to determine which human populations were responsible for it and what might have been their relationship with modern Aboriginal Australians. If the people who left the early archaeological debris at Madjedbebe were Denisovans then at least three implications follows: (1) Alan Thorne (1977) was right about a non-*sapiens* human presence in Sahul well before 50 ka; (2) the people responsible for the early deposits at Madjedbebe were relatively minor contributors to modern Aboriginal Australian ancestry; and (3) their seafaring capabilities and subsistence practices (e.g. Florin *et al.* 2020) were more sophisticated than previously appreciated. We are sceptical about any of this, just as we once were about a possible human presence halfway across Wallacea roughly a million years ago. Genetic, fossil and archaeological data continue to challenge long-standing ideas about the human experience in Sahul. We must pay more consistent attention to integrating them in modelling that experience.

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