The Evolution of Modern Behaviour and its Implications for Maritime Dispersal During the Palaeolithic

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Oceans and seas are more frequently thought to have been barriers to than enablers of movement for archaic hominins. This interpretation has been challenged by a revisionist model which suggests that bodies of water facilitated the dispersal of pre-moderns. This paper addresses the revisionist model by defining maritime dispersal as a series of cognitive and organizational problems, the capacity to solve which must have arisen during the evolution of Homo. *The central question posed is: knowing the type of social and cognitive configuration necessary for strategic maritime dispersal, and knowing the social and cognitive capacities of hominin species implied in the revisionist dispersal model, how likely is it that such species possessed the capacity to undertake purposive maritime colonization? Available data suggest that the evolution of modern cognitive architecture during the Late Pleistocene correlates positively with increasing evidence for maritime dispersal in the Upper Palaeolithic, and that behavioural modernity is implicated in the appearance of strategic maritime dispersal in Homo. Consequently, it is likely that deliberate trans-oceanic seagoing is restricted to Anatomically Modern Humans, and possibly Neanderthals.*

Oceans and their effects on hominin dispersal

Prevailing interpretations and recent challenges

Oceans are more frequently thought to have been barriers to than facilitators of movement for archaic hominins. Pre-modern human dispersals out of Africa and beyond are considered to have been conditioned and directed by bodies of water (e.g., Boivin *et al.* 2013; Dennell & Petraglia 2012; Mellars 2006; Mellars *et al.* 2013; Palombo 2013),[1] prohibiting, for example, the colonization of Australia by archaic *Homo*. Anatomically Modern Humans (AMH/Moderns), by contrast, have proven to be capable of overcoming oceanic barriers from ~50,000 years ago (Davidson 2013; Kirch 2010, 135–6; Webb 2006, 73–111). During the terminal Pleistocene and early- to mid-Holocene our species reached increasingly isolated fragments of land (notably in the Mediterranean, Caribbean, East Asia and Near Oceania), with the colonization of Remote Oceania from 3500 years ago (Athens *et al.* 2014; Wilmshurst *et al.* 2011) representing the acme of this achievement prior to the modern period. Patterning in such behaviour suggests, however, that Moderns were reluctant to abandon the security of continental environments, even if they were demonstrably capable of doing so; larger, closer islands have been preferred (or judged to be less hostile) habitats over smaller, more remote islands, following the expectations of island biogeographic theory (MacArthur & Wilson 1967). In the Holocene Mediterranean, for example, despite evident capacity to access small islands, these represent some of the last niches in the region to be colonized by expanding agropastoralist populations (Broodbank 2006; Dawson 2013). The prevailing interpretation has been, then, of bodies of water as biogeographic barriers to dispersal in *Homo*, just as they represent similar barriers (of variable permeability) to other taxa (e.g., Losos & Ricklefs 2010; Quammen 1996). This interpretation forms a vital component of the current model of hominin dispersal around the planet.

This standard model is now challenged by a revisionist model of hominin dispersal. The

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revisionist model arose from and has been primarily adopted in Mediterranean scholarship; proponents include Runnels (2013; 2014a, b; Runnels & Hammond 2012) and Simmons (2012; 2014), amongst others (e.g., Panagopoulou & Karkanas in press; Strasser *et al.* 2010; 2011; Tourloukis & Karkanas 2012). Contrary to the prevailing understanding of oceans and seas as inhibitors of the dispersal of hominins, these scholars have suggested that the Mediterranean—and by extension other bodies of water—facilitated the dispersal of pre-modern hominins. This is based on recent data from Crete and other eastern Mediterranean islands, where artefacts which bear typological similarities to Lower and Middle Palaeolithic forms (i.e. Acheulean and Mousterian) have been recorded during surface prospection (Ferentinos *et al.* 2012; Strasser *et al.* 2011). As Crete, and several other Mediterranean islands, have been truly insular since the Zanclean Flood at 5.3 million years ago (Krijgsman *et al.* 1999; before the appearance of *Homo*), it is argued that these artefacts are the signature of colonization and hence deliberate seagoing by those pre-modern hominins most usually associated with the relevant industries. Taking these data as a point of departure, it has been suggested that oceans should be viewed as environments that enabled rather than inhibited dispersal amongst pre-moderns (Runnels 2014a,b; Simmons 2014, 203–12). The paucity of Lower Palaeolithic data from other island or biogeographically remote contexts is in general regarded by these authors as a function of collection strategies not explicitly oriented towards recovery of such data, rather than being representative of patterning in hominin behaviour (Runnels 2014a).

Implications of and questions for the revisionist model

If the revisionist model were correct in asserting that oceans and seas were facilitators rather than inhibitors of movement in *Homo*, there would exist serious implications for our understanding of how and why hominins spread around the planet; not least that our ability to distinguish between probable presence *vs* absence of Lower Palaeolithic occupation is inadequate, and that we have consequently fundamentally misunderstood both the processes whereby hominins were distributed across landmasses and also the causes, forms and structural effects (such as speciation and cultural and behavioural variation) of this distribution. If the revisionist model were accurate, it would, for example, challenge the current explanation of the pre-Upper Palaeolithic absence of hominins from the Americas and Australasia and undermine attempts to explain *H. neanderthalensis* as an outcome of allopatric speciation from populations of source taxa in Africa. Consequently, although the revisionist model has gained traction primarily in Mediterranean scholarship, establishing its veracity should be of primary importance to archaeologists interested in the pattern and process of human dispersal, both regionally and at the global scale. The aim of this paper is, then, to evaluate the efficiency of the revisionist *vs* the standard model in accounting for data.

How can we interrogate the revisionist model? Thorough consideration of the quality and quantity of the Mediterranean data may be productive (see Broodbank 2014; Galanidou 2014; Phoca-Cosmetatou & Rabett 2014a). The lack of either stratified cave deposits with hominin fossil material or artefacts from sealed and radiometrically dated contexts is problematic. The absence of radiometric data from stratified contexts in particular for any of the purportedly Lower Palaeolithic material from the 'true' (i.e., insular throughout the late Pliocene and Pleistocene) Mediterranean islands severely limits the extent to which claims may be made about this material, as morphometric analyses are suggestive but not conclusive. Problems pertaining to the quality of the data themselves aside, it would be likely that any large-scale island colonization during the Lower–Middle Palaeolithic would have pronounced and palaeoenvironmentally visible effects on fragile island ecologies. The apparent lack on Mediterranean islands of ecogeographic impacts usually associated with a colonizing apex predator such as pre-modern forms of *Homo* (Leppard 2014a) might, then, be taken as indicative of a lack of colonization episodes sustainable over the long term. Finally, it should be noted that the cyclical imprisonment and release of vast amounts of water in and from the icecap(s) of the Northern Hemisphere during glacial–interstadial oscillations implies that the Pleistocene geography of the Mediterranean was more dynamic than often appreciated. For example, some islands which have remained insular during the Holocene—particularly in the Aegean, Adriatic and Tyrrhenian—were, during low sea stands associated with glacial maxima, connected to the Eurasian mainland (Lykousis 2009). In such a circumstance, artefacts from currently insular contexts with dates which straddle Pleistocene glacials can be interpreted in terms of terrestrial, and not maritime, dispersal.

The problems inherent in the data notwithstanding, this paper adopts a different approach (see also Phoca-Cosmetatou & Rabett 2014b), and in so doing aims to contribute more broadly to the study of island colonization as a behaviour in *Homo*. So far in the wider discussion, attention has primarily been fixed on the data themselves, their distribution, reliability and pertinent palaeogeographic and biogeographic

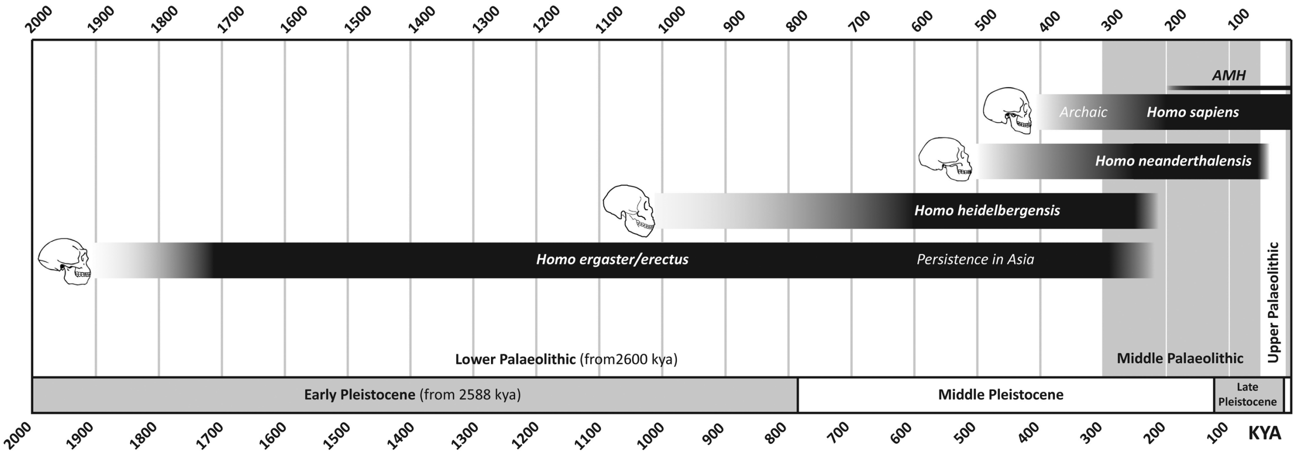

Figure 1. *Correspondence between cultural chronology, geological chronology and species prevalence, in thousands of years ago. For clarity, Australopithecines,* Homo habilis, rudolfensis *and* floresiensis *are omitted,* H. ergaster *and* erectus *considered together.*

variables. Two vital factors, which when considered in tandem have important implications for the acceptability of the revisionist model, have not yet received the attention they deserve.

First, the revised model of colonization includes in its purview species other than AMH, including but potentially not limited to *Homo ergaster/erectus, heidelbergensis* and *neanderthalensis* (see Figure 1 for correspondence between cultural and geological chronologies and species persistence). This has not been emphasized in the recent literature, and we should take care not to reduce artificially the complexity of the problem by treating the behavioural and evolutionary contexts of these species as broadly uniform. These are species which by definition display morphological and behavioural differences both between each other and between themselves and AMH, and consequently can be assumed to have varied cognitively, socially and technologically. Examining behaviour in one species, whilst informative, does not provide conclusive evidence about colonizing adaptations in another separated by genetic distance and evolutionary time.

Second (and important in the light of the previous observation), lacking in the emerging discussion is a detailed consideration of what type of process deliberate maritime colonization represents: what behaviours it involves; what logistical, technological and organizational capacities it demands; what neurological and cognitive structures necessarily underlie these behaviours and capacities; and how these might differ between the various species noted above. Purposive or active colonization (as opposed to random dispersal or passive colonization: Leppard in press) of as yet unseen habitats is not an ability innate to primates. It would be considered odd, for example, to suggest that the dispersal of the ancestors of lemurs to Madagascar from Africa between ~66–34 million years ago (Kay *et al.* 1997) was in any sense intentional or strategic; such abilities are also not obviously present in our nearest living relative, *Pan troglodytes* (Suddendorf & Corballis 2007). However, AMH have, since certainly ~50,000 years ago, exhibited capacity for deliberate trans-oceanic colonization, in which *intention* has demonstrably played a role. The ability to undertake active colonization has appeared via evolutionary processes, and in particular the evolution of the brain and certain associated types of complex behaviour; this organization must have arisen subsequent to the evolutionary divergence of our lineage from *Pan*, ~6.6 million years ago (Steiper & Young 2006).

Whether this evolutionary emergence occurred deep in the hominin lineage (prior to the appearance of the species implicated in the revisionist model), or more recently, in association with AMH, has not been considered in detail. We know that archaic species of *Homo* differed from Moderns in terms of both somatic (and particularly cranial) morphology and in behavioural organization, with a direct relationship between these factors; group size and technological complexity correlate positively if grossly with neurocranial capacity, at least in our genus (e.g., Dunbar 2012; Gamble *et al.* 2011). The vital issue is whether archaic *Homo*, thinking and acting differently from AMH, had a similar capacity for deliberate maritime dispersal. Accordingly, this paper attempts to establish what type of social and cognitive configuration is necessary for targeted and sustainable island colonization; to review the social and cognitive capacities of pre-modern hominins implied in the revisionist dispersal model; and to evaluate, on this basis, the likelihood that such species had the capacity to undertake purposive colonization. This evaluation may conceivably provide guidance when choosing between the standard and revisionist models.

In considering this problem, active maritime dispersal is framed as a cognitive and organizational problem. It is suggested that purposive or strategic colonization is a very distinct type of cognitive challenge, involving the ability to undertake a series of tasks which are rooted in complex cognitive processes. These tasks include:

(1) Modelling the existence of temporally and spatially distant (i.e. not directly observable or knowable) habitats which offer future rewards in exchange for immediate risk, and weighing these rewards against those offered more closely to home.
(2) Communicating these complex ideas to a demographically viable group and coordinating or coercing the behaviour of group members towards a defined end.
(3) Possessing the technological capacity to undertake maritime colonization.

These abilities demand certain types of neurological-cognitive organization. The pressing issue, then, is at what point in hominin evolution this organization can first (or most securely) be identified. The most recent consensus on the cognitive and organizational capacities of pre-modern hominins is considered, paying particularly close attention to cognitive processes which relate to balancing present risk *vs* future benefit, abstraction, decision-making and communication of complex concepts.

Cognition, behaviour, and maritime dispersal

What types of cognitive process and somatic action are implicated in purposive (active, or strategic) maritime dispersal? This is an inevitably complex question, answers to which must be equally inevitably speculative to a degree; this may in part explain why they have gone largely, but not entirely, unaddressed. In recent discussions of the issue of trans-oceanic colonization in pre-moderns, a focus on other topics has left the issue of the complexity of this behaviour to one side. When it has been discussed, the nature of the behaviour itself has not been an object of deliberation. An underlying theme seems to be a willingness to interpret maritime colonization as purely a technological problem (e.g., Simmons 2014, 204–5): seagoing technology and knowledge sets as a simple outcome in the wider context of the appearance of composite-additive technologies. Building on this undersubstantiated position, speculation regarding means of propulsion, stabilization devices and navigation technologies has made its way into the discussion, without serious consideration of the implications being made about the technological contexts of the species involved (see, e.g., Broodbank 2014, 269; Runnels 2014b, 274). Exacerbating this problem is the willing acceptance of evidence from experimental archaeology; in particular, that subgenre of experimental archaeology which seeks to recreate the conditions of a supposed trans-oceanic colonization event, mimic the hypothesized event and then suggest that this imitation provides corroborating evidence for it.[2]

There are, however, two notable exceptions to the general lack of recent, more reflective treatments of the question of the nature of strategic trans-oceanic colonization as a behaviour. In a pioneering paper which has not received enough attention within the recent debate, Davidson & Noble (1992) considered the extent to which the colonization of Sahul at ∼50,000 years ago might have constituted direct evidence for modern behaviour. They underscored the inherent complexity of oceangoing technology, suggesting that construction of a seagoing craft involves certain types of conception and intentionality which imply a greater degree of abstract thought than that implicated in solely reductive technologies; boat (or raft) construction involves the corralling of diverse materials, fashioning these into forms which have no practical application except as part of a functional whole, and then the composition of this whole. They further argued that the close cooperation between various individuals using various tools to achieve a unified end implied by boat construction necessarily requires language as an enabling factor.

Davidson & Noble performed a vital service by emphasizing how boat or raft construction differs from and can be considerably more complex than other types of tool manufacture. They (and other contemporary commentators) did not, however, consider the mental dynamics which underlie not only seagoing technologies, but the notion of trans-oceanic travel itself. Coolidge & Wynn, albeit in passing and with maritime dispersal not their main focus, recognized the central importance of abstract thought and the capacity to model various scenarios which must necessarily underlie deliberate dispersal or colonization:

> It [the colonization of Australia] probably required projecting future action, group contingency planning, and the production of elaborate, multi-step technologies (boats), all activities that are enabled by EWM [enhanced working memory]. (Coolidge & Wynn 2005, 20)

This brief yet important consideration (now supplemented by Davidson 2010; papers in Dennell & Porr 2014; Wadley 2013, 164; Webb 2006; Wynn & Coolidge 2010) captures three vital elements of behaviour upon which this paper expands, in a modified manner: projection of future action; group planning; and composite technological capacity. The debate has thus far paid most attention to the latter: how the cognitive-technological capacities of the constituent species of *Homo* do or do not support the contention that the species in question undertook purposive maritime colonization. It is a fundamental assertion of this paper that a far more important question concerns the type of thought which relates to future action and possible worlds. It is a complex enough task to design, build and utilize a raft to cross oceanic distance; quite another to stand on a beach, staring at the horizon, imagining distant worlds to which the raft might be paddled and on which life might be lived more fully and satisfactorily.

For various reasons that will become clear in the ensuing discussion, it is possible that the same cognitive framework is necessary for projection of future action and comprehension of composite technologies; consequently, these requirements can be combined. In contrast, Coolidge & Wynn's definition addresses group planning, and thus communication and comprehension of abstract concepts, but not the issues of coercion or decision-making: if archaic hominins theorized that long-range maritime dispersal may be in some sense beneficial, how was this goal achieved within existing social structures? It is possible to reduce the varied behaviours involved into three main types:

(1) *Ability to conceive of possible future (i.e., non-actual) states in the abstract which may be beneficial yet which are spatially and temporally remote*. The 'possible worlds' or strategic behaviour problem; transoceanic colonization of necessity involves imagining a distant future state, the adaptive benefits of which outweigh risks. This is arguably part of a larger set of cognitive processes in which abstraction from the present to non-actual desirable states is involved.

(2) *Ability to express complex ideas (involving abstraction and non-actual states) to other group members.* The issue of the emergence of language; not only the evolution of the mechanical capacity for speech, but also of a syntactical system which allows for indirect speech and abstraction.

(3) *Ability to organize, coerce, or cajole peers, mates and offspring towards a future goal such that it is achieved satisfactorily.* Successful strategic colonization events demand certain demographic thresholds, vital for logistics as well as reproductive viability. This, in turn, demands a social structure through which wishes and demands can be expressed and met.

These are inevitably generalizations abstracted from each individual and unknowable instance in which dispersal was strategic and purposeful, rather than random. On a basic level, however, it is enormously difficult to conceive of strategic colonization in the absence of any of these factors; they represent, in that sense, *necessary conditions*. If we can better understand when and in what conditions these cognitive capacities evolved, we will be able to predict more accurately when the vital cognitive components for strategic maritime dispersal were in place.

A barrier to doing so is the sheer diversity and amount of research undertaken on the evolution of these attributes in *Homo.* An exhaustive review of the available evidence for the evolution of these types of cognitive process and ensuing behaviours is likely to be compendious and perhaps rather uninformative. More productive would be to attempt to draw a limited consensus out of the varying approaches to the problem of the evolution of these types of behaviours, to establish at what stage or by what point in the evolutionary history of *Homo* we can be reasonably sure that the cognitive and behavioural architecture for successful strategic maritime dispersal was in place. A key limitation here is that successfully defining such moments of emergence in the palaeoanthropological record is inherently problematic. The goals are, then: to establish likely windows of evolutionary time in which strategic thought, language and complex social behaviour comparable to our own may have emerged; to delineate points of chronological overlap; to clarify which species of *Homo* were extant during this overlap; and to compare this to the revisionist model's expectations. It is not the intention to contribute to the many debates within the evolutionary and palaeoanthropological literature, but rather to review and extract points of broad consensus as they bear on the issue of purposive seagoing in archaic *Homo.*

Cognitive, behavioural and technological evolution in *Homo*

The emergence of strategic behaviour and the evolution of the hominin brain

Shouldering enormous risks to cross a wide, generally inhospitable environment requires substantial motivation on the part of an organism involved. In the absence of immediate and perceptible rewards, or genetic predisposition towards cyclical migration, the majority of organisms will not voluntarily assume such risk. Recognizing potential or future rewards which render this risk tolerable according to adaptive metrics and communicating this calculus to a wider group requires a very special kind of cognitive process. The ability to extrapolate to unknowable futures is an aspect of a wider development in hominin brain architecture: the capacity to model non-actual states of being and act in an attempt to bring these states about. This capacity is arguably a necessary condition for maritime dispersal in *Homo* and, consequently, the timing of its evolutionary appearance is critical.

The broad agreement on the paramount importance of abstract thought of this type within the context of explaining truly modern behaviour is matched by diverse approaches as to which physiological processes and components are involved, and to how modern behaviour might be detectable in the palaeoanthropological and archaeological record (e.g., Coolidge & Wynn 2005; Davidson 2010; d'Errico & Stringer 2011; Frith 2012; Gamble *et al.* 2011; Gowlett *et al.* 2012; Haidle 2010; Heyes 2012; McBrearty & Brooks 2000; Nowell 2010; Rossano 2010; Whiten & Erdal 2012). Consensus exists that abstract thought, planning and use of memory of experience to construct viable future scenarios lie at the core of modern cognition (e.g., Ambrose 2010; Shultz *et al*. 2012; Sterelny 2011, 811–13), but understanding how possible worlds are rendered in the human brain is a complex task situated at the intersection of evolutionary psychology, neurobiology and genetics. Unpicking this rendering is beyond the scope of this paper, but it remains important to outline current thinking on modern cognition, challenges in defining it, and attempts to establish broad consensus on its appearance.

Working memory and *executive function* loom large in the more recent literature within the wider discussion of modern cognition, and hence behaviour (Coolidge & Wynn 2001; 2005; Wynn & Coolidge 2010; 2011). This derives from the recognition that various cognitive processes share underlying structure, and that this structure is a function of the emergence of a particular form of neural architecture. In particular, the precocious development of the neocortex (i.e., encephalization) throughout the evolution of *Homo*, reaching its greatest current extent in AMH, is considered significant; multiple lines of evidence suggest that processing in the prefrontal lobes is fundamentally related to strategic cognition and abstract language (Frith 2012). That said, it also seems clear that attempting to correlate discrete subregions of the brain with equally discrete subsets of cognition is unlikely to reflect actual neurological process (Barton 2012), and that framing the problem in terms of interrelationships and complex systematics within the brain—and the evolutionary development of such features—is probably more constructive than either understanding prefrontal lobe development as the only pertinent variable (e.g., Roth & Dicke 2005), or assuming that absolute brain size and complexity of cognition exist in a purely linear relationship (Neubauer & Hublin 2012; Smaers & Soligo 2013).

The contention over how and in what terms modern cognition occurs within the human brain is exacerbated by substantive problems which relate to the data available in understanding cognitive evolution. While encephalization is recognized as central, the selective forces driving it are imperfectly understood (Bailey & Geary 2009; Dunbar & Shultz 2007), as are the neurological trajectories through which encephalization was achieved. Cranial morphometrics are instructive, although they do not allow access to cognitive process. Palaeogenetics are vital in understanding variation in *Homo* at the genotypic level (for example, presence and absence of FOXP2 variants and their relationship to language acquisition), but there remains a substantial interpretive gulf between genetic organization and neurological function. Archaeology illuminates the end-product of certain behaviours and (ideally) allows extrapolation back to these behaviours, but is hindered by the vagaries of recovery and taphonomy. Bridging behaviour, morphology, genetics and cognition is a complex task, and approaching the appearance of modern types of thought must be mediated through a mélange of probabilistic reasoning and archaeological proxies (for behaviours which are themselves proxies for cognitive process: Davidson 2010, 179). Taken in aggregate, this means that we cannot be certain at exactly what point in the evolutionary history of *Homo* modern cognition emerged. Using cranial morphometric, genetic and archaeological data in conjunction, however, allows the definition of broad areas of consensus.

Recognizing the principle of the fundamental relationship between neurophysiology and behaviour (Neubauer & Hublin 2012, 573–4), the cranial architecture of *Homo* and its development is a good place from which to begin considering the evolution of abstract, strategic thought. The evolution of this aspect of hominin morphology is illuminating, not only in gross quantitative terms of net increase in neurocranial capacity, but also in terms of which parts of the brain are implicated in this growth. The general, now-familiar trend is a profound increase in brain/overall mass ratio since the appearance of the Australopithecines in the mid Pliocene. The gracile Australopithecines (*Australopithecus afarensis, A. africanus*) had slightly greater endocranial volumes than *Pan* (Bailey & Geary 2009, 67–8), no more than ~600 cm^3 (Leigh 2012). From the appearance of *Homo*, gradual increase in brain size is evident such that *H. ergaster/erectus* displays volumes of 800–1000 cm^3 (although exhibiting considerable variability, perhaps unsurprising given the spatial and temporal persistence of this species, or collection of subspecies: Broadfield *et al.* 2001; Rightmire 2004); archaic *H. sapiens* averages 1250 cm^3, and in this overlaps with *heidelbergensis* (Conroy *et al.* 2000; Stringer 2012). Neanderthals and Moderns are broadly comparable to each other, occupying ranges from 1400–1600 cm^3 (see Holloway *et al.* 2004).

Big brains, getting bigger, have been a feature of our genus since its appearance, but this process has neither affected the brain uniformly, nor been constant.[3] First, the majority of mass growth (rather than new neural connections) has been restricted to the forebrain, and in particular the neocortex (Neubauer & Hublin 2012), which has expanded throughout the evolution of *Homo*. Second, trajectories of brain growth during the life histories of members of the species which comprise this genus diverge. Coqueugniot *et al.* (2004), working with neonate cranial data in Javan *erectus*, chart postnatal cranial growth which does not parallel similar growth in Moderns, but, rather, more closely follows juvenile development in *Pan*, suggesting that cranial architecture in *erectus* reached its adult form relatively earlier than in AMH (with probable implications for intensiveness of regimes of postnatal care). Gunz *et al.* (2012) delineate similar differences between *neanderthalensis* and Moderns. Undertaking metric studies of 10 Neanderthal newborns (including the complete Le Moustier 2 and Mezmaiskaya specimens), they demonstrate pronounced morphological differences between these examples and AMH parallels at a period crucial for cognitive development, with *neanderthalensis* achieving the characteristic 'elongated' form very early in life. By contrast, uniquely extended juvenility (and associated ongoing change in brain morphology: Kuzawa *et al.* 2014) in AMH seems to date to ~160,000 years ago, on the strength of the evidence from Jebel Irhoud (Smith *et al.* 2007). Pearce *et al.* (2013), considering mature *neanderthalensis* specimens, argue that the greatly increased size of the visual system in Neanderthals provides a false impression of endocranial capacity, in that proportionally more space would be devoted to the housing of this system. Consequently, the overlap in cranial mass between *neanderthalensis* and Moderns should not be read as passively reflecting comparable neural process. We should not lose sight of general parallels in cranial development, especially between Neanderthals and our own species (Leigh 2012), but it remains the case that pathways to and final form of adult brain architecture were different between at least three species of hominin, with enormous and probably unique investment of energy in post-natal neural development characterizing our species (Kuzawa *et al.* 2014; Neubauer & Hublin 2012).

Neurocrania with subtly different volumes and shapes might, reasonably, be supposed variably to permit certain types of cognitive process and restrict others. Variability between the cortical organization of more and less archaic hominins, and particularly trajectories of encephalization, is then of considerable interest in exploring likely behavioural variability. This is especially relevant in the context of studies (Coolidge & Wynn 2001; 2005), conducted on Moderns, suggesting a possible relationship between damage to the neocortex and altered capacities to undertake certain types of cognitive activity associated with strategic thought. Physiological studies aside, archaeological proxies—discussed below—suggest that encephalization correlates positively with increasingly elaborate behaviours over time, although this relationship is certainly not linear.

Locating the appearance of complex types of behaviour which might reflect complex types of cognitive process is a matter made difficult by competing definitions of complexity; there is, accordingly, substantial debate regarding the timing of the appearance of the suite of complex behaviours and material culture types which index 'modern behaviour'. Along a spectrum of arguments, there exist three general schools of thought; firstly, that complex behaviours implying strategic or abstract thought should be understood as a late watershed in only our species, coincident with the first extra-African dispersals of Moderns and appearance of 'symbolic' material culture ~70,000–50,000 years ago; secondly, that the key timeframe is rather 200,000–50,000 years ago, with *neanderthalensis* also capable of parallel types of behaviour or cognition; or, thirdly, that such complexity has a deep origin of over 200,000 years ago (d'Errico & Stringer 2011; McBrearty & Brooks 2000; Shultz *et al.* 2012). The nature of the emergence of such behaviours, and in particular whether a gradualist or threshold model is more appropriate, is also contentious (e.g., Gowlett *et al.* 2012; Heyes 2012; Nowell 2010, 441–2). The question of language emergence and of social organization is entangled with this debate. While in the current discussion it is preferable to deal with these three issues separately for the sake of clarity, this may artificially distinguish between what may be aspects of the same social and somatic evolutionary dynamics; yet, however the data are approached, they are suggestive of a series of key moments in cognitive-organizational evolution which have a bearing on the question addressed in this paper.

Technological development and adaptation during the evolution of Homo

Tool-use is evolutionarily ancient in the Hominidae and the primates more widely, present in both our nearer and more distant relatives (Shumaker *et al.* 2011, 73–203). Complex tool manufacture and technological adaptation to the environment more generally emerge, by contrast, subsequent to our divergence from *Pan*. Such adaptations include technologies which contain composite or additive components (rather than being simply reductive in nature), tool-construction which implies multi-component and multi-individual behaviours, and manipulation of the environment (or 'niche construction': Wadley 2013). Technologically complex behaviour is clearly not limited to purely functionally adaptive material culture, however. Artefacts associated with behaviour which seems at first blush to lack an adaptive component (symbolic or 'ritual' behaviour) also fall into this category.

There is a disconnect between the steepening encephalization quotients witnessed with the appearance of *habilis* and *ergaster/erectus*[4] 2.2–1.8 million years ago (Rightmire 2004) and the appearance of complex tools and technologies (Gamble *et al.* 2011). The technological (and by extension behavioural) conservatism of the Oldowan and Acheulean industries, whilst its extent is debatable, is suggestive of no fundamental structural change in the relationship between cognition, technology and adaptive behaviours simultaneous with the first appearance of big-brained hominins. This again underscores that we should not treat the relationship between encephalization and complexity in cognitive, social and behavioural contexts as a solely linear one; instead, the sudden appearance of more complex technologies (and arguably more elaborate forms of social organization) at 0.6–0.4 million years ago may suggest that, rather than constant change, a punctuated-equilibrium model may be more appropriate than a gradualist model. In recent treatments of the problem of the emergence of modern behaviour, this disjunct between essentially linear growth in neurocranial size and highly non-linear growth in extrasomatic complexity has been built into a robust steps *vs* gradients model (Gamble *et al.* 2011; Gowlett *et al.* 2012).

Focusing on discrete elements of technological adaptation and behaviour, Haidle (2010) and Lombard & Haidle (2012) identify a sudden and pronounced change at ~0.4 million years ago. The Schöningen spears inevitably loom large in this discussion as evidence of high-latitude active hunting of protein-rich megafauna, probably by *heidelbergensis*. It is hard to reconstruct hunt dynamics from such limited data, but targeting live Pleistocene Eurasian megafauna implies relatively high levels of cooperation and coordination, especially if the behaviours of comparable high-latitude fauna when faced with predation hint at the inherent dangers.[5] The Schöningen spears themselves are not representative of composite or additive technologies, however. Composite-additive (rather than simply reductive; i.e., biface manufacture) technologies appear in the archaeological record from ~300,000 years ago (Ambrose 2010, 138–40). The first evidence for hafting appears ~280,000 years ago (Barham 2002), potentially demonstrative of new ways of conceiving materials and components that in isolation have limited functionality. The actual method of hunting, however, probably remained approximately consistent over this period; patterns of trauma from Neanderthals suggest that hunting in this species was probably at close range (Berger & Trinkaus 1995), and this may be extended back to *heidelbergensis* (and possibly to archaic *sapiens*). By contrast, definitive evidence for the use of composite projectiles is very late; Shea (2006) would place it ~40,000 years ago. The controlled exploitation of fire is a parallel environmental adaptation that permitted expansion into new, seasonally variable niches, albeit one much harder to trace in the archaeological record. Twomey (2013), reviewing the evidence for such exploitation, argues that this behaviour appears to date from as early as 0.7 million years ago (and conceivably earlier); the main problem with these very early dates is the paucity of the evidence and establishing criteria for controlled use. Dates reported by Glikson (2013, 90) for the Lower Palaeolithic are, as he notes, controversial; more secure evidence becomes increasingly common between 0.6 and 0.2 million years ago, and prolific from ~125,000. This is unsurprisingly coincident with the presence of hominins in higher latitudes during glacials.

The question of 'symbolic' behaviours is more problematic, in terms both of defining such a behaviour and of clarifying the extent to which 'symboling' is indicative of the capacity to construct abstract, possible-world scenarios (d'Errico & Stringer 2011, 1064–6)—clearly of key importance in this discussion. Large amounts of qualitatively distinct data have been marshalled in favour of arguments for the emergence of behaviour of this type, including but not limited to cave and rock 'art' (recognizing the immense load this term bears), funerary ritual, portable non-functional objects and personal adornment, and potentially items which have been otherwise interpreted as primarily functional (such as Large Cutting Tools). There are several ways of dividing and subdividing this varied corpus (e.g., Gowlett *et al.* 2012; Rossano 2010), and similarly diverse sets of theoretical frameworks exist to approach symbolic behaviour and its relationship to cognitive dynamics. Yet however the data are approached, the dates for the appearance of this type of activity are comparatively late. This behaviour seems entirely restricted to 0.5 million years ago onwards, and perhaps—depending on definitions—entirely after 100,000, when the sheer frequency of artefacts usually associated with symbolic behaviours increases in dated contexts.

The appearance of complex (i.e., multi-stage, multi-material, composite) technologies and material culture which might be interpreted as symbolic is late in contrast to the upswing of neurocranial size in *Homo*. This has two implications which are pertinent in the current discussion. First, we might reasonably expect similar complex technologies for which we have no direct evidence—such as raft or boat construction and navigation—to appear similarly late.

Second, the cognitive framework which enables these technologies—one which permits recognition of a preferable theoretical future state which might only be achieved by focused and short-term maladaptive behaviour in the present—seems not to emerge in linear relationship with cranial capacity. While narratives of sudden enlightenment should be viewed sceptically (d'Errico & Stringer 2011), this may be suggestive of the use of threshold models in understanding the appearance of behavioural modernity. Exploring this fully is beyond the remit of this paper, but the possibility that the technological-behavioural florescence of the Middle-Upper Palaeolithic derives from a deeper cognitive unfolding, as the forebrain achieved a critical size and architectural arrangement, is intriguing. From this perspective, we should on balance assume the type of cognitive framework which enables maritime colonization to post-date this florescence. This is borne out by considering evidence for the emergence of abstract language and more complex forms of social organization.

The evolution of language

Language, comparable to the type that exists in our own species, is strongly associated in the literature with behavioural modernity, and is arguably an essential component of larger social units and their more complex inter-personal dynamics. Elaborate vocal and non-vocal communication is evident across primates, but the somatic and cognitive capacity for abstract, syntactical language used almost ubiquitously in group interactions seems to be restricted to Moderns (Reuland 2010; Sterelny 2012). Considering the role of language of this type in facilitating complex, multi-individual behaviours, we should consider some sort of linguistic ability parallel (although not necessarily isomorphic) to our own to be a necessary condition for trans-oceanic seagoing. Informed assessments regarding the point of the appearance of language in *Homo* are, then, significant.

The chief limitation in making such assessments derives from the fact that language leaves no obvious archaeological correlates. A more grounded position from which to begin involves the physiological mechanics of speech but here, too, there is contention. Lieberman (2007a, b) would place the appearance of the necessary laryngeal and epiglottal structure rather late in hominin evolution, associated with AMH. Boë *et al.* (2007), by contrast, argue that the mechanical capacity to articulate the full range of sounds with which we are familiar was also present in Neanderthals. If this were the case, we might expect these mechanics to obtain also in the most recent common ancestor, *heidelbergensis* (here, as elsewhere, limited fossil data sets and varied methods of computation may conspire to produce divergent results; Barney *et al.* 2012). In that regard, Martinez *et al.* (2012) suggest that the Atapuerca *heidelbergensis* individuals were capable of speech, based on their reconstruction of aural dynamics in the cranium, and on the similarity of the size of the vocal tract to Neanderthal equivalents. This rather tendentious argumentation is only persuasive, however, if it is accepted that *neanderthalensis* possessed language capability comparable to our own, rather than just the capacity for complex and varied vocalizations.

Simple structural configuration enabling such vocalizations does not, however, equate to language capacity at a cognitive level, the emergence of which is strongly associated with various types of brain morphology. Particularly important seems to be prefrontal growth in Broca's Area, damage to which (in Moderns) can inhibit both language and praxis. The evolutionary history of and long-term structural changes in Broca's Area are not immediately clear, however (Balzeu *et al.* 2014), and again we are left with the interpretive leap between neural architecture and cognitive process. More productive may be a focus on genetics. The gene FOXP2 appears to relate to language capacity in our own species and vocalizations in others; as with Broca's Area, absence of function in FOXP2 seems to inhibit language development in Moderns (e.g., Varga-Khadem *et al.* 1995) and some other vertebrates. It is less likely that the gene is directly responsible for this capacity, however, and more probable that it instead enables certain patterns of neural and synaptic organization associated with types of cognitive process of which language is one (see Fisher & Scharff 2009). FOXP2 is common to mammals, but the form expressed in Moderns is a relatively recent evolutionary development. How recent is exemplified by research which suggests key differences in the structure of the gene between a sample of AMH and of Iberian *neanderthalensis* (Maricic *et al.* 2012); more specifically, the presence in Moderns of transcription factor POU3F2, which appears to be implicated in the functioning of FOXP2, and its absence in the Neanderthal sample.

Approaching the genetic, morphometric and circumstantial archaeological data holistically, Shultz *et al.* (2012, 2137–8) argue for fully modern language from 100,000 years ago; d'Errico & Stringer (2011), taking a similarly broad view, opt for 200,000 onwards. Again, the relevance in the immediate context is not in delineating points of disagreement, but rather broad overlap. The emergence of language as we know it in our own species (abstract, ubiquitous, vital as a tool for social mediation) between 200–50,000 years ago would find broad support, closely associated with archaic *sapiens* and AMH. Some researchers would push this capacity further, perhaps to 0.6 million years ago and *heidelbergensis*. Beyond this, however, there is little genetic, palaeoanthropological, or archaeological data to imply the existence of language *sensu stricto* (contrary to Runnels 2014b, 274) in archaic hominins.

Group size, cooperative behaviours and hominin social organization

Punctuated-equilibrium type trajectories also seem to characterize the evolution of social organization in *Homo*, but again a brief and recent window of evolutionary time, 300–50,000 years ago, seems to be vital in terms of the nature of hominin group structure. In part, we are limited in our capacity to reconstruct social organization in that archaeological proxies must be used—often, by virtue of the wider interest in the emergence of modern behaviour, the same proxies used in arguments about symbolic material culture and behaviour, and consequently abstract thought. Indeed, the capacity for *Homo* to attain group sizes not seen in other primates is occasionally argued to accompany both the development of abstract language and thought (Ambrose 2010). The potential for group size increase, encephalization and the emergence of complex vocalization and ultimately language as social binding agents to be mutually reinforcing processes has been noted (Barrett *et al.* 2012; Dunbar 2012; Dunbar & Schulz 2007; Frith 2012).

Dunbar (2012), using cranial data and extrapolating from patterning in other primates, argues for Australopithecine and *ergaster/erectus* mean group sizes to cluster under 100 individuals; projected values for archaic *sapiens*, Neanderthals and Moderns range from 100 to slightly under 200, clustering around Dunbar's Number of ~150. Gamble *et al.* (2011) also propose very divergent group sizes for members of *Homo*, with a pronounced disjunction between *erectus* and more modern species. Drawing on varied sources of data, including dietary evidence, cranial metrics, environmental considerations and ethnographic data, Layton *et al.* (2012) suggest that forms of social organization approximating those of hunter-gatherer groups in the ethnographic present characterized *Homo heidelbergensis*; in this, their findings correspond closely with Gamble *et al.* and Dunbar, with deep evolutionary roots resulting in a socially transformative moment around 0.3 million years ago.

Clearly, group size simultaneously forecloses on some types of behaviour and permits others, but modelling the substantive difference in dynamics between larger and smaller bands is complicated. It is certainly conceivable that more complex cognitive processes may be vital in holding together larger, multi-family units with potentially competing kin groups. Recognizing and building appropriate responses to the socially-sanctioned demands of peers is probably a vital inhibitor to fissile tendencies. Robalino & Robson (2012) develop this to suggest that abstract language and capacity for abstract thought (and consequently *theory of mind*) may have existed in a feedback relationship, driving up group sizes while mitigating stresses which accompany larger group size in other primates; this is beyond the present purview, however. What is relevant is attempting to model better the relationship between group size and demographic viability. While it is evident that, all other variables being equal, a larger population will be more viable in the long term than a smaller population, greater exposure to stochastic effects towards the smaller end of the spectrum of population sizes suggests that viability does not decrease in a linear manner with size (Demetrius *et al.* 2004); for example, a population of 50 is probably more than twice as exposed to stochastic annihilation (via the 'Drunkard's Walk': de Queiroz 2014, 235–6) than a population of 100.

In the context of an increasing steepness in growth of group size as we move into the Middle Palaeolithic, the logic of demographic viability suggests that evolutionarily recent members of *Homo* would be more effective island colonists than archaic species in the genus. Even if it were possible to reconstruct a viable minimum size of colonizing population in Moderns, it would be challenging to extrapolate this back to more archaic hominins, not least because of different postnatal trajectories of growth in *Homo* and implied reproduction rates. That said, as a collection of *K*-selected species, there probably exists a minimum viable population size for hominins (and hominids more widely) below which odds of localized extinction increase exponentially, and it is conceivable that Australopithecines, with mean group sizes perhaps no larger than 40, exemplify these thresholds. Early members of *Homo* probably congregated in groups on the cusp of demographic viability when isolated from the wider metacommunity, although thereby becoming exposed to genetic drift (the speciation of *floresiensis*, if it is indeed a distinct species of hominin, from a larger-bodied ancestor is relevant here: now Dennell *et al.* 2014). This would assume a complete group or band of early hominins involved in a trans-oceanic colonization event, however—a very hard scenario to envisage in terms of motivation and dynamics. If, instead, we imagine demographically viable subsets of groups undertaking maritime dispersal after a fission event, we probably restrict ourselves to archaic *sapiens*, AMH and *neanderthalensis*.

Modelling group dynamics and size ranges for hominins is challenging. Informed model-building may suggest, however, that only recently have mean group sizes emerged in *Homo* which would generate colonizing groups suitably substantial to be insulated from the dangerous stochastic lurches of small populations. The period 300–50,000 years ago would appear to be crucial; group sizes of up to 150 individuals in Neanderthals and Moderns would have far better chances of survival in isolated insular contexts in contrast to groups of archaic hominins, comprised perhaps of fewer than 100 individuals.

The emergence of modern behaviour and patterning in strategic maritime dispersal

It is not clear when modern forms of abstract thought and the capacity to model non-actual states developed; similarly, it is not clear when spoken language capable of conveying such thoughts, or social groups capable of acting on such models, appeared. Yet it is possible, on the basis of a series of datasets, to make reasonably secure claims about temporal windows in which these capacities probably emerged in *Homo*. This is represented in Figure 2. Isolated instances of behaviour which, in the broader context of technological conservatism, seem irrepressibly more modern-like appear from around 0.6 million years ago. It is around 0.6–0.3 million years ago that the first claims for something approximating language in its current form are also made, although, depending on the importance of FOXP2 in regulating neuron growth, language as we know it may we be considerably later. This is coincident with technological developments, expansion into higher latitudes and an upswing in group sizes associated with the appearance of *Homo heidelbergensis* (Gamble *et al.*'s 2011 'second movement').

After 300,000 years ago, claims for the first symbolic behaviour might reasonably be made, alongside evidence for composite-additive technologies, increasing deliberate use of fire, and contentious evidence for Neanderthal laryngeal structures capable of reproducing the gamut of modern vocalizations. Yet it is only 70–50,000 years ago that flashes of modernity cluster into a bright continuum: the expansion of our own species across the breadth of Eurasia, including environmental niches which had hitherto resisted hominin exploitation; consistent and demonstrable use of composite and projectile technologies to achieve this exploitation; and the marking of this expansion with material symbols and abstractions. This is also the point at which the genetic elements that seem to permit the cognitive processes which underlie language are evident in our own species, coincident with modern throat morphology (Lieberman 2007a).

This reiteration of a well-established trend may seem potentially banal, but the central lesson is significant and has been overlooked in the recent literature on maritime hominin dispersal: we should expect complex behaviours, such as strategic maritime dispersal, to cluster on the right side of the spectrum of encephalization in hominins. Trans-oceanic colonization in Moderns should be unsurprising; in Australopithecines, extraordinarily surprising. For the species which lie between, it should range from possible (*neanderthalensis*) to improbable (*ergaster/erectus*). This expectation correlates with wider trajectories of behavioural complexity: neither fully sudden and late, nor gradual and linear, but rather accelerating throughout the second half of the Pleistocene. This, in turn, tracks increasing capacity for behavioural plasticity in hominins through the Quaternary; the ability to adopt new sets of strategies in the face of novel types of environment is probably adaptive, accounting for increased dispersal capacity and environmental tolerance in each species of hominin to emerge from Africa.

How does this model—J-curved behavioural complexity in *Homo*—fit with instances of trans-oceanic dispersal in the genus? The answer depends to some extent on which data are considered to be admissible examples of maritime dispersal; because of disagreements over relative dating, and paucity of absolute dates, this will remain controversial (cf. Broodbank 2014; Phoca-Cosmetatou & Rabett 2014a; Runnels 2014b). In general, however, possible

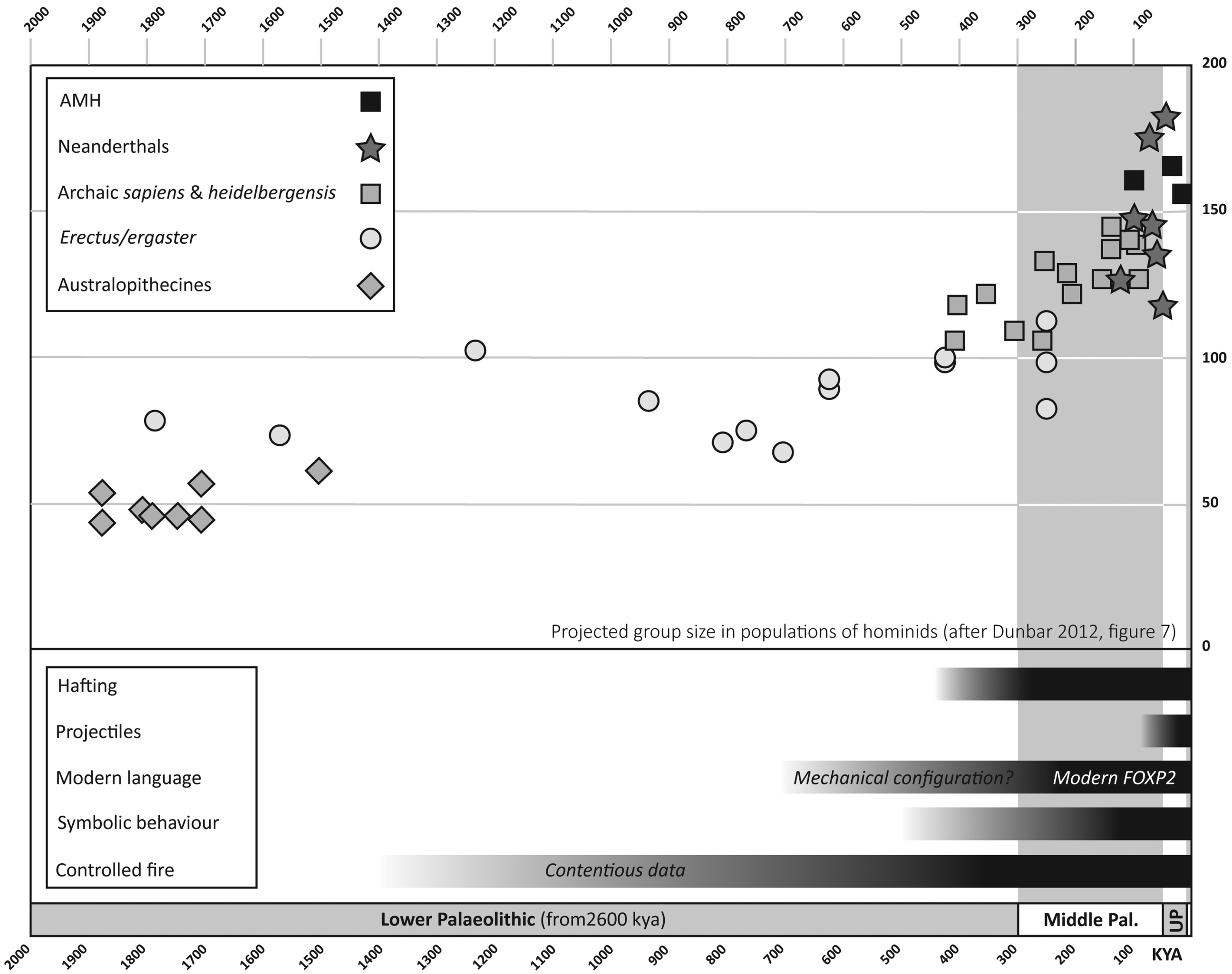

Figure 2. *Correspondence between increasing mean hominid and hominin group size (after Dunbar 2012, fig. 7, reproduced by permission) and various technological and social markers of behavioural modernity.*

maritime dispersal events are extremely rare prior to the Late Pleistocene, from ~126,000 years ago. The earliest material from Flores—concerns over the status of the later Liang Bua fossils notwithstanding—has good Lower Palaeolithic credentials, dated to 1.02 million years ago (Brumm *et al.* 2010), and is consequently an outlier. The controversial material from Crete, its satellite Gavdos, and Melos are also claimed to have a Lower Palaeolithic origin (Runnels 2014a), but the absence of radiometric dates from sealed deposits makes any tighter chronological focus impossible. Chipped stone tools allegedly adhering to a Mousterian tradition derive from the Ionian Islands and Naxos (Carter *et al.* 2014; Ferentinos *et al.* 2012), but, as the researchers in question indicate, the Middle Palaeolithic straddles glacials as well as interstadials, during which periods it is not clear how remote these islands (or their larger predecessors) would have been. This, however, is the bulk of the Early and Middle Pleistocene data; archaic *Homo* appears to have made it no deeper into Sahul than Flores, and the Mediterranean isolates remained out of reach, as did the islands in the northwest Pacific and oceanic isolates in the Indian and North Atlantic oceans. It is only after 50,000 years ago (see discussion in Leppard 2014b) that securely dated instances of maritime dispersal begin to cluster more densely, with tentative steps to continental shelf islands during the Upper Palaeolithic giving way to dispersal to truly oceanic islands in the Holocene.

The temporal distribution of these data is plotted in Figure 3, on a logarithmic scale against probable maritime distance crossed during colonization, and against proxy evidence for behavioural modernity. The patterning is quite distinct; correspondence

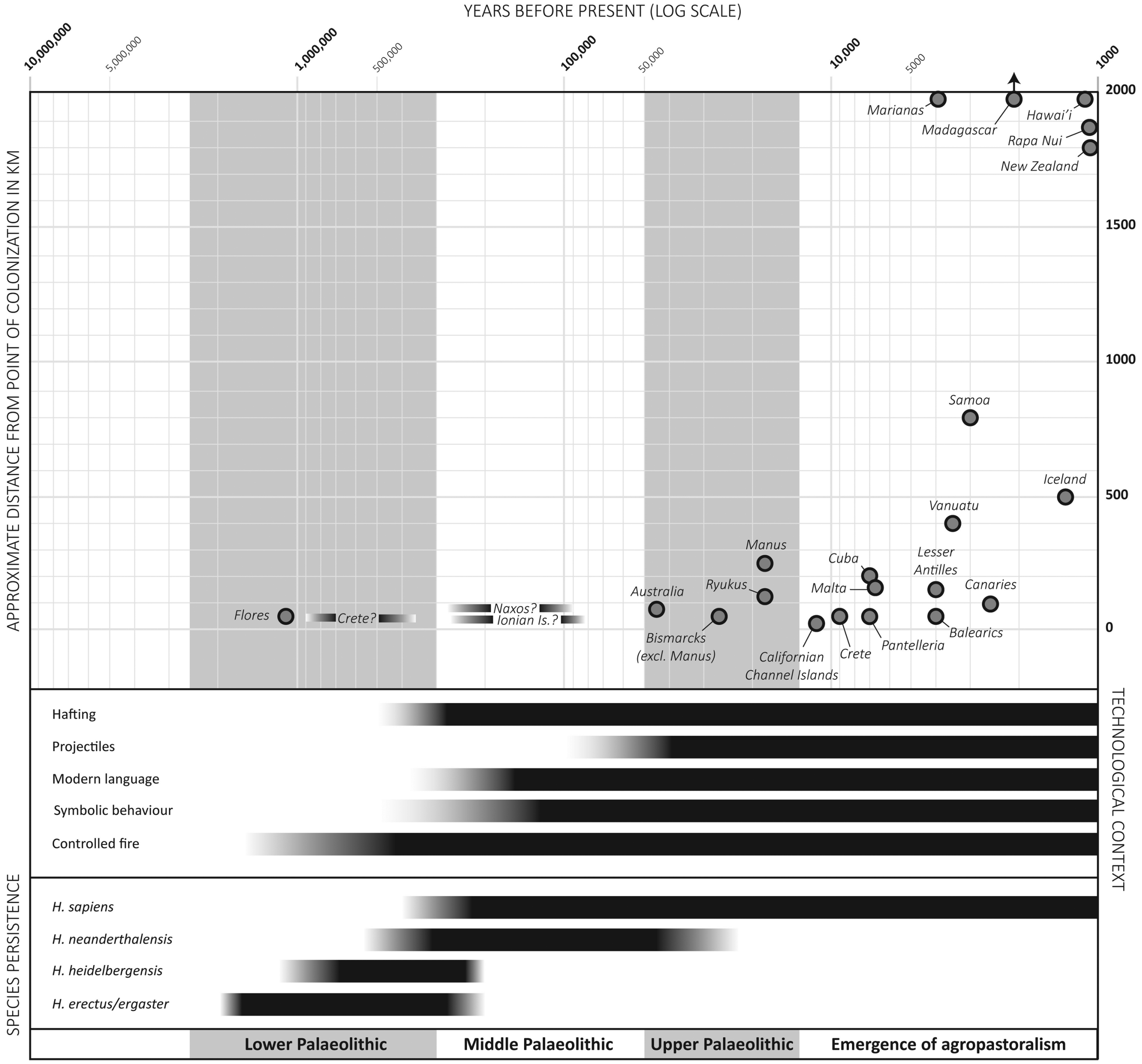

Figure 3. *Bivariate plot of definite (and contentious) maritime dispersal events on a logarithmic scale against the approximate distance from most likely point of colonization. Plotted below for comparison are various technological and social markers of behavioural modernity, and persistence of hominin species.*

between density of (increasingly long-distance) dispersal events in the Upper Palaeolithic and the late takeoff of data suggestive of modern patterns of cognition is striking; this conclusion is also arrived at by Anderson (2010). The fact that instances of trans-oceanic voyaging seem in fact to cluster in this fashion should reassure us that there is indeed some sort of meaningful, potentially causal relationship between brain size, cognitive capacity and strategic maritime behavior. As with the evidence for increasingly complex behaviour and thought, there are some isolated Middle Palaeolithic outliers, but the vast majority of maritime dispersal in *Homo* is late, and associated with Moderns.

The Flores data constitute an outlier in Figure 3, very suggestive of a precociously early maritime dispersal event probably associated with *erectus*, or similar. It must be recognized that the status of this creature remains contentious; despite attempts to find consensus (Aiello 2010), and arguments that nanism in *floresiensis* is within the bounds expected of an archaic hominin undergoing a process of insular dwarfing (Bromham & Cardillo 2007), suggestions that the Liang Bua fossils represent pathological Moderns continue to be made (e.g., Henneberg *et al*. 2014). It is not the goal of this paper to contribute to this debate. Suffice it to say that, if the Flores hominin *is* an example of insular endemism in *Homo* derived from the colonization of the Lesser Sundas by an archaic hominin associated with the Wolo Sege and Mata Menge sites, the key to reconciling this colonization with the argument developed here is interpreting the dwarfism of *floresiensis* as deriving from genetic drift in a small founder population, followed by continued reproductive isolation over evolutionary time (with peculiarly insular ecological pressures promoting nanism in this as in other medium- and large-bodied vertebrates). As Dennell *et al.* (2014) note, the most parsimonious explanation of such isolation is that initial dispersal was passive, not deliberate. The inherent statistical unlikelihood of passive maritime dispersal in large primates may then account for why this process was not repeated elsewhere in Eurasia; the current uniqueness of the Flores example in and of itself provides good reason to suppose that archaic hominins were not undertaking strategic dispersal, and passive 'sweepstake' dispersal should be built into larger models of hominin global colonization (Leppard in press).

Conclusions

Because strategic maritime dispersal is so ubiquitous in our own species, we run the risk of projecting this capacity back into deep evolutionary time without considering the claims tacitly being made in doing so about how more archaic hominins behaved and thought (Broodbank 2014). When the necessary technological, organizational and, above all, cognitive demands of successful trans-oceanic colonization are explicated clearly, however, its enormous complexity becomes evident. It is reasonable to suppose both that this complex behaviour may have an evolutionary relationship with other comparably complex behaviours (including abstract thought about potential states of being, composite-additive technologies, and creation of 'symbolic' material culture), and that behaviour of this type is underlain by a certain neurophysiological architecture.

When, in the evolution of hominins, is this most likely to have occurred? There is a disconnection between the increase in encephalization quotients and behavioural-technological conservatism in early *Homo*. The later Lower and early Middle Palaeolithic (~0.6–0.3 million years ago) by contrast witnesses technological variation, expansion into more challenging environmental niches and a cranial morphology much more comparable to our own, but evidence for behavioural modernity (averaging definitions) is still sparse. The period 300–50,000 years ago, and especially the end of this window, seems to be vital for composite technologies, large group size and organization, symbolic material culture and the genetic and morphological framework for language finding a form which is recognizably modern. It is the contention of this paper that the sudden upswing in well-attested instances of deliberate maritime dispersal after ~50,000 years ago is no coincidence, but is causally related to this emergence: specifically, such dispersal—as an example of behavioural plasticity—is an adaptive behaviour enabled by the evolution of modern patterns of cognition and social organization.

There are patchy, outlying data which predate this sudden burst of maritime dispersal activity. Maritime dispersal events which are evolutionarily ancient are extremely rare, with only the crossing of the Lombok Strait supported by radiometric dates. As the species implicated in such events (*ergaster/erectus* and preceding forms) are considered extremely unlikely to have possessed the cognitive and social frameworks necessary to facilitate strategic maritime dispersal, these events should perhaps be better understood as outcomes of passive dispersal (Dennell *et al*. 2014; Leppard in press). That such events appear to have been extraordinarily rare makes this scenario more plausible.

Middle Palaeolithic data are more problematic than the Lower Palaeolithic outliers. Dealing with Mousterian surface finds from the Mediterranean is made challenging by complexities of palaeogeographic modelling and likely variability in palaeogeographic conditions between individual glacial maxima. That said, with larger mean group sizes and evidence for more complex technological behaviours than archaic *Homo*, it may be possible that some form of intentional maritime dispersal existed in *neanderthalensis* (and potentially *heidelbergensis*?); conversely, rare passive colonization events may also be relevant. Until further data are reported from contexts known to have remained insular throughout the Pleistocene are reported, the possibility of limited Neanderthal seagoing must be considered *sub judice* (Broodbank 2006; 2014). While that remains the case, extant data are strongly indicative of deliberate, long-distance seagoing as an evolutionarily recent behaviour in *Homo*, one apparently restricted to our own species. This suggests that the standard, rather than the revisionist, model of hominin dispersal still retains the greatest efficiency in understanding the pattern and the process of global colonization.

Notes

1. While Boivin *et al.* (2013) and Mellars *et al.* (2013) disagree on the timing and nature of *Homo sapiens* dispersal, they certainly agree that directionality in such dispersal(s) was promoted by ecological attractors and ecogeographic barriers, of which latter oceans and seas are the best example.
2. Analogical reasoning of this sort may be useful in limited respects, but the genetic gulf between species means that an accurate analogue for Lower Palaeolithic seagoing will remain impossible. In general, more considered thought on what such experimental voyaging is attempting to demonstrate, and acceptable epistemological grounds for this demonstration, is required (Cherry & Leppard n.d.).
3. *H. floresiensis* is the only species of hominin which contravenes this trend. The likely unique evolutionary and ecogeographic pressures exerted on this hominin (discussed in detail below) could be understood to have overridden the otherwise general trend in non-insular evolutionary trajectories in *Homo*, especially in terms of energetic cost of encephalization in a depauperate island environment: see Kubo *et al.* (2013).
4. The recent finds from Dmanisi pose a challenge to our understanding of *erectus/ergaster*; specifically, whether it is appropriate to categorize these fossils as belonging to one species when variability within the species is so pronounced. Until a more satisfactory classificatory scheme can be devised, *erectus/ergaster* is retained as having some definitional use.
5. Evidence for carnivory in *Homo* now has a greater antiquity than previously supposed, but it is more probable that this derives from scavenging behaviours rather than active hunting (Ferraro *et al.* 2013). This should be understood in the context of a diet rich in animal protein and the symbiotic relationship between encephalization and decreasing digestive system complexity (Aiello & Wheeler 1995).

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References

Aiello, L.C., 2010. Five years of *Homo floresiensis*. *American Journal of Physical Anthropology* 142, 167–79.

Aiello, L. & P. Wheeler, 1995. The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology* 36(2), 199–221.

Ambrose, S.H., 2010. Coevolution of composite-tool technology, constructive memory, and language. *Current Anthropology* 51 (Supplement 1), 135–47.

Anderson, A., 2010. The origins and development of seafaring: towards a global approach, in *The Global Origins and Development of Seafaring*, eds. A. Anderson, J.H. Barrett & K.V. Boyle. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 3–18.

Athens, J.S., T.M. Rieth & T.S. Dye, 2014. A palaeoenvironmental and archaeological model-based estimate for the colonisation of Hawai'i. *American Antiquity* 79(1), 144–55.

Bailey, D.H. & D.C. Geary, 2009. Hominoid brain evolution: testing climatic, ecological, and social competition models. *Human Nature* 20, 67–70.

Balzeu, A., E. Gilissen, R.L. Holloway, S. Prima & D. Grimaud-Hervé, 2014. Variations in size, shape and asymmetries of the third frontal convolution in hominids: paleoneurological implications for hominin evolution and the origin of language. *Journal of Human Evolution* 76, 116–28.

Barham, L.S., 2002. Backed tools in Middle Pleistocene central Africa and their evolutionary significance. *Journal of Human Evolution* 43(5), 585–603.

Barney, A., S. Martelli, A. Serrurier & J. Steele. 2012. Articulatory capacity of Neanderthals, a very recent and human-like fossil hominin. *Philosophical Transactions of the Royal Society B* 367, 88–102.

Barrett, L., S.P. Henzi & D. Lusseau, 2012. Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society B* 367, 2108–18.

Barton, R.A., 2012. Embodied cognitive evolution and the cerebellum. *Philosophical Transactions of the Royal Society B* 367, 2097–107.

Berger, T.D. & E. Trinkaus, 1995. Patterns of trauma among Neanderthals. *Journal of Archaeological Science* 22(6), 841–52.

Boë, J.-L., J.-L. Heim, K. Honda, S. Maeda, P. Badin & C. Abry. 2007. The vocal tract of newborn humans and Neanderthals: acoustic capabilities and consequences for the debate on the origin of language. A reply to Lieberman (2007a). *Journal of Phonetics* 35, 564–81.

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

Broadfield, D.C., R.L. Holloway, K. Mowbray, A. Silvers, M.S. Yuan & S. Márquez, 2001. Endocast of Sambungmacan 3 (Sm 3): a new *Homo erectus* from Indonesia. *The Anatomical Record* 262, 369–79.

Bromham, L. & M. Cardillo, 2007. Primates follow the 'island rule': implications for interpreting *Homo floresiensis*. *Biology Letters* 3, 398–400.

Broodbank, C., 2006. The origins and early development of Mediterranean maritime activity. *Journal of Mediterranean Archaeology* 19, 199–230.

Broodbank, C., 2014. So … what? Does the paradigm currently want to budge so much? *Journal of Mediterranean Archaeology* 27(2), 267–72.

Brumm, A., G.M. Jensen, G.D. van den Bergh, M.J. Morwood, I. Kurniawan, F. Aziz & M. Storey. 2010. Hominins on Flores, Indonesia, by one million years ago. *Nature* 464, 748–52.

Carter, T., D. Contreras, S. Doyle, D.D. Mihailović, T. Moutsiou & N. Skarpelis. 2014. The Stelida Naxos Archaeological Project: New data on the Middle Palaeolithic and Mesolithic Cyclades. *Antiquity* 341, Project Gallery.

Cherry, J.F. & T.P. Leppard, n.d. Experimental archaeology and the earliest seagoing: the limitations of inference. Submitted to *World Archaeology*.

Conroy, G.C., G.W. Weber, H. Seidler, W. Recheis, D. zur Nedden & J.H. Mariam, 2000. Endocranial capacity of the Bodo cranium determined from three-dimensional computed tomography. *American Journal of Physical Anthropology* 113, 111–18.

Coolidge, F.L. & T. Wynn, 2001. Executive functions of the frontal lobes and the evolutionary ascendance of *Homo sapiens*. *Cambridge Archaeological Journal* 11(2), 255–60.

Coolidge, F.L. & T. Wynn, 2005. Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal* 15(1), 5–26.

Coqueugniot, H., J.-J. Hublin, F. Veillon, F. Houet & T. Jacob. 2004. Early brain growth in *Homo erectus* and implications for cognitive ability. *Nature* 431, 299–302.

Davidson, I., 2010. The colonisation of Australia and its adjacent islands and the evolution of modern cognition. *Current Anthropology* 51 (Supplement 1), 177–89.

Davidson, I., 2013. Peopling the last new worlds: the first colonisation of Sahul and the Americas. *Quaternary International* 285, 1–29.

Davidson, I. & W. Noble, 1992. Why the first colonisation of the Australian region is the earliest evidence of modern human behaviour. *Archaeology in Oceania* 27(3), 135–42.

Dawson, H., 2013. *Mediterranean Voyages: The Archaeology of Island Colonisation and Abandonment*. Walnut Creek (CA): Left Coast Press.

Demetrius, L., V.M. Gundlach & G. Ochs, 2004. Complexity and demographic stability in population models. *Theoretical Population Biology* 65, 211–25.

Dennell, R., J. Louys, H.J. O'Regan & D.M. Wilkinson. 2014. The origins and persistence of *Homo floresiensis* on Flores: biogeographical and ecological perspectives. *Quaternary Science Reviews* 96, 98–107.

Dennell, R. & M.D. Petraglia, 2012. The dispersal of *Homo sapiens* across southern Asia: how early, how often, how complex? *Quaternary Science Reviews* 47, 15–22.

Dennell, R. & M. Porr (eds)., 2014. *Southern Asia, Australia, and the Search for Human Origins*. Cambridge: Cambridge University Press.

de Queiroz, A., 2014. *The Monkey's Voyage: How Improbable Journeys Shaped the History of Life*. New York (NY): Basic Books.

d'Errico, F. & C. Stringer, 2011. Evolution, revolution or saltation scenario for the emergence of modern cultures? *Philosophical Transactions of the Royal Society B* 366, 1060–69.

Dunbar, R.I.M., 2012. Bridging the bonding gap: the transition from primates to humans. *Philosophical Transactions of the Royal Society B* 367, 1837–46.

Dunbar, R.I.M. & S. Shultz, 2007. Evolution in the social brain. *Science* 317, 1344–7.

Ferentinos, G., M. Gkioni, M. Gerag & G. Papatheodorou, 2012. Early seafaring activity in the southern Ionian islands, Mediterranean Sea. *Journal of Archaeological Science* 39, 2167–76.

Ferraro, J.V., T.W Plummer, B.L. Pobiner, et al., 2013. Earliest archaeological evidence of persistent hominin carnivory. *PLoS One* 8(4). doi: 10.1371/journal.pone.0062174.

Fisher, S.E. & C. Scharff. 2009. FOXP2 as a molecular window into speech and language. *Trends in Genetics* 25, 166–77.

Frith, C.D., 2012. The role of metacognition in human social interactions. *Philosophical Transactions of the Royal Society B* 367, 2213–23.

Galanidou, N., 2014. Archaic hominins on Crete: Fact or fiction? *Journal of Mediterranean Archaeology* 27(2), 260–67.

Gamble, C., J. Gowlett & R.I.M. Dunbar, 2011. The social brain and the shape of the Palaeolithic. *Cambridge Archaeological Journal* 21(1), 115–35.

Glikson, A., 2013. Fire and human evolution: the deep-time blueprints of the Anthropocene. *Anthropocene* 3, 89–92.

Gowlett, J., C. Gamble & R.I.M. Dunbar, 2012. Human evolution and the archaeology of the social brain. *Current Anthropology* 53(6), 693–722.

Gunz, P., S. Neubauer, L. Golovanova, V. Doronichev, B. Maureille & J.-J. Hublin, 2012. A uniquely modern human pattern of endocranial development: insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. *Journal of Human Evolution* 62, 300–13.

Haidle, M.N., 2010. Working-memory capacity and the evolution of modern cognitive potential: implications from animal and early human tool use. *Current Anthropology* 51 (Supplement 1), 149–66.

Henneberg, M., R.B. Eckhardt, S. Chavanaves & K.J. Hsü, 2014. Evolved developmental homeostasis disturbed in LB1 from Flores, Indonesia, denotes Down syndrome and not diagnostic traits of the invalid species *Homo floresiensis*. *Proceedings of the National Academy of Sciences* 111, 11,967–72.

Heyes, C., 2012. New thinking: the evolution of human cognition. *Philosophical Transactions of the Royal Society B* 367, 2091–6.

Holloway, R. L., D.C. Broadfield & M.S. Yuan, 2004. *The Human Fossil Record, Brain Endocasts: The Paleoneurological Evidence*. Hoboken (NJ): Wiley-Liss.

Kay, R.F., C. Ross & A.B. Williams, 1997. Anthropoid origins. *Science* 275(5301), 797–804.

Kirch, P.V., 2010. Peopling of the Pacific: a holistic anthropological perspective. *Annual Review of Anthropology* 39, 131–48.

Krijgsman, W., F.J. Hilgen, I. Raffi, F.J. Sierro & D.S. Wilson. 1999. Chronology, causes, and progression of the Messinian Salinity Crisis. *Nature* 400, 652–5.

Kubo, D., R.T. Kono & Y. Kaifu. 2013. Brain size of *Homo floresiensis* and its evolutionary implications. *Proceedings of the Royal Society B* doi.10.1098/rspb.2013.0338

Kuzawa, C.W., H.T. Chugani, L.I. Grossman, et al., 2014. Metabolic costs and evolutionary implications of human brain development. *Proceedings of the National Academy of Sciences* 111(36), 13,010–15.

Layton, R., S. O'Hara & A. Bilsborough, 2012. Antiquity and social functions of multilevel social organisation among human hunter-gatherers. *International Journal of Primatology* 33, 1215–45.

Leigh, S.R., 2012. Brain size growth and life history in human evolution. *Evolutionary Biology* 39, 587–99.

Leppard, T.P., 2014a. Modeling the impacts of Mediterranean island colonisation by archaic hominins: the likelihood of an insular Lower Palaeolithic. *Journal of Mediterranean Archaeology* 27(2), 231–54.

Leppard, T.P., 2014b. Response: The elusive insular Lower Palaeolithic and the problem of intentionality. *Journal of Mediterranean Archaeology* 27(2), 275–8.

Leppard, T.P., in press. Passive dispersal versus strategic dispersal in island colonisation by hominins. *Current Anthropology*.

Lieberman, P. 2007a. Current views on Neanderthal speech capabilities: a reply to Boë et al. (2002). *Journal of Phonetics* 35, 552–63.

Lieberman, P. 2007b. The evolution of human speech: its anatomical and neural base. *Current Anthropology* 48, 39–66.

Lombard, M. & M.N. Haidle, 2012. Thinking a bow-and-arrow set: cognitive implications of Middle Stone Age bow and stone-tipped arrow technology. *Cambridge Archaeological Journal* 22(2), 237–64.

Losos, J.B. & R.E. Ricklefs (eds.), 2010. *The Theory of Island Biogeography Revisited*. Princeton (NJ): Princeton University Press.

Lykousis, V., 2009. Sea-level changes and shelf break prograding sequences during the last 400ka in the Aegean margins: subsidence rates and palaeogeographic implications. *Continental Shelf Research* 29, 2037–44.

MacArthur, R.H. & E.O. Wilson, 1967. *The Theory of Island Biogeography*. Princeton (NJ): Princeton University Press.

Maricic, T., V. Günther, O. Georgiev, et al., 2012. A recent evolutionary change affects a regulatory element in the human FOXP2 gene. *Molecular Biology and Evolution* 30(4), 844–52.

Martínez, I., M. Rosa, R. Quam, et al., 2012. Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain. *Quaternary International* 295, 94–101.

McBrearty, S. & A. Brooks, 2000. The revolution that wasn't: a new interpretation of the origin of modern human behaviour. *Journal of Human Evolution* 39, 453–563.

Mellars, P., 2006. Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. *Proceedings of the National Academy of the Sciences* 103, 9381–6.

Mellars, P., K.C. Gori, M. Carr, P.A. Soares & M.B. Richards, 2013. Genetic and archaeological perspectives on the initial modern human colonisation of southern Asia. *Proceedings of the National Academy of the Sciences* 110, 10,699–704.

Neubauer, S. & J.-J. Hublin, 2012. The evolution of human brain development. *Evolutionary Biology* 39, 568–86.

Nowell, A., 2010. Defining behavioural modernity in the context of Neandertal and anatomically modern human populations. *Annual Review of Anthropology* 39, 437–52.

Palombo, M.R., 2013. What about causal mechanisms promoting early hominin dispersal in Eurasia? A research agenda for answering a hotly debated question. *Quaternary International* 295, 13–27.

Panagopoulou, E. & P. Karkanas, in press. The Palaeolithic of insular Greece, in *Paleoanthropology in the Balkans*, eds. K. Harvati & M. Roksandic. Dordrecht: Springer.

Pearce, E., C. Stringer & R.I.M. Dunbar, 2013. New insights into differences in brain organisation between Neanderthals and anatomically modern humans. *Proceedings of the Royal Society B* 280, 20130168.

Phoca-Cosmetatou, N. & R.J. Rabett, 2014a. Reflections on Pleistocene island occupation. *Journal of Mediterranean Archaeology* 27(2), 255–60.

Phoca-Cosmetatou, N. & R.J. Rabett, 2014b. Pleistocene island occupation in the Mediterranean: insights from a tied-biome approach to glacial refugia, in *Living in the Landscape: Essays in Honour of Graeme Barker*, eds. K. Boyle, R.J. Rabett & C.O Hunt. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 83–108.

Quammen, D., 1996. *The Song of the Dodo: Island Biogeography in an Age of Extinctions*. New York (NY): Touchstone.

Reuland, E., 2010. Imagination, planning, and working memory: the emergence of language. *Current Anthropology* 51 (Supplement 1), 99–110.

Rightmire, G.P., 2004. Brain size and encephalisation in Early to Mid-Pleistocene *Homo*. *American Journal of Physical Anthropology* 124, 109–23.

Robalino, N. & A. Robson, 2012. The economic approach to 'theory of mind'. *Philosophical Transactions of the Royal Society B* 367, 2224–33.

Rossano, M., 2010. Making friends, making tools, and making symbols. *Current Anthropology* 51 (Supplement 1), 89–98.

Roth, G. & U. Dicke, 2005. Evolution of the brain and intelligence. *Trends in Cognitive Sciences* 9(5), 250–57.

Runnels, C., 2013. Editorial: More on Palaeolithic America. *Journal of Field Archaeology* 38(2), 99–100.

Runnels, C., 2014a. Early Palaeolithic on Greek islands? *Journal of Mediterranean Archaeology* 27, 211–30.

Runnels, C., 2014b. Response: where do we stand? *Journal of Mediterranean Archaeology* 27, 272–4.

Runnels, C. & N. Hammond, 2012. Editorial: Palaeolithic America. *Journal of Field Archaeology* 37, 83–5.

Shea, J.J., 2006. The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe.*Journal of Archaeological Science* 33, 823–46.

Shultz, S., E. Nelson & R.I.M. Dunbar, 2012. Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. *Philosophical Transactions of the Royal Society B* 367, 2130–40.

Shumaker, R.W., K.R. Walkup & B.B. Beck. 2011. *Animal Tool Behaviour: The Use and Manufacture of Tools by Animals*. Baltimore (MD): Johns Hopkins University Press.

Simmons, A.H., 2012. Mediterranean island voyages. *Science* 338, 895–7.

Simmons, A.H., 2014. *Stone Age Sailors: Paleolithic Seafaring in the Mediterranean*. Walnut Creek (CA): Left Coast Press.

Smaers, J.B. & C. Soligo, 2013. Brain reorganisation, not relative brain size, primarily characterizes anthropoid brain evolution. *Proceedings of the Royal Society B* 280, 20130269. http://dx.doi.org/10.1098/rspb.2013.0269

Smith, T.M., P. Tafforeau, D.J. Reid, R. Grün, S. Eggins, M. Boutakiout & J.-J. Hublin, 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proceedings of the National Academy of Sciences* 104(15), 6128–33.

Steiper, M.E. & N.M. Young, 2006. Primate molecular divergence rates. *Molecular Phylogenetics and Evolution* 41, 384–94.

Sterelny, K., 2011. From hominins to humans: how *sapiens* became behaviourally modern. *Philosophical Transactions of the Royal Society B* 366, 809–22.

Sterelny, K., 2012. Language, gesture, skill: the co-evolutionary foundations of language. *Philosophical Transactions of the Royal Society B* 367, 2141–51.

Strasser, T.F., E. Panagopoulou, C. Runnels, et al., 2010. Stone Age seafaring in the Mediterranean: evidence from the Plakias region for Lower Palaeolithic and Mesolithic habitation of Crete. *Hesperia* 79, 145–90.

Strasser, T.F., C. Runnels, K. Wegmann, et al., 2011. Dating Palaeolithic sites in southwestern Crete, Greece. *Journal of Quaternary Science* 26, 553–60.

Stringer, C., 2012. The status of *Homo heidelbergensis* (Schoetensack 1908). *Evolutionary Anthropology* 21, 101–7.

Suddendorf, T. & M.C. Corballis, 2007. The evolution of foresight: what is mental time travel, and is it unique to humans? *Behavioural and Brain Sciences* 30, 299–351.

Tourloukis, V. & P. Karkanas, 2012. The Middle Pleistocene archaeological record of Greece and the role of the Aegean in hominin dispersals: new data and interpretations. *Quaternary Science Reviews* 43, 1–15.

Twomey, T., 2013. The cognitive implications of controlled fire use by humans. *Cambridge Archaeological Journal* 23(1), 113–28.

Vargha-Khadem, F., K. Watkins, K. Alcock, P. Fletcher & R. Passingham. 1995. Praxic and nonverbal cognitive deficits in a large family with a genetically transmitted speech and language disorder. *Proceedings of the National Academy of Sciences* 92, 930–33.

Wadley, L., 2013. Recognizing complex cognition through innovative technology in Stone Age and Palaeolithic sites. *Cambridge Archaeological Journal* 23(2), 163–83.

Webb, S.G., 2006. *The First Boat People*. Cambridge: Cambridge University Press.

Whiten, A. & D. Erdal, 2012. The human socio-cognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society B* 367, 2119–29.

Wilmshurst, J.M., T.L. Hunt, C. P. Lipo & A. Anderson, 2011. High-precision radiocarbon dating shows recent and rapid initial human colonisation of East Polynesia. *Proceedings of the National Academy of Sciences* 108, 1815–20.

Wynn, T. & F.L. Coolidge, 2010. Beyond symbolism and language: an introduction to Supplement 1, Working Memory. *Current Anthropology* 51 (Supplement 1), 5–16.

Wynn, T. & F.L. Coolidge, 2011. The implications of the Working Memory model for the evolution of human cognition. *International Journal of Evolutionary Biology* 2011, 1–12.

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