

Review



Cite this article: Haslam M. 2013 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Phil Trans R Soc B* 368: 20120421.
<http://dx.doi.org/10.1098/rstb.2012.0421>

One contribution of 15 to a Theme Issue
'Tool use as adaptation'.

Subject Areas:

behaviour, cognition

Keywords:

physical cognition, primate tool use,
demography, culture, stone tools,
Homo floresiensis

Author for correspondence:

Michael Haslam
e-mail: michael.haslam@rlaha.ox.ac.uk

'Captivity bias' in animal tool use and its implications for the evolution of hominin technology

Michael Haslam

Research Laboratory for Archaeology and the History of Art, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

Animals in captive or laboratory settings may outperform wild animals of the same species in both frequency and diversity of tool use, a phenomenon here termed 'captivity bias'. Although speculative at this stage, a logical conclusion from this concept is that animals whose tool-use behaviour is observed solely under natural conditions may be judged cognitively or physically inferior than if they had also been tested or observed under controlled captive conditions. In turn, this situation creates a potential problem for studies of the behaviour of extinct members of the human family tree—the hominins—as hominin cognitive abilities are often judged on material evidence of tool-use behaviour left in the archaeological record. In this review, potential factors contributing to captivity bias in primates (including increased contact between individuals engaged in tool use, guidance or shaping of tool-use behaviour by other tool-users and increased free time and energy) are identified and assessed for their possible effects on the behaviour of the Late Pleistocene hominin *Homo floresiensis*. The captivity bias concept provides one way to uncouple hominin tool use from cognition, by considering hominins as subject to the same adaptive influences as other tool-using animals.

1. Introduction

This review introduces the concept of 'captivity bias' as a means to discuss how differences in the diversity and frequency of animal tool use in captivity and in the wild may help us understand the behaviour and cognition of extinct hominins. This concept is supported by observations that animal tool use in captive or laboratory settings may outperform wild animals of the same species. These observations remain suggestive rather than definitive at this time, with the best available data coming from those animals that have most often been compared with tool-using hominins—the apes, macaques and capuchin monkeys. The principle underlying the captivity bias concept is that in cases where a species' tool-using ability has been argued to correlate with the cognitive ability of that species, it is important to consider the environmental conditions under which the relevant observations have been made. If tool-using ability varies by context, while underlying cognition does not, then the causal link between the two may not always be reliable. At the same time, if we can identify those aspects of the environment that promote more frequent or more diverse tool use, then we gain an additional analytical device for investigating differences in tool use between individuals and species. This study explores this line of reasoning, examining the factors that encourage or discourage technological expression over both evolutionary and ontogenetic timescales in known tool-using species. Versions of the captivity bias effect have been previously described as the 'tool paradox' [1] or 'captivity effect' [2], but the potential effect of this bias has not previously been considered in reconstructions of the cognitive and behavioural abilities of hominins (those ancestral species closer to humans than *Pan*).

Based on a review of the existing animal tool-use evidence [3,4], this study contends that the 'captivity bias' effect is not a result of the general experience

of being held captive, but derives instead from a series of atypical environmental and social circumstances generated within the captive environment. Specifically, these circumstances may include (i) increased contact between individuals engaged in tool use; (ii) guidance or shaping of tool-use behaviour by other tool-users; and (iii) increased free time and energy as a result of provisioning and lack of predation. If these (and other related) conditions are met outside of captivity, in free living populations, then I propose that it would be valuable to determine whether they result in a similar bias towards enhanced tool-use frequency or complexity.

(a) Cognition and tool use

A concise recent definition of cognition suggests that it involves ‘thinking and knowing’ [5]. Here, the term is used in a broad sense to refer to information processing within the brain, including planning, memory, learning, decision-making and perception. Of special relevance here are those processes that have an observable behavioural outcome. Investigations of cognition through animal tool use have focused particularly on what is termed physical cognition [6], assessing how animals understand and act on causal relationships between physical objects. In addition to cause and effect, animal tool manufacture and the sequential use of tools have been seen as a guide to planning abilities, where the immediate aim of accessing a reward is postponed to first create or obtain the right tool for the job [7]. It should be noted, however, that complex cognitive processes are not a prerequisite for animal tool use [8].

Many reconstructions of hominin cognitive abilities include a key characteristic that make them amenable to examination in terms of the captivity bias concept, namely that they are built on observations of tool use, usually stone tools as these survive most readily in the archaeological record [9–13]. For many living animal species, any effect of captivity bias would result in underestimation of cognitive capacities, if the sample were drawn purely from wild individuals, and we may therefore expect that: (i) if the conditions that promote captivity bias in non-human animals were not present in hominin environments, then we may systematically underestimate the cognitive capacities of tool-using hominins; and (ii) if some or all of the conditions that promote captivity bias *are* present for some or all extinct hominins, then their influence needs to be documented alongside other explanations for the patterning of hominin tool use. The existence of such a bias would not automatically determine that it would be expressed under all relevant circumstances for all tool-using animals, including hominins. However, it would offer an additional potential explanation for those circumstances where cognitive estimates of a species’ ability show a mismatch with its observed technology. By treating hominin technology as a subset of more general animal tool use, we can increase our confidence that our conclusions are not being subconsciously guided by teleological or anthropomorphic reasoning.

2. ‘Captivity bias’ in animal tool use

(a) Animal tool use in captivity and the wild

For a comprehensive catalogue of animal tool use, including captive data, the reader is referred to recent reviews [3,4].

Here, I focus primarily on vertebrate animals, and especially primates, as these have received by far the most attention from researchers both in natural and captive conditions, and they form the majority of comparisons with the evolution of human behaviour.

Table 1 provides an overview of known tool-use modes (primarily motor actions), tool manufacture and associative tool use used in captive and wild conditions by a variety of primates, based on the rationale and data presented in reference [3]. These categories were intended to allow a degree of standardization across different specific tool-use behaviours exhibited by specific animals, and they help to provide a firmer basis for cross-taxon comparisons by grouping together tool-use actions that share general manipulative or combinatorial features. For example, elsewhere in this themed issue, McGrew [14] compares chimpanzee and corvid tool use via these categories, although his approach differs slightly as he considers only habitual or customary tool use.

The available data show that captive tool use has greater diversity than in the wild among the apes, macaques and capuchin monkeys, but not in other primates. These data are likely skewed by research effort and observation effects, which is why captivity bias must remain a speculative suggestion at present rather than a firm principle, and similar data from other tool using taxa are required. Nevertheless, the species that are currently most often compared with hominins (including all the primates that use stone tools in the wild today) [15] have long histories of study both in the wild and captivity, with specific attention paid to their tool use [16,17–22]. Other primate species that are considered essentially non-tool-users in nature have also been shown to be capable of tool use under captive conditions, including Japanese macaques [23], baboons [3], cotton-top tamarins and vervet monkeys [24]. Tool use is not the only behaviour that has been observed to be more elaborate in the captive primates; for example, the number of different social signals has been demonstrated to increase in captive baboons versus their wild counterparts [25]. Note that the rearing experiences of captive animals can differ widely [26,27], and individual animals will show natural variation in their capabilities [28,29], with the result that any suggestion of captivity bias should therefore be seen as a generality rather than necessarily applying to every member of a given species. It may be also that some wild behaviours not involving tools, such as gorilla plant-food handling [30], exceed in complexity those seen in captivity, highlighting the fact that tool use does not exist in a cognitive or manipulative vacuum.

While primates have formed a significant focus of research into tool use, the same effect of more frequent and diverse tool use in captivity has been noted in animals as varied as elephants [31], keas [32], small tree finches [33], rooks [34], cockatoos [35], rodents such as degus [36] and naked mole rats [37] and even gastropods [38]. The examples listed here are illustrative rather than exhaustive—of the 418 instances of animal tool use tabulated by Bentley-Condit & Smith [4], 120 or 28.7% were found in captivity alone. For most animals, however, we do not currently have sufficient data available to judge the existence or otherwise of a captivity bias in tool use, and important avenues for future research include evaluating the effect of possible observation bias on these data, and developing criteria for quantifying the extent of the captivity bias for each taxon. For the purposes

Table 1. Primate tool use in the wild and in captivity. W, behaviour observed only in the wild; C, behaviour observed only in captivity; W C, behaviour observed in both settings. Data and tool-use categories from [3].

category	prosimians			New World monkeys			Old World monkeys			apes				
	lemurs	aye-aye		capucins	others	macaques	baboons/mandrills	others	gibbons	orangutans	gorillas	bonobos	chimpanzees	
<i>(a) tool-use modes</i>														
drop				W	W	W C	W C	W	W	W C	W	W C	W C	
throw				W C	W	W C	W C	W C	C	W C	W C	W C	W C	
drag, roll, kick, slap, push over				W		W C	W C			W C	W C	W C	W C	
brandish, wave, shake	W			W C		W	W C	W	W	W C	W C	W C	W C	
bait, entice				C		W		W C		C	C	W C	W C	
club, beat				W C	W			W		W C	W C	W C	W C	
pound, hammer				W C		W C	W C			W C	C	C	W C	
pry, apply leverage				C			W C			W C	C	C	W C	
dig				W C		C	W C	W		C	C	C	W C	
jab, stab, penetrate				W C		W				W C	C	C	W C	
reach			C	C	C	W C	W C	C	C	W C	W C	C	W C	
insert and probe				W C		W C	W C		C	W C	C	W C	W C	
scratch, rub					W	W C	W	W C	C	W C	W C	W C	W C	
cut				W C						C		C	C	
block				C						W C	C		W	
prop and climb, balance and climb, bridge, reposition		W		C		C	C	W		W C	W C	W C	W C	
hang					C				C			C	C	
contain				W C		C	C	C		C	C	C	W C	
absorb				W C		W C	C	W	C	W C	C	W C	W C	
wipe				C		C	W	W		W C	W C	W C	W C	
affix, apply, drape		W		W C	W C	W C	W C			W C	W C	W C	W C	
symbolize				C						W C	W	W C	W C	
<i>(b) tool manufacture modes</i>														
detach				W C	W	W	W	W	W	W C	W C	W C	W C	
subtract				W C	W C	W C	W C	W C	W C	W C	C	C	W C	

(Continued.)

Table 1. (Continued.)

category	prosimians		New World monkeys		Old World monkeys			apes				
	lemurs	aye-ayes	capuchins	others	macaques	baboons/ mandrills	others	gibbons	orangutans	gorillas	bonobos	chimpanzees
add, combine			C	C	C				W C	C	W C	C
reshape			W C	W	C				W C	C	W C	W C
(c) associative tool use												
sequential tool			W C		C	C			C	C	C	C
tool set			W C									W
serial tool												
tool composite (incl. meta-tool)			C						W C	C		W C
multi-function tool			W			W				W		W
secondary tool			C						C			C
wild	2	1	3	6	4	4	8	3	0	2	1	3
captive	1	0	10	3	8	4	2	6	7	16	10	5
wild and captive	0	0	16	2	10	10	3	0	22	9	15	23
total	3	1	29	11	22	18	13	9	29	27	26	31

of this paper, I will assume that the apparent captivity bias results from apes and other primates reflect reality, with the caveat that if future results prove otherwise the discussion presented here will require modification.

(b) Factors promoting captivity bias

Here, I focus on three broad topics that may promote or enable greater tool use under captive conditions: (i) increased contact between individuals engaged in tool use, leading to higher potential for the observation, maintenance and spread of tool-use innovations; (ii) guidance or shaping of individual or group tool-use behaviour by humans; and (iii) increased free time and energy as a result of provisioning and lack of predation. These topics are non-exclusive and non-exhaustive, and they are intended to provide an initially broad set of targets for identifying external influences on tool use.

In recent years, researchers have explored the relevance of the number of interacting individuals to the maintenance of traditions, showing that an increase in social contacts can allow for new ideas and techniques to be retained and spread more readily in a population [39–42]. The principle is not restricted to the human lineage [43], and wild orangutans and chimpanzees have been found to display increased complexity, success and frequency in tool use in increasingly social and higher population density settings [44–46]. Further, wild meerkats [47], captive cockatoos [35] and wild female dolphins also show that social effects can enhance tool use [48]. These examples suggest that both increased population size and density, where these promote increased contact between individuals, can facilitate the retention and spread of technological innovations and subsequently increase diversity in a species' tool-use repertoire.

Simply having increased opportunities for tool use may not be sufficient in the absence of conspecifics [49]. For social animals at least, therefore, it is plausible to suggest that a positive feedback loop of increased opportunities for repeated observation of tool-using individuals, and increased overall frequency and diversity of tool use, may be facilitated by captive conditions. In the case of tool use, the individuals with whom captive animals are coming into contact may in fact be tool-using humans, which is of particular importance for those species that are able to view humans as behavioural role models [50]. Not all species may be able to view humans in this manner, although studies of fairness in non-human primates and object manipulation in crows demonstrate its plausibility as a mechanism [51,52]. In some primate cases, the positive effect of human interaction on animal tool use has been directly observed, for example in human-raised capuchin monkeys [53], and in wild vervet monkeys that were in regular contact with humans and human facilities [54]. Experiments with captive orangutans, bonobos and other great apes [55] and non-tool-using tamarins and marmosets [56] demonstrate that human-directed training on tool-use tasks enhances performance, which might be expected for any animal amenable to operant conditioning. The human role in shaping or enabling tool use is perhaps most apparent in the studies of animals that do not use tools in the wild, through training [36] or provisioning [35] techniques, or the creation of artificial circumstances that may not occur in the wild [57]. Non-tool object manipulation may also be influenced by humans: stone handling by Japanese macaques, for example, (i) is found solely among

provisioned groups (who therefore have extra free time and energy through lowered foraging demands); and (ii) gradually disappeared from one site after provisioning was stopped [58,59]. Stone handling by rhesus macaques is also found only in captive animals [60].

An obvious difference between wild and captive conditions is the lack of natural predators in the latter, and the fact that captive animals are fed, watered and kept medically fit by humans [61]. Freed from the need to search for food or maintain vigilance for predators, captive individuals have additional time and energy to devote to exploration and play, including testing the affordances of any novel materials they may encounter [62–64]. These animals also have more time available to observe the behaviour of others, adding further impetus to the positive feedback loop suggested earlier. Suggestions that terrestriality in captivity promotes tool use among typically arboreal primates [2] may also rely, in part, on freedom from vigilance, as the captive environment provides security for these animals on the ground. A terrestriality effect cannot explain captivity bias seen in non-arboreal species, however, including elephants, gorillas and rodents.

Models that examine the origins and development of animal tool use do not suggest that there are intrinsic differences between wild and captive animals, and in fact, it is central to most models that observations made in laboratories and zoos are directly applicable to animals living in natural conditions. However, it should be clear from the foregoing that components of models that rely, even in part, on innate factors such as intelligence and manual dexterity [62] are insufficient to explain the differences between wild and captive tool-use behaviour. Extrinsic factors, whether social [65], behavioural [2] or ecological [66,67], are therefore essential to a complete explanation of how and why tool use develops. Although in a speculative form, the implications and relevance of the captivity bias effect could likely complement existing studies of technological development in each hominin species (and population within each species). For present purposes, however, we will focus on *Homo floresiensis*, a taxon that has generated controversy over both its cognitive abilities and associated technology.

3. *Homo floresiensis* and captivity bias in hominin tool use

This section contains a brief initial attempt to consider how the principles underlying the captivity bias concept may apply to an extinct animal. *Homo floresiensis* was a late-surviving so-called dwarf hominin species, going extinct only in the past few tens of thousand years [68]. It was chosen here, because the target of comparison for animal tool use has often been 'early humans' or 'early hominins' [69,70–73], and the extension of comparative studies to a geologically recent hominin species helps emphasize the potentially productive role of such comparisons for our understanding of human evolution. Importantly, for discussions of cognitive abilities, this species also presents an unprecedented small brain size for a Late Pleistocene hominin, although while brain size has been shown to correlate with innovative and tool-use behaviours in primates and birds [74], its effect on such behaviour is disputed [75,76]. *Homo floresiensis* is known from only one site, Liang Bua on the Indonesian island of Flores [77]. Its known temporal range falls within

the Late Pleistocene, from 95 000 to 17 000 years ago, although there is stone tool evidence from Flores that indicates hominin occupation from at least one million years ago (made by an unknown hominin) [78], and the Liang Bua evidence suggests that *H. floresiensis* occupied other parts of the island during drier phases [79]. The brain volume of the *H. floresiensis* holotype, LB1, has been estimated by different methods as between 380 and 426 cm³ [80–82]. This brain size is similar to that of chimpanzees, and in the preserved fossil record only *Ardipithecus ramidus* and *Sahelanthropus tchadensis*, both over four million years old, had smaller brains [83,84]. Neither of those two putative hominins are presently associated with evidence for tool use.

Archaeological material found with *H. floresiensis* skeletal elements at Liang Bua includes evidence for plant-working and consumption of *Stegodon* and Komodo dragons, as well as possible evidence for fire [85,86]. The site's excavators considered this as a whole to be support for complex cognition [68]. Much discussion has centred on the supposed sophistication of the associated stone tool assemblage (including retouched 'perforators' [87]), with some researchers considering the tools to be too advanced or similar to *H. sapiens* artefacts to have been made by *H. floresiensis*, and with the small brain of LB1 explicitly given as a primary reason for such a conclusion [88–92]. The Liang Bua lithic analysts have convincingly rebutted these claims, showing that the tools are the product of an independent lineage from *H. sapiens*, and that as an assemblage the Liang Bua tools are not any more sophisticated than Oldowan technology dating to well over one million years ago [93].

Nevertheless, the fact remains that no hominin with a brain size of ca 400 cm³ has previously been associated with knapped stone tools of any kind, and there remains no doubt that *H. floresiensis* anatomy is distinct from that of known tool-making hominins, including in the shoulder, arm and wrist configurations [94–96]. While it remains possible that *H. floresiensis* dwarfed from an isolated Southeast Asian *H. erectus* population [81], cladistics analysis suggests an earlier, non-*erectus* origin for the species [97]. In the light of the data, the questions to be asked are not whether the Liang Bua Pleistocene tools are unusually sophisticated (they are not), but rather (i) why *H. floresiensis* was a stone tool maker at all, given how physically distinct it is from other tool-making hominins, and (ii) how its lineage sustained stone tool-use traditions on Flores for what appears to be at least a million years [78].

The first factor to consider here is evidence for population interaction. We do not yet know the population size or density of *H. floresiensis*, although it has been suggested that population sizes may have increased during wetter periods on the island [79]. A testable hypothesis based on the captivity bias effect is therefore that such periods will show increased tool diversity and frequency on Flores, irrespective of whether foraging activities changed during the same periods. *Homo floresiensis* remains have been found in a single site; however, the species must have been more widespread on Flores (which is a reasonably large island at 13 500 km²) to maintain continuity over at least tens and potentially hundreds of thousands of years, including periods with very little evidence of occupation at Liang Bua. This population also survived the Toba volcanic super-eruption around 74 000 years ago on nearby Sumatra [98], and in fact, the highest concentrations of stone tools at

Liang Bua are found immediately following that event [79]. Studies of endemic primates on islands in Southeast Asia and elsewhere have shown that these populations typically have high population densities relative to mainland groups owing to release from interspecific competition [99,100], and there is no reason to assume *H. floresiensis* would have differed from this pattern. It is a reasonable hypothesis therefore that hominin encounter and interaction rates would have been higher on Flores than over a similarly sized area of mainland. This hypothesis includes encounters with artefacts left by other *H. floresiensis* individuals [101], possibly further increased through the circumscribed nature of island living. The likely cooperation necessary for hunting and transporting large or dangerous prey such as *Stegodon* and Komodo dragons [102] may have acted as an additional spur to bring individuals together.

Second, is there evidence for contact with other tool-using hominins, especially *H. sapiens*? Surrounding currents make Flores a difficult island to reach [77], and the lithic sequence shows little change over time, so on current data, the direct influence of other hominins on *H. floresiensis* tool use and manufacture is improbable. Nevertheless, the site's lithic team raised the possibility that continuities in stone technology before and after the disappearance of *H. floresiensis* at Liang Bua (near the Pleistocene/Holocene boundary) resulted from incoming *H. sapiens* groups incorporating techniques from *H. floresiensis* [87]. If this suggestion is supported by further data, then the direction of information transmission from the resident species to the new arrivals would be as expected under the captivity bias effect, where it is resident population size and interconnectedness rather than cognitive ability that determines whether technological attributes are maintained.

Third, we can consider evidence for predation reduction and increased free time. The dwarfing of *H. floresiensis* (its stature has been calculated at 1–1.1 m) [77] has been attributed to the 'island rule', in which large-bodied animals reduce in size and some smaller animals grow larger. Despite debate over its generality, this rule has been found to hold for primates [103], with the driving factors including lower levels of predation and diminished resources. One effect of diminished resources may have also been to increase range sizes, however, leading again to greater rates of contact between different groups on the island. Predation reduction was likely an important influence in *H. floresiensis* dwarfing (although predators were certainly present on the island [81]), and features in the lower limbs that favour 'low gear' locomotion and stability over speed or agility [104,105] may be indirect evidence for a relaxation of the need for rapid escape. The similarly dwarfed prey species *Stegodon florensis insularis* is found throughout the Pleistocene Liang Bua sequence, only disappearing when *H. floresiensis* does, giving one indication perhaps that over-hunting owing to resource pressures did not occur on the island. Further, Late Pleistocene *Stegodon* do not decrease in size through the Liang Bua sequence [85], and despite overall low species richness on Flores, other endemic fauna, including the Komodo dragon, a smaller varanid, and three species of giant rat also survive throughout the Liang Bua Pleistocene record [85,104].

Taken together, therefore, the available data would suggest an interconnected, cooperating, stable population on Flores, likely facing predation pressures lower than that on the mainland, but likely also lower resource availability (tempered by

the large size of the island and continued presence of large prey taxa). Interactions with other tool-using species may have been non-existent, based on lithic continuity evidence and the body size changes seen in both the hominins and other Flores fauna [85], which suggest isolation from outside influences. The long-term stability in stone tool forms suggests stable social groups, but at population densities too low to sustain cumulative changes in the technology. This maintenance of tool traditions, despite a suggested decrease in brain size of a third to a half depending on whether *Homo habilis* or early Indonesian *Homo erectus* is considered the founding population [81], was likely facilitated by increased free time granted by decreased vigilance requirements.

Although larger-brained than *H. floresiensis*, East African australopiths were manufacturing stone cutting tools from at least 2.6 million years ago [106]. Even if the Flores dwarfing process initiated from a relatively small-bodied and small-brained hominin ancestor [77], tool use at Liang Bua may be seen as a context-dependent outcome of existing behaviour, rather than an improbable *de novo* occurrence [78]. From a captivity bias perspective, *H. floresiensis*' maintenance of a variety of stone tool forms over many thousands of years, likely supported by non-stone tools, may therefore be explained, in part, as an instance of relaxed predation coupled to long-term social observation opportunities in an island setting. A prediction based on this perspective is that were *H. floresiensis* individuals ever to leave Flores (accidentally or otherwise) and reach the Southeast Asian mainland, their technological output would suffer a dramatic decline as the protective factors on Flores were removed. Although it is not the only plausible explanation, the Flores hominins could be viewed as naturally 'captive', and their technology assessed not from *a priori* expectations about brain size, cognition and anatomy but instead as another example of animal tool-use development in an enabling environment.

4. Hominins as tool-using animals

The case study included here has touched on only certain aspects of the ways in which animal tool use may provide additional options for developing our views on the behaviour of our hominin ancestors. Factors such as an increase in social contact, and the risk of predation or conflict can be linked in complex ways and, naturally, it is not only tool use that they influence, as shown for example by recent work tying the evolution of primate social living to diurnal predation [107].

Further, not every instance of increased free time and observation opportunity will automatically result in wholesale changes to toolkits, and the averaged picture of hominin technological evolution is actually one of prolonged periods of stasis (especially before the Middle Pleistocene). The key is to understand why change happens when it does, and here the animal tool-use record is useful in that it demonstrates that variations in technology characteristically involve the use of individual tools in sequence, and the

addition of new tool forms and materials to the repertoire (i.e. increases in diversity), rather than cumulative modification of existing forms. The few possible examples of cumulative change in animal tools, such as the brush-tipped termite fishing probes made by Goualougo chimpanzees [108], are important but very rare exceptions. Where changes are observed in hominin behaviours that may be expected to influence tool use, such as ranging or diet, without accompanying changes in stone tool forms, we may therefore hypothesise that either (i) additional (non-lithic) tools were being incorporated into the toolkit, or (ii) existing tools were being sequentially combined for greater energy returns or to open up new extraction niches. Further, the captivity bias effect suggests that hominin groups, even if members of the same species, will show widely varying levels of tool use as a result of both cultural and stochastic processes [33]. Cognition is irrelevant to these processes.

This discussion of the captivity bias effect is not intended to present an overarching hypothesis for all animal or even hominin tool use. It offers, instead, a complementary approach to the potentially circular arguments that assess the complexity of hominin tool use based on inferred cognition, where the tools themselves provide an important line of evidence for cognitive ability. Combined consideration of palaeoenvironmental, zooarchaeological and site occupation data (to reconstruct available resources, predator/prey abundance and information on possible group sizes from the density of material remains [109], respectively) can allow assessment of the living conditions for any hominin taxon. While these will suffer the same lacunae as any archaeological data, the independent lines of evidence that they provide may at least augment reconstructions based on cranial capacities and brain organization [110], whereas lessening reliance on often-scarce hominin fossil evidence. Variation seen among different groups of the same wild animal species [48,111,112], and between wild and captive individuals, suggests that we should focus on the specific ecological and social circumstances faced by the specific hominin groups if we want to posit anything other than a baseline cognition underlying tool use within and between those groups. The captivity bias effect posited here, while speculative at present and requiring further validation, provides a caution against generalizing findings of artefactual diversity, complexity or frequency and their behavioural implications from one hominin group to others, even of the same species, without explicit reasons for doing so.

Acknowledgements. I thank Dora Biro for organizing the Royal Society International Scientific seminar 'Tool use as adaptation', for many helpful discussions about this paper, and for assistance preparing table 1. I also thank Helen Eaton, and the anonymous reviewers for their insights.

Funding statement. Funding support was provided by the European Research Council through Starting Investigator grant no. 283959 (Primarch).

References

1. van Schaik C, Fox E, Sitompul A. 1996 Manufacture and use of tools in wild Sumatran orangutans. *Naturwissenschaften* **83**, 186–188. (doi:10.1007/BF01143062)
2. Meulman E, Sanz C, Visalberghi E, van Schaik C. 2012 The role of terrestriality in promoting primate

- technology. *Evol. Anthropol.* **21**, 58–68. (doi:10.1002/evan.21304)
3. Shumaker R, Walkup K, Beck B. 2011 *Animal tool behavior: the use and manufacture of tools by animals*. Baltimore, MD: John Hopkins University Press.
 4. Bentley-Condit VK, Smith EO. 2010 Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour* **147**, 185–221. (doi:10.1163/000579509X12512865686555)
 5. Heyes C. 2012 New thinking: the evolution of human cognition. *Phil. Trans. R. Soc. B* **367**, 2091–2096. (doi:10.1098/rstb.2012.0111)
 6. Emery NJ, Clayton NS. 2009 Tool use and physical cognition in birds and mammals. *Curr. Opin. Neurobiol.* **19**, 27–33. (doi:10.1016/j.conb.2009.02.003)
 7. Seed A, Byrne R. 2010 Animal tool-use. *Curr. Biol.* **20**, R1032–R1039. (doi:10.1016/j.cub.2010.09.042)
 8. Hansell M, Ruxton G. 2008 Setting tool use within the context of animal construction behaviour. *Trends Ecol. Evol.* **23**, 73–78. (doi:10.1016/j.tree.2007.10.006)
 9. Stout D, Toth N, Schick K, Chaminade T. 2008 Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. *Phil. Trans. R. Soc. B* **363**, 1939–1949. (doi:10.1098/rstb.2008.0001)
 10. Wynn TG. 2002 Archaeology and cognitive evolution. *Behav. Brain Sci.* **25**, 389–438.
 11. Toth N, Schick K. 1993 Early stone industries and inferences regarding language and cognition. In *Tools, language and cognition in human evolution* (eds K Gibson, T Ingold), pp. 346–362. Cambridge, UK: Cambridge University Press.
 12. Foley R, Lahr MM. 1997 Mode 3 technologies and the evolution of modern humans. *Camb. Archaeol. J.* **7**, 3–36. (doi:10.1017/S0959774300001451)
 13. Wadley L. 2010 Compound-adhesive manufacture as a behavioral proxy for complex cognition in the Middle Stone Age. *Curr. Anthropol.* **51**, S111–S119. (doi:10.1086/649836)
 14. McGrew WC. 2013 Is primate tool use special? Chimpanzee and New Caledonian crow compared. *Phil. Trans. R. Soc. B* **368**, 20120422. (doi:10.1098/rstb.2012.0422)
 15. Haslam M *et al.* 2009 Primate archaeology. *Nature* **460**, 339–344. (doi:10.1038/nature08188)
 16. Matsuzawa T (ed.) 2001 *Primate origins of human cognition and behavior*. Tokyo, Japan: Springer.
 17. Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T. 2003 Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.* **6**, 213–223. (doi:10.1007/s10071-003-0183-x)
 18. Sanz C, Call J, Boesch C. (eds) 2013 *Tool use in animals: cognition and ecology*. Cambridge, UK: Cambridge University Press.
 19. Inoue-Nakamura N, Matsuzawa T. 1997 Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **111**, 159–173. (doi:10.1037/0735-7036.111.2.159)
 20. Hayashi M, Mizuno Y, Matsuzawa T. 2005 How does stone-tool use emerge? Introduction of stones and nuts to naive chimpanzees in captivity. *Primates* **46**, 91–102. (doi:10.1007/s10329-004-0110-z)
 21. Visalberghi E, Haslam M, Spagnoletti N, Frigaszy D. 2013 Use of stone hammer tools and anvils by bearded capuchin monkeys over time and space: construction of an archeological record of tool use. *J. Archaeol. Sci.* **40**, 3222–3232. (doi:10.1016/j.jas.2013.03.021)
 22. Haslam M. 2012 Towards a prehistory of primates. *Antiquity* **86**, 299–315.
 23. Hihara S, Obayashi S, Tanaka M, Iriki A. 2003 Rapid learning of sequential tool use by macaque monkeys. *Physiol. Behav.* **78**, 427–434. (doi:10.1016/S0031-9384(02)01006-5)
 24. Santos L, Pearson H, Spaepen G, Tsao F, Hauser M. 2006 Probing the limits of tool competence: experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Anim. Cogn.* **9**, 94–109. (doi:10.1007/s10071-005-0001-8)
 25. Kummer H, Kurt F. 1965 A comparison of social behaviour in captive and wild hamadryas baboons. In *The baboon in medical research* (ed. H Vagtborg), pp. 1–46. Austin, TX: University of Texas Press.
 26. Brent L, Bloomsmith M, Fisher S. 1995 Factors determining tool-using ability in two captive chimpanzee (*Pan troglodytes*) colonies. *Primates* **36**, 265–274. (doi:10.1007/BF02381352)
 27. Menzel E, Davenport R, Rogers C. 1970 The development of tool using in wild-born and restriction-reared chimpanzees. *Folia Primatol.* **12**, 273–283. (doi:10.1159/000155297)
 28. Thornton A, Lukas D. 2012 Individual variation in cognitive performance: developmental and evolutionary perspectives. *Phil. Trans. R. Soc. B* **367**, 2773–2783. (doi:10.1098/rstb.2012.0214)
 29. Herrmann E, Call J. 2012 Are there geniuses among the apes? *Phil. Trans. R. Soc. B* **367**, 2753–2761. (doi:10.1098/rstb.2012.0191)
 30. Byrne R, Corp N, Byrne J. 2001 Estimating the complexity of animal behaviour: how mountain gorillas eat thistles. *Behaviour* **138**, 525–557. (doi:10.1163/156853901750382142)
 31. Chevalier-Skolnikoff S, Liska J. 1993 Tool use by wild and captive elephants. *Anim. Behav.* **46**, 209–219. (doi:10.1006/anbe.1993.1183)
 32. Huber L, Gajdon G. 2006 Technical intelligence in animals: the kea model. *Anim. Cogn.* **9**, 295–305. (doi:10.1007/s10071-006-0033-8)
 33. Teschke I, Cartmill E, Stankewitz S, Tebbich S. 2011 Sometimes tool use is not the key: no evidence for cognitive adaptive specializations in tool using woodpecker finches. *Anim. Behav.* **82**, 945–956. (doi:10.1016/j.anbehav.2011.07.032)
 34. Bird C, Emery NJ. 2009 Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proc. Natl Acad. Sci. USA* **106**, 10 370–10 375. (doi:10.1073/pnas.0901008106)
 35. Auersperg A, Szabo B, von Bayern A, Kacelnik A. 2012 Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo. *Curr. Biol.* **22**, R903–R904. (doi:10.1016/j.cub.2012.09.002)
 36. Okanoya K, Tokimoto N, Kumazawa N, Hihara S, Iriki A. 2008 Tool-use training in a species of rodent: the emergence of an optimal motor strategy and functional understanding. *PLoS ONE* **3**, e1860. (doi:10.1371/journal.pone.0001860)
 37. Shuster G, Sherman P. 1998 Tool use by naked mole-rats. *Anim. Cogn.* **1**, 71–74. (doi:10.1007/s100710050009)
 38. Weldon P, Hoffman D. 1975 Unique form of tool-using in two gastropod molluscs (Trochidae). *Nature* **256**, 720–721. (doi:10.1038/256720a0)
 39. Powell A, Shennan S, Thomas M. 2009 Late Pleistocene demography and the appearance of modern human behavior. *Science* **324**, 1298–1301. (doi:10.1126/science.1170165)
 40. Shennan S. 2001 Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Camb. Archaeol. J.* **11**, 5–16. (doi:10.1017/S0959774301000014)
 41. Collard M, Buchanan B, Ruttle A, O'Brien M. 2012 Niche construction and the toolkits of hunter-gatherers and food producers. *Biol. Theory* **6**, 251–259. (doi:10.1007/s13752-012-0034-6)
 42. Kline M, Boyd R. 2010 Population size predicts technological complexity in Oceania. *Proc. R. Soc. B* **277**, 2559–2564. (doi:10.1098/rspb.2010.0452)
 43. Stanley E, Kendal R, Kendal J, Grounds S, Laland K. 2008 The effects of group size, rate of turnover and disruption to demonstration on the stability of foraging traditions in fish. *Anim. Behav.* **75**, 565–572. (doi:10.1016/j.anbehav.2007.06.014)
 44. Fox E, Sitompul A, van Schaik C. 1999 Intelligent tool use in wild Sumatran orangutans. In *The mentalities of gorillas and orangutans: comparative perspectives* (eds S Parker, M Mitchell, HL Miles), pp. 99–116. Cambridge, UK: Cambridge University Press.
 45. Lonsdorf E, Ross S, Linick S, Milstein M, Melber T. 2009 An experimental, comparative investigation of tool use in chimpanzees and gorillas. *Anim. Behav.* **77**, 1119–1126. (doi:10.1016/j.anbehav.2009.01.020)
 46. van Schaik C, Ancrenaz M, Borgen G, Galdikas B, Knott C, Singleton I, Suzuki A, Utami SS, Merrill M. 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105. (doi:10.1126/science.1078004)
 47. Hoppitt W, Samson J, Laland K, Thornton A. 2012 Identification of learning mechanisms in a wild meerkat population. *PLoS ONE* **7**, e42044. (doi:10.1371/journal.pone.0042044)
 48. Mann J, Stanton M, Patterson E, Bienenstock E, Singh L. 2012 Social networks reveal cultural behaviour in tool-using dolphins. *Nat. Commun.* **3**, 980. (doi:10.1038/ncomms1983)
 49. Hopper L, Spiteri A, Lambeth S, Schapiro S, Horner V, Whiten A. 2007 Experimental studies of traditions and underlying transmission processes in chimpanzees. *Anim. Behav.* **73**, 1021–1032. (doi:10.1016/j.anbehav.2006.07.016)

50. Hirata S, Morimura N, Houki C. 2009 How to crack nuts: acquisition process in captive chimpanzees (*Pan troglodytes*) observing a model. *Anim. Cogn.* **12**, S87–S101. (doi:10.1007/s10071-009-0275-3)
51. Anderson J, Kuroshima H, Takimoto A, Fujita K. 2013 Third-party social evaluation of humans by monkeys. *Nat. Commun.* **4**, 1561. (doi:10.1038/ncomms2495)
52. Kenward B, Rutz C, Weir A, Kacelnik A. 2006 Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Anim. Behav.* **72**, 1329–1343. (doi:10.1016/j.anbehav.2006.04.007)
53. Fredman T, Whiten A. 2008 Observational learning from tool using models by human-reared and mother-reared capuchin monkeys (*Cebus apella*). *Anim. Cogn.* **11**, 295–309. (doi:10.1007/s10071-007-0117-0)
54. van de Waal E, Bshary R. 2010 Contact with human facilities appears to enhance technical skills in wild vervet monkeys (*Chlorocebus aethiops*). *Folia Primatol.* **81**, 282–291. (doi:10.1159/000322628)
55. Herrmann E, Wobber V, Call J. 2008 Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *J. Comp. Psychol.* **122**, 220–230. (doi:10.1037/0735-7036.122.2.220)
56. Spaulding B, Hauser M. 2005 What experience is required for acquiring tool competence? Experiments with two callitrichids. *Anim. Behav.* **70**, 517–526. (doi:10.1016/j.anbehav.2004.11.024)
57. Bird C, Emery NJ. 2009 Rooks use stones to raise the water level to reach a floating worm. *Curr. Biol.* **19**, 1410–1414. (doi:10.1016/j.cub.2009.07.033)
58. Leca J-B, Gunst N, Huffman M. 2012 Thirty years of stone handling tradition in Arashiyama macaques: implications for cumulative culture and tool use in non-human primates. In *The monkeys of Stormy Mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (eds J-B Leca, M Huffman, P Vasey), pp. 223–257. Cambridge, UK: Cambridge University Press.
59. Huffman M. 2008 Cultured monkeys: social learning cast in stones. *Curr. Dir. Psychol. Sci.* **17**, 410–414. (doi:10.1111/j.1467-8721.2008.00616.x)
60. Nahallage C, Huffman M. 2012 Stone handling behavior in rhesus macaques (*Macaca mulatta*), a behavioral propensity for solitary object play shared with Japanese macaques. *Primates* **53**, 71–78. (doi:10.1007/s10329-011-0279-x)
61. Beck B. 1980 *Animal tool behavior: the use and manufacture of tools*. New York, NY: Garland STPM.
62. van Schaik C, Deaner R, Merrill M. 1999 The conditions for tool use in primates: implications for the evolution of material culture. *J. Hum. Evol.* **36**, 719–741. (doi:10.1006/jhev.1999.0304)
63. Kummer H, Goodall J. 1985 Conditions of innovative behaviour in primates. *Phil. Trans. R. Soc. Lond. B* **308**, 203–214. (doi:10.1098/rsth.1985.0020)
64. Frigaszy D, Visalberghi E. 2004 Socially biased learning in monkeys. *Learn. Behav.* **32**, 24–35. (doi:10.3758/BF03196004)
65. Dean L, Kendal R, Schapiro S, Thierry B, Laland K. 2012 Identification of the social and cognitive processes underlying human cumulative culture. *Science* **335**, 1114–1118. (doi:10.1126/science.1213969)
66. Yamakoshi G. 1998 Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *Am. J. Phys. Anthropol.* **106**, 283–295. (doi:10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-0)
67. Tebbich S, Taborsky M, Fessl B, Dvorak M. 2002 The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). *Ecol. Lett.* **5**, 656–664. (doi:10.1046/j.1461-0248.2002.00370.x)
68. Morwood M *et al.* 2005 Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. *Nature* **437**, 1012–1017. (doi:10.1038/nature04022)
69. Toth N, Schick K. 2009 The Oldowan: the tool making of early hominins and chimpanzees compared. *Annu. Rev. Anthropol.* **38**, 289–305. (doi:10.1146/annurev-anthro-091908-164521)
70. Yamakoshi G. 2001 Ecology of tool use in wild chimpanzees: toward reconstruction of early hominid evolution. In *Primate origins of human cognition and behavior* (ed. T Matsuzawa), pp. 537–556. Dordrecht, The Netherlands: Springer.
71. Pruett J, Bertolani P. 2007 Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Curr. Biol.* **17**, 412–417. (doi:10.1016/j.cub.2006.12.042)
72. Hunt GR. 2000 Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proc. R. Soc. Lond. B* **267**, 403–413. (doi:10.1098/rspb.2000.1015)
73. Sirianni G, Visalberghi E. 2013 Wild bearded capuchins process cashew nuts without contacting caustic compounds. *Am. J. Primatol.* **75**, 387–393. (doi:10.1002/ajp.22119)
74. Lefebvre L, Reader S, Sol D. 2004 Brains, innovations and evolution in birds and primates. *Brain, Behav. Evol.* **63**, 233–246. (doi:10.1159/000076784)
75. Chittka L, Niven J. 2009 Are bigger brains better? *Curr. Biol.* **19**, R995–R1008. (doi:10.1016/j.cub.2009.08.023)
76. Healy S, Rowe C. 2007 A critique of comparative studies of brain size. *Proc. R. Soc. B* **274**, 453–464. (doi:10.1098/rspb.2006.3748)
77. Morwood M, Jungers WL. 2009 Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography. *J. Hum. Evol.* **57**, 640–648. (doi:10.1016/j.jhev.2009.08.003)
78. Brumm A, Jensen G, van den Bergh GD, Morwood M, Kurniawan I, Aziz F, Storey M. 2010 Hominins on Flores, Indonesia, by one million years ago. *Nature* **464**, 748–752. (doi:10.1038/nature08844)
79. Westaway KE, Morwood M, Sutikna T, Moore MW, Rokus A, van den Bergh GD, Roberts RG, Saptomo EW. 2009 *Homo floresiensis* and the late Pleistocene environments of eastern Indonesia: defining the nature of the relationship. *Quat. Sci. Rev.* **28**, 2897–2912. (doi:10.1016/j.quascirev.2009.07.020)
80. Brown P, Sutikna T, Morwood M, Soejono RP, Jatmiko E, Saptomo EW, Due RA. 2004 A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* **431**, 1055–1061. (doi:10.1038/nature02999)
81. Kubo D, Kono RT, Kaifu Y. 2013 Brain size of *Homo floresiensis* and its evolutionary implications. *Proc. R. Soc. B* **280**, 20130338. (doi:10.1098/rspb.2013.0338)
82. Falk D *et al.* 2005 The brain of LB1, *Homo floresiensis*. *Science* **308**, 242–245. (doi:10.1126/science.1109727)
83. Suwa G, Asfaw B, Kono R, Kubo D, Lovejoy O, White T. 2009 The *Ardipithecus ramidus* skull and its implications for hominid origins. *Science* **326**, 68e1–68e7. (doi:10.1126/science.1175825)
84. Brunet M *et al.* 2002 A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418**, 145–151. (doi:10.1038/nature00879)
85. van den Bergh GD *et al.* 2009 The Liang Bua faunal remains: a 95 kyr. sequence from Flores, East Indonesia. *J. Hum. Evol.* **57**, 527–537. (doi:10.1016/j.jhev.2008.08.015)
86. Culotta E. 2007 The fellowship of the hobbit. *Science* **317**, 740–742. (doi:10.1126/science.317.5839.740)
87. Moore MW, Sutikna T, Jatmiko E, Morwood M, Brumm A. 2009 Continuities in stone flaking technology at Liang Bua, Flores, Indonesia. *J. Hum. Evol.* **57**, 503–526. (doi:10.1016/j.jhev.2008.10.006)
88. Martin R, MacLarnon A, Phillips JL, Dobyns W. 2006 Flores hominid: new species or microcephalic dwarf? *Anat. Rec. A* **288**, 1123–1145. (doi:10.1002/ar.a.20389)
89. Lahr MM, Foley R. 2004 Human evolution writ small. *Nature* **431**, 1043–1044. (doi:10.1038/4311043a)
90. Richards G. 2006 Genetic, physiologic and ecogeographic factors contributing to variation in *Homo sapiens*: *Homo floresiensis* reconsidered. *J. Evol. Biol.* **19**, 1744–1767. (doi:10.1111/j.1420-9101.2006.01179.x)
91. Henneberg M, Thorne A. 2004 Flores human may be pathological *Homo sapiens*. *Before Farm.* **4**, 2–4.
92. Jacob T, Indriati E, Soejono RP, Hsu K, Frayer DW, Eckhardt RB, Kuperavage AJ, Thorne A, Henneberg M. 2006 Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: population affinities and pathological abnormalities. *Proc. Natl Acad. Sci. USA* **103**, 13 421–13 426. (doi:10.1073/pnas.0605563103)
93. Moore MW, Brumm A. 2009 *Homo floresiensis* and the African Oldowan. In *Interdisciplinary approaches to the Oldowan* (eds E Hovers, D Braun), pp. 61–69. Dordrecht, The Netherlands: Springer.
94. Larson S, Jungers WL, Morwood M, Sutikna T, Jatmiko E, Saptomo EW, Due RA, Djubiantono T. 2007 *Homo floresiensis* and the evolution of the

- hominin shoulder. *J. Hum. Evol.* **53**, 718–731. (doi:10.1016/j.jhevol.2007.06.003)
95. Tocheri M *et al.* 2007 The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* **317**, 1743–1745. (doi:10.1126/science.1147143)
96. Orr C *et al.* 2013 New wrist bones of *Homo floresiensis* from Liang Bua (Flores, Indonesia). *J. Hum. Evol.* **64**, 109–129. (doi:10.1016/j.jhevol.2012.10.003)
97. Argue D, Morwood M, Sutikina T, Jatmiko E, Saptomo EW. 2009 *Homo floresiensis*: a cladistic analysis. *J. Hum. Evol.* **57**, 623–639. (doi:10.1016/j.jhevol.2009.05.002)
98. Louys J. 2007 Limited effect of the Quaternary's largest super-eruption (Toba) on land mammals from Southeast Asia. *Quat. Sci. Rev.* **26**, 3108–3117. (doi:10.1016/j.quascirev.2007.09.008)
99. Sugardjito J, van Schaik C, van Noordwijk M, Mitrasetia T. 1989 Population status of the Simeulue monkey (*Macaca fascicularis fusca*). *Am. J. Primatol.* **17**, 197–207. (doi:10.1002/ajp.1350170303)
100. Struhsaker T, Siex K. 1996 The Zanzibar red colobus monkey *Procolobus kirkii*: conservation status of an endangered island endemic. *Afr. Primates* **2**, 54–61.
101. Frigaszy DM, Biro D, Eshchar Y, Humle T, Izar P, Resende B, Visalberghi E. 2013 The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Phil. Trans. R. Soc. B* **368**, 20120410. (doi:10.1098/rstb.2012.0410)
102. Morwood M, Cogill-Koez D. 2007 *Homo* on Flores: some early implications for the evolution of language and cognition. In *Mental states: evolution, function, nature, vol. 1* (eds A Schalley, D Khlentzos), pp. 43–73. Amsterdam, The Netherlands: John Benjamins.
103. Bromham L, Cardillo M. 2007 Primates follow the 'island rule': implications for interpreting *Homo floresiensis*. *Biol. Lett.* **3**, 398–400. (doi:10.1098/rsbl.2007.0113)
104. Meijer HJM, van den Hoek Ostende LW, van den Bergh GD, de Vos J. 2010 The fellowship of the hobbit: the fauna surrounding *Homo floresiensis*. *J. Biogeogr.* **37**, 995–1006. (doi:10.1111/j.1365-2699.2010.02308.x)
105. Jungers WL, Harcourt-Smith W, Wunderlich R, Tocheri M, Larson S, Sutikna T, Due RA, Morwood M. 2009 The foot of *Homo floresiensis*. *Nature* **459**, 81–84. (doi:10.1038/nature07989)
106. de Heinzelin J, Clark JD, White T, Hart WS, Renne P, WoldeGabriel G, Beyene Y, Vrba E. 1999 Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* **284**, 625–629. (doi:10.1126/science.284.5414.625)
107. Shultz S, Opie C, Atkinson Q. 2011 Stepwise evolution of stable sociality in primates. *Nature* **479**, 219–222. (doi:10.1038/nature10601)
108. Sanz C, Call J, Morgan D. 2009 Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* **5**, 293–296. (doi:10.1098/rsbl.2008.0786)
109. Mellars P, French J. 2011 Tenfold population increase in Western Europe at the Neandertal-to-modern human transition. *Science* **333**, 623–627. (doi:10.1126/science.1206930)
110. Smaers JB, Soligo C. 2013 Brain reorganization, not relative brain size, primarily characterizes anthropoid brain evolution. *Proc. R. Soc. B* **280**, 20130269. (doi:10.1098/rspb.2013.0269)
111. Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin C, Wrangham R, Boesch C. 2001 Charting cultural variation in chimpanzees. *Behaviour* **138**, 1481–1516. (doi:10.1163/156853901317367717)
112. Ottoni E, Izar P. 2008 Capuchin monkey tool use: overview and implications. *Evol. Anthropol.* **17**, 171–178. (doi:10.1002/evan.20185)