

A complex adaptive system may be essential for cumulative modifications in tool design

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Abstract The cumulative modification of tool designs over time is a crucial development for technological evolution. Cognitive-related prerequisites for this technological capability are innovative behaviour and the faithful inter-generational transmission and maintenance of tool designs by accurate social learning processes. Here, we investigated the hypothesis that a complex of morphological and behavioural adaptations specifically for tool skills is also required. In a novel analysis we compared the tool-associated adaptive patterns in *Homo erectus* and the New Caledonian crow. Both species provide the most convincing early *Homo* and nonhuman evidence, respectively, for the making of cumulatively modified tools. We identified probable shared traits in *H. erectus* and the New Caledonian crow that include morphological adaptations specifically for enhanced tool manipulation and a significant component of daily diet from hunting and/or processing animal food with tools. We propose that a tool-using lifestyle based on animal food that confers a reproductive advantage and evolves enhanced tool manipulation skills, together with appropriate innovative ability and social learning processes, may be essential for cumulative modification of tool designs.

Key words : adaptations, cumulative cultural evolution, *Homo erectus*, New Caledonian crow, tool manufacture

Introduction

A crucial feature in the evolution of human technology was the emergence of the ability to modify tool designs in a cumulative process over time (d'Errico & Stringer, 2011). Many animal species are known to use tools (Shumaker et al., 2011), but their modification of tools in a process of 'cumulative technological evolution' is extremely rare. One definition of cumulative technology is the production of tools that no individual could

invent in its life time (Tomasello et al., 1993; Dean et al., 2014), but this may not detect early, rudimentary cumulative modifications. Pradhan et al. (2012) used a wider definition of cumulative technology that is more focused on the increasing complexity of tool-related behavioural actions rather than of the tools themselves (e.g. using one tool to make another tool). Hunt and Gray (2003) and Hunt (2014) emphasized that an improved tool design that mostly incorporates the manufacture process of the original, simpler design may have been repeatedly invented by individuals rather than socially transmitted. Therefore, in this paper we define a cumulatively modified tool as an innovative design built on previous technical knowledge that requires a distinctly novel manufacture process and is faithfully transferred and maintained between generations until new design modifications are made. A crucial

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criterion in this definition is the little or no recapitulation of the manufacture process used to produce earlier, simpler versions of the new design.

The earliest stone-tool industry in humans is now known from 3.3 million years ago (Mya) (Harmand et al., 2015), called the Lomekwian. These tools were large flakes made by breaking rocks on a stone anvil using mostly bipolar and passive hammer techniques (Harmand et al., 2015). Oldowan tools appeared at about 2.5 Mya (Hovers, 2012; Semaw et al., 1997; Roche et al., 1999), where flake tools were produced by freehand direct percussion in a relatively simple process of knapping on a stone core. Acheulean technology, associated with *Homo erectus* (*sensu lato*), first appeared around 1.8 Mya (Lepre et al., 2011; Beyene et al., 2013) and is considered to be another key transition in cognitive evolution (Mahaney, 2015), with design form imposed on tools for the first time and elaborate production sequences (Gowlett, 2006, 2015). Although important characteristics of *H. erectus* may have been more similar to *H. habilis* than previously thought (Antón & Snodgrass, 2012), there is no doubt that they employed much more complex knapping to produce shaped tools than did earlier hominins. The Acheulean also shows marked refinement in knapping methods over time, with distinctly standardised cores first appearing around 1.2 Mya (Beyene et al., 2013). The pace of technological change in the Acheulean associated with *H. erectus* was not the rapid cumulative change produced by anatomically modern humans (Tomasello et al., 1993). Nevertheless, slowly evolving cumulative technology was probably present (Pradhan et al., 2012). For example, the elegantly shaped bifaces in the late Acheulean were probably achieved using the improved method of platform preparation to remove large, thin flakes from the faces of the biface without altering its breadth (Gowlett, 2006; Stout et al., 2014).

New Caledonian crows (*Corvus moneduloides*; NC crows hereafter) make the most complicated tools among nonhuman animals

(Hunt, 1996). For example, they are the only species besides humans to incorporate hook technology into their tool designs (Hunt, 1996; Shumaker et al., 2011). We next summarize the evidence for their cumulative evolution of not one, but two types of tool design: one made from the barbed edges of *Pandanus* species leaves (example of a tree in Figure 1a) and one from twigs (Hunt, 1996; Hunt & Gray, 2003, 2004a, 2004b). Both types of tool are made throughout the mainland (Grande Terre) and have simple and complicated design versions, thus providing the potential for cumulative modifications to have been made. The most complicated stick tool, a hooked-twig tool, is made from fresh twigs (Hunt, 1996; Hunt & Gray, 2004a; Klump et al., 2015). The manufacture process usually involves choosing a forked twig, snapping off and discarding one side of the fork leaving a stump, snapping off the remaining side of the fork with the stump at one end and removing any side extensions and leaves from it, then finally refining the stump into a pointed hook with the bill. Importantly, the manufacture process is distinctly different from that used to make non-hooked stick tools. The presence of non-hooked and hooked tools, the lack of recapitulation in the more complicated process to make hooked-twig tools and the 3D crafting of a functional hook suggest that hooked-twig tools have evolved from cumulative modifications to the manufacture of non-hooked-stick tools (Hunt, 2015). Hunt and Gray (2004a) documented a parent and its dependent juvenile making hooked-twig tools. However, there are little artefactual and behavioural data available to suggest that young crows learn the manufacture technique from experienced birds.

The evidence for cumulative evolution of pandanus tools is much stronger because of the unique artefactual record associated with the making of these tools (Hunt & Gray, 2003). NC crows make pandanus tools by removing strips of barbed leaf edge from *Pandanus* spp. trees (Hunt, 1996). The manufacture of a pandanus tool leaves a counter-

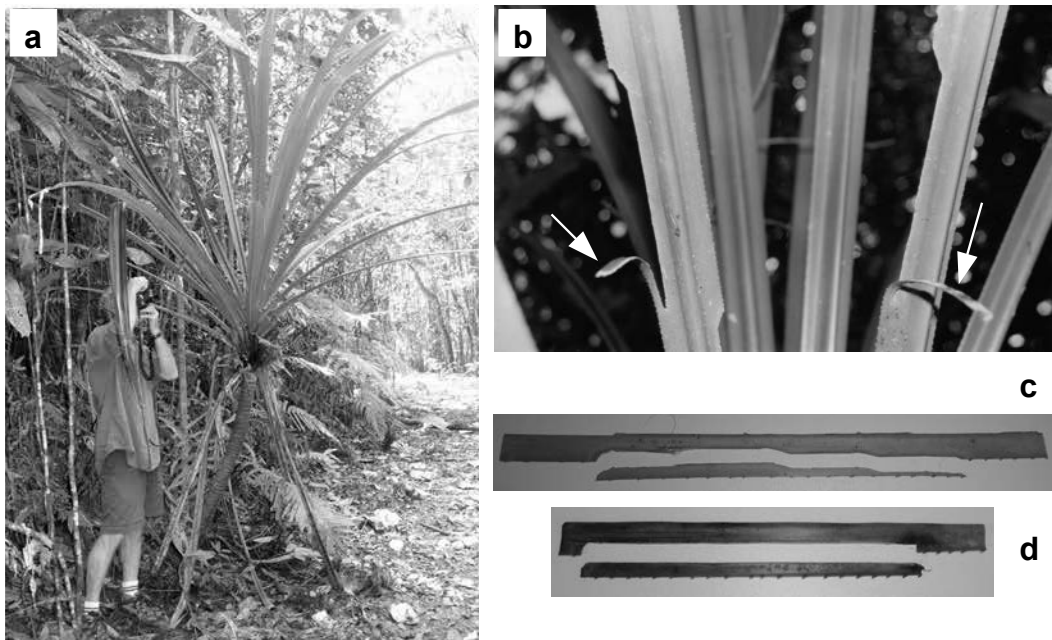


Figure 1. Images showing a young *Pandanus* sp. tree with its long, narrow leaves (a) and examples of artefacts mentioned in the text when inferring that the stepped tool design is a cumulatively modified design. (b) Two examples of leaf ripping edge (white arrows) carried out by NC crows to better access prey when the ripped sections of the leaves were located in the base of the leaf crown. The leaves have subsequently grown, moving the ripped sections away from the base of the leaf crown. (c, d) A stepped tool (c) and a wide tool (d). The tools were by made by NC crows and are next to their respective 'counterparts' that GRH removed from the leaves. Note that the wide tool is a simpler design than the stepped tool and made using a less complicated method. Also note that the method to make the more complicated stepped tool does not recapitulate the method to make the simpler wide tool. The stepped tool is 18.4 cm long and the wide tool is 18.1 cm long.

part, or section of missing leaf edge, that exactly matches the finished shape of the tool (Figure 1c,d). This is because pandanus tools are rarely, if at all, retouched after their initial manufacture (Hunt, 2000a). Thus counterparts on leaves provide a complete artefactual record of the shapes of pandanus tools made over the previous four years or so until the leaves decay (Hunt, 2000a). This record enables inferences to be made about the manufacture, origin and transmission of pandanus tool designs.

From the artefactual record we know that NC crows manufacture three distinct pandanus tool designs: wide, narrow and stepped designs (Hunt & Gray, 2003), although a possible new design was recently described (Hunt, 2014). The process to make the untapered wide and narrow tools is much

simpler than that to make the complicated tapered stepped tools as it only involves removing uniformly wide sections of leaf edge (Figure 1d). On the other hand, the manufacture of a stepped tool requires repeat sequences of cuts and rips, each sequence carried out further in from the leaf edge (Hunt, 1996; Hunt & Gray, 2003, 2004b; Figure 1c). The crows hold the wide ends of stepped tools in their bills, enabling the tapered shape to provide an apparently efficient stiff but pointed hooking implement. Each of the three distinct pandanus tool designs is an arbitrary shape unconstrained by characteristics of the raw material. As with hooked-twig tools, the manufacture of the more complicated stepped tools does not recapitulate the making of the simpler pandanus tool designs (this is clearly apparent by comparing

Figures 1c & 1d).

Artefactual and behavioural data suggest that stepped tools evolved from simpler wide-like tools. As well as making pandanus tools, NC crows rip strips of leaf edge in the centre of the leaf crown to facilitate access to prey cached there (Hunt & Gray, 2003; Figure 1b). These short sections of ripped leaf edge are often seen hanging from the leaves of *Pandanus* spp. trees and are not associated with tool making. This ripping behaviour is suggested to have been the precursor to wide-tool making as the ripped strips are most like the shapes of wide tools (Figure 1b & 1d). The data also provide a functional explanation for the innovation of the more complicated stepped-tool design (Hunt 2014). The simpler wide tools are made in only a few locations (in the south of Grande Terre and the island of Maré; Hunt & Gray, 2003) and appear to be used only for probing in *Pandanus* trees. In contrast, stepped tools are made at most sites and used in trees generally. This difference in the use of wide and stepped tools is consistent with the former, simpler design being invented initially from the ripping behaviour and subsequently modified to provide a more efficient, Swiss-army-knife-like, multi-purpose design. Furthermore, the artefactual data show that at many sites on Grande Terre only stepped tools are manufactured, and to very standardised shapes (Hunt, 1996, 2000a; Hunt & Gray, 2003). This indicates that NC crows in these areas, including juveniles, do not begin making simpler designs before making the stepped tool design. Therefore, the stepped-tool design is almost certainly transmitted and faithfully maintained across generations rather than individually invented. The transmission process involves individual and social learning (see Social learning section below).

Conclusive proof that NC crows have evolved rudimentary cumulative technology would require hard evidence that the stepped-tool design was originally invented by a NC crow(s) with experience of simpler pandanus tool designs (Dean et al., 2014;

Lewis & Laland, 2012; Hunt, 2014). Nevertheless, parsimony would suggest that a naïve crow would initially invent a relatively simple tool design that closely resembled the wide-tool-like strips that NC crows rip to access prey cached in the bases of *Pandanus* leaves, not a stepped design. Shumaker et al. (2011) also implied that the co-existence of the simpler pandanus tool designs with the more complicated stepped-tool design was evidence against cumulative modification. However, it is obvious from human technology that different ecological function is only one way that both old and modified designs can be maintained in a species' tool kit. The artefactual and behavioural data presented here are consistent with NC crows having cumulatively modified their pandanus tool technology.

It has been proposed that a suite of behavioural, cognitive and morphological adaptations for enhanced tool skills are necessary prerequisites for increased sophistication of tool designs (Hunt, 2015, Matsui et al., 2016; Visalberghi et al., in press). We tested this hypothesis within a comparative framework by examining the tool-related adaptive patterns of *H. erectus* and the NC crow. This allowed us to compare *H. erectus* with an extant species whose most complicated tool designs have a high probability of being cumulatively modified ones. We focused on behavioural and morphological adaptations considered important in early human evolution (Kaplan et al., 2000; Richerson et al., 1996) because of the difficulty in determining cognitive abilities in early humans (Whitley, 2001; Uomini, 2008, 2014; Rogers et al., 2016). Furthermore, simulation models suggest that the initial stages of cumulative technology might not require increased cognitive capabilities (Pradhan et al., 2012). Using this comparative framework we examine seven traits that may be important for enabling cumulative modification of tool designs: brain size, diet, length of juvenile dependence, genetic disposition specifically for tool use, dedicated tool manipulation morphology, tool-related forag-

ing, and social learning of tool skills.

The tool-related adaptive pattern of *H. erectus* and the NC crow

Brain size

Relative brain size rather than absolute brain size may be a more reliable predictor of cognitive performance across taxa (Kabadayi et al., 2016; Jelbert et al., 2016). The relative brain size of *H. erectus* may have been moderately larger than the relative brain size of *H. habilis*, but it was considerably smaller than the relative brain size of later *Homo* species (Falk, 2014; Holloway et al., 2009; Roth & Dicke, 2005). Amongst birds, the NC crow has a large brain for its body size (Cnotka et al., 2008). Cnotka et al. (2008) reported that the NC crow's brain was relatively larger than the brain of the carrion crow (*C. corone*), but questions have been raised about the statistical methods that were used (Medina, 2013). More recent data show that the NC crow's brain size (mean of 7.56 g for 5 birds averaging 277 g bodyweight; Cnotka et al., 2008) is comparable to that of the considerably larger rook (*C. frugilegus*) introduced into New Zealand (mean of 7.60 g for 5 birds averaging 456 g bodyweight; GRH unpublished data). This comparison suggests that the NC crow has a brain relatively larger than at least one other *Corvus* species. Further data are needed to establish if the NC crow's brain size is exceptionally large for *Corvus* species generally.

Diet

Brain size in early hominins was constrained by the amount of feeding required on a diet of raw food (Fonseca-Azevedo & Herculano-Houzel, 2012). *H. erectus* with ca. 60 billion neurons would have needed to spend nearly 9 hrs per day feeding, which was probably impossible on a chimpanzee-like diet of mostly collected food. *H. erectus* had a richer diet than previous hominins, with softer foods (Sayers & Lovejoy, 2014). Cranio-dental characteristics (e.g. teeth size and jaw anatomy) indicate that *H. erectus* was more specialised for shearing and slicing food

rather than crushing food, whereas the opposite is the case in earlier hominins and extant nonhuman apes (Ungar et al., 2006; Organ et al., 2011). Dental microwear patterns show that *H. erectus* had a broad-based diet containing both hard (e.g. nuts) and tough (e.g. meat) foods (Ungar et al., 2006; Ungar & Sponheimer, 2011). Furthermore, the cranio-dental changes in *H. erectus* also suggest that the richer diet was possible because of more processed food and a growing dependence on the use of technology (tools) (Ungar et al., 2006; Organ et al., 2011). Most diets of modern hunter-gatherer societies appear to consist of 65% plant foods, which yields an estimate of 35% meat in pre-agricultural hominins (Walker et al., 2002; Luca et al., 2010). However, some authors propose that the diet of *H. erectus* contained less meat than the diet of modern humans living in similar habitats, and that *H. erectus* was characterised by great diet flexibility according to habitat differences (Sayers & Lovejoy, 2014).

Like other *Corvus* species, NC crows are opportunistic omnivores and eat a wide range of both plant and animal food (Hannecart & Letocart, 1980; Dutson, 2011; dos Anjos et al., 2009). They eat berries and fruit when in season, as well as the succulent parts of flowers of plants such as *Freyinetia* vines (GRH personal observation). Their main animal prey are invertebrates (e.g. insect larva and adults, snails, slugs), with food such as carrion, lizards and the contents of birds' nests making smaller contributions to their diet. NC crows forage for prey by gleaning from tree surfaces and the ground or occasionally catching flying insects. They also search in vegetation and dead wood for small cached prey, with and without tools. NC crows use tools year round for hunting live prey cached in vegetation (Hunt et al., 2013), which consist of mostly invertebrates. In areas with introduced candlenut trees (*Aleurites moluccana*) they exploit the year-round rich supply of wood-boring larvae in dead wood from these trees using stick tools (Hunt, 2000b; Bluff et al., 2010). Only several

larvae are sufficient for a NC crow's daily energy needs, making a substantial amount of potential food available to competent tool users (Rutz et al., 2010). Candlenut trees are restricted to lower altitudes on sedimentary soils, and grow on only a small percentage of the NC crow's range (Hunt, 2000b). There are no quantitative data on the NC crow's diet outside candlenut tree habitat, but the prey hunted is likely to be more diverse and generally smaller. As appears to be the case with *H. erectus*, there may be an association in NC crows between a large brain providing increased technical intelligence and the use of tools to obtain a significant amount of rich food.

Length of juvenile dependence

Species can evolve to exploit complex foraging niches through extended periods of juvenile provisioning or slower development (Schuppli et al., 2016). The juvenile period in *H. erectus* may have been about 15 years (Bogin, 1999; Antón, 2003), which is more similar in length to that in modern humans (around 17 years) than to the juvenile periods in other primates (Bogin, 1999; Barrickman et al., 2008). Thus *H. erectus* juveniles had more time to learn such skills as complicated foraging techniques before foraging independently, compared to earlier hominins and nonhuman apes.

NC crow parents continue regular feeding of their juveniles for a much longer period than other *Corvus* species for which data are available (Hunt et al., 2012). NC crows on the island of Maré regularly fed their juveniles for up to 10 months, whereas more open country *Corvus* species usually feed juveniles for up to only 3 months. However, there are little or no quantitative data on the length of parental feeding in tropical forest crows other than for the NC crow (dos Anjos et al., 2009; Hunt et al., 2012). Long periods of parental feeding in birds are usually associated with the need for juveniles to learn complicated foraging skills (Ashmole & Tovar, 1968; Burger, 1980). Continued feeding by NC crow parents means that juveniles

stay on their natal range for an extended period of time where they have the opportunity to acquire and perfect complicated tool-related foraging skills.

Genetic disposition specifically for tool use

Van Schaik et al. (1999) argue that species must first be physically capable of tool use before there can be an effect of social and cognitive factors that favor the invention and social transmission of tool-assisted foraging. Van Schaik (2016) suggests that primates are unique in having no developmental canalisation for tool use. This means that tool use begins as a cultural adaptation in all species, and over time, other taxa like NC crows evolved an innate ability to use particular tools (van Schaik, 2016). Present-day innateness would thus diagnose an extended history of tool use in a species, along with specific morphology. In order for selection to act on morphology, there must be variation in a population such that some individuals have more effective anatomical features, giving them a reproductive advantage. However, this can only occur if all individuals in the population use tools.

Little is known about genetic dispositions specifically for tool use in either *H. erectus* or extant humans because nearly all humans are raised in a cultural environment that is rich with tools. Modern human infants begin to use tools from 8 months old, following a developmental trajectory involving sensorimotor manipulation and sequential planning (Rat-Fischer et al., 2012). After 24 months, demonstration by an adult plays a major role in the child's tool use acquisition (Fagard et al., 2016). This would suggest that social learning is an essential factor in human tool use, regardless of whether any innate predisposition exists.

NC crows have a strong genetic disposition to develop basic tool skills as naïve juveniles raised in captivity developed these skills from inherited tool-oriented behaviours without social contact (Hunt et al., 2007a; Kenward et al., 2005, 2006). This disposition, though, does not exclude learning and

innovation in the development and transmission of their tool behaviour (Hunt & Gray, 2007; Hunt et al., 2007b). Indeed, technological improvement in tool design is likely to be underpinned by adaptations supporting both fixed phenotypes and flexible mechanisms (Meulman et al., 2012). Their innovative foraging techniques in the wild (e.g. Hunt et al., 2002, 2007b; Hunt, 2014) and impressive problem solving ability under experimental conditions (e.g. Taylor et al., 2010, 2012) demonstrate that they can develop innovative foraging solutions, despite having a genetic disposition specifically for basic tool use.

Dedicated tool manipulation morphology

Human anatomy reflects an evolved physical capability for tool use. *H. erectus* had a modern-human-like skeleton and was a fully bipedal hominin, thus having hands free for manipulation. The hands and shoulders of *H. erectus* had anatomical features that were adapted for enhanced tool manipulation. The hand morphology of modern humans was mostly in place in pre-*Homo* species and even *Australopithecus africanus* had much more robust hands compared to the hands of chimpanzees (*Pan troglodytes*) (Kivell et al., 2011; Marzke, 2013; Skinner et al., 2015). For example, the pattern of trabecular bone in the metacarpals of modern humans was present in early hominins, indicating the use a strong precision grip (Skinner et al., 2015). The thumb in particular became more robust and enlarged and was likely an adaptation for a strong precision grip associated with tool use rather than tool making; stone-tool use places greater loading on the thumb than stone-tool making (Williams et al., 2012). Thus hand morphology in early hominins is consistent with the presence of flake production over 3 Mya.

The third metacarpal styloid process in modern humans is an adaptation for an enhanced power grip when making and using tools (Ward et al., 2014). This feature is not in the hands of *H. habilis* or earlier hominins and nonhuman apes, but was recently found in a *H. erectus* hand from 1.42 Mya (Ward et

al., 2014). Furthermore, the ability for high speed throwing in humans was based on a long sequence of morphological changes. The final changes (e.g. fully lateral glenoid position) that enhanced the storage and release of elastic energy in the shoulder to enable high-speed throwing appeared in *H. erectus* 2 Mya (Roach et al., 2013). Ballistic throwing would have provided *H. erectus* with enhanced hunting ability and possibly knapping efficiency. Importantly, the morphology for enhanced knapping and throwing was in place before the increased standardisation and refinement in Acheulean technology around 1.2 Mya (Marzke, 2013).

Its remarkably straight bill distinguishes the NC crow from other *Corvus* species, and is suggested to provide efficient visually-directed use of tools (Troscianko et al., 2012). However, it was unclear if this bill feature evolved before or after the species began using tools (Troscianko et al., 2012; Rutz & St Clair, 2012). A recent study found that the NC crow's bill has a combination of interrelated shape and structural features unique within *Corvus*, and possibly birds generally (Matsui et al., 2016). The upper mandible is relatively deep and short with a straight cutting edge, and the lower mandible is strengthened and upturned towards the tip. These novel features provide the NC crow with a precision grip to firmly hold a tool with a relatively small section of cutting edge. In this way, the tool tip can be placed in the best possible position for its visually-guided manipulation, close to the intersection of the mid-frontal and mid-sagittal planes of the bill. Thus it is highly likely that the NC crow's bill has been adapted for tool manipulation to at least some degree (Matsui et al., 2016). Similarly to early humans, selection for enhanced visually-directed manipulation and a strong precision grip when using simple tools to extract prey was probably the driving force for the NC crow's complex bill trait, which then enabled the fine manipulation required for their subsequent manufacture and use of more complicated tool designs (Matsui et al., 2016).

NC crows also have the widest binocular field of view known in birds, which was suggested to facilitate efficient tool manipulation when searching for prey (Troscianko et al., 2012). Martinho et al. (2014) subsequently reported that the wide binocular field enhanced monocular viewing of the tool tip when probing in holes. The wide binocular field allows, for example, the right eye to view the tool tip when it is positioned across the mid-sagittal line on the opposite side of the head. Nevertheless, it remains unclear if the NC crow's extreme binocular field of view evolved for enhanced tool manipulation (Rutz & St Clair, 2012).

Tool-related foraging

Tool use in foraging can either be used for capturing live prey (hunting), extracting encased plant food (e.g. nut kernel) or processing tough plant (e.g. tubers) and animal (e.g. butchering carcasses) food. Richerson et al. (1996) stated that "The basic adaptation that differentiates modern humans from other primates is co-operative food foraging using cultural adaptations (technology)". *H. erectus* was the first hominin to intensify this basic lifestyle pattern (Ungar et al., 2006).

Hunting in modern hunter-gatherers is skill-intensive and cognitively demanding, and based on long-term juvenile dependence that enables the learning of complicated foraging skills (Kaplan et al., 2009). Given their simpler technology and relatively smaller brain, one might expect that tool-assisted hunting was even more challenging for *H. erectus*. Little is known about perishable tools in the Acheulean, except that woodworking traces occur on some African bifaces dating between 1.7 and 1.4 Mya (Dominguez-Rodrigo et al., 2001). However, *H. erectus* used stone tools extensively for butchering carcasses such as elephant with Acheulean bifaces (Solodenko et al., 2015). The high concentrations of tools and tool-associated bone damage after 1.9 Mya suggest that the species depended on technology for processing animal food (Ungar et al., 2006), as well

as for extracting and/or processing plant food. Although the precise proportion of *H. erectus*'s diet that came from tool-assisted hunting is unknown, their heavy reliance on hunted meat is further corroborated by the archaeological evidence that hominins began to control fire during the Acheulean (Gowlett, 2016).

NC crows in treed habitat usually have a tool-using lifestyle which probably provides an essential part of their daily diet. As discussed in the Diet section, in woodland candlenut areas NC crows can potentially obtain a substantial part of their daily diet by using tools to extract large wood-boring grubs. In forest habitat where there are no candlenut trees, the contribution to daily diet from tool use is poorly known. That NC crows in many of these areas are observed carrying tools year-round (GRH personal observation) suggests that they may get a significant amount of food with tools. Experienced NC crows are not known to use tools to obtain difficult-to-access plant food. Thus most, if not all, of the food that NC crows obtain with tools is from hunting live animal prey.

Social learning of tool skills

H. erectus parents probably actively taught their juveniles given that they most likely lived in social groups and engaged in co-operative breeding (Burkart et al., 2009; Pradhan et al., 2012; van Schaik, 2016). The patterns of variation and similarity, along with the slow rate of cultural evolution, seen in the Acheulean technology are compatible with two modes of transmission: vertical and many-to-one (Lycett & Gowlett, 2008). Further evidence for the existence of customary active teaching in stone tool-making by *H. erectus* comes from experiments on stone-knapping skill transmission. Morgan et al. (2015) found that active teaching by gestural communication enhanced learners' ability to produce Oldowan stone flakes compared to passive imitation and emulation. Furthermore, verbal instruction gave an even greater advantage. These results support the view

that the transmission of *H. erectus*'s stone tool-making required active teaching (Uomini, 2009; Steele & Uomini, 2009; Sinclair & Uomini, 2012; Morgan et al., 2015).

NC crows mostly live and forage in small family units consisting of parents and first-year juveniles (Holzhaider et al., 2011). This family-based social system facilitates vertical transmission of foraging skills and minimizes the opportunity for horizontal transmission. On the island of Maré, parents provided considerable social scaffolding to juveniles that enable them to acquire local tool knowledge by both individual and social learning (Holzhaider et al., 2010, 2011). Mated pairs were extremely tolerant of their offspring's close proximity and the first tools that juveniles used were those of their parents or older siblings. In fact, tool artefacts may considerably assist young NC crows to acquire tool skills in the same way that is proposed for nonhuman primates (Fragaszy et al., 2013). The long period of parental feeding also gave juveniles time to learn complicated foraging skills. The high degree of relatedness within local populations suggests limited long range dispersal of birds (Abdelkrim et al., 2012; Rutz et al., 2012), which is consistent with a high degree of local standardization in the arbitrary pandanus tool designs (Hunt & Gray, 2003). The reduced opportunity for horizontal transmission in NC crows, combined with a genetic disposition specifically for basic tool use and limited dispersal, would facilitate the standardization of tool skills and increase the potential for cumulatively modified tool designs (Sterelny, 2006).

How NC crows learn to faithfully transmit pandanus tool designs remains a crucial unanswered question. Hand-raised naïve birds only randomly ripped the *Pandanus* sp. leaves that they were given and did not make any of the three known pandanus tool designs seen in the wild (Kenwood et al., 2005, 2006). Although the parents of these juveniles may not have had experience with *Pandanus* trees before their capture, it supports that idea that the knowledge to

make specific pandanus tool designs requires social input (Hunt & Gray, 2003). However, experiments with captive NC crows found that birds had poor social cognition (Jelbert et al., 2015) and solved a novel foraging problem by stimulus enhancement rather than emulation or copying (Logan et al., 2015). These experiments, though, did not involve tool making and were carried out with mature birds, not juveniles in their early months post-fledging when they are most likely to be developmentally receptive to observe and acquire their parents' foraging skills. Holzhaider et al. (2011) speculated that juveniles might faithfully acquire pandanus tool designs by 'template matching'. That is, learning or inferring the precise actions required to manufacture tools to a particular shape after only viewing the shapes of missing leaf edge resulting from tool manufacture. Inferring the required actions would seem to be beyond NC crows' cognitive ability. One might expect considerable variation in the shapes of finished tools produced by juveniles that not only learnt to match the shapes of tools to tool templates, but at the same time had to invent the cutting and ripping process used to manufacture the tools. However, the observed local standardization in pandanus tool designs is not consistent with this prediction (Hunt & Gray, 2003). Moreover, the exclusive use of template matching is extremely unlikely because juveniles would regularly observe pandanus tool making in their first months when they should be highly sensitive to observing and learning parental foraging skills.

Discussion

Our objective in this paper was using a comparative framework to learn what traits may be required for cumulatively modified tool designs to evolve. We argued in the Introduction that rudimentary cumulative modifications, using our definition, have most likely been incorporated into the tool designs of both *H. erectus* and the NC crow. Conclusive evidence for this technological

ability would be direct documentation that the inventors of the two species' respective sophisticated designs were not naïve to earlier, simpler versions but had had previous experience with them (Dean et al., 2014). This direct evidence cannot be known from the archaeological record. However, it seems valid to assume that early human innovators were not naïve based on the considerable archaeological record of stone tools. We also think the case for cumulatively modified tool designs made by the NC crow is strong even though it is based on a short, contemporary artefactual record. Thus our following discussion is based on the presence of rudimentary cumulative modifications in the tool designs of *H. erectus* and the NC crow, as defined earlier.

The tool-related adaptive pattern of *H. erectus* appears to be surprisingly similar to that of the NC crow (Table 1). Traits that seem to be shared by the two species are

(i) genetic disposition specifically for basic tool skills, (ii) high proportion of animal food in the diet, (iii) significant amount of animal food obtained with the aid of tools, and (iv) dedicated morphology for enhanced tool manipulation. Thus the crucial factor underlying their analogously-evolved, tool-related adaptive patterns is strong selection for tool use. A genetic disposition specifically for tool use in a species indicates that strong selective pressure has occurred for tool-using behaviours. Once the cognitive prerequisites are in place, morphological adaptations can evolve, further enhancing the species' success with tool use. As Taylor (2010) argues, the hominin lineages are characterised by 'artificial selection'. This means that tool use became an unavoidable aspect of daily life, when at some point, hominins were no longer able to survive *without* tool use. The morphological adaptations in *H. erectus* for enhanced tool manipulation and processing softer, richer

Table 1. Summary of tool-related characteristics for *H. erectus* and the New Caledonian crow.

	<i>H. erectus</i>	New Caledonian crow
Cumulatively modified tool design	Probable.	Probable. The strongest case for this technological feature in nonhumans.
Brain size	Modest relative increase over the brain size of <i>H. habilis</i> .	Appears to be relatively larger than the brain of at least 1 other <i>Corvus</i> species.
Diet	Versatile and richer than that of previous hominins. Large proportion of animal food in diet.	Little data on diet composition, but probably consists of a large proportion of animal food.
Length of juvenile dependence	Intermediate between <i>H. habilis</i> and <i>H. sapiens</i> .	Much longer than known care provided by other <i>Corvus</i> species.
Genetic disposition specifically for tool use	Probably present.	Present for basic tool use.
Dedicated morphology for enhanced tool manipulation	Yes. Present before increased sophistication of Acheulean tool designs.	Highly likely.
Contribution of tool-assisted foraging to diet	Probably provided a significant proportion of diet. Tools used for hunting and processing animal and plant food.	Likely to provide a large proportion of diet in many forest populations. Tools used for hunting.
Social learning in the transmission of tool designs	Vertical and horizontal social learning probably important.	Vertical social learning more important than horizontal learning.
Dependence on technology	Technology crucial for long-term survival as individuals should be less fit without tool use (e.g. because of less robust craniodental morphology).	Technology may be crucial for long-term survival of individuals in forest habitat as they may be less fit without tools (e.g. because of short bills).

food (i.e. less robust jaw and teeth anatomy) indicate that technology was probably crucial for their long-term survival (Ungar et al., 2006; Organ et al., 2011). The use of fire to cook meat resulted in our modern gut which no longer supports a diet of raw meat. Their intensified co-operative foraging and hunting lifestyle dependent on tool technology distinguish *H. erectus* from earlier hominins such as *H. habilis*. NC crows also depend on tools to a large extent, but humans have taken this dependence to an extreme because our anatomy has degenerated to become highly inefficient without the aid of tools (Taylor, 2010).

New data now allow us to hypothesise that early tool use by NC crows provided a selective advantage over those birds that did not use tools. That is, individuals that did not use tools were on average less fit for foraging in New Caledonia's primary forest. The NC crow's bill, for example, has been adapted for extended reach not because of a longer bill but because it is a short, stout bill capable of a strong precision grip to use a tool effectively (Matsui et al., 2016). Thus NC crows foraging without tools should be at a disadvantage for capturing available prey that must be often out of reach in tree holes.

The brief examination of common chimpanzees' tool use that follows provides some support for our finding that a selective advantage for tool use may be crucial for cumulatively modified tool designs to evolve. First, chimpanzees have the most diverse and flexible tool behaviour in the wild among extant nonhumans (McGrew, 2013). Paradoxically, their tools are also relatively simple with only limited modifications to basic tool designs (Shumaker et al., 2011; McGrew, 2013). Furthermore, chimpanzee tools do not show shape standardisation across geographic ranges, as seen in the Acheulean archaeological record (Gowlett, 2015) or in the pandanus tools made by NC crows (Hunt & Gray, 2003). Second, even under a wider definition of cumulatively modified tool designs than we use in this

paper only a few chimpanzee populations show any sign of possibly manufacturing such designs (Pradhan et al., 2012 and references therein). We emphasise that we are only focusing on tool design, as opposed to the development of more complicated tool behaviour over time without cumulatively modified tools such as using tool sets to achieve a goal. Two of the most promising examples of cumulatively modified tools come from chimpanzees that either form a 'brush' on one end of a stick tool for more efficient extraction of termites (Sanz et al., 2009) or a point to make a stick spear to capture small vertebrates in tree holes (Pruetz & Bertolani, 2007). These modifications are made at the end of an existing manufacture process. That is, an individual makes a tool using a past manufacture technique (i.e. recapitulation), then uses a novel modification to improve the tool (e.g. forming a brush or point on the end of a stick). In contrast to the lack of recapitulation in NC crows' stepped tool manufacture, this makes it difficult to rule out modifications to existing tool designs from individual learning. As far as we know, there are currently no data showing that the modified brush and spear tool designs are transmitted socially, a crucial criterion for cumulative technology. Moreover, the brush and spear tools only seem to be made by a limited number of individuals in each population, which is more consistent with individual learning.

Last, there is currently no evidence that chimpanzees have a genetic basis specifically for tool use (Biro et al., 2013; Visalberghi et al., in press). In fact, some chimpanzee populations have never been seen to use stick tools (Whiten et al., 1999; Reynolds, 2005). That captive chimpanzees performed better in the trap-tube problem when using their hands than when using stick tools also suggests a lack of an avian-like inherited disposition for tool use (Seed et al., 2009). The contextually diverse tool use in chimpanzees is consistent with the recent finding that "...object play in younger immatures, especially males, mainly concerns preparation

for adulthood in terms of practicing general motor skills.” (Koops et al., 2015). That is, chimpanzees seem to have an inherited disposition more to do with the generalized use of objects rather than specifically for tool use. The strong cultural clustering of tool behaviours between different chimpanzee groups also indicates that their tool traditions are socially learned (Whiten et al., 1999). Furthermore, there is no evidence that chimpanzees have dedicated morphology for enhanced tool manipulation (Biro et al., 2013). It has been suggested that the more robust metacarpals in some chimpanzees from Cameroun might reflect both their increased knuckle-walking and nut-cracking behaviour (Lazenby et al., 2011). However, the authors state that the greater robustness would reflect the functional loading during ontogenetic development, therefore it cannot be an adaptive trait for tool use.

The lack of evidence of a genetic underpinning and adaptive morphology specifically for tool use suggest that chimpanzees’ foraging-associated technology has little effect on individual fitness. This is consistent with the hypothesis that chimpanzees’ tool designs are relatively simple because their technology is maintained by learning processes without an underlying genetic basis specifically for tool use (Hunt et al., 2013; Visalberghi et al., in press). In other words, until tool use confers an important reproductive advantage for individual chimpanzees their tool designs will remain relatively simple.

Large brain size and associated increased intelligence in humans, and life history characteristics such as extended juvenile dependence, may have co-evolved in response to a richer diet of difficult-to-acquire food (e.g. requiring tool use) (Kaplan et al., 2000). Our comparative findings indicate that NC crows provide an extant, nonhuman model with which to investigate this hypothesis. NC crows have relatively large brains for an avian species and provide an exceptionally long period of parental care to their juveniles. They also use tools exclusively, or

almost exclusively, for hunting live prey, and this foraging technique that is practised year-round probably provides a large component of their diet in forest habitat. Thus a large proportion of the animal food in the diet of both *H. erectus* and the NC crow seems to be associated with tool-assisted foraging. In contrast, the chimpanzee diet generally consists of mainly fruit (McGrew et al., 1988; Potts et al., 2011), with a significant proportion of other plant foods (e.g. leaves, nuts, pith, shoots, tubers, wood), a few vertebrates such as colobus monkeys or bush babies, invertebrates such as ants or termites, and honey (McGrew, 2014; Lambert, 2015). Therefore, chimpanzees generally have a diet of mostly plant food collected without tools (ca. 95%), a small percentage (ca. 2%) consisting of meat and insects, and around 3% encased food (Kaplan et al., 2009). The complex tool designs made by *H. erectus* and the NC crow that are associated with a hunting way of life suggest a novel hypothesis: that a tool-assisted hunting and/or animal processing lifestyle is an important prerequisite for enabling the cumulative modification of tools.

Why might such a lifestyle increase the need for more complicated tools compared to using tools to acquire non-animal food? First, animals need to be captured before they can be killed and eaten. They have a brain that provides them with species- and situation-specific defence mechanisms, and they generally move to escape and/or cache themselves, which can make capturing them difficult. The use of hooked tools by NC crows, for example, may provide more efficient tools to deal with prey defences and thus increase prey capture rates compared to capture rates using non-hooked tools. Second, using tools to butcher carcasses may have been much easier with tools that provided, for example, more efficient cutting edges. Indeed, the evolution of stone-tool refinement in early hominins led to handaxes that were more efficient than flakes for butchering carcasses (Galán & Domínguez-Rodrigo, 2014). In contrast, encased or tough plant food is simply

collected and usually only requires pounding with tools to extract the edible parts. Thus improvements to hunting or animal-processing tools may provide relatively greater foraging success and associated increased fitness compared to improvements to pounding tools. In conclusion, we propose that a tool-using lifestyle based on animal food that confers a reproductive advantage and evolves enhanced tool manipulation skills, together with appropriate innovative ability and social learning processes, may be essential for cumulative modification of tool designs to evolve in a species.

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