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Is primate tool use special? Chimpanzee and New Caledonian crow compared

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The chimpanzee (*Pan troglodytes*) is well-known in both nature and captivity as an impressive maker and user of tools, but recently the New Caledonian crow (*Corvus moneduloides*) has been championed as being equivalent or superior to the ape in elementary technology. I systematically compare the two taxa, going beyond simple presence/absence scoring of tool-using and -making types, on four more precise aspects of material culture: (i) types of associative technology (tools used in combination); (ii) modes of tool making; (iii) modes of tool use; and (iv) functions of tool use. I emphasize tool use in nature, when performance is habitual or customary, rather than in anecdotal or idiosyncratic. On all four measures, the ape shows more variety than does the corvid, especially in modes and functions that go beyond extractive foraging. However, more sustained field research is required on the crows before this contrast is conclusive.

1. Introduction

Until recently, the chimpanzee was the consensus choice as the most accomplished tool-user of living, non-human species. So say all the textbooks in biological anthropology, based on 50+ years of data on wild chimpanzees, starting with Goodall's [1] findings at Gombe, Tanzania. New findings on the elementary technology of chimpanzees continue to emerge, both from nature and from captivity [2–6].

In the past 10 years, the chimpanzee's paramount position has been challenged by three other primate taxa: Sumatran orangutan (*Pongo abelii*), a great ape from Sumatra [7,8]; bearded capuchin (*Cebus* (*Sapajus*) *libidinosus*), a New World monkey from Brazil [9–11]; and Burmese long-tailed macaque (*Macaca fascicularis aurea*), an Old World monkey from Thailand [12,13]. These diverse taxa are treated elsewhere in this issue, so no more need be said here about them, except to note that each of these taxa has yielded novel findings, compared with chimpanzees.

More surprisingly, the most impressive challenger to primate supremacy has come not from another mammal, but from a bird, the New Caledonian crow (NCC) from the South Pacific [14–16]. This species is the tip of the Corvidae spear, exemplifying the resurgence in research on the behaviour and cognition of this radiation of crows, jays, raven, rook, jackdaw, etc. [17–19]. The corvidologists' claims are sustained and notable (italics mine):

> These population-level features [handedness and shaping] are *unprecedented* in the tool behaviour of free-living non-humans... [20, p. 403]

> NC Crows in the wild manufacture and use tools in ways *more sophisticated* than do other non-humans... [21, p. 307]

> The *only credible evidence* of technological evolution in nonhumans to date comes from New Caledonian crows. [22, p. 291]

> 'In the wild, [NC] crows manufacture, and use...the *most sophisticated* animal tools yet discovered...' [23, p. 313]

These claims have taken root: in the latest edition of their influential textbook, Manning & Dawkins [24, p. 282] state '...if we wished to demonstrate tool use in animals then probably by far the best subject would be the New Caledonian crow...' In Shumaker *et al.*'s [25] encyclopaedic second edition of Beck's monumental 'bible' on animal tool behaviour, their final chapter raises seven key issues or 'myths'. Three of these reflect the topic tackled in this paper:

Myth no. 3: 'Only primates use and make tools'.

Myth no. 4: 'New Caledonian crows use and make tools as well as, or even better than, chimpanzees'.

Myth no. 6: 'Chimpanzees are the most proficient animal tool users'.

The proposition in myth no. 3 is provocative but long-ago falsified, although it highlights an important distinction, between merely using found objects versus modifying objects, in order to improve their function. Tool users occur widely across animal taxa, whereas tool makers are a far more select subgroup. The aim of this paper is to answer the question posed in its title by comparing the two main contenders, chimpanzee and NCC. My emphasis is to go far beyond the 'do-they or do-they-not' tally of using or making of tools, which always has been a simplistic dichotomy.

2. Two other 'myths'

Before proceeding, two other common misunderstandings need to be cleared up, although these amount to painful 'home-truths' for some primatologists. First, most of the 200+ species (and some taxonomic splitters would double that number!) of the Order Primates never or rarely use tools, in nature or in captivity [25]. When they do, most cases are typically one-off anecdotes or idiosyncratic aberrancies, such as human-reared individuals. When captive primates use tools, they often have been laboriously trained to do so, in contrived laboratory settings. Only the four genera named above, of the 30+ genera of primates, are naturally technical; the other genera are technically no different from other mammals.

More pointedly, most apes do not use tools either. Of the six genera of the two families of living apes, Hylobatidae and Pongidae/Hominidae, only two species, *Pan troglodytes* and *Pongo abelii*, convincingly use tools in nature [25]. Despite decades of field study, neither gibbons nor gorillas nor bonobo (*Pan paniscus*) are proven tool-users. All of these non-technological taxa now have been studied long-term at close range, but none shows habitual or customary tool use. Instead, there are isolated descriptions of occasional incidents [26]. Moreover, even in the absence of behavioural data, no artefacts discarded by these other species have been detected, despite persistent searching. Especially striking is the contrast between two pairs of sibling species: chimpanzee versus bonobo, and Sumatran versus Bornean orangutan. In both pairings, the former species uses multiple types of extractive foraging technology but the latter none, despite living in similar habitats. Most dumbfounding is that *all* great ape taxa experimentally tested in captivity *are* proficient tool-users when placed in facilitating, scaffolded circumstances [27]. This is most confusing!

3. What is tool use?

The closest thing to a standard definition of tool *use* is Shumaker *et al.*'s [25], which is unwieldy and long but comprehensive and time-tested (see the electronic supplementary material tables for all definitions). Their definition of tool *making* is simpler and shorter but equally heuristic. Until recently, these two categories sufficed for comparative exercises, with more tool-using species than tool-making ones, apparently confirming the presumption that the latter is more cognitively demanding than the former.

However, in recent years, these minimal categories have proved to be inadequate for capturing the rich variety of animal technology. There has been an explosion of phenomena and terminology to describe more precisely the complexity of the phenomena uncovered. These newer categories have emerged piecemeal, often confusingly, with the same label being attached to different behaviours, or different labels being attached to the same behaviour [28,29]. I rely on Shumaker *et al.*'s scheme as the closest thing to a standard taxonomy, although I have done some tweaking.

Furthermore, rather than just classify tool *use* by type, Shumaker *et al.* [25] sought to characterize it by a second-order elaboration: 'alteration of form, position, or condition of an object, organism or user'. This they called a '*mode*' (p. 13). Linked with this is a third-order classification by the consequences of tool use, which is called '*function*'. This latter scheme is necessary if one wishes to go beyond description to the evolutionary adaptedness of tool use. For example, one of their modes is 'pry, apply leverage', which is defined as to 'push or pull on an object (the tool), using a fulcrum'. The function of this prising action is to 'amplify mechanical force'.

The corresponding exercise applied to tool *making* yields four more modes. For example, the manufacturing mode of 'subtract' is to 'remove and discard a portion of a tool or an eventual tool so the tool can be used, or used more efficiently' (p. 14). This mode of tool making functions as 'structural modification of an object or an existing tool by the user or a conspecific so that the object/tool serves, or serves more effectively, as a tool'.

Finally, these definitions say nothing about the *frequency* with which a behavioural pattern occurs in an individual, population or species. Shumaker *et al.*'s [25] scheme merely distinguishes between presence versus absence, in which the former could be just one individual doing one act one time, that is, a minimal anecdote. Clearly, one-off, rare or idiosyncratic events do not deserve the same status as commonplace ones. Whiten *et al.* [30] accordingly distinguished among *customary* patterns (occurring in all or most able-bodied members of at least one age–sex class), *habitual* ones (seen repeatedly in several individuals, consistent with some degree of social transmission) and *present* ones (clearly identified but neither customary nor habitual). Here, I combine 'customary' and 'habitual' (versus 'present'), as the former two often are not clearly differentiated in published reports. All patterns reported meet this frequency criterion, unless otherwise noted.

4. Comparing chimpanzee and crow

I compare the two pre-eminent taxa of mammal and bird by modes of tool use, modes of tool making, functions of tool use and associative technology. Shumaker *et al.* [25] did a similar analysis for three of these four tool categories, but they combined all birds into a single unit. They also combined wild versus captive into a single category of usage. Finally, new findings have enriched the picture.

The chimpanzee is a medium-sized, semi-terrestrial, hominid mammal with prehensile fingers and toes. The species naturally inhabits at least 20 tropical, sub-Saharan African countries and is widespread elsewhere in zoos and laboratories. It readily breeds in all settings, given appropriate resources. In nature, chimpanzees live in groups that regularly subdivide into parties of ever-changing composition ('fission–fusion'). They aggressively defend a group territory against neighbours, even to the point of fatality. Males are philopatric, but females often leave their natal groups and settle elsewhere to reproduce.

NCC is a medium-sized, volant, corvid bird with prehensile feet. In nature, the species inhabits the South Pacific island of Grande Terre in New Caledonia and a smaller offshore island (Mare). It occurs in only four settings in captivity, where breeding seems to be rare. In nature, the crows live in small family groups, but these encounter one another often [23,31].

Despite these differences, the two taxa have many traits in common. Both are omnivores, consuming plants, vertebrates and invertebrates. Both inhabit a range of ecotypes, from closed forest to open grassland, including former farmlands. Both are large-brained, for their taxonomic class and order [32,33, but cf. 15]. Both show impressive vocal communication that includes dialect differences across populations [34,35]. Both make simple shelters ('nests'), although these serve different functions. Both have been studied in nature, in laboratories and in ingenious field experiments [36]. Finally, both habitually make and use tools.

5. Components of elementary technology

First, I compare chimpanzee and NCC on Shumaker *et al.*'s five components of complex technology [25] (see electronic supplementary material, table S1 for definitions). Chimpanzees show all five in nature and captivity.

All known long-studied groups (communities) of chimpanzees have *tool kits* [37]. These repertoires range in size from 8 to 22 tool types, among the eight habituated groups for which there are published ethnographic data [38]. The median size is *ca* 20, but the three Ugandan study sites (Budongo, Kanyawara, Ngogo) have significantly smaller tool kits, for reasons yet unknown.

Chimpanzees leave behind *assemblages* of tools and their remnants at tool-use sites (*ateliers*), after sessions of extractive foraging. When coupled with observations, these tools can be matched to the individual users. Otherwise, lacking direct data, these discards can be analysed archaeologically [39]. Abandoned tools sometimes are reused later by the same or different individuals.

Chimpanzees *craft* many tools made of vegetation. A termite fishing probe is stripped of leaves, peeled of bark, split longitudinally and clipped at one end and frayed at the other [40].

Like all great apes after weaning, chimpanzees daily *construct* sleeping platforms (nest, bed), in which boughs, branches, twigs and leaves are combined into a single integrated whole [41–44]. Typically, these simple shelters are used only once, but they persist, sometimes for months, gradually degrading, although recognizable scars may persist for the lifetime of the tree used [45].

A chimpanzee shows tool-use *multi-functionality* by using a melon-sized stone as: hammer (pounding mode, functioning to amplify force), missile (throwing mode, functioning to extend user's reach), or signal enhancer (brandishing mode, functioning to create or augment signal value of social display). However, using thin, stripped-down, flexible probes of vegetation to fish for terrestrial termites versus arboreal ants is *not* multi-functional, as both the mode ('insert and probe') and function ('extend user's reach') are the same, despite the prey and context differing greatly.

How do NCC compare? They too show four modes in nature, but apparently one (multifunctionality) only in captivity.

In nature, NCC make tools of leaf, twig or stem to fish out insect prey, and some are clearly *crafted*, involving at least two steps. Most notable is the sculpting of hook tools from particularly detached twigs [14,16,46], a form of non-human extractive technology shown only by NCC. Whether detaching bits of a flat object such as a *Pandanus* leaf is three- or only two-dimensional is unclear, but folding the leaf to create a new shape surely qualifies [22]. Wire-bending by captive crows to make hooked tools, albeit with artificial raw materials, shows comparable extractive function [47, but cf. 48].

The NCC's *tool kit* is usually given as three components: straight stick tools, hooked stick tools and complex shapes of barbed leaf [15], but elsewhere grass-stem probing for lizards [49,50] and candle-nut dropping onto rocks [29] are described. Different populations of NCC have differing tool kits [16,51].

Assemblages of tools accumulate at sites where the crows extract prey from stumps or logs, but it is not always clear whether these are natural feeding sites or artificially provisioned ones. Detailed analyses of these collections of artefacts, such as spatial distribution, identification of debitage, etc. are beginning to be done [52].

Like all other passerines, NCC *construct* nests for depositing eggs and rearing nestlings.

Captive crows use familiar sticks both as tools to retrieve food items and to investigate novel objects [53], but this has yet to be seen in nature.

6. Modes of tool use

Here, I compare NCC and chimpanzees on 22 modes of tool use [25] (the electronic supplementary material, table S2 gives definitions). Chimpanzees show all 22 modes, but two of these (cut, hang) have been seen only in captivity.

Absorb. Wild chimpanzees use crushed leaves as 'sponges' to extract drinking water from tree holes [54,55]. This is a chimpanzee universal, found in all populations subject to long-term study [30].

Affix, apply, drape. Wild chimpanzees apply faeces to surfaces, such as buttress roots of trees, in order to extract passed seeds for re-ingestion (W. C. McGrew *et al.* 1976–1979, unpublished data). Wild chimpanzees drape themselves around the neck with vines or animal skins while walking quadrupedally [54]; in one case, a strip of colobus skin was knotted, creating a necklace [56]. No case of apes affixing with adhesive an object is known.

Bait, entice. Wild chimpanzees, especially juveniles, use objects to attract the attention of potential playmates [54]. More interestingly, chimpanzees solicit their companions to groom them by engaging first in 'leaf grooming', in which the normal patterns of grooming, often accompanied by 'lip-smacking' vocalizations, are directed non-functionally to a leaf [54].

Block. Wild chimpanzees use leafy twigs as 'gloves' for hands and feet or as 'cushions', when climbing or sitting in spiny trees, such as kapok (*Ceiba pentandra*) [57]. Chimpanzees sometimes leave tools in the 'fishing holes' of termite mounds, effectively keeping them from being closed by the termites [58]. These may function as plugs or stoppers to facilitate later reuse, or they may be just oversights; more investigation is needed. Gashaka chimpanzees sometimes leave thick sticks inserted into beehive entrances, apparently for the same function (V. Sommer & A. Pascual-Garrido 2013, unpublished data).

Brandish, wave, shake. Wild chimpanzees, especially adult males, show all of these patterns (and more) in agonistic displays, making use of both attached and detached vegetation [54].

Balance and climb, prop and climb, reposition, bridge. Koehler's [59] captive chimpanzees vertically balanced poles and climbed them to get bananas suspended overhead. Chimpanzees escaped from an enclosure by dismantling their climbing frames and using the poles as ladders to clamber over a high fence [60]. The same chimpanzees jammed sticks into seams in a fence, creating 'pitons' that they used to climb up and over [61].

Club, beat. Wild chimpanzees hit one another or other species with various objects, especially sticks, but also with dead prey [54].

Contain. Wild chimpanzees fold leaves to make simple containers for drinking water [55]. Captive chimpanzees readily use human-supplied containers but also create their own, such as filling an empty coconut shell with water and carrying it elsewhere to drink [62].

Cut. Wild chimpanzees have not been seen to slice with an object but instead use their teeth. Captive chimpanzees readily learn to use sharp-edged objects, and both chimpanzees and bonobos make functional stone flakes that cut rope [63].

Dig. Wild chimpanzees at Issa, Tanzania, use woody objects to dig up tubers for food [64].

Drag, roll, kick, slap, push over. Chimpanzees drag objects, including uprooted saplings, in bipedal agonistic displays [54]; youngsters drag piles of leaves in invitation to potential play partners [65]. All known chimpanzee populations drum on buttress roots of trees in acoustic communication, using the palms of the hands (slap) and soles of the feet (stamp) [66]. Chimpanzees push over rotting tree stumps as part of agonistic display [54].

Drop. Agitated wild chimpanzees drop branches onto humans and other threatening large mammals; this is a chimpanzee universal [54].

Pound, hammer. West African chimpanzees use stones or wooden hammers to crack open nuts on stone or wooden anvils [67,68]. Chimpanzees pound hand-held, hard-shelled fruit on stone or wooden anvils, as technically assisted, percussive food processing [69]. When the anvil is portable, it is tool use; when the anvil is fixed (e.g. boulder, root, outcrop), it is not [25].

Hang. Captive chimpanzees reposition ropes, cloth, etc. and play, rest or locomote on them. Wild chimpanzees have not been seen to do so, perhaps lacking the appropriate raw materials.

Pry, apply leverage. Wild chimpanzees use sticks as levers to widen entrance holes to honeybee colonies in tree cavities or underground [70,71].

Probe. Chimpanzees insert linear objects, usually vegetation, into cavities to extract their contents. This foraging ranges from delicate threading of a flexible probe in termite or ant fishing [1,72] to 'dip-sticking' honey from a bees' nest [6].

Reach. Chimpanzees use elongate objects to poke at or retrieve other objects, ranging from a sleeping conspecific to a found dead animal [54].

Scratch, rub. Chimpanzees scratch inaccessible parts of their bodies (e.g. back) with sticks [54].

Stab, jab, penetrate. Chimpanzees use sharpened, sturdy sticks as 'skewers' to dislodge bushbabies from their sleeping holes [73]. Central African chimpanzees use stout sticks to force passageways in the soil, providing access to underground termite colonies [6].

Symbolize. Chimpanzees, usually males, clip leaves in courtship. Repeated tearing of the leaves acoustically attracts the attention of the sought-after female [74]. This *may* be an arbitrary signal to the female, in which the sight and sound of leaf-clipping *may* represent the libidinous state of the male. However, seeking to show by observation alone that *any* act is symbolic is well-nigh impossible methodologically. Captive chimpanzees readily learn to use symbols, for example, in simple token economies, numerosity, etc. [70].

Throw. Chimpanzees throw objects, usually sticks or stones, at conspecifics, prey or predators, or hurl objects without aiming as part of agonistic displays [1,54].

Wipe. Chimpanzees use leaves as napkins to wipe clean their or companion's body surface of blood, sap, semen, faeces, etc. [54].

NCC show four modes of tool use in nature and four in captivity.

Drop. Wild NCC drop candlenuts (*Aleurites moluccana*) from branches onto rocks below, in order to crack them open [50]. Such standardized (aimed?) release from a specific launching site seems to be unique to NCC, but many species of corvids drop food objects onto hard surfaces [75]. Captive crows drop stones as tools to raise levels of liquid, thus gaining access to floating objects [76] or to collapse a platform to release an object [77].

Pry, apply leverage. Crows in captivity bend segments of wire to make a hooked tool, by using the lip of a glass cylinder as a fulcrum [47]. (Strictly speaking, the bending is tool making, not using.)

Insert and probe. Wild crows insert elongated segments of various kinds of vegetation (leaf, petiole, stem, twig) into cavities or crevices, in order to extract prey items (e.g. long-horned beetle larvae) contained therein [14,15,78–81].

Reach. Captive crows use probes to retrieve objects from behind barriers [28,51] or to investigate novel, artificial objects [53], but this has not been seen in nature.

Jab. NCC use grass-stems to dislodge lizards from crevices, and this behavioural pattern may be common in farmland habitats [50]. Jabbing to flush prey from their refuges is common in NCC (C. Rutz 2013, personal communication).

7. Modes of tool making

Shumaker *et al*. [25] distinguished four modes of tool manufacture (see the electronic supplementary material, table S3 for definitions). Chimpanzees show all four of these.

Detach. Chimpanzees disconnect, usually by hand or mouth, plant parts from their source, whether woody or non-woody;

the detached objects range in size from leaf to entire sapling [62]. Such detachment varies greatly in precision and force applied, from gross stripping to pointed plucking.

Reduce. Chimpanzees separate extraneous elements from a detached, incipient tool, discarding what is removed (*debitage*), such as removing the leaves from a twig, so that it can be inserted as a probe into a narrow passageway.

Reshape. Chimpanzees fold leaves into crude, spoon-like containers to drink water from a tree hole [55].

Combine. Chimpanzees pick and crush individual leaves into a single sponge-like mass for absorbing water, either from a tree-hole or a puddle [54,67].

NCC show three of the four modes of tool making.

Detach. Using the bill, NCC tear strips from the spiny-fringed leaves of *Pandanus* trees, producing probes [14]. Some populations repeat the technique with successive, narrower tears, thus producing a 'stepped' tool [21]. The process is rarely observed but it leaves behind the artefactual 'negative' of the tool that is taken away, which can be analysed archaeologically.

Reduce. NCC remove and discard side-twigs, leaflets and bark from woody twigs in the process of making hooked probes [16,20]. They shorten non-hooked stick tools before or during use [15].

Reshape. In finalizing the making of a hook tool, the crows 'sculpt' the hook from the existing fork of a twig, by bending the end of the twig, removing small pieces of wood, and sharpening the point [16,20,46]. They fold the wide tools made of *Pandanus* leaf [22].

There seems to be no record of crows joining or connecting two or more components to make a single tool.

8. Functions of tool use

Shumaker *et al*. [25] distinguished seven classes of function in tool using (see the electronic supplementary material, table S4 for definitions). Chimpanzees show six of these seven, lacking only *hide/camouflage* (i.e. conceal user). However, one captive chimpanzee regularly conceals stones (but not itself), in order to retrieve them later to throw at human targets [81].

Amplify force. Chimpanzees hold or propel by hand objects that increase the impact of the tool being used. Often the action is ballistic, with the inertia supplied by muscular extension and centripetal force. Examples: throw, club, pound, pry, dig, stab.

Augment display. Chimpanzees use objects to enhance the signal value of displays in agonism, courtship and play. Examples: drag, brandish, entice, drape.

Control substances. Chimpanzees use objects to manage fluids (e.g. blood, semen, etc.) for consumption or removal. Examples: absorb, contain, wipe.

Enhance comfort. Chimpanzees use objects to facilitate rest, locomotion or hygiene. In nature, they cushion their hands and feet from thorny bark with leafy twigs [57]. A more ubiquitous example is the nest or sleeping platform, but it is not a tool, as noted above [82]. Examples: bridge, block.

Extend reach. Chimpanzees hold, propel or release objects by hand, foot or mouth that expand access to goal objects in three-dimensional space. Such tools may be used to repel or retrieve objects on or in a substrate. Examples of modes: drop, hang, reach, insert and probe.

Symbolize. Chimpanzees appear to use objects to signal, abstract or represent reality. Wild chimpanzees play with 'dolls', by directing typical cradling and other caregiving behaviour to inanimate objects, such as lengths of woody vegetation [83]. Whether this is sign or symbol or neither is hard (or impossible?) to discern in nature, but fantasy play occurs in both wild and captive apes; much of it involves objects as instigating devices [84].

NCC show two of the seven functions of tool use.

Extend reach. Crows hold or release objects in the beak that expand their access to goal items by contact or through space. Probes stuck into cavities fish out larvae or winkle out lizards.

Amplify force. Wild crows dropping nuts onto a hard substrate enlist gravity's force to crack them open. Controlled release from a proven point in space increases the probability of success [29]. Captive crows learn to drop stones into a vertical tube to release a reward, even without specific training [77].

9. Modes of associative technology

Here, I compare chimpanzee with NCC on Shumaker *et al*.'s five modes of associative technology (see the electronic supplementary material, table S5). Chimpanzees show all five: three are habitual or customary in the wild, but two (sequential and secondary) are presently known only in captivity (see review in [70]).

The best-known chimpanzee tool *set* is the use of a stout perforating tool to open a passage, followed by a thin, flexible probe for fishing out subterranean termites [6,54]. Sets of up to five components have been recorded for dipping honey from bees' hives [85]. The order of use of tool types in a set is obligatory: a dipstick cannot be used to extract honey from a cavity until the cavity has been punctured.

The iconic *composite* tool is hammer and movable anvil to crack open nuts [39,68]. One without the other is useless for processing small, dense, hard-shelled objects. (Another form of percussive technology, the use of a fixed anvil alone to pound open larger objects, does not qualify as tool use. Chimpanzees smash large fruits such as baobab (*Adansonia digitata*) directly on root or boulder anvils, without hammers [69]. Similarly, Nimba chimpanzees 'cleave' basketball-sized *Treculia africana* fruits with stone hammers and anvils, but evidence for this plant 'butchery' remains preliminary [86].)

A less co-dependent form of composite tool in nature occurs in dipping for army ants (*Dorylus* spp.) [87]. Chimpanzees use long, stiff wands of vegetation to extract ants from their subterranean nest, but the anti-predatory defence of the biting ants is fierce and painful. By elevating themselves off the ground, via bending over a nearby sapling and perching on it, the ape reduces its exposure to the swarming ants below. Creating the perch increases the effectiveness of the wand's use, but only indirectly, as the perch does not act directly on the wand.

The closest thing to a *metatool* in wild chimpanzees may be their use of 'wedge stones' to modify the orientation of an anvil stone, in nut-cracking [68]. A wobbly or tilting anvil may be stabilized or levelled by inserting one or more smaller stones beneath it. However, this is positional modification (see definition of tool use in electronic supplementary material, table S1), not structural modification.

Secondary tool use has been induced in the laboratory: captive chimpanzees and bonobos readily use one stone to fracture another, then use the resulting sharp-edged pieces

Table 1. Summary of chimpanzee (*Pan troglodytes*) and new Caledonian crow (*Corvus moneduloides*) compared on five aspects of tool-use (from [25]). (First number before comma is types seen in nature, second is for captivity.)

species	components of elementary technology ($n = 5$)	modes of tool use ($n = 22$)	modes of tool making ($n = 4$)	functions of tool use ($n = 7$)[a]	modes of associative technology ($n = 5$)
chimpanzee	5,5	20,22	4,4	6,6	5,5
New Caledonian crow	5,4	4,4	3,3	2,2	0,2

[a]Shumaker *et al.*'s criteria for 'symbolize' are operationally problematic, but chimpanzee fantasy play seems to meet them.

to cut rope, which gains them access to a food-item (Garufi, unpublished data and [63]). This may amount to a crude form of stone knapping, in which the cobble strikes the core.

Chimpanzees in captivity have been known for decades to use tools *sequentially*, that is, use one tool to acquire another; this task is induced artificially by placing the additional tools behind artificial barriers [70]. Such a challenge is hard to imagine in nature, although wild bearded capuchin monkeys use stones to knock free from the substrate embedded stones, which then become hammers [10].

Shumaker *et al.*'s *construction* is not tool use, but it is associative technology, in that two or more objects are physically combined to create a functional item. Every wild chimpanzee past weaning daily builds at least one sleeping platform (a.k.a. nest, bed) of fresh vegetation. These interwoven pallets comprise bent and broken boughs and branches and are lined with leafy twigs [41–45].

NCC in nature appear to show no associative technology, that is, combinations of tools, but do show sequential tool use and tool sets in captivity.

Experimental induction of *sequential* tool use has been demonstrated and replicated: the crows spontaneously used a short stick to retrieve a long stick from beyond a barrier, then used the long stick to retrieve a bait from a deep hole. An extended version of this task involves an extra step, whereby three tools are necessary to solve the problem [88]. A variant design has the crows obtaining the first tool by pulling up a string, then using it to extract a long-enough tool from a toolbox, then using the long tool to extract food from a cavity [89].

Captive crows showed a tool *set* when they pulled a string to obtain a short stick, then used the stick to retrieve a longer stick, which was then used to extract food from a hole [90].

At least two studies of captive NCC have claimed to show metatool use [28,88], but both used definitions that differ from Shumaker *et al.*'s. In one case, the metatool was defined as 'to use one tool on another' [28, p. 1504]; in the other it was defined as 'a tool directed towards other tools' [89, p. 2]. In Shumaker *et al.*'s scheme, this is sequential tool use.

NCC construct nests for rest and reproduction, but their architecture seems not to have been compared systematically with that of chimpanzees or any other primates.

10. Conclusion

No one disputes that chimpanzees and NCC are excellent makers and users of tools, or that each is the paramount technologist of their respective taxonomic orders. But when we move beyond mere species tallies of presence versus absence of types of tool use, a wide gap opens. (see summary in table 1). Both taxa show all five components of elementary technology. For the 22 modes of tool use, the apes again show all but the crows only four. For the four modes of tool making, the two taxa come close to equivalence: four by the apes versus three by the crows. For the seven functions of tool use, the apes show all but one, but the crows only two. Of the five types of associative tool use, the apes show all but the crows only two.

Overall, what emerges, especially from modes of tool use, is that the NCC is a relatively specialized extractive forager, using a variety of tools to access embedded food items. In this regard, NCC may well match the chimpanzee, as shown by the modes of tool making employed by both. However, the ape's technology goes far beyond subsistence, notably into social and self-maintenance realms, neither of which is expressed by the crow, as seen in the ranges of functions displayed. Finally, despite the impressive range of social cognition displayed by other corvid species [17–19], it is unclear whether NCC's cognition extends into higher-order cognition, such as theory of mind [16,70,89]. Thus, the chimpanzee is a truly generalist technologist, more akin to the other hominins than to any other living non-hominin species [37].

So, why have so many strong claims been made about crow and ape equivalence? One possibility is novelty. Chimpanzee technology is old hat, being known for more than 50 years in nature [1], and almost 100 years in captivity [59]. NCC technology is striking and fresh, especially against the background of absent natural tool use in the rest of the corvid radiation. A more substantial explanation for the contrast may be that field studies of NCC lag decades behind that of chimpanzees [91]. The apparent differences may reflect that much less research effort has been spent so far on the crows, by comparison with the apes. When continuous close-range observations of the crows are achieved, much more may be revealed [92]. This is an exciting prospect.

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