

Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*

Gavin Raymond Hunt

Department of Psychology, University of Auckland, Auckland 92019, New Zealand (grhunt10@hotmail.com)

The main way of gaining insight into the behaviour and neurological faculties of our early ancestors is to study artefactual evidence for the making and use of tools, but this places severe constraints on what knowledge can be obtained. New Caledonian crows, however, offer a potential analogous model system for learning about these difficult-to-establish aspects of prehistoric humans. I found new evidence of human-like specialization in crows' manufacture of hook tools from pandanus leaves: functional lateralization or 'handedness' and the shaping of these tools to a rule system. These population-level features are unprecedented in the tool behaviour of free-living non-humans and provide the first demonstration that a population bias for handedness in tool-making and the shaping of tools to rule systems are not concomitant with symbolic thought and language. It is unknown how crows obtain their tool behaviour. Nevertheless, at the least they can be studied in order to learn about the neuropsychology associated with early specialized and/or advanced population features in tool-making such as hook use, handedness and the shaping of tools to rule systems.

Keywords: early humans; handedness; New Caledonian crows; population-level specialization; rule systems in tool-making; tool behaviour

1. INTRODUCTION

Understanding human evolution requires knowledge of the behaviour and neurological faculties of our early ancestors. One underlying reason for searching for this knowledge is an attempt to determine how language and the modern 'symbolic' mind evolved (e.g. Gibson & Ingold 1993; Deacon 1997). Because behaviour and brains do not fossilize, the making and use of tools has a crucial role in providing clues about the above aspects of early humans. This is far from ideal because an artefactual record of tool behaviour is not a reliable indicator of the behaviour and neurological faculties of tool-makers (Lieberman 1991). Most archaeological material associated with tool behaviour involves stone tools which first appear in the artefact record around 2.5 million years (Myr) ago (Semaw *et al.* 1997). Three main, overlapping chronological periods in the early tool-making of our ancestors are recognized.

- (i) Before around 1.5 Myr ago, humans appear to have only made simple stone tools, which were mostly flakes struck or broken from the same side of a core (Toth 1985a). No organic tools are known from this period.
- (ii) Between around 1.5 and 0.1 Myr ago, stone tool-making was characterized by bifacial cores such as 'hand axes' formed by flaking on several sides and both faces of a core (Noble & Davidson 1996). Evidence for the early manufacture and use of organic tools is extremely rare, but sophisticated wooden spears were being made in Europe at least around 0.4 Myr ago (Thieme 1997).
- (iii) Prehistoric tool-making in the last 100 000 years by *Homo sapiens* sees the appearance of much greater innovation and fine tool-making, with bone as well

as wood and stone (Oakley 1961; Mellars 1989; Yellen *et al.* 1995).

At some time in this history of tool-making, two features which are thought to indicate the early signs of a modern-like mind became widespread: right-handedness in tool behaviour and the fashioning of tools to a precisely predetermined shape.

The strong population bias (i.e. occurring in significantly more than half the population) for right-handedness in modern humans is linked to specialization of the brain's left hemisphere for the control of sequential, purposeful behaviours (Corballis 1991) and has probably resulted in more precise manual skills compared to ambidexterity (Ward & Cantalupo 1997). Two competing views propose that left hemisphere specialization for the organization of non-tool-related manipulatory skills predates human evolution. One view is that selection for handedness occurred in the common primate ancestor of monkeys and humans and, consequently, caused this specialization (MacNeilage *et al.* 1987). Alternatively, mounting evidence of laterality (structural and functional) in non-humans suggests that this specialization is phylogenetically very ancient and was present in the common four-limbed ancestor of birds and mammals (Rogers 1989; Bradshaw 1991; Bisazza *et al.* 1998). Although tool use possibly led to increased left hemisphere specialization of the brain for the organization of manipulatory skills, Deacon (1997) suggested that the strong bias for right-handedness in modern humans was much more likely to be driven by language and the need for (left) hemispheric specialization in speech processing rather than tool behaviour. Thus, a strong population bias for biologically related right-handedness in early human tool behaviour might indicate not only modern-like cerebral specialization and coordination skills but also

symbolic thought and the use of language. Toth (1985*b*) reported a strong population bias for right-handedness in the knapping of stone tools 1.4–1.9 Myr ago. However, there appear to be reasons to doubt that this has been shown (Noble & Davidson 1996; Pobiner 1999). A population bias for right-handedness in the manipulatory skills of humans has therefore only been documented with certainty back to 5000 years ago (Coren & Porac 1977).

The finished shape of a one-piece tool manufactured prior to use is achieved by (i) 'trial-and-error', that is, the removal of material until an acceptable form is obtained although not precisely predetermined (Wynn 1979; Wynn & McGrew 1989), or (ii) using a 'rule system' (Isaac 1976), that is its form is precisely predetermined before its manufacture begins. Trial-and-error shaping of tools is different from trial-and-error learning because it can still involve '... well-defined intentions and techniques' but, in contrast to the shaping of tools to a rule system, it cannot control more than one shape variable at a time (Wynn & McGrew 1989, p. 390). Shaping tools to a rule system is generally assumed to also require foresight, planning and the shaping of tools to 'mental templates' (Oakley 1961; Isaac 1976; Wynn 1979; Tattersall 1998), behaviour which might point to symbolic thought and the use of language as well (Noble & Davidson 1996). In the literature (e.g. Mellars 1989), human tools complying with the following three criteria are thought to have been shaped to a rule system.

- (i) The imposition of form on raw material in the 'sculpted' sense requiring the simultaneous control of more than one shape variable in a way which indicates that the shape of the finished tool is important.
- (ii) Skilled tool-making technique(s).
- (iii) The morphological standardization of finished tools.

The necessary strictness of these criteria in establishing that the finished shape of a tool is precisely predetermined with a high degree of certainty means that tools failing to meet them could still be shaped to a rule system.

Hand axes have long been considered the first stone tools shaped to rule systems (Oakley 1961; Wynn 1979; Toth 1985*a*; Tattersall 1998). However, recent ideas have suggested that they were cores primarily for knapping flake tools (Davidson & Noble 1993; Noble & Davidson 1996). Nevertheless, bifacial cores indicate the use of consistent, different and probably improved knapping techniques compared to earlier tool-making (Noble & Davidson 1996). Thus, although very recent prehistoric humans could clearly shape stone tools to rule systems (e.g. late Palaeolithic arrowheads) (Oakley 1961), there is some doubt that earlier humans did. The three throwing spears found by Thieme (1997, p. 809), though, appeared to have been '... manufactured to the same pattern...' and resembled aerodynamically efficient '... modern javelins...', suggesting that early *Homo* species may have been shaping one-piece wooden tools to rule systems.

New Caledonian crows (*Corvus moneduloides*, hereafter crows) live on mainland Grande Terre and nearby Maré Island (Délacour 1966), two of the larger islands of the French Territory of New Caledonia in the tropical southwest Pacific. The first report of crows using tools in foraging appears to have been made in 1909 (Hunt 2000), but it was only recently discovered (Hunt 1996) that they

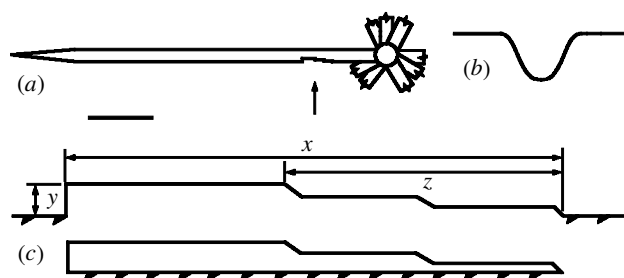


Figure 1. (a) Stylized cross-section of the leaf crown of a pandanus tree (viewed from above) showing the (clockwise) three-spiral configuration of mature leaves around the trunk. Only one leaf is drawn complete and only a small number of leaves are shown below the cross-section. A stepped-cut tool counterpart (arrowed) is drawn on the left edge of the entire leaf. Scale bar, 35 cm. (b) Cross-section of a mature pandanus leaf (variation in leaf thickness not shown). Scale bar, 2.5 cm. (c) A generalized-shaped counterpart on a section of pandanus leaf edge (top) and the resulting stepped-cut tool (three steps) (bottom); barbs run along the leaf edge. x (tool length), y (tool width) and z (length of the tapered section) show the measurements taken off counterparts. Scale bar, 2 cm.

manufacture and use two types of hook tool: a crochet-hook-like, hooked twig held in the bill by the non-hooked end and a flat, narrow section of *Pandanus* sp. (screw pine) leaf edge with naturally occurring, saw-toothed barbs along one edge facing away from the working end of the tool. The way the crows made, held and used these tool types indicated that they were using hooks to aid prey capture. I found that crows in higher altitude rainforest on two adjacent mountains (Mount Cindoa and Pic Ningua) regularly used these hook tools to extract prey from cracks and holes in trees and branches and amongst their epiphytes. Individuals used hook tools repeatedly at many sites in different trees and also often cached their tools on their perches for short periods when not using them. It is unknown whether crows inherit or individually learn their tool behaviour.

Crows make pandanus tools by removing short sections of barbed edge from pandanus leaves (figure 1). A pandanus tool's shape at its removal is faithfully recorded in the matching counterpart (previously termed a 'cut-out') on the leaf edge (Hunt 1996) (figure 1*a,c*). Because pandanus tools appear to be rarely if at all modified after removal (Hunt 1996), tool counterparts provide a complete artefact record of the numbers and shapes of these tools manufactured in past years (pandanus leaves stay on trees for approximately four years at Pic Ningua; G. R. Hunt, unpublished data). This overcomes problems such as unfinished tools, those modified after first use and an incomplete artefact record that can confound studies of stone tools and chimpanzees' (*Pan troglodytes*) stick tools, but not the problem that, once a tool is made, it might be discarded if it was defective in some way (McGrew *et al.* 1979; Davidson & Noble 1993).

Most of the pandanus tools that crows made at Pic Ningua were very regular-shaped, tapered, 'stepped-cut tools' (Hunt 1996) (figure 1*c*). This shape gives sturdy but pointed tools because birds hold the wide ends in their bills. The crows used these tools to search for prey often with some force while holding them lengthways and

aligned with the bill (Hunt 1996). The shape of these tools is more complex than the shape of a thin, less sturdy, untapered strip of pandanus leaf edge that I saw a crow using as a tool at Parc Rivière Bleue (Hunt 1996). From my previous work I also noticed that the counterparts were more often on the left edges of leaves (as in figure 1*a*). I investigate here whether the manufacture of pandanus tools might exhibit 'handedness' and whether stepped-cut tools might be shaped to a rule system as defined above. The main rationale for this is to see whether crows might provide an extant species for learning about the behaviour and neurological faculties associated with the early stages of advancement in tool-making.

2. METHODS

The monocotyledon pandanus trees that crows use for tool-making have long, thin, leathery leaves with a central reinforcing trough which runs longitudinally along their length (figure 1*a, b*). Leaves spiral in three ranks outwards and upwards at the top of a narrow trunk in an anticlockwise (ACL) or clockwise (CL) direction (figure 1*a*). New leaves continually emerge near vertically one after the other around the centre of the leaf crown then 'migrate' to its base over approximately four years when they finally drop from the trees. Most leaves on these pandanus trees (except juveniles) are mature, usually of 2–3 m in length and have their longitudinal axis near the trunk at an angle of *ca.* 45° or more to the trunk. Crows remove tools from the left edges (LEs) and right edges (REs) of CL and ACL spiralling leaves, mostly near the trunk; more than two tools removed along the same edge of a leaf is uncommon. Ease of access for a crow to either the LE or RE of a leaf near the trunk is probably not equal because of the spiralling configuration of the leaves. The trailing edges on the spiralling leaves tend to be more exposed, that is the LE on CL leaves (as in figure 1*a*) and the RE on ACL leaves. Leaves spiral unidirectionally on younger, shorter trunked trees and usually bidirectionally (a change in spiral direction may be associated with fruiting; G. R. Hunt, personal observation) on older trees which can grow to at least 5–6 m in height.

In late 1997, I sampled the pandanus tool-making of crows on Grande Terre (*ca.* 400 km long and averaging 50 km wide) at two study sites. I removed pandanus tool counterparts from leaves at Mount Panié (20°35' S, 164°46' E) and Pic Ningua (21°45' S, 166°8' E), mountains which are 190 km apart. The site at Mount Panié had a wetter climate (annual rainfall over 3000 mm), was at a lower altitude (300–500 m above sea level (asl)) and was on a different rock type (sedimentary rocks) compared to the site at Pic Ningua (annual rainfall 1000–2000 mm, 1000–1100 m asl and ultrabasic rocks) (Angleviel & Biliquy 1992). Because these factors contribute to the high localized endemism of New Caledonian flora (Jaffré 1993), the plant and associated invertebrate communities at each site also probably varied. Crows live in forest throughout Grande Terre (G. R. Hunt, personal observation). My previous observations of crows at Pic Ningua suggested that they live in small groups of adults and young in rainforest and are relatively sedentary on the territories they live in year round.

I removed counterparts from a pair of (single-trunked) pandanus trees (one with CL and one with ACL leaves) at eight locations at both sites within a contiguous *ca.* 100 ha area of rainforest. I initially chose a pandanus tree without knowledge

of the number of counterparts on its leaves or the direction(s) its leaves spiralled in. I sampled it if its leaves spiralled predominantly (five out of the 32 trees) or exclusively in one direction and a minimum number of counterparts were present for analyses ($n=10$ at Pic Ningua and $n=20$ at Mount Panié). I chose the second tree of a pair by the same method, except that its leaves spiralled in the opposite direction to those on the first tree. The distances between pairs of trees at each site were at least *ca.* 100 m and between trees within pairs up to *ca.* 20 m. The maximum distance between any two pairs of trees was *ca.* 1.8 km at Pic Ningua and *ca.* 1.0 km at Mount Panié. I removed all distinct and possible counterparts (undamaged and damaged) from a tree's leaves or recorded the edges they were on if this was not possible (ten counterparts on two trees). I kept the counterparts in 70% alcohol to prevent distortion from drying.

I also recorded the leaf-spiral direction on the first ten juvenile or young pandanus trees (with little or no visible trunk) that I approached around paired trees to check for any bias in leaf-spiral direction on young trees. The juvenile and young trees were quite widely scattered around each pair of sampled trees.

I described how the crows removed stepped-cut tools from pandanus leaves from examination of 62 unfinished tools at varying stages of manufacture that I found on leaves and the bill marks on these, 103 tools with and without matching counterparts and over 1500 counterparts. I collected this artefactual material between 1993 and late 1997.

To analyse the shapes of the tools the crows removed from counterparts, I first measured tool length, that is the length of barbed-leaf edge removed from each counterpart (measurement x in figure 1*c*). I then traced the outlines of all undamaged counterparts onto paper. The crows finally removed a stepped-cut tool from the leaf at the tool's wide end using different techniques. It was often difficult to tell whether the last step (i.e. of steps made sequentially inward from the leaf edge and away from the pointed end of the tool) was a step formed from the pointed end of the tool or resulted from removal at the wide end. Therefore, to qualify as the last step, its length (parallel to the leaf edge) had to be at least 1.5 cm which minimized the chance of misidentification of steps. On each outline I measured (on a transparent sheet of 1 mm grids placed over the outline) (i) the length of the tapered section and (ii) the width of the removed leaf section at right angles from the leaf edge to the top of the last step (measurements z and y , respectively, in figure 1*c*). I also counted the number of steps per tool when they were well defined.

I normalized the tool length data using logarithmic transformation and counterpart numbers on trees by square-root transformation before I carried out ANOVA tests on them. I used the Spearman coefficient of correlation for correlation tests, which is indicated by r_s .

3. RESULTS

I had previously observed up to four individual crows carrying tools together and up to nine birds at a time at the study site at Pic Ningua (Hunt 1996), but over the seven days I spent at Mount Panié the most crows I observed at a time was two and only one out of a pair ever carried a tool. There were hundreds of pandanus trees suitable for tool-making spread throughout each study site and crows had removed tools from leaves on

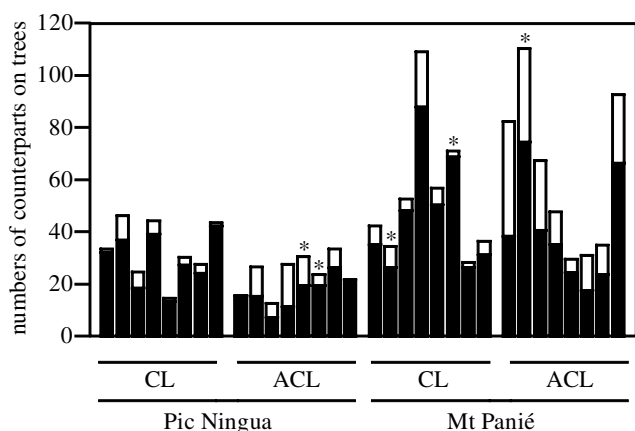


Figure 2. Numbers of pandanus tool counterparts on the LEs (filled symbols) and REs (open symbols) of individual trees at Pic Ningua and Mount Panié. ACL, anticlockwise-spiralling leaves and CL, clockwise-spiralling leaves. An asterisk indicates a tree whose leaves spiralled bidirectionally but mostly in the direction indicated. The trees were paired at each site as follows: the first tree from the left with CL leaves and the first tree from the left with ACL leaves and so forth.

many of them, resulting in probably thousands of counterparts on trees from tool-making over recent years. The crows removed tools from young and old pandanus trees at both study sites, but at Pic Ningua, in contrast to Mount Panié, birds used young trees with trunks shorter than 1 m in length much less often and many older, longer trunked trees there had unidirectionally spiralling leaves. Thus, the trees I sampled at Pic Ningua generally had longer trunks than those I sampled at Mount Panié. Crows at both sites nearly always removed tools from leaves well over 1 m in length as I rarely saw counterparts on short, immature leaves. I observed that the width of the horizontal area of leaf edge available for tool-making on each side of a pandanus leaf (figure 1*b*) was little different, but was commonly narrower on leaves at Mount Panié compared to leaves at Pic Ningua because of generally wider leaves at Pic Ningua.

I collected 448 counterparts (388 undamaged) from the 16 pandanus trees (mean per tree = 28 and s.d. = 10.3) sampled at Pic Ningua and 919 counterparts (715 undamaged) from the 16 trees (mean = 57 and s.d. = 28.1) sampled at Mount Panié. Damage to counterparts mostly occurred by overlap with other counterparts and at both sites the number damaged on a tree was correlated with the total number of counterparts present (Mount Panié $r_s = 0.74$ and Pic Ningua $r_s = 0.63$; $p < 0.01$ and $n = 16$). There were only two cases at each site when I was unsure whether the missing leaf edge resulted from the removal of a tool. The numbers of counterparts on trees with CL and ACL leaves did not differ at Mount Panié ($F_{1,14} = 0.20$ and $p > .60$) or Pic Ningua ($F_{1,14} = 2.9$ and $p > 0.10$) (figure 2).

Only one out of the 16 trees at each site had more counterparts on REs than LEs (figure 2). The per cent use of LEs on CL leaves was almost identical at Pic Ningua (89%) and Mount Panié (87%), but less similar on ACL leaves (71 and 65%, respectively). As might be expected, the crows used LEs more than REs to make tools on both CL leaves (Pic Ningua, $F_{1,14} = 62.6$ and

$p < 0.0001$, and Mount Panié, $F_{1,14} = 41.5$ and $p < 0.0001$), and ACL leaves (Pic Ningua, $F_{1,14} = 9.4$ and $p < 0.01$, and Mount Panié, $F_{1,14} = 4.69$ and $p < 0.01$) (figure 2). In a generalized linear model (GLM), the edge-use ratios were significantly smaller (i.e. high but lower use of LEs compared to REs) on trees with ACL leaves compared to those with CL leaves (table 1); access was probably poorer to leading LEs on ACL leaves. To a lesser degree, the ratios were also associated with an interaction between the mean length of the counterparts on LEs and site differences; the ratios were smaller and counterparts longer at Mount Panié, but the inverse occurred at Pic Ningua. The ratios appeared to be unaffected by space constraints on leaf edges because the total number of counterparts on trees was not selected as an explanatory term in the minimal model. Out of the four leaf-spiral-direction-leaf-edge categories at both sites, REs on CL leaves were used least, which was consistent with the crows' preference for LEs combined with a leaf edge access effect. The number of juvenile and young trees that I recorded around sampled trees did not differ at Pic Ningua (35 and 45, respectively; $\chi^2_1 = 1.25$ and $p > 0.20$) or Mount Panié (41 and 39, respectively; $\chi^2_1 = 0.05$ and $p > 0.80$).

Over 99% of the resulting tools from the 1103 undamaged counterparts were obviously tapered to a point at one end and on average the length of the tapered section was slightly more than 50% of a tool's total length (table 2). At Pic Ningua and Mount Panié, the tapered edges on most (85 and 79%, respectively) of these tools had a distinctly stepped profile (e.g. figure 1*c*) where the number of steps per tool was well defined. Out of the remaining tapered tools, only a small number were removed in a way which suggested possible inexperience in tool-making (e.g. leaf edge barbs facing towards the pointed end of the tool; see the inset in figure 4). The manufacture of stepped-cut tools by crows involves one-sided use of the bill to execute a patterned sequence of precision 'cut-rip' actions to make a tapered, stepped edge (figure 3*a*). These tools are very different in shape compared to the raw material (i.e. a pandanus leaf). The cut-rip technique requires not only positioning the tip of the bill just above a rip to make steps but also the accurate positioning of a cut in relation to the end of a rip from the previous cut. A cut made before the end of a rip results in obvious damage to the tool (figure 3*b*), but this type of damage occurred only rarely in the over 100 completed tools that I collected. A cut after a rip terminates (figure 3*c*) could potentially result in difficulty with tool removal, but evidence of problematic tool removal (e.g. tools 'misshapen' and/or not 'cleanly' cut out) was also rare from my examination of the 1103 undamaged counterparts.

The two-dimensional (2D) shapes of the stepped-cut tools differed in interesting ways within and between sites by variation in three main tool characteristics (figure 4): length, width and the number of steps per tool. Each of these variables showed a capacity to vary independently of the other two at both sites. For example, compared to the most commonly made shape class at both sites (class 14), the crows made longer tools which were still relatively thin with relatively few steps (classes 22–23 and 26) and shorter tools which were relatively wide with relatively more steps (classes 5–6 and 8). They made relatively few

Table 1. Generalized linear model of edge-use for tool-making

(The data were modelled to a binomial response variable which was the proportion of the counterparts on the LEs of a tree's leaves; $n = 16$ trees at both sites. Leaf-spiral direction: ACL, 1; and CL, 0. Site: Mount Panié, 1; and Pic Ningua, 0. The F -statistics and probability levels are when each effect was fitted last in the model. The full model included two-way interactions and main effects only; only significant interaction effects are given, indicated by a multiplication sign between effects. The F -statistics were corrected for overdispersion. The minimal model includes all significant effects.)

effect	F	d.f.	p -value	estimate	s.e.
maximal model					
mean counterpart length on LE	3.22	1	0.087	—	—
site	1.94	1	0.180	—	—
number of counterparts on tree	0.35	1	0.559	—	—
leaf-spiral direction	0.57	1	0.457	—	—
minimal model					
leaf-spiral direction	—	—	—	-1.33	0.249***
counterpart length on LE	—	—	—	0.57	0.237*
site	—	—	—	8.80	4.267*
counterpart length on LE \times site	—	—	—	-0.56	0.255*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 2. Summary data and ratio for stepped-cut tools

(The measurements are shown in figure 1c.)

	mean (cm)	s.e.	n	range
Mount Panié				
length				
both edges	19.13	0.1950	715	7.00–35.4
left edge	20.57	0.1963	515	9.70–35.4
right edge	15.44	0.3696	200	7.00–35.4
width	0.86	0.0073	715	0.30–1.50
number of steps	3.53	0.0334	565	2.00–7.00
length of tapered section	10.22	0.1803	565	2.20–25.5
tapered section/length	0.53	0.0058	565	0.17–0.92
Pic Ningua				
length				
both edges	16.54	0.1244	388	7.40–30.1
left edge	16.29	0.1396	306	7.40–30.1
right edge	17.49	0.2487	82	13.10–26.1
width	0.96	0.0066	388	0.40–1.70
number of steps	3.03	0.0192	329	1.00–5.00
length of tapered section	8.96	0.1053	329	0.00–14.5
tapered section/length	0.54	0.0055	329	0.00–0.96

tools of the shape classes that would be expected for tools shorter (class 1) and longer (class 27) than class 14 from a close relationship between length, width and the number of steps. However, there was only one record (class 8 at Mount Panié) of crows making short or narrow tools with many (more than four) steps (classes 7–9, 16 and 25) or long or wide tools with few (one to two) steps (classes 3, 12 and 19–21), which would be expected. Birds mostly made tools with three or four steps at Mount Panié (46 and 38%, respectively, of the 565 tools in figure 4) and Pic Ningua (89 and 7%, respectively, of the 329 tools) in all tool length categories. Only one out of the 894 tools in figure 4 (at Pic Ningua) had one step (i.e. an untapered strip of leaf edge, 23.1 cm long and 0.4 cm wide). The examples of shapes of actual stepped-cut tools removed from the counterparts (figure 4) show that there was also

variation in the position and spacing of the stepped cuts along the tapered edge, the angle of the stepped cuts, the width of individual steps and the shape of the wide ends of tools.

Greater uniformity in the shapes of the pandanus tools occurred at Pic Ningua than at Mount Panié, as indicated by figure 4 and the lower standard errors in table 2. For example, at Pic Ningua 60% of the 329 tools were in class 14 (15–24.9 cm long, 0.7–1.09 cm wide and with three to four steps). In fact, the shapes of these tools were much more uniform than even this indicates because 89% of the 197 tools in class 14 were 15–19.9 cm long and had three steps. At Mount Panié, 44% of the 565 tools were in class 14 and, of these, only 25% were 15–19.9 cm long with three steps but 35% were 20–24.9 cm long and had four steps.

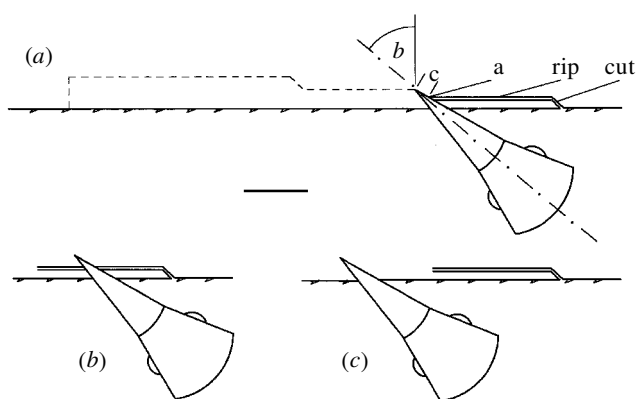


Figure 3. (a) Standard manufacturing method for a stepped-cut tool (the tool in figure 1c). Crows first make a cut to form the pointed end of the tool and then rip a thin strip of leaf edge away from the trunk to position a. When making cuts, the longitudinal axis of the birds' bills is offset from right angles to the leaf edge at an average of ca. 50° (angle *b*). The mean angles of the second cut were 54° (s.d. = 13.6°) on 24 counterparts from one of the sampled trees at Mount Panié, and 61° (s.d. = 4.6°) on 23 counterparts from one tree at Pic Ningua. Crows can make cuts at right angles to the leaf edge, for example when cutting out the wide ends of tools. Crows make a cut with the leaf edge (the soon-to-be tool) between their mandibles. Only one side of the bill at the tip (region c) makes a cut which prevents damage to the tool. To make cuts to form steps, the bill is positioned so that the cut is angled from the end of the rip (position a) from the last cut inwards from the leaf edge. Cut(s) at the wide end to remove the tool complete its manufacture and are made using the left side of the bill. Crows remove tools from REs in exactly the same way, but with the left side of the head mostly angled towards the leaf edge. The dashed line outlines the yet-to-be-completed tool. The tip of the bird's bill is drawn approximately to scale from bill marks on leaf material. Scale bar, 2 cm. (b) The position of the bill to make a stepped cut before the end of a rip. Note that this would result in the rip continuing into the tool. (c) The position of the bill to make a stepped cut after a rip terminates.

In separate logistical regression analyses, the tools (in figure 4) the crows made at Mount Panié were longer ($F_{1,890} = 72.4$ and $p < 0.0001$), narrower ($F_{1,890} = 222.8$ and $p < 0.0001$) and had more steps on them ($F_{1,890} = 152.5$ and $p < 0.0001$) than those the crows made at Pic Ningua when corrected for the variation in each of the other two main shape characteristics. In a GLM analysis to see what factors might be influencing tool length (table 3), the length and width of a tool and the number of steps on it were significantly associated, that is longer tools were generally wider and had more steps. There were two interesting significant interactions between the effects (tables 2 and 3). First, at Mount Panié tools on LEs were longer than those on REs, whereas the inverse occurred at Pic Ningua. Second, the tools were long and narrow at Mount Panié but shorter and wider at Pic Ningua.

4. DISCUSSION

The high use of LEs compared to REs for tool removal at both sites demonstrates functional lateralization or

handedness in crows' pandanus tool-making at least at the local population level. There were no obvious physical environmental factors which explained this preference for the use of LEs over REs. First, the similar strong bias for the use of LEs at both sites suggests that the variation in habitat characteristics and the numbers of counterparts on trees had minimal influence on the edges that crows used. Second, this bias existed regardless of leaf-spiral direction and the likelihood of a disadvantage of using LEs on ACL leaves because access to these leading edges was probably poorer. Third, I observed little lateral asymmetry in the pandanus leaves that I removed counterparts from. Fourth, it seems unlikely that crows used LEs out of habit because of a greater frequency of trees with CL leaves (whose LEs are probably more accessible) and/or that they targeted CL leaves as I found equal numbers of juvenile and young trees with CL and ACL leaves and no difference in the frequency of use of trees with CL and ACL leaves for tool-making. Lastly, counterparts were also common on older trees with leaves spiralling bidirectionally and much more often on the LEs of these leaves than REs (G. R. Hunt, unpublished data).

Stepped-cut tool-making appears to meet the three criteria outlined in §1 for tools shaped to a rule system. First, making these tools involves the 2D sculpting of pandanus leaves. This is obvious from the range of shapes of stepped-cut tools and that the likelihood of accidentally ripping off a tapered or stepped-tapered shape is extremely low because of the strong longitudinally parallel fibres (G. R. Hunt, personal observation). The sculpting of a tapered edge also requires the simultaneous control of two shape variables (length and width) and the shape of a stepped-cut tool seems to be important. Its sturdy, pointed form appears highly functional (see §1) and manufacturing it involves appropriately different techniques to shape the tapered and 'blunt' edges at opposite ends of a tool. The removal of a well-defined, stepped-tapered edge is not obligatory (e.g. see the middle tool in the inset in figure 4) but shows an appropriate exploitation of an important physical characteristic (strong parallel fibres) of pandanus leaves. It requires minimal cutting action with the bill, whereas making a straight tapered edge should be much more difficult because it would require scissor-like cutting along the entire length of the edge. Crows also very rarely make stepped-cut tools with leaf edge barbs facing inappropriately towards the pointed ends of tools (see figure 4). Thus, the shape of a stepped-cut tool is clearly determined more by the crow than the material and appears to be important in relation to function and the use of an efficient method in forming a tapered edge.

Second, the shape of a stepped-cut tool is not simple and, in order to sculpt these tools from pandanus leaves, crows employ an ingenious technique requiring precision manipulation of their bills. The technique is more complex than that needed to remove an untapered strip of leaf edge because sculpting a stepped-tapered edge involves, for example, precise positioning of the bill relative to the end of a rip to form the second and additional steps. Thus, the technique of stepped-cut tool-making is skilful and a comparatively complex way of manufacturing a pandanus tool.

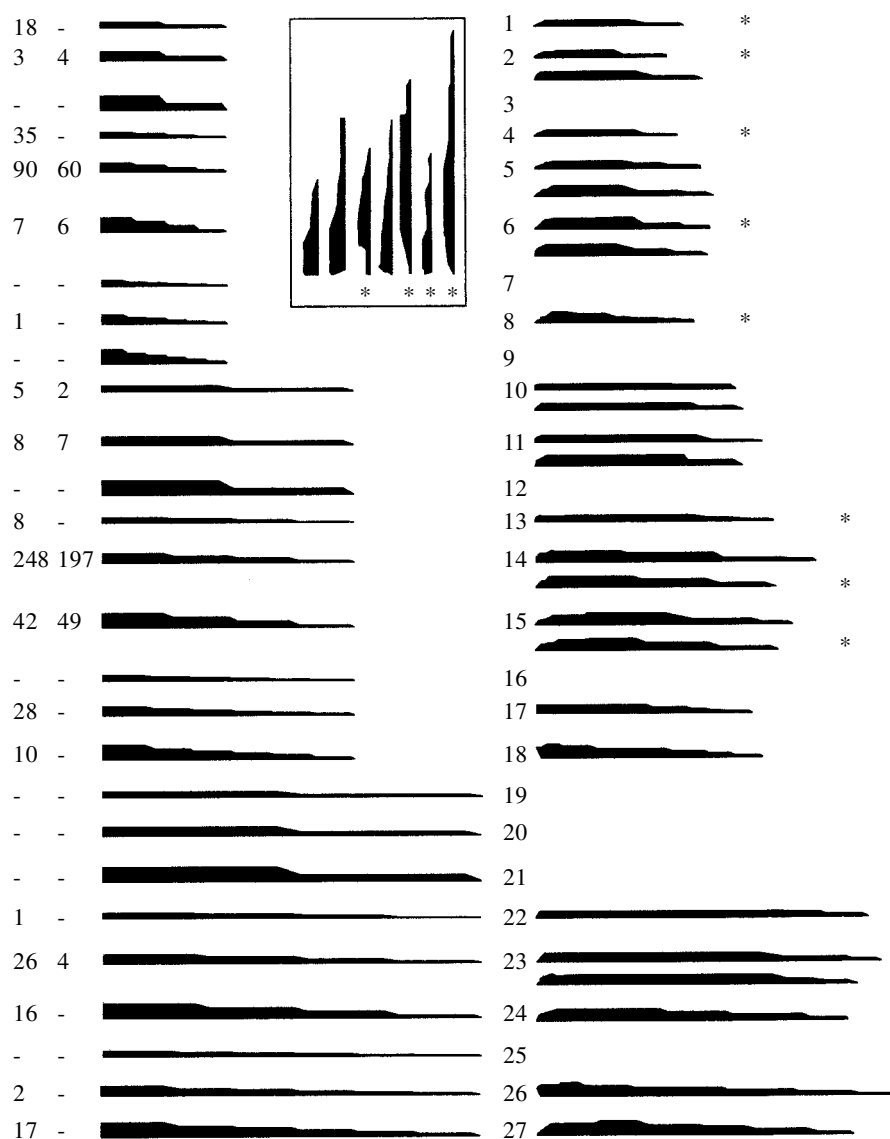


Figure 4. Comparison of the variation in the shapes of the stepped-cut tools (data taken from counterparts) at Mount Panié and Pic Ningua. Each tool on the left is a generalized representation of one of the 27 possible shape classes (numbered 1–27 between the two sets of tool shapes) which result from variation in the tool length, tool width and the number of steps per tool when these variables are separated into three categories. The categories are as follows. Length: (a) 5–14.9 cm, (b) 15–24.9 cm and (c) >24.9 cm. Width: (a) 0.3–0.69 cm, (b) 0.7–1.09 cm and (c) >1.09 cm. Steps per tool: (a) one to two steps, (b) three to four steps and (c) more than four steps. The numbers of tools in each shape class at Mount Panié (left column, $n = 565$) and Pic Ningua (right column, $n = 329$) are next to the wide ends of the tools; the data include only those tools where the number of steps per tool were well defined (a minus sign indicates that no tools were recorded). The variation in the angle of the stepped cuts is only an artefact of computer scaling. For scale, the tools are 10, 20 and 30 cm in length. The steps per tool are two, four and six. Each tool on the right is an example (randomly selected by drawing numbers when $n > 1$) of the shape of an actual tool from each shape class at each site. When two tools appear in a shape class, the top tool is from Mount Panié and the bottom one from Pic Ningua. The tools in the inset are examples of actual shapes which suggested possible inexperience in tool-making. The two tools from the left are from Pic Ningua and the other five are from Mount Panié. The two tools from the right in the inset are the only examples I found with the leaf edge barbs facing towards the pointed end of the tool, that is the crows removed these tools working towards not away from the trunk. An asterisk beside the shape of an actual tool indicates that the tool was removed from the RE of a leaf. The bottom edge is barbed on all tools outside the inset and the RE on those inside the inset.

Lastly, there was a high degree of morphological standardization in the shapes of the completed pandanus tools because (i) crows mostly made stepped-cut tools when they could make, for example, untapered tools, and (ii) the stepped-cut tools were highly similar in shape given the matrix of forms that they could take. Standardization related to the first point clearly resulted from crow behaviour and to the second point probably from crows'

use of a consistent manufacturing technique (e.g. a preference for making tools with three or four steps). Further research is needed in order to establish what factors determine this consistency of technique. Mechanical constraints are obviously involved, such as the difficulty in making very narrow tools with many steps. Systematic behavioural constraints on the tool-making process might also best explain the consistent patterns seen in the

Table 3. *Generalized linear model of stepped-cut tool length*

(The length data were modelled to a normal distribution; Mount Panié $n = 565$ and Pic Ningua $n = 329$. Edge: LE, 1 and RE, 0. The χ^2 -statistics and probability levels are when each effect was fitted last in the model. See the legend to table 1 for details.)

effect	maximal model			minimal model	
	χ^2	d.f.	p -value	estimate	s.e.
site	15.509	1	<0.001	-9.7	1.673***
edge	5.572	1	0.018	1.4	1.449**
leaf-spiral direction	1.659	1	0.198	-1.0	0.475 ^{n.s.}
width	0.956	1	0.328	2.7	1.862***
steps per tool	0.080	1	0.777	1.1	0.191***
site \times edge	34.725	1	<0.001	4.1	0.568***
width \times site	23.183	1	<0.001	10.1	1.687***
edge \times spiral direction	5.477	1	0.019	1.4	0.541**
width \times edge	4.910	1	0.027	-3.6	1.392*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and n.s., not significant.

lengths of tools, such as shorter tools on REs compared to LEs at Mount Panié and the inverse at Pic Ningua. The constraints associated with the raw material, such as leaf length and leaf thickness, might not greatly influence, for example, the lengths of the stepped-cut tools. The tools were nearly always removed from mature leaves many times longer than their length and the lengths of the tools varied widely even when removed from the same sides of leaves on the same tree (G. R. Hunt, unpublished data) where leaf thickness should be similar. It is difficult to see any mechanical and/or physical constraints on the tool-making process similarly 'constraining' the shapes of stepped-cut tools at both sites within a relatively extensive range of possible shapes. One possible explanation might be foraging-related selection for appropriately shaped tools. The use, for example, of relatively long and short tools could conceivably result in lower foraging success because of difficulty of manipulation or poorer 'reach', respectively. That American crows (*Corvus brachyrhynchos*) are reported to maximize the energy obtained from walnuts in walnut-dropping behaviour (Cristol & Switzer 1999) suggests that crows could have potentially evolved or learned to make appropriately shaped pandanus tools to provide, on average, maximum foraging success.

The crows were specialists in sculpting stepped-cut tools because they rarely made untapered tools and there was little indication of complete inexperience in removing stepped-cut tools. They also importantly shaped these tools before they used them, using a 'one-step' manufacturing process which should have rarely, if at all, involved 'retouching' once a tool was separated from the leaf. Therefore, when a crow manufactured a stepped-cut tool from a pandanus leaf there seems little doubt that its tapered, stepped form was predetermined by a rule system before manufacturing began. At Pic Ningua in particular, the shapes of the stepped-cut tools (Hunt 1996; this study) indicated that replication-like manufacturing of a specific, predetermined, tapered, stepped form was occurring. The rule system must be stored in neural memory as, for example, experienced crows do not copy other tools or tool-makers when making hooked-twig tools (G. R. Hunt, personal observation). Experiments can only establish the type (learned and/or innate), form

(e.g. step-by-step instructions or the final shape of a tool) and location of this memory. However, it is not necessary to know the mechanism(s) behind a process such as the shaping of tools to a rule system to show that it occurs (De Waal 1999).

Crows might prefer LEs for tool-making because of, for example, social tradition or an innate predisposition for using these edges. An island-wide preference for LEs would be strong evidence for the latter. This study suggests that such a preference might exist and work planned for 2000 looking at additional sites will give a much better indication as to whether or not the bias for LEs is widespread. That a crow's right eye and right side of the bill appear to be mostly used when removing stepped-cut tools from LEs (figure 3) is consistent with a biological explanation because specialization of the right-eye system for object-related tasks in the binocular field has been found in chickens and pigeons (Rogers 1996; Güntürkün 1997). A rule system for stepped-cut tool-making stored in the neural memory might facilitate lateralized tool-making even if a preference for a particular edge is not determined biologically. This is because of the need to access that memory and the fact that most neural pathways from a bird's eye are connected to the opposite side of the brain (Rogers 1996). Specialization of the right-eye system has also been found for access to long-term memory of cache sites in food-caching marsh tits (*Parus palustris*) (Clayton 1993). Caching is also common behaviour in *Corvus* sp. and has been observed in crows (Hunt 2000). Careful experimentation will also be needed in order to establish the mechanism(s) behind crows' handedness in pandanus tool-making.

Chimpanzees are the only non-human primates which extensively make and use tools in the wild (Beck 1980). They have been proposed as a homologous model system for learning about the behaviour and cognitive capabilities of the humans who made so-called Oldowan stone tools (those before ca. 1.5 Myr ago) (Wynn & McGrew 1989). They do not appear to be a suitable model system for learning about the humans who made later stone tools because of '... the looseness in chimpanzee tool-use traditions ... and very little, if any, accumulation of modifications over time ...' (Nagel *et al.* 1993, p. 185). In addition,

handedness is unknown in the tool-making of free-living chimpanzees at the population level. However, to this author's knowledge, no studies have investigated this aspect of their tool behaviour. Research, though, has not found a population bias for handedness in the tool use of free-living chimpanzees (review by McGrew & Marchant (1997) and references therein).

It has been suggested that the chimpanzees of the Tai Forest, Ivory Coast, have a 'predefined' (Boesch & Boesch 1990) or 'preconceived' (Boesch 1996) idea of a finished stick tool because they mostly made these tools before using them and they were similar in length and diameter. Chimpanzees in other localities commonly modify their stick tools after first use (Boesch & Boesch 1990). Tai chimpanzees' stick tools may meet the third criterion (morphological standardization) for tools shaped to a rule system, but the morphological similarity is largely caused by the shape of a stick tool being determined more by the material than the tool-maker (Isaac 1976; Lieberman 1991). For example, at feeding sites Tai chimpanzees usually chose branches within arm's reach and stick tools essentially only varied in two ways (length and diameter) due to lack of sculpting (Boesch & Boesch 1990). As Lieberman (1991, p. 159) stated about chimpanzees' stick tools, '... neither the technique used... nor the [finished tool] is very "abstract" in the sense of departing profoundly from the initial material—the branch with twigs and leaves'. This contrasts with the standardized shapes of stepped-cut tools which can vary in many ways because their form is sculpted and due more to crow behaviour than the material. Chimpanzees' stick tools do not meet the first and second criteria because making these tools usually only involves simple techniques such as removal of leaves or shortening and no sculpting (Boesch & Boesch 1990). Stick tool-making is also considered to involve the control of only one shape variable (e.g. length or diameter) at a time (Wynn & McGrew 1989). Thus, there is little artefactual or behavioural evidence to suggest that chimpanzees shape their stick tools to rule systems as defined here (Wynn & McGrew 1989).

The shaping of stepped-cut tools to a rule system points to the possibility that crows have progressed in their tool-making because this capacity is an advanced feature in human tool-making (e.g. Isaac 1976; Mellars 1989). This possibility is also supported by crows' manufacture and use of hook tools, which again is an advanced feature in human tool behaviour. Hooks appeared late (<100 000 years ago) in the tool-making of humans (Oakley 1961; Yellen *et al.* 1995) and the use of such features requires an understanding of the complex functional relationships between the properties of a tool and their effects on objects (Caron *et al.* 1988). To the author's knowledge, the manufacture and use of hooks by crows is unprecedented in the tool behaviour of free-living non-humans (Hunt 1996). Boesch (1996) claimed that Sugiyama & Koman (1979, p. 523) had reported hook use by chimpanzees in Guinea, however the authors concluded unambiguously that the animals had little understanding of how to make or use '...an effective hook-type stick-tool'. The latter has support from experiments showing a lack of cause-effect recognition by captive chimpanzees when given the choice of using either the forked (forks widely spaced) or flat-edge side of a rake to pull a small object towards

them (Nagel *et al.* 1993). Trial-and-error shaping of tools by chimpanzees would be consistent with the simple technical level of their tool traditions in the wild (McGrew *et al.* 1979; Boesch & Boesch 1990) which do not appear to have accumulated innovations (Nagel *et al.* 1993; Tomasello *et al.* 1993; Tomasello 1996; Boesch & Tomasello 1998). In contrast, the range of shapes of pandanus tools also suggests the possibility of progress in crows' tool-making. Compared to the rarely made untapered tools, stepped-cut tools appear to have more functionally appropriate attributes (i.e. a tapered pandanus tool provides both a sturdy and a pointed tool whereas an untapered one can only be either pointed or sturdy depending on its width) and are manufactured by a more involved technique (discussed above). As far as the author is aware, pandanus tool-making is the only reported use of pandanus leaves by *Corvus* sp. and there is no comparable behaviour to the shaping of this material for tools in crows or other Corvidae in the wild. Crows' use of pandanus leaves, then, may have evolved independently in New Caledonia and only in association with tool behaviour.

Many intriguing but unanswered questions are raised by crows' tool behaviour such as whether or not they learn their tool-making skills (Plotkin 1997). *Corvus* sp. in general are opportunist social foragers and resourceful at obtaining food without tools (e.g. Cristol & Switzer 1999) which has contributed to their human-like dispersal around the world in a wide range of habitats (Coombs 1978). In captivity, they can learn novel ways of obtaining food and resources by manipulating objects individually or from observing conspecifics (Reid 1982; Heinrich 1995; Fritz & Kotschal 1999) and are reported to be capable of insight (Heinrich 1995). The characteristic capacity of *Corvus* sp. for 'intelligent' behaviour may be related to their relatively highly developed forebrain (Voronov *et al.* 1994) which is responsible for avian learning and intelligence (Gill 1989). It would not be surprising, then, if a species of *Corvus* showed advanced tool behaviour (Plotkin 1997) and it would be equally unsurprising if crows at least in part learn their tool know-how. Crows do show flexibility in tool behaviour, which is seen as evidence of learning in chimpanzees (McGrew 1992) such as the making and use of two types of (hook) tool at a site (Hunt 1996) and distinctly different tool traditions in close proximity (Hunt 2000).

It is becoming increasingly recognized that birds make highly suitable model systems for learning about the relationships between human behaviour and neurology, such as vocal learning and memory and also asymmetry in the processing and memory associated with vision-related behaviours (Rogers 1996; Clayton & Soha 1999; Doupe & Kuhl 1999). The data I have presented here show that crows offer an extant model system for learning about the behaviour and neurological faculties associated with an early stage of advancement in tool-making. I found new evidence of human-like specialization in crows' manufacture of hook tools from pandanus leaves: functional lateralization or handedness and the shaping of tools to a rule system. These population-level features are unprecedented in the tool-making of non-humans and provide the first demonstration that a population bias for handedness in tool-making and the shaping of tools to rule systems are not concomitant with symbolic thought and language. It

is generally assumed (e.g. Isaac 1976; Tattersall 1998) that our early ancestors obtained their tool behaviour socially, but it is unknown how crows obtain their tool behaviour. At the least, crows provide an extant species for learning about the neuropsychology associated with early specialized and/or advanced population features in tool-making, such as handedness, hook use and the shaping of tools to rule systems, including an opportunity to see whether left-hemisphere specialization of the brain for the organization of sequential, manipulatory behaviours in tool-making might indeed be phylogenetically very ancient. If crows' tool behaviour involves cultural transmission, they also offer the opportunity for studying tool-making which might be similar to tool-making by pre-modern humans where cognitive, behavioural and social processes may have resulted in largely repetitive rather than innovative tool manufacture, and symbolism and language were rudimentary or absent (e.g. Dibble 1989; Davidson & Noble 1993; Potts 1993).

I thank E. DuFaily for accommodation, C. Lambert (Service des Parcs et Réserves Terrestres, Province Sud) and C. Papineau (Service Forêts-Bois et Environnement, Province Nord) for permission to work at Pic Ningua and Mount Panié, respectively; Tony Whitaker for identifying the Mount Panié site and M. Corballis, A. Kacelnik, D. Penny, A. Robertson and L. Rogers for their comments on drafts of this work. I am particularly grateful to C. Veltman and two anonymous referees for their comments which resulted in a more rigorous and substantially improved paper.

REFERENCES

- Angleviel, F. & Biliquy, O. (eds) 1992 *Atlas de Nouvelle Calédonie*. Noumea, New Caledonia: Editions du Cagou.
- Beck, B. B. 1980 *Animal tool behaviour: the use and manufacture of tools by animals*. New York: Garland.
- Bisazza, A., Rogers, L. J. & Vallortigara, G. 1998 The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neurosci. Biobehav. Rev.* **22**, 411–426.
- Boesch, C. 1996 The question of culture. *Nature* **379**, 207–208.
- Boesch, C. & Boesch, H. 1990 Tool use and tool making in wild chimpanzees. *Folia Primatol.* **54**, 86–89.
- Boesch, C. & Tomasello, M. 1998 Chimpanzee and human cultures. *Curr. Anthropol.* **39**, 591–614.
- Bradshaw, J. L. 1991 Animal asymmetry and human heredity: dextrality, tool use and language in evolution—10 years after Walker (1980). *Br. J. Psychol.* **82**, 39–59.
- Caron, A. J., Caron, R. F. & Antell, S. E. 1988 Infant understanding of containment: an affordance perceived or a relationship conceived? *Dev. Psychol.* **24**, 620–627.
- Clayton, N. S. 1993 Lateralization and unilateral transfer of spatial memory in marsh tits. *J. Comp. Physiol. A* **171**, 799–806.
- Clayton, N. S. & Soha, J. A. 1999 Memory in avian food caching and song learning: a general mechanism or different processes? *Adv. Stud. Behav.* **28**, 115–173.
- Coombs, F. 1978 *The crows: a study of the corvids of Europe*. London: B. T. Batsford Ltd.
- Corballis, M. C. 1991 *The lopsided ape*. New York: Oxford University Press.
- Coren, S. & Porac, C. 1977 Fifty centuries of right-handedness: the historical record. *Science* **198**, 631–632.
- Cristol, D. A. & Switzer, P. V. 1999 Avian prey-dropping behavior. II. American crows and walnuts. *Behav. Ecol.* **10**, 220–226.
- Davidson, I. & Noble, W. 1993 Tools and language in human evolution. In *Tools, language and cognition in human evolution* (ed. K. R. Gibson & T. Ingold), pp. 363–388. Cambridge University Press.
- Deacon, T. 1997 *The symbolic species: the co-evolution of language and the human brain*. London: Allen Lane The Penguin Press.
- Délaour, J. 1966 *Guide des oiseaux de la Nouvelle-Calédonie et de ses dépendances*. Paris: Delachaux & Niestlé.
- De Waal, F. B. M. 1999 Cultural primatology comes of age. *Nature* **399**, 635–636.
- Dibble, H. L. 1989 The implications of stone tool types for the presence of language during the Lower and Middle Palaeolithic. In *The human revolution: behavioural and biological perspectives on the origins of modern humans* (ed. P. Mellars & C. B. Stringer), pp. 415–432. Princeton University Press.
- Doupe, A. J. & Kuhl, P. K. 1999 Birdsong and human speech: common themes and mechanisms. *A. Rev. Neurosci.* **22**, 567–631.
- Fritz, J. & Kotrschal, K. 1999 Social learning in common ravens, *Corvus corax*. *Anim. Behav.* **57**, 785–793.
- Gibson, R. & Ingold, T. (eds) 1993 *Tools, language and cognition in human evolution*. Cambridge University Press.
- Gill, F. B. 1989 *Ornithology*. New York: W. H. Freeman & Co.
- Güntürkün, O. 1997 Avian visual lateralization: a review. *NeuroReport* **8**, iii–xi.
- Heinrich, B. 1995 An experimental investigation of insight in common ravens (*Corvus corax*). *Auk* **112**, 994–1003.
- Hunt, G. R. 1996 Manufacture and use of hook-tools by New Caledonian crows. *Nature* **379**, 249–251.
- Hunt, G. R. 2000 Tool use by the New Caledonian crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu*. (In the press.)
- Isaac, G. L. 1976 Stages of cultural elaboration in the Pleistocene: possible archaeological indicators of the development of language capabilities. *Ann. NY Acad. Sci.* **280**, 275–288.
- Jaffré, T. 1993 The relationship between ecological diversity and floristic diversity in New Caledonia. *Biodiv. Lett.* **1**, 82–87.
- Lieberman, P. 1991 *Uniquely human: the evolution of speech, thought, and selfless behaviour*. Cambridge, MA: Harvard University Press.
- McGrew, W. C. 1992 Tool-use by free-ranging chimpanzees: the extent of diversity. *J. Zool. Lond.* **228**, 689–694.
- McGrew, W. C. & Marchant, L. F. 1997 Using the tools at hand: manual laterality and elementary technology in *Cebus* spp. and *Pan* spp. *Int. J. Primatol.* **18**, 787–810.
- McGrew, W. C., Tutin, C. E. G. & Baldwin, P. J. 1979 Chimpanzees, tools, and termites: cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man* **14**, 185–214.
- MacNeilage, P. F., Studdert-Kennedy, M. G. & Lindblom, B. 1987 Primate handedness reconsidered. *Behav. Brain Sci.* **10**, 247–303.
- Mellars, P. 1989 Major issues in the emergence of modern humans. *Curr. Anthropol.* **30**, 349–385.
- Nagel, K., Olguin, R. S. & Tomasello, M. 1993 Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J. Comp. Psychol.* **107**, 174–186.
- Noble, W. & Davidson, I. 1996 *Human evolution, language and mind: a psychological and archaeological inquiry*. Cambridge University Press.
- Oakley, K. P. 1961 *Man the tool-maker*. London: British Museum (Natural History).
- Plotkin, H. 1997 *Evolution in mind: an introduction to evolutionary psychology*. London: Allen Lane The Penguin Press.
- Pobiner, B. L. 1999 The use of stone tools to determine handedness in hominids. *Curr. Anthropol.* **40**, 90–92.
- Potts, R. 1993 Archeological interpretations of early hominid behavior and ecology. In *The origin and evolution of humans and humanness* (ed. D. Tab. Rasmussen), pp. 49–74. Boston, MA: Jones and Bartlett Publishers.

- Reid, J. B. 1982 Tool-use by a rook (*Corvus frugilegus*), and its causation. *Anim. Behav.* **30**, 1212–1216.
- Rogers, L. J. 1989 Laterality in animals. *Int. J. Comp. Psychol.* **3**, 5–25.
- Rogers, L. J. 1996 Behavioral, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. *Neurosci. Biobehav. Rev.* **20**, 487–503.
- Semaw, S., Renne, P., Harris, W. K., Feibel, C. S., Bernor, R. L., Fesseha, N. & Mowbray, K. 1997 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* **385**, 333–336.
- Sugiyama, Y. & Koman, J. 1979 Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. *Primates* **20**, 513–524.
- Tattersall, I. 1998 *Becoming human: evolution and human uniqueness*. Orlando, FL: Harcourt Brace & Co.
- Thieme, H. 1997 Lower Palaeolithic hunting spears from Germany. *Nature* **385**, 807–810.
- Tomasello, M. 1996 Do apes ape? In *Social learning in animals: the roots of culture* (ed. C. M. Heyes & B. G. Galef), pp. 319–346. New York: Academic Press.
- Tomasello, M., Kruger, A. C. & Ratner, H. H. 1993 Cultural learning. *Behav. Brain Sci.* **16**, 495–552.
- Toth, N. 1985a The Oldowan reassessed: a close look at early stone artifacts. *J. Archaeol. Sci.* **12**, 101–120.
- Toth, N. 1985b Archaeological evidence for preferential right-handedness in the Lower and Middle Pleistocene, and its possible implications. *J. Hum. Evol.* **14**, 607–614.
- Voronov, L. N., Bogoslovskaya, L. G. & Markova, E. G. 1994 A comparative study of the morphology of forebrain in corvidae in view of their trophic specialization. *Zool. Zh.* **73**, 82–96.
- Ward, J. P. & Cantalupo, C. 1997 Origins and functions of laterality: interactions of motoric systems. *Laterality* **2**, 279–303.
- Wynn, T. 1979 The intelligence of later Acheulean hominids. *Man* **14**, 371–391.
- Wynn, T. & McGrew, W. C. 1989 An ape's view of the Oldowan. *Man* **24**, 383–398.
- Yellen, J. E., Brooks, A. S., Cornelissen, E., Mehlman, M. J. & Stewart, K. 1995 A middle stone age worked bone industry from Katanda, Upper Semliki Valley, Zaire. *Science* **268**, 553–556.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.