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Diversification and cumulative evolution in New Caledonian crow tool manufacture

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Many animals use tools but only humans are generally considered to have the cognitive sophistication required for cumulative technological evolution. Three important characteristics of cumulative technological evolution are: (i) the diversification of tool design; (ii) cumulative change; and (iii) high-fidelity social transmission. We present evidence that crows have diversified and cumulatively changed the design of their pandanus tools. In 2000 we carried out an intensive survey in New Caledonia to establish the geographical variation in the manufacture of these tools. We documented the shapes of 5550 tools from 21 sites throughout the range of pandanus tool manufacture. We found three distinct pandanus tool designs: wide tools, narrow tools and stepped tools. The lack of ecological correlates of the three tool designs and their different, continuous and overlapping geographical distributions make it unlikely that they evolved independently. The similarities in the manufacture method of each design further suggest that pandanus tools have gone through a process of cumulative change from a common historical origin. We propose a plausible scenario for this rudimentary cumulative evolution.

Keywords: tool manufacture; cultural evolution; New Caledonian crows; pandanus tools

1. INTRODUCTION

Many animals use tools, but tool manufacture is rare (Beck 1980). Rarer still is cumulative technological evolution, which is essential for the development of complex material culture (Tomasello *et al.* 1993; Boyd & Richerson 1996; Tomasello 1999). Modern humans evolved their sophisticated technology by the faithful transmission of tool design through social learning. The skills underlying this high-fidelity social transmission are reported to include an understanding of physical relationships and functional properties of objects (Tomasello & Call 1997; Tomasello 1998; Povinelli 2000), an understanding of intentions and goals of others (Heyes 1993; Tomasello & Call 1997; Tomasello 1998, 1999), and the ability for fine object manipulation (Diamond 1992; Whiten 2001). Animals other than humans are generally presumed to lack the necessary neural hardware and cognitive sophistication for this level of tool behaviour (Tomasello *et al.* 1993; Boyd & Richerson 1996; Tomasello 1999). Even chimpanzee *Pan troglodytes* tool manufacture is often haphazard (Kummer & Goodall 1985; Nagel *et al.* 1993; Tomasello *et al.* 1993) and their tools show no evidence of incremental change over time (Tomasello *et al.* 1993; Boesch & Tomasello 1998). The extent to which chimpanzees understand the functional properties of objects is also contentious (Nagel *et al.* 1993; Tomasello & Call 1997; Povinelli 2000).

Hunt (2000*a*) suggested that the complex-shaped stepped pandanus tools New Caledonian crows *Corvus moneduloides* make to extract prey from rainforest vegetation (Hunt 1996) may have evolved from simpler tools. Three important characteristics of cumulative technological evolution are: (i) diversification of tool design; (ii) cumulative change to tool lineages; and (iii) faithful transmission of tool design through social learning (Isaac 1976; Tomasello *et al.* 1993; Foley & Lahr 1997). Diversification occurs when a new tool design is added to one or more existing, related designs. This forms a branching sequence of tool evolution from a single ancestral design, in contrast to the independent development of similar designs. Diversification is clearly observed in the evolution of human stone tools from simple Oldowan-type cutting flakes and hammer stones to the diverse range of shaped tool types (e.g. knives, blades, arrowheads, axeheads) made at the end of the Palaeolithic (Oakley 1961; Isaac 1976; Foley & Lahr 1997).

The cumulative nature of natural selection is an essential requirement for adaptive biological evolution (Dawkins 1988). A similar cumulative process in tool design has allowed humans to develop progressively more sophisticated tool lineages; the evolution of the axe is a good example (Oakley 1961). This cumulative change is a 'ratchet-like' process where design changes are retained at the population level until new improved designs arise (Tomasello *et al.* 1993; Tomasello 1999). This is possible because tool design is transferred faithfully between individuals. In this way, an individual does not need to reinvent or recapitulate past designs to obtain the new design. Tools made by non-human animals such as chimpanzees are not the result of the ratchet effect (Tomasello *et al.* 1993; Boesch & Tomasello 1998) even though they may result from modification of raw material. Tool modifications that chimpanzees make usually only involve the removal of material in a stepwise process where the toolmaker proceeds through past versions (e.g. leafy stick, then stick with leaves removed) to arrive at the finished product (e.g. stick with leaves and bark removed) (Boesch & Boesch 1990). Such a tool may be produced by a unique set of modifications that incorporates past knowledge, but as it also recapitulates one or more earlier tool versions there is uncertainty as to whether the final design was predetermined before manufacture began.

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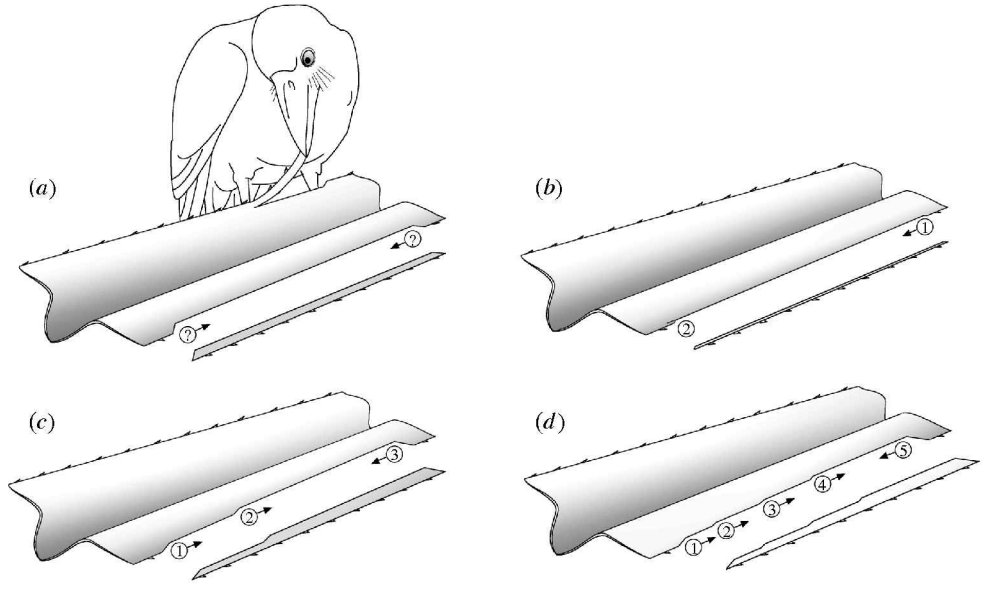

Figure 1. Principal manufacture technique for each pandanus tool design (also see § 2). (*a*) A crow making a basic cut and rip with the bill on the left edge of a section of pandanus leaf with an action that could be similar to that used in leaf ripping. The ripped strip is held between the bird's mandibles. The bill tip is level with the rip and only the left side of the bill, in this case, makes the short cut in from the leaf edge. The leaf section is *ca.* 5 cm wide and the leaf-edge barbs face away from the trunk towards the tip of the leaf at right. A wide tool is drawn alongside its counterpart shape on the right edge. Circles below the counterpart indicate when a cut with the bill is made. Numbers inside the circles give the temporal sequence of cuts (see *b–d*); question marks indicate that the sequence of cuts cannot be inferred. An arrow attached to a circle indicates an associated rip and its direction. (*b–d*) The same symbols and leaf section as in (*a*) describe the techniques used to manufacture a narrow tool, a one-step tool and a three-step tool, respectively. An arrow is missing from the second cut to make a narrow tool (*b*) because birds make a rip towards the trunk then appear to nip the hanging strip off the leaf before the end of the rip. To form a step on stepped tools (*c*,*d*), a crow holds the leaf edge between the mandibles and positions its bill tip close to and above the termination of the previous rip (Hunt 2000*a*). It then makes a step by cutting the leaf across the fibres with only one side of the tip of the bill before ripping the leaf longitudinally. The body of the tool is held further back in the mandibles and is rarely damaged due to the cutting of steps.

Social transmission is the only known transmission mechanism associated with both diversification and cumulative change in tool design. Cumulative tool evolution by social learning requires cognitive and behavioural skills that enable the development and high-fidelity transfer of distinct designs (Heyes 1993; Tomasello *et al.* 1993). Social learning is not required for tool use in woodpecker finches *Cactospiza pallida*, but seems to depend on a special learning disposition that involves trial-and-error experience during a sensitive period in early development (Tebbich *et al.* 2001). Acquisition of tool skills by chimpanzees also seems to involve mainly individual trial-and-error, combined with simpler social learning mechanisms such as 'stimulus enhancement' and 'emulation learning' (Paquette 1992; Nagel *et al.* 1993; Tomasello 1996; Tomasello & Call 1997; Celli *et al.* 2001). These methods of obtaining tool knowledge do not allow the finished design of tools to be transferred with high fidelity between individuals, and therefore would prevent any cumulative change from occurring in chimpanzee and finch tools.

We investigated New Caledonian crows to see if there was evidence of diversification and cumulative evolution in their tool manufacture. Crows manufacture two distinct types of tool to facilitate the capture of invertebrates in trees: one from twigs and similar material (Hunt 1996, 2000*b*; Hunt & Gray 2002), and the other from the long barbed edges of *Pandanus* species leaves (Hunt 1996, 2000*a*; Hunt *et al.* 2001). The monocotyledon pandanus trees, or screw pines, that crows use for tool manufacture consist of a leaf crown situated at the top of a narrow trunk. Their long (generally 2–3 m), narrow, leathery leaves have strong parallel fibres, which run longitudinally along their length and barbs along each edge facing away from the trunk. The manufacture of pandanus tools provides a unique opportunity for study because of the artefact record of tool 'counterparts' on leaves. The tool shapes that crows fashion from leaf edges are faithfully recorded in their counterparts, the outlines remaining on the leaf edge (Hunt 1996, 2000*a*; Hunt *et al.* 2001) (figure 1). This provides a complete artefactual history of the shapes and number of pandanus tools made at a site over the *ca.* 4 years that leaves stay on trees (Hunt 2000*a*). We collected counterparts between March and July 2000 to survey the current variation in pandanus tool manufacture throughout New Caledonia. Our specific objectives were: (i) to quantify the physical differences in the shape of pandanus tools; (ii) to describe any local and geographical differences in tool design; and (iii) to determine whether or not these differences might relate to ecological factors.

2. MATERIAL AND METHODS

(a) *Extent of the survey and site selection*

New Caledonian crows occur throughout mainland Grande Terre ($> 16\,000$ km^2) and nearby Maré Island (< 100 km^2), where birds were introduced from the mainland after European

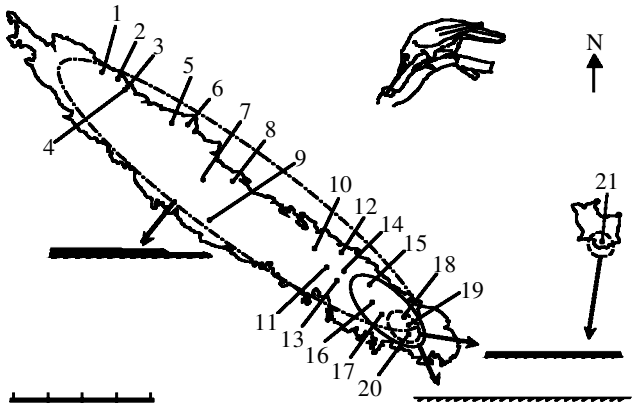

Figure 2. The 21 sites on New Caledonia's Grande Terre and Maré where we collected tool counterparts from pandanus leaves. Sites are grouped by tool design. Sites where a tool design accounted for less than 5.0% of the classified counterparts are not included (see table 1). The relative differences in the lengths of the tool symbols indicate significant differences in the mean lengths of classified tools for each design ($F_{2,5101} = 391.8$, $p < 0.0001$). Scale bar, 100 km.

colonization began *ca.* 1850 (Délacour 1966). Field observations by G.R.H. (e.g. observations for over 2 years at Pic Ningua) indicate that crows in the rainforest live relatively sedentary lifestyles. In rainforest on non-ultrabasic rocks, trees with counterparts are usually concentrated along high, damp ridges. On ultrabasic rocks (mostly in the lower third of Grande Terre), they are much more common on slopes. Four sites we sampled were chosen because we knew crows made pandanus tools at the locations. These sites were Mt Aoupinié, Pic Ningua, Mt Panié and Parc Rivière Bleue. Otherwise, we visited locations on Grande Terre and Maré where vegetation and terrain indicated that counterparts were more likely to occur, and collected them if they were present. On Grande Terre, we only visited one location (Mt Tchingou southwest of Mt Tonine) within the distribution of the sites that we sampled where we did not find counterparts. We visited six sites southeast of Parc Rivière Bleue but did not find counterparts on pandanus leaves, although crows were present at some of these locations. To our knowledge, the sites that we sampled on Grande Terre covered the geographical range of pandanus tool making there, and a wide variation in altitude (60–1600 m above sea level) and annual rainfall (1500–3500 mm). Sites were mostly in isolated locations and accessible only by foot. The mean distance from a sample site to the closest adjacent sample site was 11.9 km (s.e. = 1.24, $n = 20$). This sampling design reduced the possibility of overlap in the ranges of family groups and allowed us to investigate potential environmental influences on tool manufacture.

(b) *Sampling trees at sites*

Because numbers of counterparts on individual trees varied considerably (range 1 to more than 100), we used two collection methods to minimize any sampling bias. At sites 1–3 and 11, where the number was generally high (more than nine per tree), we sampled two trees at each of five locations at least 100 m apart. The locations were at regular intervals on transect lines, along contours and/or directly up slopes depending on the terrain and whereabouts of trees. We selected one tree at a location from a distance without knowledge of the number or shapes of counterparts on its leaves. We removed all actual and possible counterparts if there were more than nine counterparts present. Leaves on pandanus trees spiral in three ranks outwards and upwards at the top of a narrow trunk, in either an anticlockwise or clockwise direction (Hunt 2000*a*). Leaf-spiral direction might influence the shapes of tools (Hunt 2000*a*), so the second tree was that closest to the first tree with leaves spiralling in the opposite direction and (usually) more than nine counterparts (2 of the 10 trees at site 1 had more than 10 counterparts). At all other sites we followed transects, contours or ridges collecting all actual and possible counterparts from trees that we could see had them on their leaves. We rejected trees at these sites when their trunks were more than *ca.* 2 m high. Counterparts were common on shorter trunked trees. We removed and individually labelled all actual and possible counterparts and preserved them in 70% ethanol to minimize shape distortion.

(c) *Determination of tool shapes, tool manufacture techniques and data analyses*

To describe the shapes of tools that crows manufactured, we traced the outlines of all undamaged (wet) counterparts of wide and stepped tools onto 1 mm grid paper. From each outline, where possible, we measured tool length (the length of leaf edge removed) and tool width. For wide tools, we estimated the average width over the length of the counterpart. Measures for width and the length of the tapered section on stepped tools are described in Hunt (2000*a*). We recorded the number of steps on each stepped tool, or the minimum number that could be determined. Finally, we recorded the average width of the point, or the narrow end, on a stepped tool. The length and width of narrow tools were taken directly from counterparts. To obtain the shapes of wide and stepped tools in figure 3, we only included tools with a complete set of measurements: length and width for wide and narrow tools; length, width, length of tapered section, width of point and number of steps for stepped tools. The spacing and width of steps on the shapes of stepped tools, though, are arbitrary.

We inferred the manufacture techniques for the wide, narrow and stepped tools that crows removed from the counterparts in three ways. First, it is quite common for crows to begin manufacture of narrow and stepped tools but not complete the process. This gives us a good indication of the sequence of actions birds use to make these two designs. We have found few incomplete attempts at manufacturing wide tools and therefore do not know at which end (i.e. nearest the leaf tip or the trunk), if any, crows mostly begin manufacture. Second, bill marks are sometimes present on tools and counterparts. This evidence shows that the bill is used in manufacture and indicates its position to carry out cutting and ripping actions. Third, from a counterpart we can occasionally get an idea of the nature of individual rips (e.g. length) when convergent ones do not exactly align, as often happens when birds make wide tools. Finally, in July 2002 we observed one crow at Pic Ningua making over 40 multi-stepped tools. This confirms that crows do manufacture the stepped design starting from the narrow end, as Hunt (1996, 2000*a*) has previously inferred from artefactual evidence. Manufacture techniques probably vary somewhat for each design; therefore we present what we consider to be the predominant technique used.

After visual examination of the counterparts that we (G.R.H.) collected on the survey, it was obvious that crows manufactured pandanus tools of distinctly different designs. G.R.H. visually assigned counterparts to these design categories, together with an additional category for unclassifiable tools. To check G.R.H.'s classification of the counterpart shapes, R.D.G. independently

Table 1. Site data for classified pandanus tool counterparts.
(Sites 1–20 are listed geographically from northwest to southeast of Grande Terre (see figure 2). Column 3 gives the approximate mean altitude above sea level (a.s.l.) of the trees sampled. Column 4 gives the number of trees from which we removed counterparts. Columns 6–8 are percentages of classed tools in column 5; we could not classify 67 (1.2%) tool counterparts. In only 21 cases were we unsure if missing leaf edge was a tool counterpart. Narrow tools are probably overestimated because unfinished narrow, ripped strips left hanging from leaves can decay and fall off. This is much more unlikely to occur with unfinished stepped and wide tools because of their greater width.)

	site no.	altitude (m a.s.l.)	trees (*n*)	classed tools (*n*)	wide tools (%)	narrow tools (%)	stepped tools (%)
Mt Ignambi	1	730	10	164	0.6	0.0	99.4
Mt Colnett	2	570	10	279	0.7	0.0	99.3
Mt Panié (I)	3	420	10	593	0.2	0.0	99.8
Mt Panié (II)	4	1615	92	164	1.8	0.0	98.2
Mt Tonine	5	940	62	168	1.2	0.0	98.8
Mt Köhîdagé	6	800	48	169	2.4	0.0	97.6
Mt Aoupinié	7	770	67	261	1.9	0.0	98.1
Sommet Arago	8	820	24	296	1.0	0.0	99.0
Mt Këiyöumâ	9	710	70	294	0.0	0.0	100.0
Mt Nakada	10	1090	53	286	0.0	0.0	100.0
Pic Ningua	11	1100	10	206	0.5	0.0	99.5
Forêt de Saille	12	880	57	191	1.0	0.0	99.0
Mt St Vincent	13	1050	22	183	1.1	0.0	98.9
Pic Kambwi	14	1010	9	85	0.0	3.5	96.5
Mt Humboldt	15	950	45	251	0.0	85.3	14.7
Mt Ouin	16	1100	39	582	0.0	78.4	21.6
Mt Dzumac	17	980	51	300	0.7	44.0	55.3
Mt Bleue	18	800	64	202	5.9	43.6	50.5
Rivière Bleue	19	160	103	396	39.9	22.0	38.1
Mt Pouédihi	20	360	51	309	73.1	26.2	0.7
Maré Island	21	60	25	104	100.0	0.0	0.0
totals			922	5483			

reclassified 200 randomly selected counterparts. Classification was of counterpart shapes drawn onto tracing paper by G.R.H., not of actual counterparts. This was a conservative method because details of manufacture associated with the leaf material were lost when the shapes were traced. There was high concordance of R.D.G.'s independent classification with that of G.R.H.'s after chance agreement was taken into account (kappa coefficient: $\kappa = 0.94$).

We used generalized linear models to look for significant ecological correlates with tool variables. We first tested if the width of the leaf edge (continuous response variable) could be predicted by tool design (categorical variable). We then used the mean altitude of the sampled trees and the estimated annual rainfall at each site to see if they could significantly predict different response variables: the ratio of multi-step to one-step tools, the mean length of stepped tools, the presence versus absence of wide tools, the presence versus absence of narrow tools and the presence versus absence of stepped tools. We recorded the altitude of the trees that we sampled using an altimeter and 1 : 25 000 or 1 : 50 000 topographical maps. Annual rainfall at sites was taken from a meteorological map for New Caledonia drawn up by the Service de la Météorologie, Nouméa. This map was based on rainfall recorded continuously at locations throughout the territory between 1961 and 1990.

3. RESULTS

(a) *Extent of the survey*

We collected counterparts from pandanus leaves at 20 sites throughout Grande Terre and at one site on nearby Maré (figure 2). The sites on the *ca*. 400 km long Grande Terre covered the *ca*. 300 km of its length (excluding the extreme ends of the island) where we found that crows made pandanus tools. The numbers of counterparts we collected at each site varied (table 1; mean number classed = 261.1, s.e. = 28.8, $n = 21$), depending on the collection method, the time we had available, and their frequency on individual trees. The 922 trees from which we obtained 5550 counterparts (table 1) constituted only a small percentage of the pandanus trees with counterparts on their leaves. Pandanus tool manufacture by crows is therefore common and geographically widespread in New Caledonia.

(b) *Pandanus tool designs*

The shapes of the pandanus tools we obtained from tool counterparts fell into three distinct tool designs, each with a different method of manufacture (figure 1) and a different geographical distribution (figure 2). Counterparts of the previously discovered tapered, stepped tools were easily distinguishable from those of untapered tools. Untapered counterparts could be further separated into either wide tools or narrow tools. Wide tools were significantly wider and shorter than narrow tools (legend to figure 3). These shape differences meant that we could confidently visually classify over 98% of counterparts to either one of the three designs (see explanation of table 1 and § 2).

Manufacture of each tool design involves a unique series of actions (figure 1). Each action usually consisted of a basic cut and rip with the bill (figure 1*a*). Two such

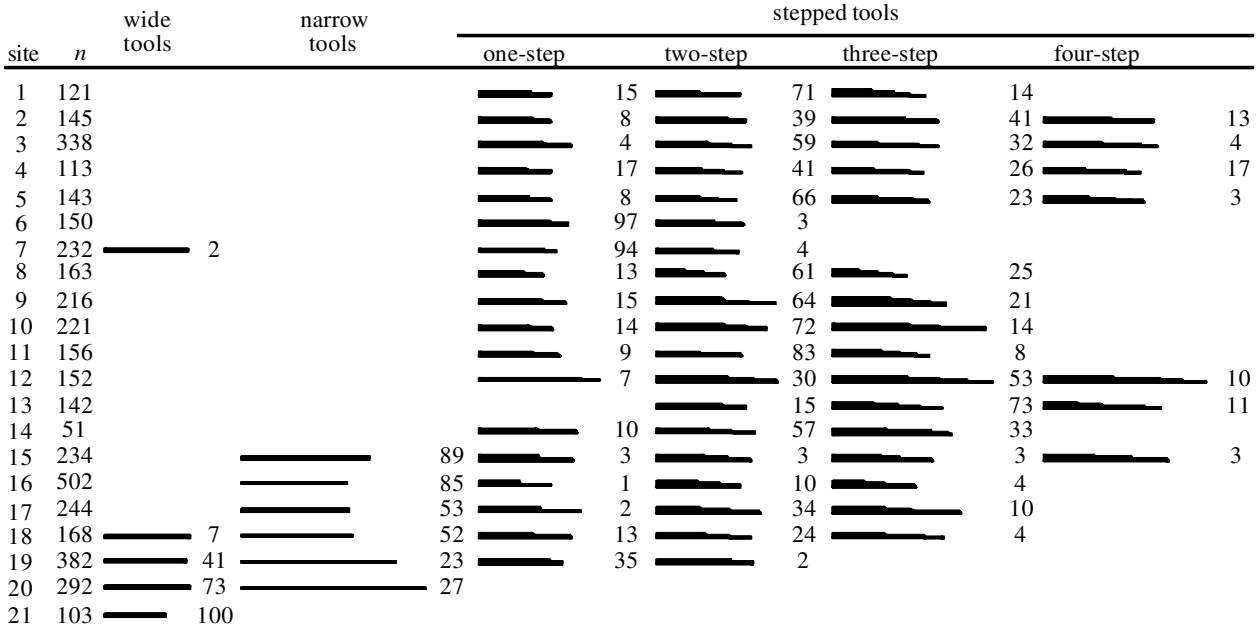

Figure 3. Variability in the design and shape of pandanus tools across collection sites. A shape was drawn only when $n > 4$ and provides an indication of the average shape (see § 2 for how shapes were drawn). The relative frequency (%) of a shape is to the right of the shape (percentages were rounded to whole numbers). Wide tools average 14.7 ± 0.15 cm (mean ± s.e.m.) in length and 0.47 ± 0.005 cm in width ($n = 512$); narrow tools 23.4 ± 0.24 cm ($n = 1022$) and 0.14 ± 0.002 cm ($n = 1008$); one-step tools 15.7 ± 0.14 cm and 0.59 ± 0.006 cm ($n = 728$); multi-step tools 19.3 ± 0.13 cm ($n = 2571$) and 0.91 ± 0.004 cm ($n = 2421$). The width of the narrow end on stepped tools averages 0.22 ± 0.01 cm ($n = 3347$). For scale, the wide tool at site 18 is 16 cm long.

actions are typically used for wide-tool manufacture (figure 1*a*), one towards and one away from the tree trunk. The making of a narrow tool also involves two sequential actions, but in this case a relatively long rip is made towards the tree trunk then crows seem to nip the hanging strip off the leaf just before the end of the rip (figure 1*b*). Manufacture of a one-step tool requires three sequential actions (figure 1*c*). Each additional step on the tool requires an additional cut–rip action, with a three-step tool, for example, requiring five sequential actions (figure 1*d*). Stepped tools are different from wide and narrow tools in that their width is different at each end of the tool. Consequently, birds must appropriately vary the distance in from the leaf edge that they place their bill when making a rip. At no stage in the process of making a tool is one of the other designs or varieties of stepped tool made then modified. That is, there is no recapitulation in pandanus tool manufacture.

(c) *Geographical distribution of pandanus tool designs*

On Grande Terre, stepped tools accounted for 5% or more of counterparts at 19 of the 20 sites (figure 2; table 1). Multi-step tools (two or more steps) were made much more frequently than one-step tools at 16 of these 19 sites (figure 3). Wide tools accounted for 5% or more of counterparts at sites only in the southeast of the island. We only found narrow tools in the southeast of Grande Terre and only wide tools on Maré. Therefore, all three designs co-occurred in a region only in the southeast of Grande Terre. They occurred at the same site, each with frequencies of 5% or more, only at adjacent sites 18 and 19.

(d) *Ecological factors and pandanus tool manufacture*

Variation in the raw material, altitude and rainfall does not appear to be a significant causal factor of the different geographical distributions of the designs. Leaf characteristics (e.g. length, thickness, width of leaf edge) should not influence the design of pandanus tools because we commonly found different designs on the same tree and even on the same leaf. The generalized linear model showed that the width of a leaf edge was a poor predictor of tool design ($F_{3,4438} = 0.90$, $p = 0.44$), after accounting for significant variation in the width of leaf edges between sites ($F_{20,4438} = 115.2$, $p < 0.0001$). Also, the rejection of some trees with longer trunks was unlikely to have influenced the detection of designs because the mean length of the trunk on trees that we sampled at sites was not significantly different between wide (1.45 ± 0.22 m, mean ± s.e.m., $n = 4$ sites), narrow (1.59 ± 0.16 m, $n = 6$) and stepped (1.72 ± 0.11 m, $n = 19$) designs ($F_{2,26} = 0.66$, $p > 0.05$). Annual rainfall and altitude did not significantly predict the ratio of multi-step to one-step tools (altitude: $F_{1,17} = 1.54$, $p = 0.23$; annual rainfall: $F_{1,17} = 0.14$, $p = 0.71$) or the mean length of stepped tools (altitude: $F_{1,17} = 0.005$, $p = 0.98$; annual rainfall: $F_{1,17} = 3.04$, $p = 0.10$) at sites. Annual rainfall was also not significantly associated with the presence of each design at sites (data from figure 1), but altitude was a significant predictor of the presence of wide tools ($F_{1,18} = 21.42$, $p < 0.0001$) and stepped tools ($F_{1,18} = 24.52$, $p < 0.0001$). Stepped tools were mostly made at higher altitudes, but at Mt Panié and Parc Rivière Bleue we found counterparts well below 500 m above sea level (table 1). Therefore, the significant

Table 2. Coefficient of variation (CV) values for each tool design.

tool design	variable	no. of sites	mean CV (%)/s.e.
wide	length	4	19.6/2.01
	width	4	23.0/1.85
narrow	length	6	25.0/0.76
	width	6	36.7/2.29
stepped	length	19	24.6/1.74
	width	19	19.6/0.61
	no. of steps	19	28.3/1.81

altitude effect may be an artefact of the restricted distribution of crows that commonly make wide tools in forest at low altitude in the southeast of Grande Terre and on Maré.

(e) *Site fidelity in the shape and design of pandanus tools*

Pandanus tools, like human tools, have high fidelity at sites in both the shape and the type of a design manufactured. At 18 of the 21 sites, at least 70% of the tools that we recorded were a single design (table 1). The shapes of stepped tools were also highly similar locally as demonstrated by the making of either one-, two- or three-step tools at percentages of over 50% at sites (figure 3). This was extreme at sites 6, 7 and 19 where one-step tools accounted for over 90% of stepped tools. Hunt (2000*a*) showed at two sites that the shapes of stepped tools were highly similar given the range of their shapes made at a site. In the current study, the variation in the shapes of each of the three designs at sites was also relatively low (table 2). Furthermore, we have evidence for high similarity in the shapes of stepped tools over more than 10 years at Pic Ningua. The shapes of pandanus tools were sampled there in November 1993 (Hunt 1996), November 1997 (Hunt 2000*a*) and in 2000. As leaves stay on pandanus trees at the site for *ca*. 4 years, this effectively gave a 10.5-year record of tool manufacture. Over 99% of the undamaged counterparts in each of the three samples were stepped tools. Low coefficient of variation values for the three samples combined (CV for length = 14%; CV for steps = 19%) show that the shapes of these tools varied little over the 10.5 years.

4. DISCUSSION

We set out to survey the variation in crows' pandanus tool making throughout New Caledonia to see if there was any evidence of design diversification and cumulative evolution. Inferences about past events are inevitably speculative to some degree. In the following discussion we outline the reasons why the most likely explanation for our results involves a history of tool design diversification and cumulative evolution.

(a) *Diversification*

Four reasons suggest that it is likely that the three pandanus tool designs diversified from a common origin. First, tool making by imposing form on material has rarely evolved in animals (Hunt 1996), and innovation events are rare even in human technology (Boserup 1981). The relatively low evolutionary probability of tool manufacture means it is unlikely that pandanus tools would have evolved more than once in New Caledonian crows. Second, there is an underlying similarity in the basic cutting and ripping actions that crows use to make pandanus tools. Third, each tool design has a continuous geographical distribution, and all three distributions overlap only at one end of Grande Terre. This geographical pattern is consistent with a unique origin for pandanus tools and of each design, not multiple independent developments (Whiten *et al.* 2001). Fourth, a prerequisite for both diversification and cumulative change is the transmission of the finished design between individuals with high fidelity. If this does not occur then distinct design variants at the population level cannot develop, and beneficial modifications to tools will not be retained in the population. If crows developed stepped tools by individual trial-and-error we would expect to find ample evidence of learning, not just to become proficient at making the local stepped design but also to develop it. Stepped tools at each site occur in a wide range of shapes, some of which seem to indicate obvious inexperience at tool making (Hunt 2000*a*). Evidence of stepped-tool invention-like intermediate designs (e.g. wide tools) is absent or rare at the many sites where stepped tools predominate. At Pic Ningua, where we have taken samples over 10.5 years, more than 99% of tools manufactured were stepped tools. Assuming that mated crows, like other *Corvus* (Wilmore 1977), usually breed each year, we would not expect such a high percentage of stepped tools if juveniles developed them by trial-and-error learning. The high site fidelity in tool design is not related to any obvious ecological factor such as forest structure or prey type. We did not examine these ecological variables directly, but rather did so by looking at variation in altitude and rainfall at sites. Tropical rainforest structure and composition (Givnish 1999), and the abundance and diversity of associated invertebrate prey for birds in a region (Wolda 1987), are known to vary predictably with altitude and annual rainfall. Few of these variables were significant predictors of tool design.

(b) *Cumulative change*

The diversification of pandanus tool designs means that at least two of the three designs must have evolved from cumulative change(s) to earlier versions. This is because each design results from a unique, non-recapitulating manufacture process (figure 1). Multi-step tools seem the obvious candidate for a cumulatively evolved design. The manufacture of these tools requires the most involved manufacture technique (see figure 1) and their regular shapes are little constrained by physical constraints associated with the raw material (Hunt 2000*a*). These two points make it very likely that multi-step tools evolved from simpler tools.

Two general characteristics of cumulative change in human technology are: (i) later tool designs are more efficient than earlier ones (French 1994); and (ii) earlier technologies eventually become rarer than later technologies. Do multi-step pandanus tools have practical advantages over wide and narrow tools? Unlike these untapered tools, a multi-step tool is conspicuously wider and tapered, making it both stiff at the base but also pointed at the working end. These two features are likely to facilitate

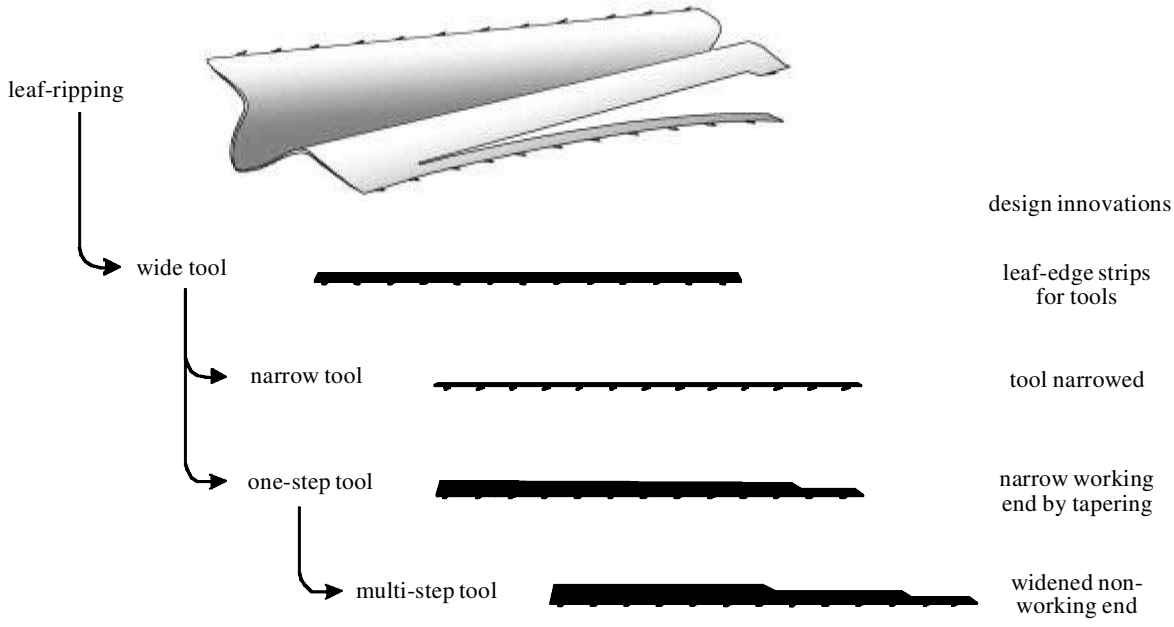

Figure 4. Proposed evolutionary history of the diversification and cumulative change in pandanus tool designs. Design innovations associated with the initial use of pandanus leaf as tools (wide design) and subsequent design changes (narrow and stepped designs) are briefly described at right of each tool. The section of pandanus leaf is *ca.* 5 cm wide.

controlled manipulation and reduce buckling when the tool is held near the base and inserted into sites to search for prey (see crow drawing in figure 2). In other words, stepped tools appear to have these combined characteristics of 'good design' (i.e. '...attributes that an intelligent and knowledgeable engineer might have built into [multi-step tools] in order to achieve some sensible purpose...' (Dawkins 1988, p. 24)) that probably provide certain functional advantages over wide and narrow tools. Stepped tools are by far the main pandanus tools manufactured by crows.

(c) *Proposed evolutionary history of diversification and cumulative change*

We have presented a case for diversification and cumulative change in crows' pandanus tools for which a temporal sequence of design change is implicit. A plausible behavioural precursor to the manufacture of pandanus tools is the leaf ripping that crows carry out in pandanus trees (figure 4). Birds often rip wide (> 0.5 cm) strips of leaf edge towards the trunk in non-tool behaviour where they remain hanging from leaves (Hunt 1996). This ripping is only recent at the bases of the tightly bunched young upright leaves at the centre of the leaf crown not on older, individually separated leaves. The strips are ripped by crows presumably attempting to capture prey concealed in the tightly packed leaves. This ripping may have led to crows removing strips for use as tools. Wide tools might plausibly be the basal pandanus tool design (figure 4) for two reasons: (i) they are more similar in width than narrow tools to the torn strips that crows rip on pandanus leaves; and (ii) they have simpler shapes and require a less complex manufacture technique than stepped tools.

We propose that selection for narrow-tipped foraging tools led to the independent evolution of both the narrow and stepped designs from the wide design. Differences in their method of manufacture indicate that narrow and stepped tools are distantly related, as does the absence of narrow tools at many sites where crows make stepped tools. Several lines of evidence indicate that the evolution of multi-step tools involved: (i) the development of one-step tools from wide-tool manufacture by a taper at the working end; then (ii) the widening and further tapering of one-step tools by additional steps to evolve multi-step tools. First, the small numbers of wide tools, but not narrow tools, made at sites where stepped tools predominate suggest the stepped design descended from the wide design. Second, wide tools were only made extensively with one-step tools (at site 19) but not with multi-step tools. At site 19, the shapes of wide and one-step tools were very similar and their widths did not differ significantly ($z = 0.50$, $p = 0.62$, $n = 288$) (figure 3). Last, a high degree of fidelity exists at sites in the presence of either one-step or multi-step tools (figure 3); over 90% of stepped tools at sites 6, 7 and 19 were one-step tools, whereas over 80% of tools at 14 of the 16 other sites were multi-step ones.

(d) *Conclusion*

Our findings are the first indication that a non-human species may have evolved rudimentary cumulative technology. We do not have direct evidence for the social transmission of tool design between crows, but this seems probable. In both birds and primates there has been progressive encephalization of the brain in areas that seem to deal with so-called 'intelligent' behaviour (Rehkämper & Zilles 1991; Rehkämper *et al.* 1991). This brain specialization is associated with innovation, social intelligence and tool use (Lefebvre *et al.* 2002; Reader & Laland 2002). *Corvus* species in particular have relatively large avian brains (Portmann 1947; Lefebvre *et al.* 2002) and are renowned for their considerable social learning abilities (Fritz & Kotrschal 1999; Heinrich 1999) and innovative behaviour (Lefebvre *et al.* 1997, 2002). Tool manufacture in New Caledonian crows shows striking flexibility and

innovation. These crows manufacture hook tools from a wide variety of raw materials (Hunt 1996; Hunt & Gray 2002), make a range of stick-type tools as well as pandanus tools, and have the ability to modify novel material appropriately to solve new tool tasks (Weir *et al.* 2002). New Caledonian crows therefore provide a unique opportunity to identify the cognitive and neural features that are required for sophisticated tool manufacture and cumulative technological evolution.

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REFERENCES

Beck, B. 1980 *Animal tool behaviour: the use and manufacture of tools by animals*. New York: Garland.

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.

Boserup, E. 1981 *Population and technological change*. University of Chicago Press.

Boyd, R. & Richerson, P. J. 1996 Why is culture common, but cultural evolution is rare? *Proc. Br. Acad.* **88**, 77–93.

Celli, M. L., Tomonaga, M., Udono, T., Teramoto, M. & Nagano, K. 2001 Learning processes in the acquisition of a tool using task by captive chimpanzees. *Psychologia* **44**, 70–81.

Dawkins, R. 1988 *The blind watchmaker*. London: Penguin Books.

Délacour, J. 1966 *Guide des oiseaux de la Nouvelle-Calédonie et de ses dépendances*. Paris: Delachaux & Niestlé.

Diamond, J. 1992 *The rise and fall of the third chimpanzee*. London: Vintage.

Foley, R. A. & Lahr, M. M. 1997 Mode 3 technologies and the evolution of modern humans. *Camb. Archaeol. J.* **7**, 3–36.

French, M. J. 1994 *Invention and evolution: design in nature and engineering*. Cambridge University Press.

Fritz, J. & Kotrschal, K. 1999 Social learning in common ravens, *Corvus corax*. *Anim. Behav.* **57**, 785–793.

Givnish, T. J. 1999 On the causes of gradients in tropical tree diversity. *J. Ecol.* **87**, 193–210.

Heinrich, B. 1999 *Mind of the raven*. New York: Cliff Street Books.

Heyes, C. M. 1993 Imitation, culture and cognition. *Anim. Behav.* **46**, 999–1010.

Hunt, G. R. 1996 Manufacture and use of hook-tools by New Caledonian crows. *Nature* **379**, 249–251.

Hunt, G. R. 2000*a* Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proc. R. Soc. Lond.* B **267**, 403–413. (DOI 10.1098/rspb.2000.1015.)

Hunt, G. R. 2000*b* Tool use by the New Caledonian crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu* **100**, 109–114.

Hunt, G. R. & Gray, R. D. 2002 Species-wide manufacture of stick-type tools by New Caledonian crows. *Emu* **102**, 349–353.

Hunt, G. R., Corballis, M. C. & Gray, R. D. 2001 Laterality in tool manufacture by crows. *Nature* **414**, 707.

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.

Kummer, H. & Goodall, J. 1985 Conditions of innovative behaviour in primates. *Phil. Trans. R. Soc. Lond.* B **308**, 203–214.

Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997 Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549–560.

Lefebvre, L., Nicolakakis, N. & Boire, D. 2002 Tools and brains in birds. *Behaviour* **139**, 939–973.

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.

Oakley, K. P. 1961 *Man the tool-maker*. London: British Museum (Natural History).

Paquette, D. 1992 Discovering and learning tool-use for fishing honey by captive chimpanzees. *Hum. Evol.* **7**, 17–30.

Portmann, A. 1947 Etudes sur la cérébralisation chez les oiseaux. II. Les indices intracérébraux. *Alauda* **15**, 1–15.

Povinelli, D. J. 2000 *Folk physics for apes: the chimpanzee's theory of how the world works*. Oxford University Press.

Reader, S. M. & Laland, K. N. 2002 Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441.

Rehkämper, G. & Zilles, K. 1991 Parallel evolution in mammalian and avian brains: comparative cytoarchitectonic and cytochemical analysis. *Cell Tissue Res.* **263**, 3–28.

Rehkämper, G., Frahm, H. D. & Zilles, K. 1991 Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (insectivores and primates). *Brain Behav. Evol.* **37**, 125–143.

Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. 2001 Do woodpecker finches acquire tool-use by social learning? *Proc. R. Soc. Lond.* B **268**, 2189–2193. (DOI 10.1098/rspb.2001.1738.)

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. 1998 Uniquely primate, uniquely human. *Devl Sci.* **1**, 1–30.

Tomasello, M. 1999 *The cultural origins of human cognition*. Boston, MA: Harvard University Press.

Tomasello, M. & Call, J. 1997 *Primate cognition*. New York: Oxford University Press.

Tomasello, M., Kruger, A. C. & Ratner, H. H. 1993 Cultural learning. *Behav. Brain Sci.* **16**, 495–552.

Weir, A. A. S., Chappell, J. & Kacelnik, A. 2002 Shaping of hooks in New Caledonian crows. *Science* **297**, 981.

Whiten, A. 2001 Imitation and cultural transmission in apes and cetaceans. *Behav. Brain Sci.* **24**, 359–360.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 2001 Charting cultural variation in chimpanzees. *Behaviour* **138**, 1481–1516.

Wilmore, S. B. 1977 *Crows, jays, ravens and their relatives*. London: David & Charles.

Wolda, H. 1987 Altitude, habitat and tropical insect diversity. *Biol. J. Linn. Soc.* **30**, 313–323.

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