CURRENT BIOLOGY

Causes and consequences of tool-shape variation in New Caledonian crows

Shoko Sugasawa,[1,]* Barbara C. Klump,[1] James J. H. St Clair,[1] Christian Rutz[1,2,]*

[1]Centre for Biological Diversity, School of Biology, University of St Andrews, Sir Harold Mitchell Building, St Andrews KY16 9TH, UK
[2]Lead Contact
*Correspondence: ss244@st-andrews.ac.uk (S.S.), christian.rutz@st-andrews.ac.uk (C.R.)

SUMMARY

Hominins have been making tools for over three million years [1], yet the earliest known hooked tools appeared as recently as 90,000 years ago [2]. Hook innovation is likely to have boosted our ancestors' hunting and fishing efficiency [3], marking a major transition in human technological evolution. The New Caledonian crow is the only non-human animal known to craft hooks in the wild [4, 5]. Crows manufacture hooked stick tools in a multi-stage process, involving [4, 6, 7]: the detachment of a branch from suitable vegetation; 'sculpting' of a terminal hook from the nodal joint; and often additional adjustments, such as length-trimming, shaft-bending, and bark-stripping. While tools made by a given population share key design features [4, 6, 8], they vary appreciably in overall shape and hook dimensions. Using wild-caught, temporarily-captive crows, we experimentally investigated causes and consequences of variation in hook-tool morphology. We found that bird age, manufacture method and raw-material properties influenced tool morphology, and that hook geometry in turn affected crows' foraging efficiency. Specifically, hook depth varied with both detachment technique and plant rigidity, and deeper hooks enabled faster prey extraction from the provided tasks. Older crows manufactured tools of distinctive shape, with pronounced shaft curvature and hooks of intermediate depth. Future work should explore the interactive effects of extrinsic and intrinsic factors on tool production and deployment. Our study provides a quantitative assessment of the drivers, and functional significance, of tool-shape variation in a non-human animal, affording valuable comparative insights into early hominin tool crafting [9].

RESULTS AND DISCUSSION

Tool use is extremely rare across the animal kingdom, and the ability to make tools from raw materials is rarer still [5]. Tool manufacture usually involves the detachment of material, and some basic modifications [5]. Chimpanzees, for example, break-off and fray plant stems to make termite-fishing probes [10], trim the tips of branches to produce pointed hunting tools [11], or fold and chew leaves into ‘sponge’-like bundles to soak-up drinking water [12] (for reviews of chimpanzee tool-manufacture behaviour, see refs [5, 13]). These actions require notable skill, but they contrast with the precise crafting of pre-determined, three-dimensional shapes that is characteristic of early hominin tool making [9]. Interestingly, the New Caledonian (NC) crow provides a non-human example of such behaviour: in some populations, these birds fashion hooked foraging tools from branched vegetation in an elaborate, multi-stage process [4, 6, 7].

To make a hooked tool, NC crows carefully remove a branch from a suitable plant (often by making cuts just above and below the joint), snip-off unwanted leaves and trim the shaft, and finally ‘sculpt’ a neat terminal hook from the wooden material of the nodal joint [4, 6, 7] (according to our earlier analyses, active hook ‘processing’ occurs in *ca.* 80% of tool-manufacture episodes; [7]). Frequently, they add further design features [4, 7, 14], by vigorously bending the tool shaft (which induces curvature that may improve tool ‘ergonomics’; [7, 15]), or by stripping off bark at the functional end (which may alter its mechanical properties; [4, 7]). During foraging, birds use the hooked tip for snagging arthropods hiding in deadwood and vegetation [4, 16]. Some animal species use plant materials that have pre-existing or coincidentally-formed hooks as tools. NC crows excise foraging tools from the barbed edges of screwpine leaves [4, 17], woodpecker finches have been observed to use thorny blackberry twigs to extract embedded prey [18], and orangutans occasionally reach for vegetation with naturally-hooked branches [19, 20]. Interestingly, for algae harvesting, chimpanzees not only select stems with natural barbs/hooks (bends can become more pronounced as a result of heavy use), but they also produce hooks by stripping away side branches or leaves (leaving behind stem bases) [21, 22]. But, to the present day, the NC crow remains the only non-human species known to sculpt hooks in the wild [4, 5], providing a valuable comparison to our ancestors' production of fish-hooks [3] and barbed spears [2].

Despite considerable interest, surprisingly little was known until recently about the curious hook-tool-making of NC crows. The discovery of the behaviour in the 1990s was based on the observation of just four tool-manufacture episodes [4], and it was only years later that two birds could be lured to a baited feeding table, affording close-up views of the production of another 10 tools [6]. Over the past few years, our team has identified three adjacent crow populations – in dry forest, farmland, and a beachside settlement, respectively – where birds routinely forage with hooked tools (Figure 1), creating exciting opportunities for systematic studies [7, 8, 14]. Our work with free-ranging and temporarily-captive crows has revealed that, although hooked tools generally share certain design features, they vary appreciably in overall shape (such as the degree of shaft curvature) and specific dimensional properties (such as hook depth). For example, while some tools only have a very small extension at the functional tip, others exhibit well-defined, deep hooks. This raises questions about the functional significance of tool morphology: Are some hooked tools more efficient than others, and if so, what does it take to make such a tool?

In the present study, we investigated experimentally what extrinsic and intrinsic factors (crow age, manufacture method, and plant properties) determine the morphology of hooked tools, and how tool morphology in turn affects crows' foraging efficiency. Using recently established protocols [7, 14], we trapped crows in our farmland study site and held them temporarily in field aviaries – a method that has been shown to be both scientifically productive [7, 14, 23], and well-tolerated by this species [24]. During experimental trials, we allowed subjects to manufacture hooked stick tools from a choice of their preferred plant material, forked stems of the shrub *Desmanthus virgatus* [8], and observed how they subsequently used these tools to extract bait from naturalistic foraging tasks (Figure 2; for details, see Methods and ref.

[7]). Tools were recovered after trials, identified from video footage, and measured using digital reference photographs.

Adult crows manufactured distinctive tools (adults *vs.* immatures: Mahalanobis distance [*MD*] = 3.67, $p < 0.001$; adults *vs.* juveniles: *MD* = 2.68, $p = 0.07$; immatures *vs.* juveniles: *MD* = 2.04, $p = 0.09$) – with pronounced shaft curvature and medium-sized hooks (hook depth, mean ± s.d. – adults: 1.21 ± 0.64 mm; immatures: 1.04 ± 0.92 mm; juveniles: 1.83 ± 1.59 mm; hook depth by itself did not differ significantly between age classes: $\chi^2_2 = 2.33$, $p = 0.31$) – that appeared less variable in overall shape than those made by younger individuals (s.d. of canonical variates 1 and 2 – adults: 0.45, 0.43; immatures: 1.12, 1.07; juveniles: 1.02, 1.12) (Figure 2A). This suggests that tool-making skills, or preferences for certain tool shapes, change as birds mature [6]. For example, older individuals may converge on similar designs through individual trial-and-error learning (see ref. [25]) and/or the social transmission of tool-related information (either via observation of other birds, or interaction with their tools; [26]). Future work should investigate the ontogeny of hook-tool-making, ideally under controlled experimental conditions [27].

NC crows in our study population use two main methods for releasing (basic) hooked stick tools from plants – ‘cutting’ and ‘pulling’ (figure S1; for video clips illustrating these actions, see Additional file 1 of ref. [7]). Our main experiment demonstrated that, with relatively standardised plant materials, cutting (13 cases, only one of which without subsequent hook processing) enables the production of significantly deeper hooks (comparison between cut and pull: $t = -2.21$, $p = 0.03$; trend for longer hooks, $t = -1.73$, $p = 0.09$; Figures 2B and 2D); while this increases tool efficiency (see below), it necessitates two separate actions – one cut above and one below a branching joint. In contrast, pulling (20 cases, two of which without hook processing) leads to shallower hooks on average, presumably as less material remains at the tool tip for sculpting after detachment, but it has the advantage that a single action yields a basic tool. Sometimes, a single cut is combined with a pull (cut–pull: 6 cases; pull–cut: 2 cases; figure S1), producing hooks of intermediate depth (Figure 2B). A trade-off between tool efficiency and manufacture costs provides a potential explanation for the co-existence of different release techniques in our study population (for further discussion, see below).

It has been suggested that hooked stick tools have evolved from basic non-hooked stick tools through a process of ‘cumulative’ modification [7, 23, 28]. In fact, the cost-efficient single-step pulling method observed in our study population resembles the production of basic non-hooked stick tools – where crows swiftly snap-off twigs from nodal joints [29, 30] – and may therefore represent an evolutionary precursor of more involved multi-step manufacture techniques (as described in refs [6, 7]). Over time, crows may have gradually improved tool efficiency further, by processing the hook, stripping the bark off the functional end, and/or bending the tool shaft (Figure 2D; [4, 7, 14, 15]; cumulative refinement of tool designs has previously been suggested for the tools NC crows make from screwpine leaves – see ref. [17]). Interestingly, with some plant species, pulling apparently does not produce hooks [4], and crows exclusively employ the cutting technique [6]; similarly, in chimpanzees only some plants appear suitable for the production of brush-sticks [31]. We suspect that comparable effects of raw-material properties on manufacture methods, and ultimately on artefact morphology, are widespread in animal tool-use and construction behaviour [5, 32, 33].

In a companion experiment using seven NC crows from our main sample, we found that the properties of plant raw materials influenced several aspects of hooked tool morphology. After controlling for the effect of manufacture method, hook depth increased significantly with stem rigidity ($\chi^2_1 = 10.04$, $p = 0.002$; Figure 2C). Hook length ($\chi^2_1 = 3.63$, $p = 0.06$) likewise increased with increasing material score (no effect of manufacture method), as did overall tool dimensions (tool length: $p = 0.02$; length from the non-hooked end to the maximum curvature point: p

= 0.05; Figure 2C). The increase in tool length with increasing material score may simply be due to the fact that tool shafts of higher rigidity were difficult to sever close to the joint. Interestingly, the relative position of the maximum curvature point changed little across material scores ($p = 0.62$), resulting in a relatively consistent overall tool shape as tool dimensions increased (see Methods). While this may reflect allometric properties of the plant material, crows often actively adjust tool curvature through shaft bending [7, 15], presumably in an effort to keep the hook centred in the field of binocular vision during deployment [14, 34]. Although many studies have investigated tool-material selectivity in primates (e.g., [10, 35]), the effects of material properties on the morphology of *manufactured* tools remain poorly documented (e.g., [31, 36]). Our work on NC crows has shown that plant properties affect aspects of manufacture behaviour [7], as well as the morphology of the resulting tools (present study). Such research on extant tool-using animals provides a valuable window into early human tool making where the relationships between raw materials, crafting techniques, tool morphology, and tool functionality remain a topic of great interest [9, 37, 38].

Having identified three significant drivers of variation in NC crow tool morphology – bird age, manufacture method and raw-material properties – we next examined whether hook geometry in turn affects foraging efficiency. As a simple performance metric, we measured how long it took our subjects to extract two types of ‘prey’ (dead spiders, and worm-like cylinders of meat) from standardised holes drilled into wooden logs [23] – tasks that resemble foraging scenarios routinely encountered by wild crows [4, 16]. We found that extraction speed increased significantly with hook depth ($z = 2.80$, $p = 0.005$; Figure 2E), with spiders being extracted more quickly on average than vermiform prey (spider in wide hole *vs*. vermiform prey in wide hole: $z = 3.67$, $p < 0.001$; spider in wide hole *vs*. vermiform prey in narrow hole: $z = 3.65$, $p < 0.001$; no significant difference in slopes: $\chi^2_2 = 1.56$, $p = 0.46$).

Including trials where crows were offered human-made exemplar hooked tools allowed us to extend the range of hook depths over which extraction efficiency could be measured, and confirmed the pattern observed with crow-made tools only ($z = 2.56$, $p = 0.01$). To our knowledge, this is the first demonstration that variation within a specific design feature of crafted animal tools can affect foraging performance, adding to studies that found similar effects for researcher-deployed replica hominin [39, 40] and chimpanzee tools [41].

Based on the findings from our two experiments, one might expect that experienced adult crows use the more controlled cutting technique, to produce deep hooks that enable faster prey extraction. We found instead that adults frequently used pulling (for details, see figure S1), yielding hooks of intermediate depth (see above). This may be because there are yet-to-be-investigated costs associated with deeper hooks, including increased manufacture effort, high rates of hook damage, and/or reduced performance in very tight crevices such as beneath tree bark. Such hidden costs would imply the existence of an optimal hook depth. Thus, although we still do not know whether foraging performance with hooked stick tools increases with age (and, hence, experience; see refs [42, 43]), it is conceivable that older birds optimise returns from a given tool by trading-off extraction speed against one or more other factors. In general, it remains an important challenge for future studies, to assess – with larger sample sizes and dedicated experimental designs – how different extrinsic and intrinsic factors *interact* to drive variation in tool morphology, and ultimately tool- and foraging efficiency.

CONCLUDING REMARKS

In human and animal archaeology, our understanding of the development, form and function of lithic artefacts is substantially greater than for those made of bone, wood, and other plant materials [44]. Relatively perishable materials, however, are thought to have been used at least as frequently as stone by early humans [44, 45], suggesting that our knowledge of their technologies is based on a biased subset of both raw materials and tool types. Many extant animal species make tools and other constructions using organic materials [5, 32, 33, 46], allowing us to search for general relationships with a wide range of raw materials, artefacts and construction behaviours. NC crows provide an excellent model in this regard, given the diversity of plant materials and tool shapes they use [4], and – perhaps uniquely among non-humans – their capacity to craft tool types with multiple distinct design features, most notably the hooked stick tools discussed here [14]. Further research on these relatively complex tools will contribute to our understanding of how early hominin technology advanced and diversified.

STAR METHODS

Please see below.

SUPPLEMENTAL INFORMATION

Supplemental information includes one figure.

AUTHOR CONTRIBUTIONS

All authors conceived of, designed and conducted experiments, and planned analyses; S.S. scored videos, extracted data and performed statistical analyses, except for the experiment examining the effect of plant properties on tool morphology, for which B.C.K. collected, extracted and analysed data and provided draft text sections; S.S. and C.R. wrote the manuscript, which was edited and approved by all co-authors; and C.R. secured funding and supervised the project.

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FIGURE CAPTIONS (2)

Figure 1. A wild New Caledonian crow holding a hooked stick tool
Apart from the distinctive terminal hook, which is used for snagging arthropod prey, the tool exhibits two additional crow-induced design features that are typical for this particular population – pronounced curvature of the tool shaft, and stripped bark near the functional end. Photo: Pedro Barros da Costa.

Figure 2. Causes and consequences of morphological variation of hooked stick tools crafted by wild-caught New Caledonian crows
(A) Age-dependent variation in tool shape. Points are subject-level averages (calculated for at least three different tools), with colour-coding indicating bird age (black, adult; grey, immature; pink, juvenile). Schematic illustrations of tools were produced from CVA, representing tool shapes at the extremes of canonical variates 1 and 2. Sample size (main experiment): 117 tools made by 14 crows.
(B) Hook length (blue) and hook depth (red) of tools (mean ± s.e.m. [mm]) manufactured using the ‘cut’ or ‘pull’ method, or a mixed technique (for details, see text and figure S1). Sample size (main experiment): 41 tools made by 13 crows.
(C) Tool length (green), length to maximum curvature point (orange), hook length (blue) and hook depth (red) of tools (mean ± s.e.m. [cm or mm]; for details, see panel *D*) crafted by crows from plant materials of increasing rigidity (scores 1–8). Sample size (companion experiment): 28 tools made by 7 crows.
(D) Morphological landmarks and measurements superimposed on a representative crow-made hooked stick tool. Summary statistics of measurements (mean ± s.d.) for crow-made tools were as follows – tool length: 14.31 ± 4.75 cm; length from the non-hooked end to the maximum curvature point: 9.29 ± 3.86 cm; hook length: 4.43 ± 2.13 mm; hook depth: 1.26 ± 1.11 mm. Sample size (main experiment): 122 tools made by 17 crows.
(E) Extraction time (natural log-transformed; mean ± s.e.m [sec] per tool) for dead spiders (left) and vermiform pieces of meat (right; data for wide and narrow holes pooled) as a function of hook depth (mm). Sample size (main experiment): 21 tools made and deployed by 11 crows; 13 human-made tools deployed by 8 crows. While the fitted lines are for linear mixed models that exclude unsuccessful bait-extraction attempts (16 holes, with 8 tools made by five crows) (for statistical results, see main text), a corresponding mixed-effect Cox proportional hazards model including these cases confirmed the significant effect of hook depth ($z = 2.34$, $p = 0.02$; for details, see Methods).

STAR METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Corvus moneduloides	[7, 23]	N/A
Software and Algorithms		
R version 3.1.2	[47]	http://www.R-project.org/
R package ‘lme4’	[48]	http://cran.r-project.org/package=lme4
R package ‘lmerTest’	[49]	http://cran.r-project.org/package=lmerTest
R package ‘glmmADMB’	[50]	http://glmmadmb.r-forge.r-project.org/
R package ‘coxme’	[51]	http://cran.r-project.org/package=coxme
R package ‘survival’	[52]	http://cran.r-project.org/package=survival
R package ‘MuMIn’	[53]	http://cran.r-project.org/package=MuMIn
ImageJ	[54]	https://imagej.nih.gov/ij/
MorphoJ	[55]	http://www.flywings.org.uk/morphoj_page.htm
Solomon Coder	N/A	http://solomoncoder.com

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Christian Rutz (christian.rutz@st-andrews.ac.uk).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

From 17 September to 28 November 2012, and from 24 August to 28 October 2013, we trapped 41 NC crows in our farmland study site near Bourail, New Caledonia (for map, see ref. [56]). We sexed birds based on their body size (males are bigger than females; five birds were sexed genetically) and assigned them to rough age categories based on the colouration of their gapes (as birds mature, gape colouration changes from all-pink, through mottled intermediate stages, to all-black) [7]. While our ageing technique is known to be imperfect (there is variation in how fast birds transition from pink to black), it is suitable for identifying very young birds (which also beg persistently) and old birds (there is no evidence for reversals, from black to pink), and provides a useful proxy for individuals’ developmental stage. Future studies would ideally conduct experiments with known-age subjects, although achieving sufficient sample sizes would be very challenging.

Crows were housed individually in field aviaries (except for dependent young trapped with adults, which were kept together), and cared for as described in detail elsewhere [7, 14]. To assess birds' natural tool behaviour, we provided in each housing aviary an extraction task (a log with meat-baited drilled holes) and locally preferred plant materials for tool manufacture (stems of the shrub *Desmanthus virgatus*; [8]); only crows that were confirmed to make hooked stick tools progressed to the experiments described below (for rationale, see refs [7, 14, 23]).

METHOD DETAILS

Manufacture and deployment of tools

In our main experiment, wild-caught New Caledonian crows were given standardised opportunities for hook-tool manufacture (multiple stems of *D. virgatus*) and deployment (prey hidden in drilled holes in wooden logs; see below). Subjects were tested individually in an experimental chamber, which was adjacent to, and of the same size as, the housing aviaries. Food was removed approximately one hour prior to the trial, but birds always had access to water. We provided two food logs, containing 12 wide and 6 narrow drilled holes (1.2 cm diameter × 7 cm depth, or 0.9 × 7 cm), baited with a dead spider or a worm-like prey item (a cylindrical piece of meat drilled out of a beef or pork heart, of *ca*. 0.8 × 2.1 cm), a log with 10 stems of the plant material inserted into drilled holes (material log), and half of a log split lengthwise for the subject to stand on whilst processing tools (manufacture log) (for details of experimental set-up and protocol, see ref. [7]). Of 31 trials which provided valid data, 8 trials also had a choice of non-hooked sticks presented on the material log, but we collected morphological data only for hooked stick tools.

Each trial was recorded with a Panasonic camcorder (HC-V700 or HDC-SD 900) by an observer in a hide outside the experimental chamber, and lasted for 90 minutes or until the subject had extracted all bait. The observer collected tools in the experimental chamber, labelled them, and took digital photos under standardised conditions (laid out flat on grid paper; camera perpendicular to tool plane; good lighting). Here, 'tools' are considered to be pieces of material that crows had detached from plant stems, processed and inserted into a hole. Tools were identified by S.S. (and distinguished from plant debris that accumulates during routine tool manufacture) based on video footage, observers' notes taken during trials, and our reference photographs. Of the 163 identified tools, 41 tools were non-hooked stick tools made from *D. virgatus*, or damaged, and were not included in morphometric analyses. Overall, we collected morphological data for 122 hooked stick tools made by 17 crows (3 males and 14 females; 5 adults, 8 immatures and 4 juveniles).

The main experiment had two treatments: the ‘crow-made tool’ treatment and the ‘human-made tool’ treatment [23]. The latter, which was a control condition from a companion study [23], was included in our analyses of tool performance (see below), to explore crows’ foraging efficiency over a wider range of hook depths (crow-made, 1.26 ± 1.11 mm *vs.* human-made, 1.90 ± 0.68 mm [mean ± s.d.]). The same experimental procedure was used as for the crow-made tool treatment, except that three experimenter-made hooked stick tools were presented, instead of raw plant material for manufacture. We ran 8 trials where the subjects readily used the 24 supplied tools (8 trials × 3 tools). All 8 subjects also participated in the crow-made tool treatment described above (1 male, 7 females; 3 adults, 4 immatures, 1 juvenile), and the order of trials was randomised.

Manufacture of tools from plant materials of varying properties

In a companion experiment, we investigated the influence of raw-material properties on hook-tool morphology. As described in detail elsewhere [7], three fieldworkers were tasked to independently score the material properties of plant stems. We opted for an approach based on professional judgement, as it would have been difficult to take reliable biomechanical measurements [46] either before trials commenced (measurements result in the destruction of specimens) or afterwards (crows often flex tools vigorously during manufacture and deployment; [15]).

Seven crows from the main sample (1 male, 6 females; 3 adults, 4 immatures) were each provided with a choice of eight stems of *D. virgatus*, ranging from green and flimsy (material score 1) to woody and rigid (material score 8), and a food log with a single meat-baited extraction hole (for details, see ref. [7]). After each tool manufacture (and subsequent bait extraction, or 15 minutes without bait extraction), the tool and any plant debris were removed, and the extraction hole was rebaited, enabling each subject to produce a series of tools from stems of different material properties. At the analysis stage, tools that had been deployed (and not broken) by crows were identified by B.C.K. from video footage (28 tools manufactured by 7 subjects), and subsequently measured from digital imagery as described below.

QUANTIFICATION AND STATISTICAL ANALYSIS

Factors affecting tool morphology

For each tool, we established the coordinates of five landmarks from our digital photos using ImageJ software [54], which were subsequently used to derive four basic dimensional properties (Figure 2D). We checked error associated with digitising landmarks by re-analysing 20 tools (14 subjects; >15% of the entire dataset), and by comparing digitising error and inter-individual variation (as a reference for biologically meaningful variation) using Procrustes ANOVA [57]. The digitising error was negligible compared to between-crow variation (0.01% for centroid size and 0.8% for shape).

To examine tool shape, we first separated shape information from tool-size and orientation information through Procrustes superimposition, producing Procrustes coordinates [58]. Using canonical variate analysis (CVA), we then tested whether the configuration of Procrustes coordinates varied across age groups (Figure 2A). To achieve this, canonical variates (CV) were calculated that best separated the tool coordinates from different age groups, and group centroids were subsequently used to test for age differences. Canonical variates provided graphical outputs of how tool shape varies between age groups, and allowed us to draw exemplary tools for the extremes of canonical variates 1 and 2 (Figure 2A). *P*-values were adjusted for multiple comparisons using Holm's method [59], and significance was assessed at $\alpha = 0.05$. Additionally, we ran a linear mixed model (LMM; 'lmer' function of the 'lme4' package in R; [48]) with hook depth (square-root transformed to normalize errors) as the dependent variable, age class (adult, immature or juvenile) as the independent variable, and subject identity as a random term (to account for non-independence of multiple tool manufactures per bird).

We investigated whether crows' manufacture method influenced tool morphology (Figure 2B), using tools for which the manufacture method could be determined from video footage [7]. In particular, we focused on the behavioural action the subject used to detach a (basic) tool from the plant stem, since this is a critical step in the production of hooked tools. There are two different actions: 'cut' (detachment at the point where the subject was gripping) and 'pull' (detachment away from the gripping point) (for video clips illustrating these actions, see Additional file 1 of ref. [7]), and it has been suggested that the former may afford crows more control over the resultant shape of hooks. As illustrated in figure S1, our subjects employed three release techniques, using two cuts (panel B), a single pull (C), or a combination of a cut and a pull (D) (in an earlier study, the latter two were classed as 'pulling' and cases pooled for data analyses due to modest sample sizes; [7]). We ran LMMs ('lmer' function of the 'lmerTest' package in R; [49]) with hook length or hook depth (square-root transformed to normalize errors) as the dependent variable, the behavioural action (cut, both or pull) as the independent variable and subject identity as a random term. We only investigated the influence of manufacture method on hook length and hook depth, since tool length and length to maximum curvature point were (potentially) determined at other stages in the tool-manufacture sequence.

To investigate the influence of both manufacture method and raw-material properties on tool morphology, we ran generalised linear mixed models (GLMMs) with tool length, length to maximum curvature point, or the relative position of maximum curvature point (length to maximum curvature point / tool length) as the dependent variable (gamma error structure with log-link function; ‘glmmadmb’ function of the ‘glmmADMB’ package in R; [50]), and LMMs with hook length or hook depth as the dependent variable (square-root transformed to normalize errors). All models had material score as the independent variable and included subject identity as a random term. LMMs contained the manufacture method (cut, both or pull) as an additional independent variable, given its effect on tool morphology (see above). We determined the best model by dropping (the) main effect(s) (the full model for hook depth, and the univariate model with material score as independent variable in all other cases). The significance of main effects in all LMMs and GLMMs was assessed using likelihood-ratio tests (best model against the null model, except in the case of hook depth where the *p*-value refers to the comparison of the best model against the reduced model). We additionally performed CVA for these tools with Procrustes coordinates as the response variable and the material score as independent variable, but found no influence of material properties on overall tool shape.

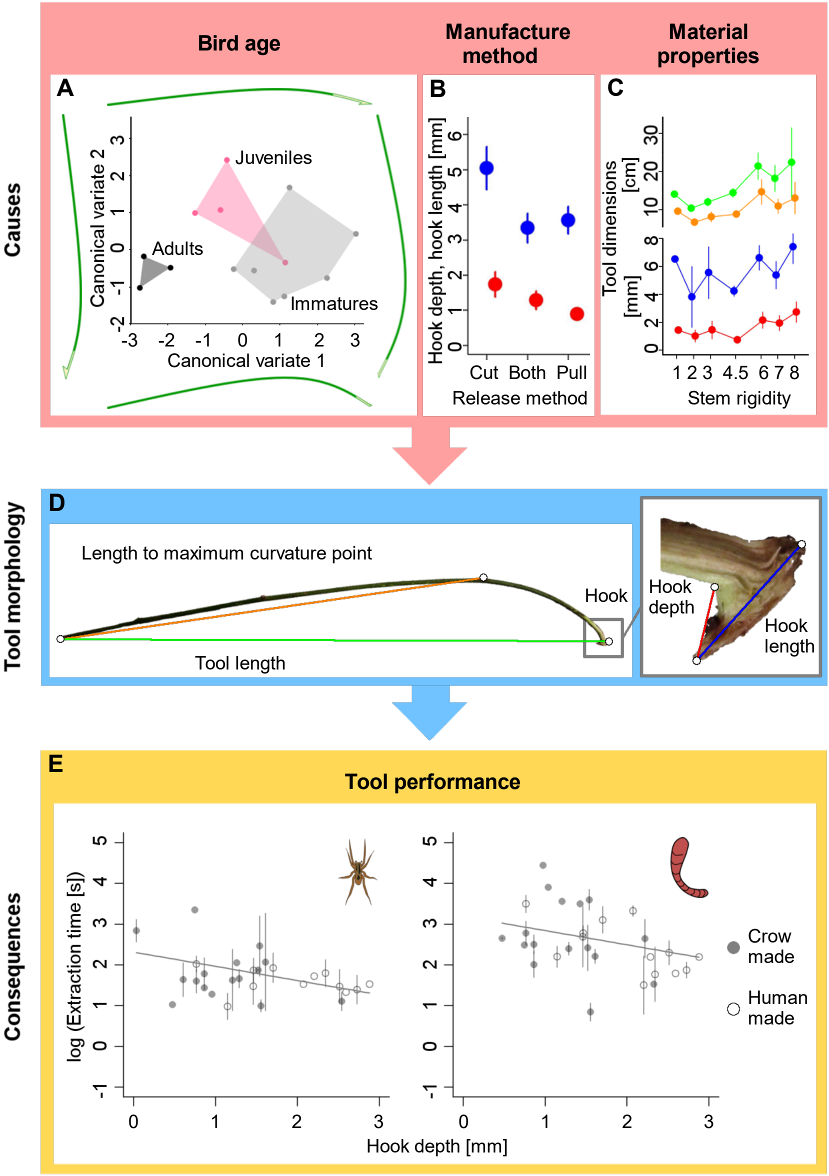
All data analyses were carried out in R [47] or MorphoJ software [55].

Effects of tool morphology on foraging performance

From videos of 17 trials with crow-made tools, and all 8 trials with human-made tools (see above), a hypothesis-naïve observer (Caitlin Higgott) scored crows’ probing behaviour using Solomon coder software [23], and S.S. subsequently established the probing histories of individual tools (see above). Out of a total of 450 extraction holes available to subjects in those trials, 213 were probed by a single hooked stick tool and therefore used for analyses; the remaining 237 holes were excluded as crows did not probe into them, or probed into them with two or more tools, unidentifiable tools, and/or non-hooked stick tools.

To assess foraging efficiency, we measured how long a bird probed with a particular tool in baited holes before prey was either extracted or the trial was over. While Cox proportional hazards models (‘coxme’ function of the ‘coxme’ package in R; [51]) are the method of choice for analysing such right-censored ‘survival’ data [23], our dataset contained only few cases where bait was targeted with tools but not extracted (5 crows, 8 tools, 16 holes; of the 8 tools, 5 tools made by 4 crows were used for extractions from other holes), and model assumptions ('cox.zph' function with rank transformation in the 'Survival' package in R; [52]) were not met for one of two analyses (crow-made tools only). We therefore used LMMs instead ('lmer' function of the 'lme4' package in R; [48]), to analyse the sample of successful bait extractions (100 and 97 holes from crow- and human-made tool treatments, respectively). Models were fitted with extraction time (log-transformed for normalisation) as the dependent variable, morphological parameters (tool length, hook length, hook depth and length to maximum curvature point divided by tool length; see above) and task type as independent variables, and tool identity and subject identity as random terms (to account for the non-independence of data from individual crows and tools); task type was defined based on bait type and the size of the extraction hole (spider in a wide hole; vermiform prey in a wide hole; vermiform prey in a narrow hole). In the analysis including human-made tools, we added treatment (crow- or human-made tools) as an independent variable, and treatment nested within subject identity as a random term (to account for the fact that birds engaged with multiple tasks in the two discrete treatment trials). Task type and treatment were included in models since previous work had demonstrated their importance [23].

We fitted all possible combinations of explanatory variables, and compared models based on AICc, delta weight and Akaike weight, and averaged the estimated outputs of models with delta weight <2 ('dredge function' and 'model.avg' function of the 'MuMIn' package in R; [53]). As strong correlations between predictors result in unreliable estimates in model averaging [60], and original values of tool length and length to maximum curvature point were highly correlated ($r = 0.92$, $p < 0.001$), we removed the latter and instead used the ratio of the two (tool length divided by length to maximum curvature point; $r = 0.40$, $p < 0.001$). There was no other combination of predictors that was strongly correlated (all $|r| \leq 0.40$).


Causes
Bird age
Manufacture method
Material properties
A
Canonical variate 2
Canonical variate 1
-3 -2 -1 0 1 2 3
-2 -1 0 1 2 3
Juveniles
Adults
Immatures
B
Hook depth, hook length [mm]
0 1 2 3 4 5 6
Cut Both Pull
Release method
C
Tool dimensions [cm]
10 20 30
[mm]
0 2 4 6 8
1 2 3 4.5 6 7 8
Stem rigidity
Tool morphology
D
Length to maximum curvature point
Hook
Tool length
Hook depth
Hook length
E
Tool performance
Consequences
log (Extraction time [s])
-1 0 1 2 3 4 5
0 1 2 3
Hook depth [mm]
Crow made
Human made

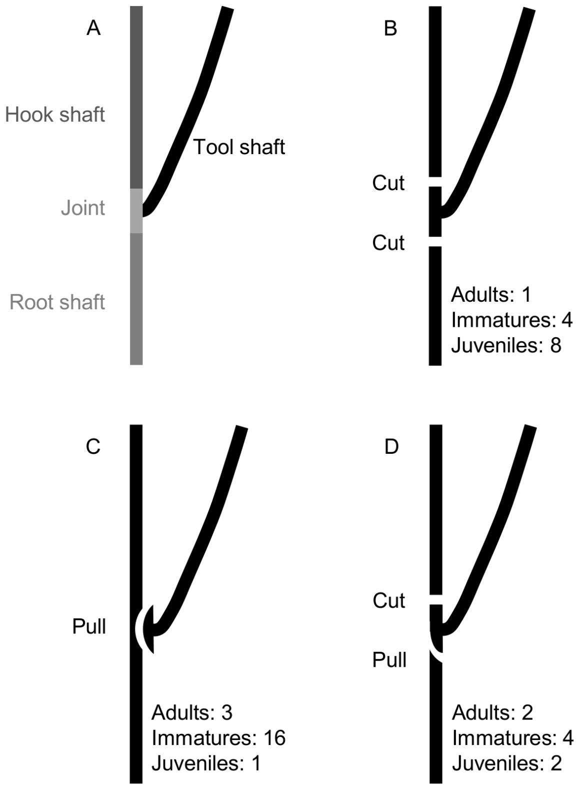


Figure S1. New Caledonian Crows' Manufacture Methods for Producing Hooked Stick Tools from Forked Plant Stems, Related to Figure 2B

(A) Schematic drawing of a stem, and terminology used to describe plant sections. Subjects in the present study detached a basic hooked stick tool from the plant stem by either: (B) cutting the hook shaft above the joint and the root shaft below the joint; (C) pulling by gripping at the tool shaft and detaching at the joint; or (D) cutting the hook shaft above the joint and then pulling by gripping at the tool shaft and detaching at the joint, or by gripping at the joint and detaching at the root shaft (these actions also happened in reverse order: first pulling by gripping at the joint and detaching at the root shaft, and then cutting the hook shaft above the joint). When crows detached the main stem at the root shaft below the joint as their first action (B or D), they trapped plant material beneath their feet so they could process it further by bill. Note that detachment by cutting at the tool shaft results in a non-hooked stick tool – these manufacture episodes are not considered here. Panels (B) to (D) provide counts of manufacture episodes, and basic demographic information. Subjects of the different age categories employed the three release techniques as follows – adults: three birds exclusively used either B, C or D, and one bird used both C and D; immatures: one bird used both B and C, one bird exclusively used C, and three birds used both C and D; juveniles: two birds exclusively used B, one bird used both B and C, and one bird used both B and D.