Raw-material selectivity in hook-tool-crafting New Caledonian crows

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Animals that manufacture foraging tools face the challenge of identifying suitable raw materials amongst a multitude of options. New Caledonian crows exhibit strong population-specific material preferences for the manufacture of hooked stick tools, but it is unknown how they identify their favourite plants. We investigated experimentally whether crows pay attention to the stems of plants (from which the tools are made) and/or their leaves (which are usually discarded during manufacture, but may enable rapid and reliable species identification at a distance). Subjects were highly selective in choice trials with multiple plant species. Two additional treatments with experimental leaf–stem combinations revealed that birds can identify their preferred plant species by its stems alone, and possibly also its leaves. These findings encourage future experiments that investigate whether New Caledonian crows attend to features of the stem that are required for the production of efficient hooked stick tools. Our study provides one of the most detailed assessments to date of how non-human animals identify raw materials for tool manufacture.

1. Introduction

It is well documented that several animal species can select tools with appropriate properties for solving foraging problems [1–4]. In some cases, the underlying mechanisms have been investigated in detail, notably for hammer selection in nut-cracking primates, which can involve both kinaesthetic feedback obtained during object handling [2] and visual assessment [5]. In contrast, much less is known about how animals identify suitable raw materials for tool *manufacture*. For example, chimpanzees in some communities appear to prefer certain plant species for tool production [6–10], yet it remains unclear how exactly they recognise these materials amongst the multitude of options available in their forest habitats (a question that applies to animal construction behaviour more generally; [11]).

New Caledonian (NC) crows *Corvus moneduloides* use a variety of tool types for extractive foraging, and are the only non-human animal known to fashion hooks in the wild [12,13]. In some areas, birds use several different plants for manufacturing hooked stick tools, while in others, they strongly prefer a single species – as in one of our study populations where crows favour the non-native perennial shrub *Desmanthus virgatus* [14]. It is still unknown why this population exhibits such a strong preference for *D. virgatus*, and how individuals manage to locate these relatively small plants in the forest understory where they have a patchy distribution and often grow intertwined with other species.

Crows make hooked stick tools from forked plant stems, detaching branches in a way that preserves nodal joint material from which a hook can subsequently be 'sculpted' by bill; twiglets and leaves are usually discarded during tool production [13,15,16]. Since the tool is made from the stem material, crows may focus on this part of the plant when making their choices, paying particular attention to branching angle, stem thickness and node structure, which will all affect the morphology and biomechanical properties of the manufactured tool [13,14,17]. Leaves, in contrast, have no functional significance, but may be easier to assess from a distance than stems (which may also be obscured by vegetation), and crows could use them as a cue for locating suitable raw material efficiently in a forested environment. Thus, it is conceivable that NC crows attend to both stems and leaves, potentially employing a two-step strategy, first using leaves as a short-cut to identify the correct plant species (in a similar way, perhaps, as a field botanist would do), before paying attention to the dimensional properties of stems.

To investigate which plant features NC crows attend to when sourcing raw materials for hooked stick tool manufacture, we presented wild-caught, temporarily captive subjects with a choice of plant stems (figure 1*a*), some of which had been experimentally grafted with heterospecific leaves (for treatments and ethical considerations, see table 1). We selected three plant species that share features believed to be important for tool manufacture (figure 1*b*): (i) their preferred species, *D. virgatus*; (ii) *Leucaena leucocephala*, which has similar bipinnate leaves; and (iii) *Melaleuca* sp., which crows in and around our study area occasionally use for making hooked stick tools ([18], and unpublished data).

2. Methods

Between 28 August and 07 October 2015, we individually tested 10 NC crows that had been trapped in our farmland study site at the border of the Gouaro-Déva reserve, and were confirmed hook-tool users (for methods, see [14,17]).

The experiment consisted of five consecutive treatments (A–E; two pilot birds only participated in a subset; table 1), where crows were presented with locally sourced plant materials (figure 1*b*) and a wooden log with a single meat-baited hole (16 mm wide, 70 mm deep). At the beginning of each treatment, a small piece of meat ('teaser') was positioned on the log to attract the bird's attention. Each treatment lasted for *ca.* 10 min after the bird's initial interaction with the set-up, but ended earlier if the bait was extracted. At the end of each treatment, until completion of the full set, M.C. removed the bird's manufactured tool and any plant debris, prepared the plant material for the next treatment out of view before placing it in the aviary, and re-baited the set-up (bait and teaser) in full view of the subject. Each subject received only one trial per treatment (with the exception of CK6; see table 1), to avoid unwanted learning effects that could have complicated the interpretation of results and/or altered birds' natural material preferences. All trials were filmed by B.C.K. from a hide outside the aviary using a Panasonic HD camcorder.

For each treatment, we scored from video (for details, see supplementary figure 1) when a subject first touched or detached plant material, and manufactured a tool. All videos were scored in random order by B.C.K., using 'Solomon Coder' software (http://solomoncoder.com), and trials by two crows (20%) were re-scored by M.C. to assess inter-observer agreement (supplementary table 1). All statistical analyses were based on B.C.K.'s original scores. We used exact binomial tests ('binom.test' in R [19]) to assess whether subjects handled *D. virgatus* material more frequently than expected by chance.

3. Results

NC crows in our experiment strongly preferred *D. virgatus* for tool manufacture (note that some manufactured tools were non-hooked; see table 1). Subjects touched the *D. virgatus* stem, and manufactured a tool from it, significantly more often than expected by chance (treatments A and D; for statistics, see table 1), even when it was presented with experimentally-grafted *Melaleuca* sp. leaves (treatment-C). The importance of the stem was further highlighted by crows' reluctance to interact with plant material when no *D. virgatus* stem was present (no indication of an age effect; table 1). In treatment-B, both stems were *Melaleuca* sp. – a material that is occasionally used in our study area [18] – yet only six subjects touched a stem, and only four of them manufactured tools (three of which were non-hooked stick tools). Interestingly, all four crows that made a tool selected the stem with grafted *D. virgatus* leaves, despite the striking similarity of *D. virgatus* and *L. leucophala* leaves (figure 1*b*), suggesting that they recognised *D. virgatus* by its leaves alone and attended to these when making a choice. Birds did not exhibit a preference for stems or leaves in treatment-E, although we cannot rule out that they found it difficult to assess the materials placed behind the display screens (table 1).

4. Discussion

We have found that, when sourcing raw materials for hooked stick tool manufacture, NC crows attended to the part of the plant – the stem – from which the tool is crafted (treatment-C). When stems of their preferred species (*D. virgatus*) were not available (treatment-B), most birds failed to engage with plants, presumably because they considered *Melaleuca* sp. stems unsuitable for tool manufacture. Since all subjects readily handled plant material in a subsequent choice trial offering stems of all three species (treatment-D), we can rule out that low participation was due to lack of motivation.

Interestingly, those birds that did manufacture tools in treatment-B, consistently chose the stem with grafted *D. virgatus* leaves, suggesting that leaves serve as an associatively-learned cue. Given their performance in treatment-C, it seems unlikely that these subjects did not recognise that *Melaleuca* sp. – rather than *D. virgatus* – stems had been provided in treatment-B; instead we suspect that they may have had a lower acceptance threshold for stem material, and/or were familiar with making tools from *Melaleuca* sp. [18]. As in one of our earlier studies, where crows had been given suboptimal *D. virgatus* stems [16], most tools were non-hooked, perhaps indicating that this material is more difficult to work with. While leaves have no functional significance, and are usually discarded during tool manufacture [15,16], they may help crows identify their preferred plant species in the wild. The ability to reliably recognise suitable raw materials is expected to enhance foraging efficiency, by avoiding costly interaction with materials that are difficult to process during tool manufacture and/or that yield substandard tools (for NC crow studies, see [13,16,20]).

Our findings set the scene for experiments that test whether NC crows assess – prior to handling materials – features of the stem that are required for the production of efficient tools. They may, for example, examine whether stems possess a well-formed fork and whether the nodal joint offers sufficient wooden material for crafting a hook. Recent experiments have demonstrated that NC crows attend to subtle (functional) features of both raw materials [21] and finished tools [17], and can fashion objects that replicate aspects of recently-encountered templates [22,23], so it seems plausible that birds employ a fairly specific 'search image' and scrutinise plant features of functional significance. If this is confirmed by future work, the species would afford invaluable comparative insights into the process of careful raw-material selection that appears to be a prerequisite for the crafting of relatively complex tools, informing debates about material preferences and shape standardisation observed in hominin tool making [24].

Ethics. Research was approved by our local ethical review committee (31 July 2015) and New Caledonian authorities (permit 2445-2014/ARR/DENV).

Data accessibility. Raw data are reported in table 1.

Authors' contributions. C.R. secured funding and supervised the project; B.C.K. and C.R. designed experiments; B.C.K. and M.C. conducted experiments; B.C.K. scored videos and analysed the data, with input from C.R.; M.C. re-scored some videos; B.C.K. and C.R. wrote and revised the paper, and M.C. contributed to editing; all authors approved the final version and agree to be held accountable for the work performed.

Competing interests. We have no competing interests.

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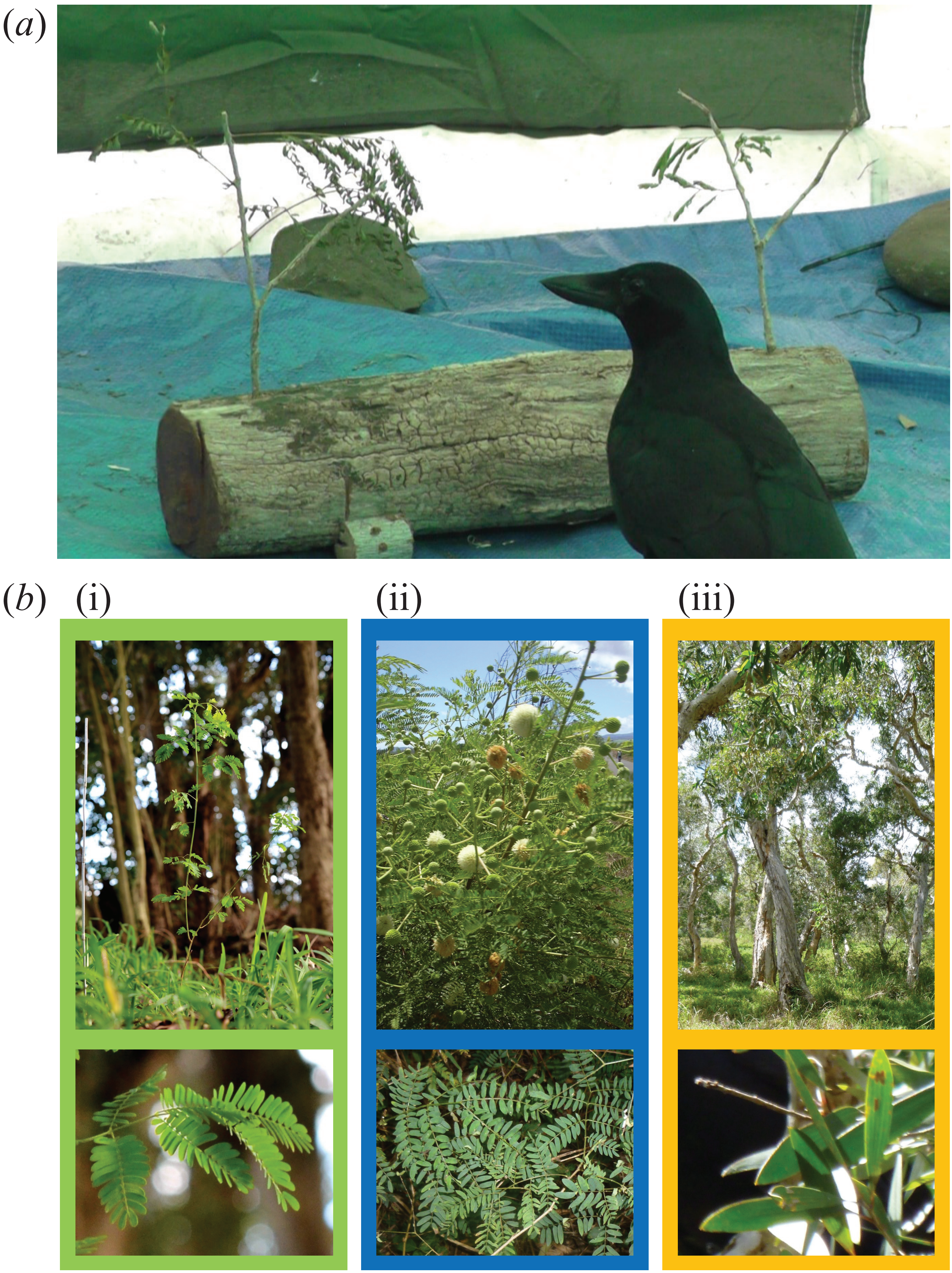
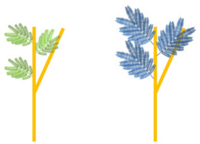
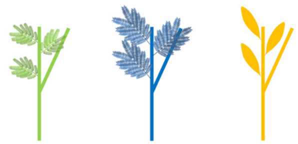
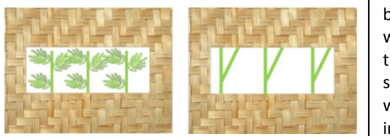
Figure 1. Experimental set-up. (*a*) A New Caledonian crow examining plant options in treatment-B (for details, see table 1). (*b*) Plant species that can potentially be used for hooked stick tool making (key features: relatively small stem diameter, and a suitable fork; [14,16]) and close-up of leaves: (i) *Desmanthus virgatus* (green; photos by James St Clair); (ii) *Leucaena leucocephala* (blue; top photo by Forest & Kim Starr); and (iii) *Melaleuca* sp. (yellow).

Table 1. Experimental rationale and results. Colour coding of the schematic drawings is the same as that used for plant species in figure 1*b*.


(a)
(b)
(i)
(ii)
(iii)

Treatment[a]	Schematic	Rationale	Subjects' behaviour D = ***Desmanthus virgatus*** (green), L = ***Leucaena leucocephala*** (blue), M = ***Melaleuca*** sp. (yellow); X = no interaction; NA = subject did not receive treatment											Preference (for *D. virgatus*[b])
			Subject ID[c]	EV7	CN7	AN2	AM1	AM2	HJ3	CU0	CK6	EA670182	HA5	
			Gape score[d]	1	5	35	60	75	97	99	100	100	100	
A Preference[e]		To confirm birds' preference for *D. virgatus*.	Touch Detach Manufacture Extraction[f]	D D D yes	D D D yes	D D D yes	D D D yes	D D D[g] yes	D D D yes	D D D yes	D D D yes	D D X X	D D D yes	10/10, ***p* < 0.001** 10/10, ***p* < 0.001** 9/9, ***p* < 0.001**
B Leaves[h,i,j]		To investigate if birds pay attention to leaves when choosing raw materials.	Touch Detach Manufacture Extraction[f]	X X X X	X X X X	D D D yes	D X X X	D D D[g] yes	D D D[g] no	D D D[g] yes	X X X X	L X X X	X X X X	5/6, *p* = 0.2* 4/4, *p* = 0.125* 4/4, *p* = 0.125*
C Stems[h,i,j]		To investigate if birds pay attention to stems when choosing raw materials.	Touch Detach Manufacture Extraction[f]	D D D[g] no	D D D yes	D L L yes	D D D yes	L L D yes	D D D yes	D D D yes	D D D no	D D X X	D D D yes	9/10, ***p* = 0.02** 8/10, *p* = 0.11* 8/9, ***p* = 0.04**
D Control[e,i,j]		To rule out motivational issues, to establish that birds retained their preference for *D. virgatus*, and to observe how crows react to glued leaves in a non-grafted condition.	Touch Detach Manufacture Extraction[f]	D D D no	D D D yes	NA NA NA NA	D D D yes	M D D yes	D D D yes	D D D yes	D D D[g] yes	D D X X	D D D yes	8/9, ***p* < 0.001** 9/9, ***p* < 0.001** 8/8, ***p* < 0.001**
E Order[h]		To investigate in which order birds inspect leaves and stems when choosing raw materials. In the cut-out window of one screen, only leaves of *D. virgatus* were visible from the front, while in the other one, only stems were visible.	Touch Detach Manufacture Extraction[f]	X X X X	NA NA NA NA	NA NA NA NA	X X X X	leaves X[k] leaves[k] yes	X X X X	stems stems stems yes	leaves stems stems[g] yes	X X X X	leaves leaves leaves yes	**Preference for leaves** 3/4, *p* = 0.625 1/3, *p* = 1 2/4, *p* = 1

[a]Birds received treatments either in the order A–B–C–D–E or A–C–B–D–E (randomised), with the exception of subject CK6, which was extremely unsettled during the first presentation of B and C (as were birds in adjacent aviaries) and was re-run on these treatments (A–[C–B]–D–E–C–B); results are reported for the re-runs. Stems in each treatment were matched as closely as possible in terms of general appearance [16,17], and the position of stems on the material log was randomised.
[b]All binomial tests are two-tailed. Given our clear expectation of subjects' preference for *D. virgatus* [14,16,17], asterisks are used to denote cases where a one-tailed test would yield a trending *p*-value.
[c]Subjects are identified by their ring codes. All birds had participated in earlier experiments, but had never been given the opportunity to manufacture tools from material other than *D. virgatus*.
[d]Gape score (% black colouration) is provided as a proxy of bird age (older birds tend to have darker gapes; see [16]). Subjects are ordered by gape score.
[e]Expected probability for binomial test (three options), P = 0.33.
[f]In all cases without extraction, crows probed with the tool in the extraction hole (for definition of 'tool manufacture', see supplementary figure 1*b*).
[g]This tool was non-hooked.
[h]Expected probability for binomial test (two options), P = 0.5.
[i]For these treatments, all leaves were removed from the stems and three leaves of either the corresponding (D) or a different species (B, C) were attached with heat glue onto the hook shaft (for terminology, see supplementary figure 1*a*).
[j]New Caledonian crows are likely to experience 'apparent' leaf grafting in the wild, due to the intertwining growth of plants, where leaves of one species are in close proximity to the stems of another species. Nevertheless, since we presented experimental leaf–stem combinations to wild-caught birds that were released again after the experiment, it was of utmost importance to ensure that our treatments did not alter subjects' natural material preferences (even though this imposed constraints on our experimental design). In each treatment, we presented at least one stem of a plant species that is known to be used for hooked stick tool manufacture [14,18]. Importantly, we confirmed through treatment-D that subjects retained their preference for *D. virgatus* after experiencing experimental leaf–stem combinations. Finally, gluing leaves onto the hook shaft only (for terminology, see supplementary figure 1*a*) ensured that crows did not have to touch any glued parts when manufacturing tools.
[k]Here, the subject removed the complete stem from the log and probed with the root shaft (for terminology, see supplementary figure 1*a*), without detaching any material.

ELECTRONIC SUPPLEMENTARY MATERIAL

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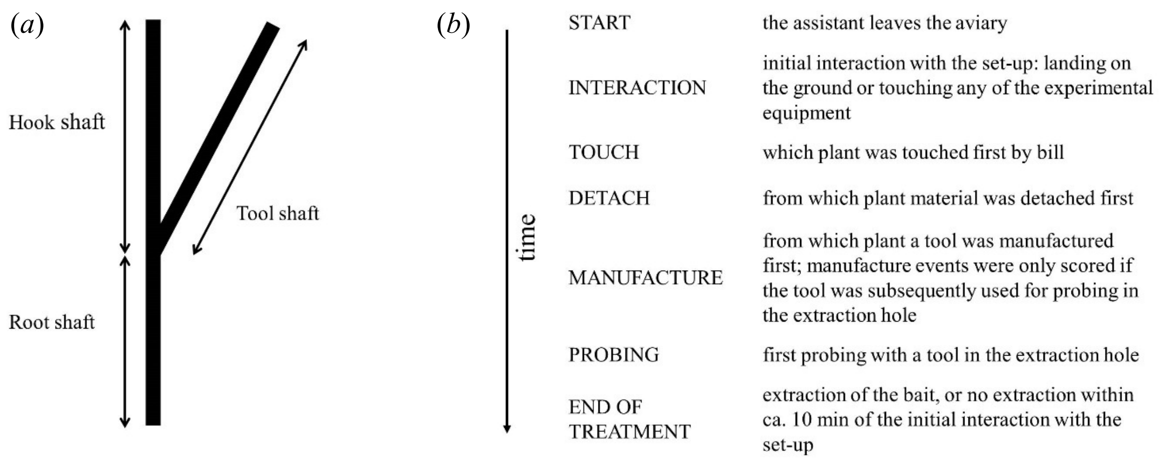

Supplementary figure 1. Terminology and key events. (*a*) Terminology for stems with a single fork. All side branches suitable for hooked stick tool making but one were removed, and all leaves were removed from the tool shaft. (*b*) Key events scored during video analyses.

Supplementary table 1. Inter-observer agreement. (*a*) Cohen's kappa coefficients for key events (see supplementary figure 1*b*). (*b*) Correlation coefficients for the time it took birds to express certain behaviours.

(*a*)

First plant…	**Cohen's kappa coefficient**
…touched	$\kappa = 0.58^a$
…material detached from	$\kappa = 1$
…tool manufactured from	$\kappa = 1$

[a]Both disagreements for 'touch' were due to a misinterpretation of the scoring definition. Re-scoring of these cases by M.C. after clarification resulted in an adjusted $\kappa = 1$.

(*b*)

Time of first…	**Correlation coefficient**
…interaction	$r = 1, p < 0.001$
…touch	$r = 1, p < 0.001$
…detachment	$r = 1, p < 0.001$
…manufacture	$r = 1, p < 0.001$