

Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites

Lucas A. Bluff^{1,*,\dagger,\ddagger}, Jolyon Troscianko², Alex A. S. Weir¹,
Alex Kacelnik¹ and Christian Rutz^{1,*,\ddagger}

¹Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

²School of Biosciences, University of Birmingham, Birmingham B15 2TT, UK

New Caledonian crows *Corvus moneduloides* use tools made from sticks or leaf stems to ‘fish’ woodboring beetle larvae from their burrows in decaying wood. Previous research on this behaviour has been confined to baited sites, leaving its ecological context and significance virtually unexplored. To obtain detailed observations of natural, undisturbed tool use, we deployed motion-triggered video cameras at seven larva-fishing sites. From 1797 camera hours of surveillance over 111 days, we recorded 317 site visits by at least 14 individual crows. Tool use was observed during 150 site visits. Our video footage revealed notable variation in foraging success among identifiable crows. Two nutritionally independent, immature crows spent considerable time using tools, but were much less successful than local adults, highlighting the potential role of individual and social learning in the acquisition of tool-use proficiency. During systematic surveys of larva-fishing sites, we collected 193 tools that crows had left inserted in larva burrows. Comparing these tools with the holes in which they were found, and with raw materials available around logs, provides evidence for tool selectivity by New Caledonian crows under natural conditions. Taken together, these two complementary lines of investigation provide, to our knowledge, the first quantitative description of larva fishing by wild crows in its full ecological context.

Keywords: extractive foraging; social learning; tool use; *Agrianome fairmairei*; *Aleurites moluccana*; *Corvus moneduloides*

1. INTRODUCTION

Woodboring (‘xylophagous’) beetle larvae are a rich but well-protected food resource. Their predators typically employ specialist morphology to overcome the structural defence formed by a larva’s xylem surroundings. For example, pileated woodpeckers *Drycopus pileatus* excavate beetle larvae by removing wood with chisel-like bills (Raley & Aubry 2006), while aye-eyes *Daubentonia madagascariensis* gnaw into larva burrows with powerful incisors, before skewering larvae with an elongate digit (Sterling 1994). The use of tools to extract xylophagous beetle larvae is rare, being apparently restricted to humans *Homo sapiens* (Bodenheimer 1951), Galapagos woodpecker finches *Cactospiza pallida* (Tebich *et al.* 2002) and New Caledonian crows *Corvus moneduloides* (hereafter ‘crows’).

In New Caledonia, decaying trunks of candlenut trees *Aleurites moluccana* (electronic supplementary material, figure S1) commonly house larvae of the longhorn beetle *Agrianome fairmairei* (Cochereau 1970). Crows ‘fish’ for larvae by probing their burrows with leaf petioles of *A. moluccana* (hereafter ‘leaf-stem tools’), or twigs from

various plant species (hereafter ‘twig tools’) (Hunt 2000). These tools are used to irritate the larva until it bites the tool tip and can thus be extracted (Hunt 2000, see movie S1 in the electronic supplementary material). Research to date has been conducted at baited sites, where either live or dead larvae were experimentally presented in natural burrows, holes drilled into logs, or Perspex-sided boxes (Hunt 2000; Hunt *et al.* 2006). The use of baited sites enhances opportunities for close observation, but it precludes the collection of behavioural data under natural conditions (McGrew 1992; Rutz *et al.* 2007).

The paucity of studies on such a rare and interesting behaviour results from the difficulty of observing this species’ natural foraging behaviour (Rutz *et al.* 2007). Previously, in 841 h of video- and radio-tracking crows in our study area (2005–2007), which includes sites containing many beetle-infested fallen logs, we have observed only three instances of potential larva fishing. Here, we describe the deployment of motion-triggered video cameras at larva-fishing sites visited by a population of individually marked crows, addressing three main objectives. First, to determine the extent of natural larva fishing and whether tool use is an obligate feature of the task, we quantified the frequency of tool use and larva extraction at unbaited, naturally degrading logs. Second, while individual crows are known to specialize in the type of tools they use (Hunt & Gray 2007), the finer details of variation between individuals within a single form of tool use have not previously been investigated under field conditions. In particular, we examined

* Authors for correspondence (lucas.bluff@sci.monash.edu.au; christian.rutz@zoo.ox.ac.uk).

† Present address: School of Biology, Monash University, Victoria 3800, Australia.

‡ These authors contributed equally to the study.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.1953> or via <http://rspb.royalsocietypublishing.org>.

whether individual crows differ in their extraction behaviour, especially their tool-use competence. Finally, given the potential for social learning of tool skills (Hunt 2000; Kenward *et al.* 2006), and the claim that this species may culturally transmit aspects of its tool technology (Hunt & Gray 2003), we documented opportunities for young crows to learn about tool-assisted foraging individually, or from older individuals.

Over the same period as the video surveillance was conducted, we systematically scanned foraging sites throughout the area to collect the tools left behind by crows (electronic supplementary material, figure S2). Previous field and laboratory experiments have offered differing perspectives on the degree of tool selectivity shown by crows (Chappell & Kacelnik 2002, 2004; Hunt *et al.* 2006), but whether selectivity occurs under natural conditions is unknown. By comparing the dimensions of tools with those of the burrows in which they were found, and with the locally available supply of raw materials, we can examine the hypothesis that crows select tools from the environment on the basis of task affordances.

2. MATERIAL AND METHODS

(a) Study site and subjects

New Caledonian crows inhabit the islands of Grande Terre and Maré, some 1200 km east of mainland Australia. While this species is known to make three distinct types of tool, including complex shapes cut from the barbed edges of *Pandanus* spp. leaves (Hunt 1996), the research we describe here only concerns the use of non-hooked stick-type tools (i.e. leaf-stem tools and twig tools; §1). This appears to be the only tool type used by crows for larva fishing in our dry forest study area in the Tabou and Taro valleys (21°33' S, 165°19' E; electronic supplementary material, figure S3) of the Parc Provincial de Gouaro-Déva, on the central west coast of Grande Terre. On current evidence, crows source the majority of their larva-fishing tools from the leaf litter around *A. moluccana* logs (this study and J. Troscianko, L. A. Bluff & C. Rutz 2006–2009, unpublished data; Hunt 2000; Hunt *et al.* 2006), although they may occasionally use material from trees or bushes (J. Troscianko, L. A. Bluff & C. Rutz 2006–2009, unpublished data; see also Hunt 2000). Since October 2005, as part of an ongoing project on the socio-ecology of wild crows, we have marked a substantial proportion of this local population with coded wing tags and colour rings (we refer to individuals by ring code throughout). Details of crow marking, sexing and ageing, and a description of local diet, are provided in the electronic supplementary material.

(b) Motion-triggered video surveillance

Our focal study area contained some 20 dead trunks of *A. moluccana* at any one time, which were subject to occasional degradation by humans and feral pigs *Sus scrofa*, in addition to their use by crows. Between 29 October 2006 and 16 February 2007, we deployed four customized, motion-activated, digital video-recorders at seven different *A. moluccana* sites (electronic supplementary material, figures S3 and S4). While some 'sites' contained more than one 'log' (e.g. sites A and Q), video cameras were always used to monitor one log at a time. Following an initial trial of one unit in the nearby Vallée des Cannes (ca 2 km E), from 8 November onwards, we deployed all units in the focal study area. We

chose sites where the presence of fresh frass ('sawdust' excreted by xylophagous insects) and crow tools (see below) indicated good larvae and crow activity, and changed recording locations when old sites were depleted or more attractive ones became available (electronic supplementary material, figure S4). These displacements allowed us to map foraging activity in the area as a whole (although three logs were under observation for extended periods of time). We allowed all sites to degrade naturally, including those fitted with video cameras, i.e. we never baited sites or opened up wood to expose larva burrows. For part of the study, one camera was deployed to monitor an active crow nest in the study area.

It is likely that we recorded all crow visits to sites under active video surveillance. While surveillance was not continuous over the entire study period (e.g. owing to battery and memory limitations), we attempted to service the units at intervals that minimized periods of inactivity. Details of video-recorder specifications and deployment are provided in the electronic supplementary material.

(c) Video scoring

Foraging bouts were scored in random order by the same observer (L.A.B.), using replays and slow motion to facilitate interpretation where necessary. A foraging bout was defined as all footage at a particular site, within which crows were not absent for longer than 2 min. Events and durations were recorded at the levels of individual crows (for each bout) and individual tools (for each crow bout). For each bout, the following data were scored: date and time, location, identity of crows present, number of tools used, number of larvae extracted and minutes of footage during which the crow was present (see the electronic supplementary material).

(d) Sampling of tools and raw materials

During two field seasons (4 December 2005 to 2 February 2006 and 8 October 2006 to 25 February 2007), we regularly searched for tools that had been left behind by crows at dead *A. moluccana* sites, with additional opportunistic sampling during radio tracking and other field activities. Between 17 November 2006 and 7 February 2007, we conducted a standardized tool-site survey at intervals of 2–7 days (mean distance between sites = 241.4 ± 20.5 m; sites A–P in the electronic supplementary material, figure S3). These surveys yielded samples of tools (twigs and leaf stems found unambiguously inserted into holes or crevices in dead wood, or into the substrate immediately below) and of 'potential tools' (twigs and leaf stems found lying on the surface, within 1 m of decaying wood, at video-recording sites). Tools were photographed *in situ* before collection, and we also recorded the dimensions of the holes in which they were found. At certain sites, we collected complementary samples of the raw materials available to crows on the ground (where crows source most tools; see §2a), using two different methods. First, 'control plot' samples were collected by clearing loose vegetable matter from 0.7×0.7 m quadrats during each tool survey. Single control-plot quadrats were established near (ca 2–3 m) 11 sites under circumstances that, as much as was possible, matched those of the focal log (e.g. presence/absence of overhanging vegetation). Second, 'leaf litter' samples were obtained through haphazard sampling of the forest floor, from within ca 10 m of selected focal logs (see the electronic supplementary material, figure S3), at the end of the study period (on 25 February 2007).

Tools and potential tools were measured in a pooled and shuffled order (J.T.), while raw-material samples were measured separately but also in a haphazard order (L.A.B. and J.T.). In all cases, the location and date of collection were masked from the measurer. Mass, length and diameter were measured for tools and potential tools, while mass and length were measured for raw materials. Details of sampling and measurement methods are provided in the electronic supplementary material.

(e) *Statistical analysis*

We modelled tool dimensions as dependent variables and hole dimensions as covariates. Canonical correlations (Tabachnik & Fidell 2007) were used to select tool length and hole depth as representative variables, which also facilitated comparison with previous studies. Model fit for general linear models (GLM) was checked with diagnostic scatter plots, using standardized residuals, and transformations were applied where necessary. All results remained qualitatively unchanged when data were modelled with general linear mixed models (GLMM; with site identity fitted as a random effect) instead of GLMs. However, as many crow tools were found outside pre-defined sites, and as many sites had only small sample sizes, data exclusion substantially reduced the power of GLMMs, and we report GLM results throughout, which are based on the full dataset. The empirical distributions of tools and raw materials were compared with the non-parametric statistic of stochastic difference (δ) and its effect-size equivalents, as well as Welch's *t*-test for ranks (Vargha & Delaney 2000).

We used SPSS 16.0, MINITAB 15.0, and GENSTAT 11 for statistical modelling. All tests are two-tailed, and means are reported with their standard errors. Further analysis details are provided in the electronic supplementary material.

3. RESULTS

(a) *Video surveillance*

(i) *Foraging activity*

Over a period of 111 calendar days, video surveillance was active for at least 1797 camera hours on 201 camera days (16.19 ± 1.14 h of surveillance per day). We recorded 317 crow visits to five *A. moluccana* sites, by at least 14 different individuals. Of these, 10 crows were marked with wing tags and were readily identifiable from video footage (see movies S1–S3 in the electronic supplementary material), and another two birds wore rings but had lost their wing tags (table 1).

Crows were typically active at *A. moluccana* logs for less than 1 per cent of surveillance time on any given day (range: 0–9.9%; electronic supplementary material, figure S4). Foraging activity varied considerably over the study period, and reflected at least partly the breeding cycle of a resident pair that nested in close proximity to surveillance sites (male, HC4; female, AK9; offspring, HS8). Early peaks (9 and 13 September 2006) were largely caused by high-intensity foraging by HC4 to provision the brooding female (confirmed by nest-camera observation). The second, prolonged period of elevated activity (2 January 2007, onwards) coincided with the fledging of HS8, two offspring from another nearby pair (male, HK9; female, EK6; offspring, HM0 and HM5), and two unmarked offspring from an unknown nest. There was no strong evidence from

video footage, or our general field observations, that breeding pairs effectively deprived other individuals of access to larva-fishing sites.

(ii) *Tool deployment*

Crows used tools in 47 per cent ($n = 150$) of bouts, deploying on average 1.57 ± 0.09 tools per bout (range: 1–6). Within bouts, individual tools ($n = 234$) were inserted by individual crows into 3.05 ± 0.194 holes (range: 0–18), which is most probably an underestimate, as assessment of individual holes was constrained by video resolution. In the cases where a tool's fate at the end of a bout could be determined ($n = 168$), 40 per cent ($n = 67$) were carried off-screen by the crow, 33 per cent ($n = 56$) were dropped on the ground, 14 per cent ($n = 24$) were left lying on the log and 13 per cent ($n = 21$) were left inserted into a hole. Crows were observed to use tools found in holes in 7 of the 105 cases where tools were obtained on-screen, although this frequency was most probably affected by our systematic removal of tools from holes.

(iii) *Extraction success*

Approximately 7 per cent ($n = 23$) of all recorded visits by crows to foraging sites resulted in the capture of one or more larvae. Success in larva extraction was spatially localized and temporally sporadic. For example, 16 of the total 35 observed extractions occurred at site A on 26 November 2006. Cases in which more than one larva was extracted in a single bout ($n = 18$) accounted for more than half of all extractions. Of the 35 recorded extractions (across at least six individual crows, of which four were marked, and two or more unmarked), 25 cases (71%) were immediately preceded by the use of a tool in the same hole (see movie S1 in the electronic supplementary material). These 25 hole–tool pairings that immediately preceded extraction events represent a small percentage (4%) of all observed pairings of tools with holes ($n = 713$), and so the vast majority of such pairings were unsuccessful. We cannot infer to what extent this overall success rate was the product of (i) a low abundance of larvae in accessible burrows, (ii) failure by crows to locate accessible larvae, or (iii) failure by crows to extract a larva once it had been located.

(iv) *Individual differences in foraging behaviour*

Individual crows varied substantially in the time they were observed foraging at camera sites, and in the number of larvae they extracted on video (table 1). The most successful crow was HC4, an adult male, who extracted 15 larvae in a total of 80 min present at camera sites. The highest extraction efficiency of four larvae in 18 min was observed in HE1, an immature male. By contrast, the two individuals who were observed foraging most often, and for the greatest total duration, were surprisingly unsuccessful: EK2 obtained only one larva in 305 min on-camera, and HK2 failed to extract any larvae in 195 min. Both were immature second-year birds, the offspring of the resident breeding pair (HC4, AK9) from a brood in 2005. While we do not have sufficient longitudinal gape-coloration data to estimate precisely the age difference between these immature siblings and the

Table 1. Summary statistics for autonomous video footage, for marked and unmarked (pooled) New Caledonian crows. (Birds EK6 and AK9 did not have wing tags at the time of video recording, but could often be distinguished by their rings or their association with other crows. Crows that were marked, but could not be positively identified, were recorded as 'identity uncertain'. While three unmarked crows were seen simultaneously on one occasion, the real number of unmarked individuals filmed is likely to be higher.)

crow ID	sex	age class	family group	bouts	bouts	larvae	larvae	tools used	tool/hole pairings	time present (HH:MM:SS)	time spent in tool use (%)
				with tools	without tools	obtained with tools	obtained w/out tools				
EK2	male	immature	A	48	26	1	0	79	267	05:05:02	61.0
HK2	male	immature	A	44	24	0	0	70	237	03:15:37	61.2
HE1	male	immature	—	4	8	4	0	9	17	00:18:18	61.9
HC4	male	adult	A	11	15	8	7	18	43	01:20:09	48.5
EK6	female	adult	B	8	10	3	0	19	45	01:18:29	46.6
AK9	female	adult	A	2	2	0	0	6	11	00:17:04	15.9
EK0	female	adult	—	0	1	0	0	0	0	00:01:46	0
HK4	male	adult	—	0	1	0	0	0	0	00:00:13	0
HM5	male	juvenile	B	0	3	0	0	0	0	00:12:38	0
HS8	female	juvenile	A	2	2	0	0	3	3	00:06:13	34.9
HM0	male	juvenile	B	1	1	0	0	1	0	00:02:14	94.0
unmarked crows	—	—	—	22	33	9	3	29	82	02:06:27	35.8
identity uncertain	—	—	—	8	41	0	0	9	8	00:31:24	9.6

older immature HE1, the most likely age difference is a full breeding cycle, i.e. roughly 12 months.

Both EK2 and HK2 used tools more frequently and for a greater proportion of foraging time than did more successful foragers (table 1). However, in a quantitative comparison across crows ($n = 6$ individuals observed for more than 5 min each, excluding juveniles), relative measures of tool-use intensity (proportion of time spent in tool use; number of tools used per hour; number of tool-hole pairings per hour) were not significantly related to either success rate (larva extractions per hour), or overall success (number of extracted larvae) (Pearson's r , $p > 0.2$ in all cases). Because of limited sample sizes within and among crows, these results should be interpreted cautiously.

Male HC4 extracted seven of a total of 15 larvae without the use of a tool. He achieved four of these extractions by a powerful, 'woodpecker-like' use of the bill to chisel away the dead wood surrounding a larva. Other crows, and HC4 on other occasions, regularly performed such chiseling within periods of tool use (see Hunt 2000, and case study in the electronic supplementary material). The remaining three larvae extracted by HC4 without tools were simply picked from their burrows, nearby in the same log, within 30 s of each other.

(v) Opportunities for social learning

Video footage showed two or more crows simultaneously present at foraging sites in 12 per cent ($n = 32$) of 268 observed bouts. This occurred most often among related crows: nine bouts included the simultaneous presence of a parent and one or more offspring (e.g. see movies S2 and S3 in the electronic supplementary material), while in 14 bouts a pair of siblings was present simultaneously with or without their

parents. However, in four bouts, an immature crow was filmed simultaneously with an adult known not to be its parent (EK2 with EK6 once, HK2 with EK6 thrice).

The same tool was observed to be used by multiple crows within the same bout in at least five instances. For example, at 08.34 on 7 February 2007, EK2 was using a tool in a larval burrow, when it was displaced by EK6, who proceeded to use the same tool in the same hole (see also scene 3 of movie S2 and scene 1 of movie S3 in the electronic supplementary material). It is likely that similar events occurred more frequently but could not be confirmed owing to insufficient video quality.

Begging was recorded at larva foraging sites on 22 occasions, by four marked juvenile or immature crows (EK2, HK2, HM0 and HM5) and at least one unmarked crow. Such begging was typically directed at a parent. In one case, begging was associated with a parent provisioning its nutritionally dependent offspring with *A. fairmairei*: on 3 February 2007 at 18.16, EK6 extracted a larva and immediately fed it to HM5 (scene 2 of movie S2 in the electronic supplementary material). By contrast, HC4 extracted three larvae in a single bout in the presence of its nutritionally independent, but frequently begging, offspring (EK2 and HK2) without feeding them (see movie S3 in the electronic supplementary material).

While it proved difficult to quantify the attention paid by juvenile and immature crows to the foraging actions of their parents (e.g. as the offspring might be watching its parent while foraging itself), a description and video summary of one such bout may provide an informative case study (included in the electronic supplementary material).

(b) Tools and raw materials**(i) Tool properties**

We found 193 tools inserted into holes and crevices in logs, 18 tools lying in open hollows and 47 tools inserted into frass on, or immediately below, logs. In addition, 230 possible tools were found lying at the base of logs at camera sites. Although we cannot attribute tools to individual crows, we are confident that the collected tools represent an adequate sample of tools used among crows in the study area, because (i) video surveillance showed that individual sites were visited by several individuals and (ii) the area searched for tools incorporated multiple crow home ranges (C. Rutz, L. A. Bluff & J. Troscianko 2005–2008, unpublished data).

Summary statistics of tool and hole properties are presented in table S1 in the electronic supplementary material. Pooling across sites, twig tools were longer on average than leaf-stem tools (GLM, $F_{1,256} = 4.45$, $p = 0.036$). After controlling for the effect of length (GLM, $F_{1,255} = 33.98$, $p < 0.001$), leaf stem and twig tools did not differ significantly in maximum basal diameter (GLM, $F_{1,255} = 0.126$, $p = 0.717$). For sites with at least 10 tools (A, F, J, L, N and Q; $n = 130$ tools), tool length did not differ significantly between sites (GLM, $F_{5,123} = 0.91$, $p = 0.479$), after controlling for tool type.

From examining inserted tools whose apical and basal ends could be determined, there was no evidence that crows preferentially used one end of the plant material as the functional end (two-sided binomial tests: $n = 87$ leaf-stem tools, of which 51 with basal end inserted, $p = 0.133$; $n = 132$ twig tools, of which 70 with basal end inserted, $p = 0.541$). Apically and basally inserted tools did not differ significantly in length (controlled for tool type; GLM, $F_{1,216} = 2.44$, $p = 0.120$), suggesting that there was no strong sampling artefact caused by sticks falling from holes prior to collection (for a discussion, see §4d).

(ii) Do crows select tools from the available raw materials?

Pooling data across sites, the distributions of stick lengths differed significantly between tool, potential tool, control plot and leaf-litter samples (two sample Kolmogorov–Smirnov tests, in all cases $p \ll 0.001$; figure 1). The largest stochastic differences were found between the tool samples and, respectively, control plots (stochastic difference $\delta = 0.61$, which is equivalent to a conventional ‘large’ effect size; Vargha & Delaney 2000) and leaf-litter samples ($\delta = 0.41$, large). By comparison, the stochastic difference between control plot and leaf-litter samples was minor ($\delta = 0.09$, small). The null hypothesis of no stochastic difference between samples could be rejected ($p \ll 0.001$) for all comparisons except those between control plot and leaf-litter samples ($p = 0.089$, which exceeds the Bonferroni-corrected threshold probability of 0.016), demonstrating that crow tools are a non-random sample from the available raw materials. In all comparisons, the sample of potential tools was intermediate between actual tools and the available raw materials (control plots and leaf-litter samples).

Further evidence for selectivity comes from the observation that crows use significantly more *A. moluccana* leaf stems (overall frequency in the tool sample) than expected from this material’s availability in either control plots (χ^2 -test: $\chi^2_1 = 35.608$, $p < 0.001$), or leaf-litter samples

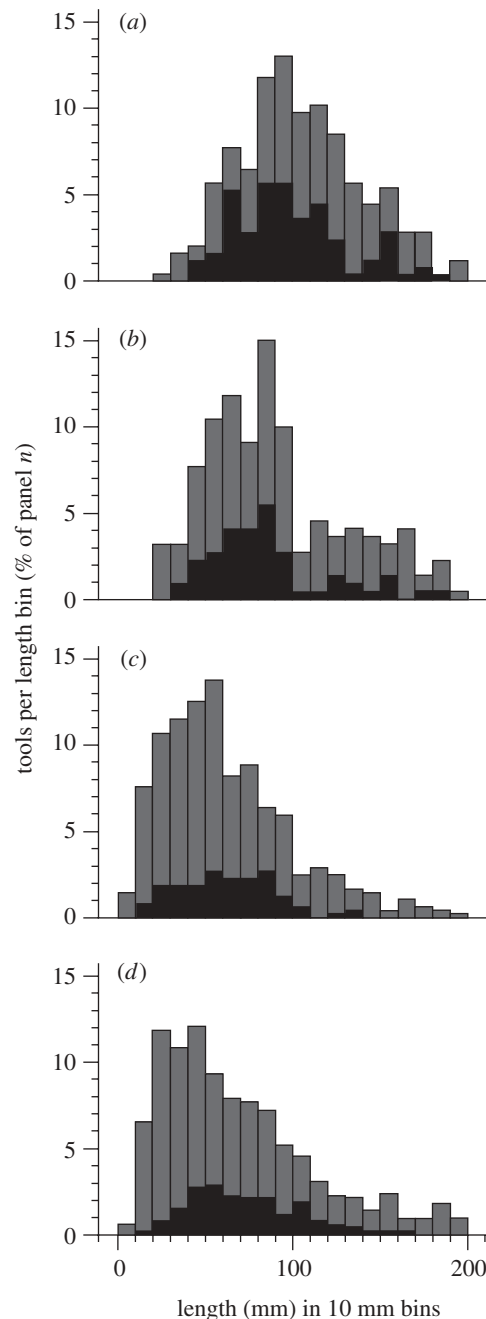


Figure 1. Histograms of the lengths of New Caledonian crow tools, possible tools, and control plot and leaf litter raw-materials samples (pooled across sites). Data for both leaf-stem tools (black bars) and twig tools (grey bars) are shown. The y-axis represents the percentage of the overall cell total that is contributed by each length bin. Data for individual sites are shown in figure S5 in the electronic supplementary material. (a) Tools ($n = 258$); (b) possible tools ($n = 230$); (c) control plot ($n = 502$) and (d) leaf litter ($n = 878$).

($\chi^2_1 = 37.238$, $p < 0.001$). Control plot and leaf-litter samples did not differ significantly in the proportion of *A. moluccana* raw material ($\chi^2_1 = 0.405$, $p = 0.525$; figure 1).

(iii) Is tool selection related to hole properties?

We took depth measurements from 186 holes in which tools were found, of which 10 were larger cavities not associated with larva burrows (table S1 in the electronic supplementary material shows full dataset). Pooling all tools found in larva-type holes ($n = 176$), hole depth

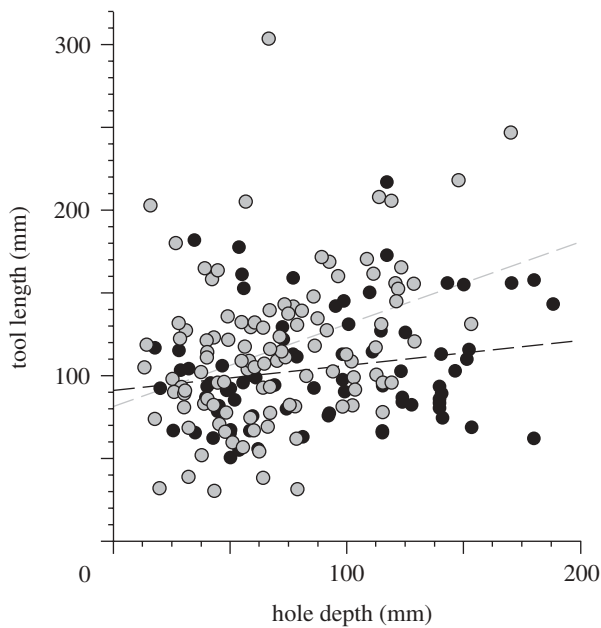


Figure 2. Relationship between the length of inserted New Caledonian crow tools ($n = 176$) and the depth of holes in which they were found (raw data). Longer tools were found in deeper holes (GLM, $F_{1,173} = 16.74$, $p < 0.001$), after accounting for twig tools (grey) being longer on average than leaf-stem tools (black) (GLM, $F_{1,173} = 5.54$, $p = 0.020$). This tool-length/hole-depth relationship remained significant after omission of the unusually long twig tool.

was a significant predictor of tool length after controlling for the significant effect of tool type (figure 2). There was a marginally non-significant interaction between tool type and hole depth (GLM, $F_{1,172} = 3.56$, $p = 0.061$), with a steeper slope for twig tools than leaf-stem tools (figure 2). When data were restricted to tools found at sampling sites with at least 10 tools each (A, F, J, L, N and Q; $n = 93$ tools), hole depth remained a significant predictor of tool length (GLM, $F_{1,85} = 4.98$, $p = 0.028$), after accounting for the non-significant effects of tool type (GLM, $F_{1,85} = 0.70$, $p = 0.405$) and site (GLM, $F_{5,85} = 0.57$, $p = 0.720$). Thus, while there was considerable variation, tools found in deeper holes were on average longer than tools found in shallower holes.

4. DISCUSSION

An individual larva of the beetle *A. fairmairei* is a valuable food item, albeit one that is well defended by the woody tissue in which it lives. New Caledonian crows overcome this defence by using tools; most larvae obtained by crows are 'fished' out with sticks or leaf stems. Previous research on this behaviour has been constrained by the need for direct human observation, which in practice requires provisioning of crows with larvae (Hunt 2000; Hunt *et al.* 2006). This approach permits only limited ecological and behavioural inference, owing to the experimental modification of the abundance of larvae and/or of the difficulty of their extraction. We circumvented these constraints with the use of motion-triggered video monitoring of naturally decaying, larva-infested logs. Our video surveillance showed that at such sites, in contrast to baited areas, larva fishing is sufficiently infrequent to frustrate attempts at research by direct observation.

Autonomous video monitoring of chimpanzee *Pan troglodytes* foraging at termite nests yielded comparably low rates of attendance (Sanz *et al.* 2004), highlighting the value of automated video surveillance for documenting and quantifying rare foraging events in natural ecological contexts (see also Sanz *et al.* 2009). While sample sizes in our study are comparatively small, they represent the outcome of some 1800 h of surveillance at tool-use hot-spots; accumulating such a dataset through direct human observation would have been impractical.

(a) Frequency of tool use and larva extraction

Infested *A. moluccana* logs often contain hundreds of larvae and would therefore appear to constitute a highly aggregated food supply, ready to be exploited by crows. However, our video surveillance suggests that the depletion rate per log averages only one larva per 50 daylight hours. This rate reflects both the infrequency of attendance by crows (<1% of our total surveillance time) and their comparatively low rate of success when present (one larva every 25 min on average; 93% of crow visits did not lead to a larva extraction). Crows used tools on roughly half (47%) of all visits to larva-fishing sites, and successful crows achieved most of their extractions through the use of tools. Taken together, we infer that the overall rate of extraction is typically limited by the accessibility of larvae to crows, rather than their absolute abundance in the environment. This accessibility is by no means constant, as it reflects the larva-fishing competence of individual crows and the position of individual larvae within logs, among other factors.

(b) Individual differences in foraging behaviour

Quantitative trapping and marking of birds enabled us to compare the tool-use competence of known wild individuals. One immature crow foraged unsuccessfully at larva-foraging sites for a total duration exceeding 3 h, while another achieved only a single larva extraction over 5 h of foraging. By contrast, an older immature crow and two adults enjoyed much higher rates of foraging success at the same locations, despite having lower attendance times. Furthermore, our video dataset provided several examples (see case study in the electronic supplementary material), where young crows foraged simultaneously with adults, but only the latter managed to extract larvae. It is unclear whether the foraging success of the two younger crows was more limited by their ability to locate larvae or to extract them when located. Both individuals were of a sufficient age (390 days or older at the start of this study) to perform the basic mechanics of tool manufacture, and both used tools frequently during video-recorded foraging and did not differ from older crows in the median number of tools used per bout. In a previous field season, one of the two (EK2) was first observed to use tools some 86 days after fledging, which matches the development of basic tool-use ability by four captive juveniles at 63–79 days of age (Kenward *et al.* 2005, 2006). Thus, while fishing for live larvae certainly requires a higher degree of motor control than extracting inert rewards in captivity, we have no reason to believe that the younger immature crows in this study were unusually incompetent. We therefore suggest (i) that the process of finding and extracting *A. fairmairei*

larvae requires a high level of acquired skill and (ii) that this ability typically develops by individual or social learning over more than a year post-fledging.

(c) Opportunities for individual and social learning

Juveniles forage less proficiently than adults in many other bird species (Wunderle 1992), and field studies of other tool-using species have indicated that maturation of tool-related foraging skills can take considerable time. For example, the development of proficient stone tool nut-cracking in chimpanzees requires 3–5 years (Boesch & Boesch-Achermann 2000; Biro *et al.* 2003), while the efficiency of human hunter-gatherers in skilled foraging peaks between 25–35 years of age (Kaplan *et al.* 2000). Thus, reduced efficiency of larva foraging among young crows is not unexpected. Yet, while we did not measure the energy consumption of the two young crows in this study, their almost complete lack of success suggests that they lost more energy in foraging than they gained either from larvae (including any they may have obtained from their father), or other prey found incidentally in and around the decaying logs. Similarly, captive New Caledonian crows engage in tool-based foraging attempts before having the skills that make this behaviour profitable (Kenward *et al.* 2006). If this proves generally true, we suggest that the immediate energetic cost of learning complex tool-related skills (namely the lost opportunity of foraging elsewhere by less demanding means) is offset by future benefits, most probably in the provisioning of offspring with tool-derived food sources.

There are many aspects of larva fishing that may require learning, for example, identification of active logs, location of larvae within logs, selection of appropriate tools and contingent reaction to larva behaviour. However, if learning occurs by practice, it would not be driven at this stage of development by direct food reinforcements. Rather, it seems to be the consequence of an inherited motivational system aimed at fostering tool-related competence (Kenward *et al.* 2006).

Likewise, there is considerable scope for social learning of aspects of larva fishing. Apart from observing foraging adults (this study; Hunt 2000), young crows may indirectly gain information through encountering the non-random sub-sample of raw materials present in the immediate vicinity of foraging sites. Our video surveillance demonstrated that substantial numbers of tools are left behind at tool sites and that immature crows adopt these tools, including ones that they have found inserted in holes (see also Hunt 2000). These observations are corroborated by indirect evidence: the sticks in our potential tools sample were more similar in their properties to actual tools than to sticks from both raw-material samples, suggesting that many of them were in fact crow tools. The deposition of used tools by skilled foragers creates the opportunity for acquiring information about (i) the properties of profitable holes, (ii) the properties of tools, and (iii) the relationship between holes and tools.

(d) Selection of larva-fishing tools

We found that crows do not sample randomly when selecting larva-fishing tools from the available raw materials. First, the length distribution of tools was

statistically different from the distributions of both the existing leaf litter and newly fallen debris (cf. Hunt *et al.* 2006). Second, leaf stems of *A. mollucana* appear to be used more often for larva fishing than twigs of other species, based on the relative availability of raw materials in the local environment. In isolation, these results could be explained by simple ergonomic factors intrinsic to crow morphology. However, we also found an association between tool length and hole depth, which is more difficult to explain, and could reflect matching by crows. This is not a complete surprise, given that laboratory work with captive individuals has shown that crows possess the ability to make visual assessment of task demands and select or manufacture tools of appropriate dimensions (Chappell & Kacelnik 2002, 2004; Wimpenny *et al.* 2009). But whether the same selection process operates in the wild has been questioned: a length-selection experiment found that a wild individual made reactive selection for longer tools only when the initial tool proved too short (Hunt *et al.* 2006). There are many reasons why, under natural conditions, a tool-hole matching ability may be difficult to detect. Larvae are generally hidden in opaque burrows and covered with frass, so visual assessment is more difficult than for a transparent experimental box. Crows are further constrained by the availability of raw materials, as they must search for comparatively rare long tools rather than select at will from an experimental array. Also, as we found here, the tool-to-hole relationship is rarely one-to-one (as in experimental contexts); wild crows visiting natural logs sometimes use a range of tools to probe many different holes. Considering these factors, it is striking that our data revealed a significant positive relationship between tool length and hole depth.

This result could either occur as an artefact, or from crows matching tools and holes. An artefactual relationship between tool length and hole depth could arise from a size bias in our detection of tools in holes, or from the persistence of tools in holes until collected. While we consciously tried to reduce the likelihood of the former by thorough examination of holes, we can address the latter possibility (long sticks tend to fall out of short holes before collection) with our data; a stick's centre of gravity is closer to its basal end, so an apically inserted tool would be more likely to fall from a given hole than would a basally inserted tool of the same length. We found no difference in length between apically and basally inserted tools (see §3b(i)), suggesting that there was no systematic bias owing to sticks falling from holes. It could also be argued that our tool sample is biased against successful tools, given that these are removed from holes in the process of larva extraction. Three lines of evidence suggest that any effect of such bias would be weak. First, the proportion of successful tool-hole pairings was sufficiently low (4%) that their complete exclusion would be highly unlikely to affect the outcome of statistical tests. Second, tools are frequently used in multiple holes, and are reused over time, thus the presence of a tool in a given hole does not directly reflect its past success, or its potential future use. Finally, as crows adopt tools found in holes, there is no evidence that these are inferior to other available materials.

Following the above considerations, it appears that crows do match tools and holes during natural foraging, but how this is achieved remains unclear. The least

cognitively demanding explanation would seem to be passive matching, in which haphazard combination of tools and holes is followed by a tendency to persist longer with a given tool and hole, if these 'fit together'. Taking site-level means for six sites with at least 10 tools each, there was no correlation between hole depth and tool length ($r = -0.131$, $p = 0.8$), suggesting that matching occurred at the level of the individual hole, rather than at the level of the log, but this deserves further investigation with more data. In any case, active matching could be achieved by a variety of mechanisms: (i) visual hole inspection and *a priori* tool selection (*sensu* Chappell & Kacelnik 2002); (ii) reactive selection of longer tools for deeper holes (*sensu* Hunt *et al.* 2006); and (iii) reactive selection of deeper holes once a long tool has been acquired. These possibilities are not mutually exclusive, and further subtleties, such as context dependence, may be unravelled by experimental manipulation.

5. CONCLUDING REMARKS

Our two complementary lines of investigation—motion-triggered video surveillance and systematic collection of tools and raw materials—provided, to our knowledge, the first quantitative description of larva fishing by wild crows in its full ecological context. Enhancing our understanding of these birds' foraging behaviour (with and without tools) is important, considering that the scarcity of tool use across species seems to be largely an ecological issue. If formidable cognitive prerequisites constrain the frequency at which tool use evolves, then the rarity of the evolution of such cognitive capacities would itself be puzzling (Hansell & Ruxton 2008). We note that the capacity for tool use has recently been demonstrated in hand-reared captive rooks *Corvus frugilegus*, a species that does not habitually use tools in the wild (Bird & Emery 2009). This observation supports our view that the process of adaptation towards tool use may occur mostly through the evolutionary acquisition of motivational mechanisms, rather than by enhancing general intelligence. Plainly, if tool use was generally advantageous, one would expect to see it expressed more widely among different species and different habitats. The ecological significance of tool use for individual species and the ecological correlates of tool use among species are therefore timely foci for continued field research.

Fieldwork was carried out with permissions from the Centre de Recherches sur la Biologie des Populations d'Oiseaux (France) and the Direction de Ressources Naturelles (Province Sud, New Caledonia), and was in accordance with the University of Oxford's procedures for local ethical review.

We thank Nicolas Barré, Serge Blancher, Jacques Paimbou-Ayouma, Brian Etheridge, Risto Juvaste, Ian Owens, Ben Sheldon, two anonymous referees and French and New Caledonian authorities. This study was supported by the BBSRC (grant BB/C517392/1), the Rhodes Trust (L.A.B.) and Linacre College (C.R.). C.R. is a BBSRC David Phillips Fellow (grant BB/G023913/1). Full acknowledgements are provided in the electronic supplementary material.

REFERENCES

Bird, C. D. & Emery, N. J. 2009 Insightful problem solving and creative tool modification by captive nontool-using

- rooks. *Proc. Natl Acad. Sci. USA* **106**, 10 370–10 375. (doi:10.1073/pnas.0901008106)
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T. 2003 Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.* **6**, 213–223. (doi:10.1007/s10071-003-0183-x)
- Bodenheimer, F. S. 1951 *Insects as human food: a chapter in the ecology of man*. The Hague, The Netherlands: Dr W. Junk Publishers.
- Boesch, C. & Boesch-Achermann, H. 2000 *The chimpanzees of the Tai forest*. Oxford, UK: Oxford University Press.
- Chappell, J. & Kacelnik, A. 2002 Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Anim. Cogn.* **5**, 71–78. (doi:10.1007/s10071-002-0130-2)
- Chappell, J. & Kacelnik, A. 2004 Selection of tool diameter by New Caledonian crows *Corvus moneduloides*. *Anim. Cogn.* **7**, 121–127. (doi:10.1007/s10071-003-0202-y)
- Cochereau, P. 1970 Observations sur la faune des bois en voie de décomposition en forêt Néo-Calédonienne. *Cah. ORSTOM Ser. Biol.* **12**, 123–127.
- Hansell, M. & Ruxton, G. D. 2008 Setting tool use within the context of animal construction behaviour. *Trends Ecol. Evol.* **23**, 73–78. (doi:10.1016/j.tree.2007.10.006)
- Hunt, G. R. 1996 Manufacture and use of hook-tools by New Caledonian crows. *Nature* **379**, 249–251. (doi:10.1038/379249a0)
- Hunt, G. R. 2000 Tool use by the New Caledonian crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu* **100**, 109–114. (doi:10.1071/MU9852)
- Hunt, G. R. & Gray, R. 2003 Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. Lond. B* **270**, 867–874. (doi:10.1098/rspb.2002.2302)
- Hunt, G. R. & Gray, R. 2007 Parallel tool industries in New Caledonian crows. *Biol. Lett.* **3**, 173–175. (doi:10.1098/rsbl.2006.0603)
- Hunt, G. R., Rutledge, R. B. & Gray, R. D. 2006 The right tool for the job: what strategies do wild New Caledonian crows use? *Anim. Cogn.* **9**, 307–316. (doi:10.1007/s10071-006-0047-2)
- Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. 2000 A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* **9**, 156–185. (doi:10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7)
- Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnik, A. 2005 Tool manufacture by naïve juvenile crows. *Nature* **433**, 121. (doi:10.1038/433121a)
- Kenward, B., Rutz, C., Weir, A. A. S. & Kacelnik, A. 2006 Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Anim. Behav.* **72**, 1329–1343. (doi:10.1016/j.anbehav.2006.04.007)
- McGrew, W. C. 1992 *Chimpanzee material culture: implications for human evolution*. Cambridge, UK: Cambridge University Press.
- Raley, C. M. & Aubry, K. B. 2006 Foraging ecology of pileated woodpeckers in coastal forests of Washington. *J. Wildl. Manag.* **70**, 1266–1275. (doi:10.2193/0022-541X(2006)70[1266:FEOPWI]2.0.CO;2)
- Rutz, C., Bluff, L. A., Weir, A. A. S. & Kacelnik, A. 2007 Video cameras on wild birds. *Science* **318**, 765. (doi:10.1126/science.1146788)
- Sanz, C., Morgan, D. & Gulick, S. 2004 New insights into chimpanzees, tools, and termites from the Congo basin. *Am. Nat.* **164**, 567–581. (doi:10.1086/424803)

- Sanz, C., Call, J. & Morgan, D. 2009 Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* **5**, 293–296. (doi:10.1098/rsbl.2008.0786)
- Sterling, E. J. 1994 Aye-ayes: specialists on structurally defended resources. *Folia primatol.* **62**, 142–154. (doi:10.1159/000156771)
- Tabachnik, B. G. & Fidell, L. S. 2007 *Using multivariate statistics*, 5th edn. Boston, USA: Pearson.
- Tebbich, S., Taborsky, M., Fessl, B. & Dvorak, M. 2002 The ecology of tool-use in the wood-pecker finch (*Cactospiza pallida*). *Ecol. Lett.* **5**, 656–664. (doi:10.1046/j.1461-0248.2002.00370.x)
- Vargha, A. & Delaney, H. D. 2000 A critique and improvement of the *CL* common language effect size statistics of McGraw and Wong. *J. Educ. Behav. Stat.* **25**, 101–132.
- Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C. & Kacelnik, A. 2009 Cognitive processes associated with sequential tool use in New Caledonian crows. *PLoS One* **4**, e6471. (doi:10.1371/journal.pone.0006471)
- Wunderle, J. M. 1992 Age-specific foraging proficiency in birds. *Curr. Ornithol.* **8**, 273–234.