



*Citation for published version:*

Rutz, C, Klump, B, Komarczyk, L, Leighton, R, Kramer, J, Wischnewski, S, Sugasawa, S, Morrissey, M, James, R, St Clair, J, Switzer, R & Masuda, B 2016, 'Discovery of species-wide tool use in the Hawaiian crow', *Nature*, vol. 537, pp. 403-407. <https://doi.org/10.1038/nature19103>

*DOI:*

[10.1038/nature19103](https://doi.org/10.1038/nature19103)

*Publication date:*

2016

*Document Version*

Peer reviewed version

[Link to publication](#)

This is the author accepted manuscript of an article published in final form and available online via:  
<https://doi.org/10.1038/nature19103>

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Published as: Rutz *et al.* *Nature* **537**, 403–407 (2016) doi:10.1038/nature19103

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# Discovery of species-wide tool use in the Hawaiian crow

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**Only a handful of bird species are known to use foraging tools in the wild<sup>1</sup>. Amongst them, the New Caledonian crow *Corvus moneduloides* stands out with its sophisticated tool-making skills<sup>2,3</sup>. Despite considerable speculation, the evolutionary origins of the species' remarkable tool behaviour remain largely unknown, not least because no naturally tool-using congeners have yet been identified that would enable informative comparisons<sup>4</sup>. Here we show that another tropical corvid, the 'Alalā *C. hawaiiensis* (Hawaiian crow), is a highly dexterous tool**

**user. Although ‘Alalā became extinct in the wild in the early 2000s, and currently only survive in captivity<sup>5</sup>, at least two lines of evidence suggest that tool use is part of the species’ natural behavioural repertoire: juveniles develop functional tool use without training, or social input from adults; and proficient tool use is a species-wide capacity. ‘Alalā and New Caledonian crows evolved in similar environments on remote tropical islands, yet are only distantly related<sup>6</sup>, suggesting that their technical abilities arose convergently. This supports the idea that avian foraging tool use is facilitated by ecological conditions typical of islands, such as reduced competition for embedded prey and low predation risk<sup>4,7</sup>. Our discovery creates exciting opportunities for comparative research on multiple tool-using and non-tool-using corvid species. Such work will in turn pave the way for replicated cross-taxonomic comparisons with the primate lineage, enabling valuable insights into the evolutionary origins of tool behaviour.**

The foraging behaviour of many corvid species remains poorly studied<sup>8</sup>, leaving open the possibility that there are undiscovered tool users in this genus<sup>4</sup>. We identified the ‘Alalā as a promising candidate for further investigation (see p. 161 in ref. 4), based on its morphological<sup>9,10</sup> and ecological<sup>4</sup> similarity with the tool-using New Caledonian crow (Fig. 1, c and d; Extended Data Fig. 1a). Following a precipitous decline in the late 20<sup>th</sup> century<sup>5</sup>, the world’s entire ‘Alalā population currently resides in two captive facilities where birds are being bred for future releases<sup>11</sup> (Figs 1f, 2b). After studying anecdotal reports<sup>12,13</sup>, the instigating authors learned from facility staff that tool use had indeed been repeatedly observed over the years (Supplementary Video 4; see Methods), leading to the collaborative project reported here.

We tested 104 of the 109 surviving ‘Alalā (five birds were excluded for health reasons *a priori*), and found that 78% of them

spontaneously used tools to probe for out-of-reach food (Fig. 2f). While tool-use competence (that is, whether or not a bird used tools) was very similar for males and females (Fig. 2c), it varied strongly across age classes (Fig. 2d): 93% of all sexually mature subjects (third year of life or older<sup>5</sup>) were confirmed as tool users, compared with 47% of younger birds. In the majority of cases, birds used tools in their very first trial, usually within minutes of gaining access to the experimental apparatus, a wooden log with six extraction tasks (Fig. 2a; Extended Data Fig. 2a). Most subjects handled stick tools in a highly dexterous manner (Supplementary Videos 1 and 2) and extracted bait from several tasks (median 4, range 0–6;  $n = 64$  tool users that had been tested individually). All but one successful extractions from vertical and horizontal crevices and drilled horizontal holes were completed in <60 seconds of probing time, with vertical holes proving slightly more challenging (Fig. 2g). During experimental trials, birds routinely selected tools of appropriate dimensions, replaced unsuitable tools, and transported non-supplied sticks to the log. Tool modification was frequent (shortening: 67% of  $n = 64$  tool users that were tested individually; other modifications: 8%), and we even observed tool manufacture from plant materials (14%) (Supplementary Video 2). ‘Alalā have relatively straight bills and highly mobile eyes (Extended Data Fig. 1; Supplementary Video 5) – features that are thought to facilitate dexterous handling of bill-held tools in New Caledonian crows<sup>9,14</sup> (for craniofacial morphology of other extant crows, and two extinct Hawaiian species, see Fig. 1, b and f).

Our discovery of a species-wide capacity for tool use raises the possibility that ‘Alalā possess genetic predispositions similar to those reported for New Caledonian crows<sup>15,16</sup>. To examine this hypothesis, we reared seven naïve juvenile ‘Alalā in two social groups under controlled conditions, without opportunities to observe tool-proficient adults. All birds eventually used sticks and other objects in an attempt

to reach hidden food during probe trials (Fig. 3b; Extended Data Fig. 2b; Extended Data Table 1), and four were successful (Fig. 3c; Supplementary Video 3; a fifth subject later used tools successfully on the log task). Towards the end of the 5-month observation period, we documented an increase in the handling of stick-type and similar objects (Fig. 3a), possibly in response to increased exposure to tool-use opportunities (Fig. 3c), but ‘Alalā did not perform stereotyped probing or rubbing behaviours that are precursors of functional tool use in New Caledonian crows<sup>16</sup>. ‘Alalā also appeared to spend less time manipulating stick-type and similar objects 3–5 weeks post-fledging than New Caledonian crows, with some estimates even lower than for non-tool-using ravens *C. corax*<sup>17</sup> (Fig. 3d), although these comparisons should be treated cautiously due to differences in study protocols.

While our rearing experiment demonstrated conclusively that naïve ‘Alalā can independently develop functional tool use, environmental conditions are likely to affect behavioural development. At the population level, we detected only minor differences between birds that had been raised (and tested) at the two facilities (Fig. 2c), despite some variation in enrichment regimes. In groups of young ‘Alalā, we often observed birds interfering with each other’s attempts to use tools, for example by stealing sticks (Supplementary Video 3). We examined possible social-interference effects in a separate experiment, in which birds were tested both in their usual housing group (of 6–7 subjects) and individually. Tool-use behaviour was generally rare amongst ‘Alalā in their second year of life, irrespective of experimental condition, but it was clearly suppressed by the presence of group mates in subjects that were a year older (Fig. 2e).

Using detailed housing data and computer simulations, we next examined the social connectivity of our study population, by tracing potential transmission pathways (Fig. 3e, right) in time-ordered contact networks (1996–2013; Fig. 3e, left). Based on highly

conservative assumptions (instantaneous, deterministic information transfer), we estimated that between one (unrestricted transmission) and eight (more realistic, age-biased transmission<sup>18</sup>) independent information sources would be required to reach all confirmed tool users by 2013 ( $n = 74$  birds, excluding the 7 isolated subjects of our rearing experiment). This indicates that, despite considerable social mixing, it is unlikely that a single ‘innovation’ event can explain the observed species-wide distribution of tool competence. ‘Alalā clearly possess a propensity to ‘discover’ tool-assisted foraging solutions independently, which most likely results from genetically canalised, persistent object-exploration behaviour; further experiments are now required to quantify the relative contributions of individual and social learning<sup>19</sup>.

It is well-known that naturally non-tool-using animal species sometimes use tools in captivity, especially when the behaviour is shaped or otherwise encouraged<sup>1</sup>. The ‘Alalā’s case is unusual in several regards: almost all adult birds expressed tool behaviour (Fig. 2c); tool users swiftly solved even demanding extraction tasks (Fig. 2g); and naïve subjects independently acquired tool skills (Fig. 3c). Comparison with naturally non-tool-using corvids reveals another difference. Most ‘Alalā and New Caledonian crows exhibit a striking degree of dexterity during stick handling, while captive rooks *C. frugilegus* appear to have less control over their tools<sup>20</sup> (Supplementary Video 6). We have observed rook-like tool handling in the seven juveniles of our rearing experiment, but this was unusual amongst older ‘Alalā, suggesting that tool control improves with practice; we note, however, that even highly proficient adults would have had relatively limited tool-use experience during their lifetimes.

‘Alalā once lived in dry- and wet-forest habitats on Hawai‘i Island (Fig. 1f) where they foraged for a variety of fruit, invertebrates and other items<sup>5,21</sup>. Wild birds have been observed to engage in woodpecker-like extractive foraging, flaking bark and chiselling wood

with their powerful bills<sup>5,21,22</sup>, just as New Caledonian crows are known to do<sup>4,23</sup>. But, apart from one suggestive observation of a bird transporting a twig in its bill (P. Crosland, cited in ref. 22) – at a time of year (late June) when nest construction was unlikely<sup>5</sup> – we have found no reports of tool-related behaviour in the wild. Tool use may have been relatively infrequent, confined to particular habitats, or difficult to observe (Extended Data Table 2). Alternatively, the last wild ‘Alalā may have no longer used tools, for example, if island-wide habitat degradation<sup>24</sup> had forced them to switch to alternative foraging modes – a scenario with important implications for forthcoming reintroduction attempts<sup>11</sup>.

Anecdotal observations of avian tool use are relatively common, yet very few species routinely use foraging tools in the wild<sup>1</sup> (for well-known examples, see Fig. 1g). Unfortunately, since the ‘Alalā is extinct in the wild, and tools made from plant materials are perishable, we may never know whether birds once used tools under natural conditions. Current evidence strongly favours this scenario, but otherwise, our study would have uncovered a truly remarkable capacity for highly dexterous tool behaviour in a naturally non-tool-using corvid. Future studies should chart the (development of) object-related behaviour of other species under similar conditions in captivity, with an initial focus on the rook, which is the ‘Alalā’s sister species<sup>6</sup> (Fig. 1a) and a rapid learner of tool skills when trained appropriately<sup>20,25</sup>.

‘Alalā and New Caledonian crows are only distantly related<sup>6</sup> (Fig. 1a), suggesting evolutionary convergence of tool-related adaptations. In fact, interspecific differences in the ontogenetic development of functional tool use support the hypothesis of convergence rather than homology. As for possible ecological drivers, both species<sup>4,26</sup> – as well as the stick-tool-using Galápagos woodpecker finch<sup>7</sup> – evolved on remote tropical islands (Fig. 1e) where competition for embedded prey is likely to be reduced and predation risk low. These conditions, which

have previously been predicted to facilitate tool behaviour<sup>4,7</sup>, may vary across island environments, but are presumably less common on adjacent mainland habitats, providing a possible explanation for the striking rarity of avian tool use<sup>1</sup>.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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**Supplementary Information** is available in the online version of the paper.

**Acknowledgements** This paper is dedicated to the people – far too many to name individually – who have prevented the ‘Alalā’s extinction, and who are working tirelessly towards its successful reintroduction into the wild. For contributions to the present study, we thank: Rob Fleischer for facilitating initial contacts; San Diego Zoo Global’s staff for assistance with experiments; Caitlin Higgott for help with video scoring; Darren Parker for constructing the consensus phylogeny; several photographers for providing images for Fig. 1; Steve Thompson for help with graphic design; Graeme Ruxton for statistical advice; and five reviewers for excellent comments. Research was conducted with

permission from San Diego Zoo Global's IACUC animal welfare committee (Project ID#12-017), and with funding from the Biotechnology and Biological Sciences Research Council, UK (BBSRC; grant BB/G023913/2 to C.R., and studentship to B.C.K.), the University of St Andrews (C.R.), JASSO (S.S.), and the Royal Society of London (M.B.M.). Funding for the captive 'Alalā propagation programme was provided by the U.S. Fish and Wildlife Service, Hawai'i Division of Forestry and Wildlife, Moore Family Foundation, Marisla Foundation, several anonymous donors, and San Diego Zoo Global.

**Author Contributions** C.R. conceived of, initiated and led the project, and secured funding; R.A.S. and B.M.M. led the captive 'Alalā propagation programme, with support from R.L., J.K. and L.K.; C.R., J.J.H.S.C. and B.C.K. designed behavioural experiments; B.C.K., J.J.H.S.C. and C.R. conducted the species-wide tool-use assay, and L.K. performed the ontogeny experiment, with help from R.L., C.R., J.J.H.S.C. and B.C.K.; B.C.K. scored videos and extracted behavioural data, except for ontogeny trials, which were scored by S.W. and processed by S.S.; L.K., J.K., B.M.M. and C.R. collated and checked data on the life histories of captive birds; M.B.M. and B.C.K. assessed bird-performance data; R.J. and C.R. conducted social-diffusion simulations; C.R. and B.C.K. coordinated manuscript preparation, analysed data and prepared figures and videos; and C.R. wrote the manuscript, which was edited by B.C.K., J.J.H.S.C., R.J. and B.M.M., and approved by all co-authors.

**Author Information** Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). The authors declare the following competing financial interests: five co-authors were (R.L., J.K., R.A.S.), or still are (L.K., B.M.M.), employees of San Diego Zoo Global, which is a not-for-profit organisation. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to C.R. ([christian.rutz@st-andrews.ac.uk](mailto:christian.rutz@st-andrews.ac.uk)).

**MAIN TEXT FIGURES (3)**

**Figure 1 | Phylogenetic and biogeographical context of tool behaviour in crows.** **a**, Phylogeny for the genus *Corvus* (blue, posterior probabilities  $\geq 0.90$ ; scale bar, estimated substitutions per site). **b**, Variation in craniofacial morphology (adapted from ref. 8, Lynx Edicions). **c**, One of the last wild ‘Alalā (27 February 1998, Kealakekua, Hawai‘i; photo: Jack Jeffrey Photography). **d**, New Caledonian crow (photo: M. Griffioen). **e**, Location of Hawai‘i and New Caledonia (globe: Google Earth, NASA, U.S. Geological Survey). **f**, Hawai‘ian corvids (skulls adapted from ref. 26, American Ornithologists’ Union; photo: C.R.), and historical ‘Alalā distribution (from ref. 11, USFWS). **g**, Discovery timeline for well-known habitual avian tool users (photos: A. Gandolfi/naturepl.com; D. Pintimalli; D. Brinkhuizen; J. Troscianko), with landmark chimpanzee reports by Darwin<sup>27</sup> and Goodall<sup>28</sup> for reference.

**Figure 2 | Species-wide tool-use behaviour in ‘Alalā.** **a**, Captive birds using stick tools to extract bait from experimental logs. **b**, Development of the world’s ‘Alalā population and results of species-wide tool-use assay (birds shown survived at least until post-fledging age; inset data from ref. 29, Elsevier). **c–e**, Tool-use competence across: **c**, sexes (M, male; F, female) and facilities (subdivided according to where subjects were raised and tested); **d**, age classes; and **e**, different test conditions (tested individually or in a group). **f, g**, Bird performance: **f**, outcome of trials and **g**, extraction speed for different tasks. Panels **b–g** refer to the standardized tool-use assay (Extended Data Fig. 2a); **g** only includes successful extractions from the first individual trial where birds used tools.

**Figure 3 | Development of tool-use behaviour in naïve, juvenile ‘Alalā.** **a**, Object-handling rates (bill only) estimated from focal-bird observations (week 1 commenced 3 September 2012; ‘sticks’ are all stick-type objects, fern sections and branched pieces of plant; correlation coefficients). **b**, Group A on experimental platform. **c**, Behavioural development as documented through weekly probe trials, from week 3 onward (action types are defined in Extended Data Table 1; for ①–③, see Methods). **d**, Comparison of object-manipulation times (bill, and foot-grasped<sup>17</sup>) 3–5 weeks post-fledging (weekly means; note that  $n < 5$  birds for some values) between ‘Alalā, New Caledonian (NC) crows<sup>17</sup> and non-tool-using ravens<sup>17</sup>. **e**, Potential for social diffusion across the ‘Alalā contact network (1996–2013, cumulative results; hatching blocks out the 7 isolated subjects of the rearing experiment): co-housing matrix (left) and reachability matrix (right).

## METHODS

**Study population.** ‘Alalā were studied in two captive breeding facilities operated by San Diego Zoo Global. With the species considered extinct in the wild<sup>11,30</sup>, the world’s population consisted of 109 individuals (58 males; 51 females) in early 2013, with: 64 birds housed at the Keauhou Bird Conservation Center (KBCC), Hawai‘i Island; 44 birds at the Maui Bird Conservation Center (MBCC), Maui; and a single individual off-exhibit at San Diego Zoo Safari Park, California. The captive stock originated from a few founder individuals that had been collected from the wild since the 1970s, as described in detail elsewhere<sup>11,29–32</sup>. All birds available for testing in our study (referred to throughout by their studbook numbers) were of known ancestry, sex (determined through genetic analysis of blood samples<sup>33</sup>) and age, and had been reared in captivity (see Fig. 2b). Male #67 had hatched from one of the very last eggs laid by a wild pair, and three other subjects (#77, #78, #86) had temporarily lived in the wild (they had been released in the late 1990s, but were later returned to captivity<sup>30</sup>).

Adult birds were kept as breeding pairs, or sometimes as singletons, and immatures were housed in groups of up to 8 individuals, to facilitate their socialisation<sup>34</sup>. All aviaries at the two main facilities are multi-chambered, spacious outdoor enclosures (varying in size from *ca.* 3.0×6.0×3.7 m to 7.3×17.0×5.5 m), which are open to the elements, but have a roofed section for shelter. At the KBCC (purpose-built in 1996), the ground is covered in lava stones, with patches of live vegetation, while at the MBCC (repurposed building in use since 1986, with later extensions), some aviaries have concrete flooring. Standard fittings include a variety of branches and ropes for perching, a nesting platform, and a large water bath. All birds have access to cut vegetation (‘browse’) and sticks year-round, and pairs receive supplies of assorted nesting material during the breeding season.

Enrichment protocols have changed over the years and varied slightly between facilities. Initially, all enrichment given to ‘Alalā was made of natural materials (e.g., fresh browse, and logs of deadwood), but this was supplemented with artificial items (e.g., food hidden inside dog toys, or wrapped in newspaper) from 2008 at the KBCC (and at the latest from 1999

onwards at the MBCC); a human-imprinted male (#35) was given artificial items as early as 2000. Food items were hidden in holes and crevices in wooden logs, or tossed into water baths, intermittently since at least 1997, and about once or twice a week since 2004, at the KBCC (since 1999 at the MBCC), and baited PVC tubes were presented from late 2012 onwards (since 2007 at MBCC). While this enrichment provided opportunities for tool use, in the vast majority of cases bait could also be obtained by bill alone, in contrast to the extraction tasks of our formal behavioural assay (see below). Importantly, to the best of our knowledge, the use of tools to extract hidden food was never demonstrated to birds at either facility.

**Behavioural assay.** We conducted a species-wide assay of tool-use competence, using a standardised food-extraction task set (see below). Following pilot experiments with two subjects (female #94, and her son #134) in August 2012 and January 2013, we tested all healthy birds in both facilities between 23 January and 27 February 2013. With five birds excluded from experiments *a priori* for medical reasons, and one male tested later in the year (#67; tool use confirmed on 31 August 2013), our final sample comprised 104 subjects, which was over 95% of the world's 'Alalā population at the time (see Fig. 2b). Since we effectively tested an entire species, it was not necessary to use inferential statistics to support findings.

The experimental set-up consisted of (Extended Data Fig. 2a): a Koa *Acacia koa* log containing four drilled holes and two crevices, each baited with a quarter of a neonate mouse (or other preferred food in early trials at KBCC); 12 sticks of varying lengths as potential tools scattered in front of the log; and assorted native plant materials (KBCC), or two dead branched stems (MBCC; native materials not readily available), from which tools could be manufactured, wedged firmly into a wooden board to stand upright (for further details, see Extended Data Fig. 2a). The four different types of extraction task were designed to resemble foraging problems New Caledonian crows regularly solve with tools in the wild<sup>2,4,23</sup>. At both facilities, we used the same two near-identical logs to run trials in parallel. Encouraged by earlier anecdotal observations during routine enrichment sessions (see Supplementary Video 4), we usually also placed a piece of mouse head in the aviary's water bath, to see whether the subject(s) would

fish it out with a stick; this complementary task proved useful, as it often attracted birds' attention, and confirmed tool-use behaviour in one female (#95) that failed to engage with the main log set-up.

Trials were scheduled to last for approximately 1.0–1.5 hours, but were terminated earlier on a few occasions at the start of the study, whilst the test protocol was being established ( $n = 6$  trials), or when all bait had been extracted ( $n = 24$ ), cameras failed ( $n = 2$ ) or due to experimenter error ( $n = 1$ ). Food bowls were usually removed shortly before trials commenced, but birds sometimes found food scraps in their aviaries, and always had *ad libitum* access to water. An experimenter placed the fully-baited experimental log and the board with plant materials on the ground, before scattering the sticks underneath a large cotton sheet, out of view of the subject(s). Before removing the sheet and leaving the aviary, several small food items were conspicuously placed on top of the log, to encourage approach and exploration of the set-up, and the water bath was baited (see above). At the KBCC, birds could be filmed with experimenter-operated video cameras through tinted or one-way-mirror observation windows, while at the MBCC, all trials had to be filmed with static video cameras hidden inside a rainproof box, placed *ca.* 1.5–3.0 m away from the experimental set-up. Subjects were temporarily isolated for individual testing ( $n = 83$  birds), but we also ran some trials with pairs early on in the study ( $n = 3$  birds) and some with larger groups where isolation was impossible due to aviary layout ( $n = 18$  birds). For logistical and ethical reasons, birds remained in visual contact with other 'Alalā in adjacent chambers even when tested individually. Subjects that did not show tool-related behaviours in their first trial were re-tested for varying amounts of time (Fig. 2f). Immature 'Alalā are usually housed in groups (see above); to examine experimentally how social context affects the expression of tool behaviour, we tested a sample of birds in their second and third year of life, both in their usual housing group and individually (Fig. 2e).

Video footage from experimental trials was scored in randomised order by the same observer (B.C.K.) using Solomon Coder software<sup>35</sup>, and a subsample of 10 trials was re-scored by a second observer (S.S.) to estimate inter-observer agreement (Cohen's  $\kappa$  for 'extraction type' [tool/bill/not-extracted] = 0.97,  $n = 70$  cases; correlation coefficient  $r$  for 'time spent

probing with a tool' = 0.99,  $P < 0.0001$ ,  $n = 38$  probing bouts); all analyses are based on the original data. Two main types of data were generated by our standardised behavioural assay. First, we used trials to establish whether or not birds used tools – irrespective of deployment context and extraction success (see Fig. 2, b and f). Second, for those birds that did use tools, we examined aspects of tool handling, modification (and possible manufacture) and deployment, and quantified the speed with which they extracted bait from the log's holes and crevices (see Fig. 2g; trials included only when birds had been tested individually). Formal species comparisons are pending, but when extracting meat from vertical holes, 'Alalā's performance ( $n = 52$  birds that probed; 63% of attempted extractions successful; cumulative probing time until extraction [median, range]: 26.8 s, 3.2–215.6 s; see top-left panel of Fig. 2g) is broadly comparable to that of New Caledonian crows (more difficult, deeper and narrower holes<sup>3</sup>:  $n = 15$ ; 49%; 42.3 s, 5.8–161.6 s; unpubl. data).

Visual-field measurements require that subjects' heads are held completely still for *ca.* 30–45 minutes<sup>9</sup>. While such temporary restraint is tolerated well by most birds, it cannot currently be used with 'Alalā, given the species' critical conservation status. Since the width of the binocular field is determined to a large degree by lateral eye-movement amplitude (correlation,  $r = 0.82$ ,  $P = 0.02$ ,  $n = 7$  *Corvus* spp.; data from table 1 in ref. 9), we opportunistically assessed – during behavioural trials, and when handling subjects for routine health checks – how much birds can rotate their eyes forward during full convergence (see Extended Data Fig. 1b; Supplementary Video 5).

**Ontogenetic patterns.** To gain insights into possible genetic predispositions<sup>15,16,36</sup>, we studied the development of object-oriented behaviour in seven juvenile 'Alalā that had been bred and puppet-reared<sup>37</sup> at the KBCC in 2012 (hatch dates between 20 June and 16 July). Subjects were housed in two mixed-parentage groups (offspring of five different pairs) of three (Group A: subjects #206, #207, #208) and four birds (Group B: #200, #201, #204, #205), respectively. Following the facility's standard procedures, birds were transferred from fledgling aviaries (*ca.* 2.0×1.8×2.3 m) to large outdoor aviaries after they had acquired basic flight skills, at 61–

69 days-old. From 15 September onwards, the groups were housed in adjacent aviary chambers (each *ca.* 3.0×12.0×5.5 m), with visual contact through a wire-mesh partition, but they never saw adults during the full duration of our study. Furthermore, all staff were briefed never to use ‘tools’ (of any kind) in front of subjects, both during formal observation sessions and in all other contexts, including general husbandry activities (due to an oversight, large metal tongs were used on a few occasions, to scrape old food from logs). Since subjects were co-housed in groups, individuals that only expressed tool use later in the experiment could potentially have learned from those that used tools earlier (see Fig. 3c). This means that only the very first tool behaviour expressed in either of the two experimental groups was certain to be an independent ‘discovery’<sup>15,19</sup>.

We collected two main datasets. First, we employed a standard focal-bird observation protocol<sup>15–17</sup> to document the natural development of object-oriented behaviour. Up to three days per week (usually on Tuesday, Thursday and Saturday), we conducted a morning (between *ca.* 6:30–11:00 hrs) and an afternoon (*ca.* 12:00–16:00 hrs) session, aiming to collect *ca.* 5 minutes of video footage per subject (i.e., 3 × 2 sessions × 5 min = 30 min, per subject per week). To avoid biases, the order in which groups were observed, and the order in which subjects were observed within sessions, was pseudo-randomised, and session start times were varied slightly within the above-mentioned time windows. Second, once per week (usually on Fridays), we conducted a ‘probe trial’ to assess subjects’ tool-use competence. We presented each group for *ca.* 15–20 minutes with a wooden platform, containing food-baited vertical holes and crevices (Extended Data Fig. 2b). The rationale of our study design was to monitor the development of the subjects’ tool-related behaviour (see Fig. 3c) with minimal environmental ‘scaffolding’; note that, in contrast, the New Caledonian crows raised in an earlier study had *ad libitum* access to extraction tasks<sup>15,16</sup>.

Platforms were initially baited with waxworms and cereal treats, but from 5 October 2012 onwards, we switched to mouse heads, neonate mice, and bright-red ‘Ōhelo *Vaccinium reticulatum* berries<sup>38</sup>. By January 2013, subjects in both groups showed keen interest in the hidden food, and often handled objects near the platform. For two reasons, however, their tool-use attempts largely failed: they sourced inappropriate materials as tools (e.g.,



decaying pieces of fern), and even when suitable sticks were found, they struggled to extract food from tasks. We addressed these problems by providing sticks of assorted length (6 of 10–15 cm; 6 of 20–25 cm), loosely placed in the centre of the platform (sticks were never handled in view of the birds, and never pre-inserted into tasks), and by adding horizontal holes and crevices from which food was presumably easier to extract. These changes implemented, we concluded our experiment by providing birds with abundant opportunities to practice their tool-use skills (see entries ①–③ in Fig. 3c; trial length extended to *ca.* 30 min), with: a week of almost daily platform trials (23–29 January 2013; pooled data shown as ①); two re-test trials about a week later (4 and 6 February 2013; pooled data shown as ②); and another 1.5 weeks of exposure to the platform and a range of other extraction tasks without observation (8–18 February 2013), followed by a final platform trial on 20 February 2013 (entry ③). For reference, when protocols were altered on 23 January 2013, subjects were 151–181 days post fledging.

Following standard protocols, subjects received near-daily aviary enrichment (sometimes immediately prior to observation sessions), including a variety of food items that required processing but were accessible by bill alone. The exception to this were baited opaque PVC tubes, which were presented on a single day in weeks 11, 12, 16, 19 and 24 (with week 1 commencing on 3 September 2012), to assess how birds' tool-related performance on this task compared to that expressed during formal probe trials with the more demanding platform-mounted set-up (see above). These sessions were not included in focal-bird analyses shown in Fig. 3a, but some object insertions were documented slightly ahead of formal platform probe trials (see Fig. 3c).

Videos from all observation sessions were scored with JWatcher software<sup>39</sup> in randomised order by two hypothesis-naïve observers (S.W. and Caitlin Higgott), who achieved very high inter-observer agreement for a subsample of three sessions (correlation coefficients for handling rates for the object categories shown in Fig. 3a,  $r = 0.96–0.99$ , all  $P < 0.0001$ ,  $n = 10$  scores for each test); sessions for post-fledging weeks 3–5 (data from fledgling aviaries included) were scored with a particularly detailed scheme, with some behaviours coded as states, rather than as events, for time-budget

analyses (weekly sample sizes were 3, 5 and 7 birds, respectively; Fig. 3d). We wrote code in R<sup>40</sup> for extracting data from raw JWatcher output files, to calculate either object-handling rates (Fig. 3a; data for ‘sticks’ and ‘stones’ analysed with simple correlations) or time budgets (Fig. 3d; calculated for the time focal subjects were in view). Except for cross-species comparisons (see below), we plotted temporal data by calendar week (Fig. 3, a and c), rather than by bird age or time since fledging, since the development of the younger birds in Group A may have been accelerated through observing the older members of Group B in the adjacent aviary chamber. In videos of probe trials, we scored which behavioural actions subjects had performed near or on the platform, ranging from merely approaching the set-up to successfully using tools to extract bait (action types are numbered in the panels of Fig. 3c, and descriptions are provided in Extended Data Table 1).

For cross-species comparisons, we extracted data on the development of object-oriented behaviour in New Caledonian crows and common ravens *C. corax* from figure 2 in ref. (17). For ‘stick’ manipulation, we only used data from untutored New Caledonian crows (2 subjects)<sup>17</sup>, and the object category ‘perch’ included all non-portable aviary fixtures. These species comparisons are for indicative purposes only (Fig. 3d), as the three studies considered varied in a range of factors, including details of subject housing, access to objects and extraction tasks, observation conditions and behavioural scoring (note considerable variation for ‘stick’ estimates for ‘Alalā), and the species in question are known to exhibit different rates of juvenile development<sup>4,5,8</sup>.

**Historical observations.** Prior to the commencement of our study, ‘Alalā had regularly been observed using tools in both captive facilities. Staff did not consider these cases particularly noteworthy, as they were aware that the behaviour had been previously described for the congeneric New Caledonian crow. To provide context for our study, we collated information on these earlier, opportunistic observations, trying to locate written records<sup>12,13</sup> and conclusive photo or video evidence (see Supplementary Video 4). It is worth noting that our sample of well-documented historical observations constitutes only a small fraction of the observations made by facility staff over the years.

**Correlates of phenotypic variation.** To examine the influence of environmental and/or social factors on tool-use competence, we reconstructed our subjects' lifetime housing histories – that is, the time they had spent at different facilities, their allocation to particular aviaries and chambers, and their co-housing with other birds – using paper files and electronic spreadsheets held at the KBCC and MBCC.

First, we conducted some basic checks, to see whether competence was related to being raised (first two years of life), or kept, in a particular facility (see Fig. 2c). Next, we used our detailed housing data to investigate how well our study population was admixed socially, by simulating<sup>41</sup> the flow of information – such as tool use – across birds<sup>42,43</sup>. Using all dated housing entries in our database ( $n = 1,501$  for 135 birds in 1996–2013), we first generated contact networks that specified which crow dyads were in potential visual contact at any given time, by sharing an aviary or occupying adjacent aviaries/chambers with a see-through wire-mesh partition (cumulative 'co-housing matrix' shown in Fig. 3e, left). Since the expression of 'Alalā tool behaviour is strongly age-dependent (Fig. 2d), and studies in other systems have shown that learning is often particularly effective during a 'sensitive window' early in life<sup>18</sup>, we considered only the subset of co-housing events in which one of the birds was adult (>2-years-old) and the other an immature (<2-years-old). Our idealised simulation model assumed that, if the adult had the information at the time of co-housing, it was expressed and transmitted instantaneously to the immature. The information was never lost, so both the adult (and the immature, once old enough) could pass it on in subsequent co-housing events. We then traced (computationally) for all potential 'innovators' of information all possible transmission pathways through the time-ordered contact networks, identifying those reaching confirmed tool users by 2013 (grey dots in Fig. 3e, left, refer to immature recipients that were not among the confirmed tool users in 2013); the results are summarised in the 'reachability matrix' (Fig. 3e, right). From this matrix we computed<sup>44</sup> the smallest number ( $m$ ) of independent innovation events (rows) needed to ensure that every tool user (column) is reached. For the transmission dynamics described,  $m = 8$ . To establish a lower-bound estimate, we relaxed the transmission rules so that

information could be passed between birds of all ages, yielding  $m = 1$ . Both simulations assumed highly conservatively that transmission was not only instantaneous but also deterministic (yet, we would expect considerable between-dyad variation in transmission probabilities due to differences in social-learning opportunities and phenotypic plasticity<sup>18,45</sup>), but inevitably had to ignore possible pathways created by birds for which exact aviary information was unknown (16.3% of 1,501 housing entries). As explained in the main text, these analyses helped us characterise the ‘social connectivity’ of our study population, but further behavioural experiments are required to demonstrate social learning in ‘Alalā.

**Phylogenetic relationships.** To examine phylogenetic relationships within the genus *Corvus*, we built a consensus tree (see Fig. 1a) from sequence data that had previously been archived in GenBank by two independent studies<sup>6,46</sup> (note that *C. macrorhynchos culminatus* had erroneously been logged as *C. culminatus* in GenBank<sup>6</sup>). Where more than one sequence was available for a given species, we aligned them and produced a consensus sequence. We then aligned each region (CR, GAPDH, ND2, ND3, and ODC) separately using MAFFT<sup>47</sup>, and concatenated these alignments. For species that did not have coverage for a particular region, these regions were coded as Ns. We used this alignment to generate a consensus tree, using MrBayes<sup>48</sup> ( $n_{\text{gen}} = 10,000,000$ ). Uncertainty about the specific status of some taxa affects the total number of species within the genus<sup>6,8,46</sup> (e.g., recent authors<sup>46</sup> treated *C. violaceus* and *C. minutus* as distinct species, rather than as subspecies of, respectively, *C. enca* and *C. palmarum*<sup>8</sup>), but not the gross topology of the phylogenetic tree. Importantly, although more work is required to resolve the close relationships of *C. moneduloides*<sup>4,6,46</sup>, our analyses confirmed that the two tool-using species *C. hawaiiensis* and *C. moneduloides* are only very distantly related<sup>49</sup>. While our concatenation method enabled us to maximise data coverage, it complicated the estimation of divergence times, but according to an earlier study, the last common ancestor would have lived in the mid-Miocene, *ca.* 11 million years ago (see figure 2 in ref. 46).

The ‘Alalā is the only survivor of at least five species of crow that once inhabited the Hawaiian archipelago<sup>5,26,30</sup>. To assess variation in craniofacial

features, we used previously published photos (figure 3 in ref. 26) of the fossil skulls of two extinct species (*C. impluviatus*, *C. viriosus*), and adapted (mandibles closed; flipped horizontally; re-coloured) and re-sized them for direct comparison with the portrait photo of a live ‘Alalā (adult female #94; see Fig. 1f). The evolutionary history of this species assemblage remains unknown, but variation in bill morphology indicates well-differentiated foraging behaviour<sup>50,51</sup>. The distribution of an undescribed species with “a bill modified for hammering”<sup>5</sup> may be of particular relevance<sup>4</sup> for understanding the evolutionary ecology of tool behaviour in ‘Alalā.

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**EXTENDED DATA FILES (2 Figures; 2 Tables)****Extended Data Figure 1 | Craniofacial morphology of tool-using ‘Alalā and**

**New Caledonian crows.** **a**, Although some other *Corvus* species<sup>8</sup> have relatively straight bills – in terms of culmen- and commissural-line projections – they usually lack the pronounced distal angle of the gonys that is characteristic of the tool-using (i) ‘Alalā (adult female #191, 8 January 2015) and (ii) New Caledonian crow (adult female #CR6, 6 October 2013; photo: P. Barros da Costa), and also have larger distal protrusions of the upper mandible. Despite the overall similarity of the two species<sup>4,10</sup>, ‘Alalā are larger and more robust birds (see Fig. 1, c and d), and exhibit modest bill curvature, comparatively smaller eyes, and notable intraspecific variation in bill shape. The scale bar applies to all four images. **b**, ‘Alalā have markedly forward-pointing eyes, with high lateral eye-movement amplitudes, enabling (i) a considerable degree of convergence (#96, 17 February 2014; note that the red-brown plumage colouration is an image artefact; no adjustments have been made). The movement of (ii) both eyes (#201, 9 August 2014), or (iii) just one eye (red arrow; #206, 9 August 2014), can often be observed during the handling of birds for routine health checks (the white marker on the bills is a removable scale bar; see Supplementary Video 5). Although the ‘Alalā’s visual field could not be measured in this study (see Methods), these features are likely to produce a large field of binocular overlap, which in New Caledonian crows is thought to aid tool manufacture and deployment<sup>9</sup>. **c**, When ‘Alalā hold stick tools in a transverse grip, (i) the slight curvature of the birds’ bill can force the non-functional end of the tool close to the eye (as would be predicted from earlier work; see figure 5 in ref. 9), (ii) which may cause discomfort or even injury (red arrow indicates nictitating membrane, which the bird closed temporarily to protect its eye); (iii) this may explain why the vast majority of individuals prefer to hold tools in a frontal grip (adult male #134, 21 January 2013; transverse grip observed in only 11 of 104 subjects tested on the standardised log task).

**Extended Data Figure 2 | Food-extraction tasks for investigating tool-use**

**behaviour in captive ‘Alalā.** **a**, A species-wide assay of tool-use competence was conducted by presenting birds with a baited Koa *Acacia koa* log (length, *ca.* 78 cm; diameter, *ca.* 16 cm), containing two vertical holes (depth, *ca.* 5.0 cm; diameter, *ca.* 2.3 cm), two horizontal holes (*ca.* 5.4 cm; *ca.* 2.3 cm), one vertical crevice (width × depth, *ca.* 2.4 × 6.4 cm) and one horizontal crevice (height × depth, *ca.* 2.3 × 6.8 cm); all estimates of dimensions are averages for the two log set-ups used in experimental trials (see Methods). Sticks for potential tool use were scattered in front of the log (length classes: 3 of 0–5 cm; 3 of 10–15 cm; 3 of 20–25 cm; and 3 of 30–35 cm), and assorted plant materials for potential tool

manufacture were provided on a wooden stand nearby (KBCC: 2 ‘Ōhi‘a lehua *Metrosideros polymorpha* stems, 2 Koa stems, 1 fern frond, 2 dead branched stems; MBCC: 2 dead branched stems). It is worth noting that, since subjects had access to suitable tools during trials, current data likely underestimate the species’ tool-making capabilities. **b**, The tool-use competence of seven juvenile birds was assessed once per week over a 20-week period (and more often towards the end of the study period; see Methods), using a baited wooden platform (ca. 50 × 50 cm) with four vertical holes (depth, ca. 4.5–5.4 cm; diameter, ca. 2.0–2.7 cm) and two vertical crevices (width × length × height, ca. 2.5 × 21.2 × 7.3 cm and ca. 2.4 × 13.5 × 8.0 cm). From late January 2013 onwards, a second replica platform was used to enable parallel testing of both experimental groups. During the final stages of the experiment, the four vertical holes were substituted with horizontal holes (by rotating the wooden blocks), and two horizontal crevices were added (not shown here; see Supplementary Video 3).

**Extended Data Table 1 | Behavioural actions scored for captive, juvenile ‘Alalā during standardised probe trials.** Action types correspond to the numbers shown on the *y*-axes of panels in Fig. 3c; for a photo of the baited experimental platform, see Extended Data Fig. 2b. Action types are grouped into: approach to and interaction with the platform, not directly involving objects (no shading); object dropping near or on the platform (grey); object combinations and insertions (includes unsuccessful tool use) near or on the platform (light blue); and successful bait extractions with tools from platform tasks (dark blue).

\*These actions were possible only after the platform set-up had been modified during the final stages of the experiment (see Methods).

†‘Tool-assisted bait extractions’ were scored according to which parts of an extraction sequence a bird performed. Full sequences involved tool insertion, movement of the tool, and bait acquisition (insert → move → acquire), but in some cases, birds failed to acquire the bait they had brought within reach because another subject took it (insert → move), or they used a tool for extraction that had previously been inserted by another subject (move → acquire). Bait extractions were often highly dynamic, involving multiple birds (see Scene B of Supplementary Video 3). Note that there were no tool-assisted bait extractions from holes.

‡‘Stick-type object’ is an elongated object that could potentially be used as a tool; some side branches may remain, but the object must have a potentially functional end that could be inserted into holes or crevices (some sticks were provided on the platform during the final stages of the experiment; see Methods). Note that, for the purpose of estimating object-handling rates and manipulation



times for Fig. 3a and 3d, respectively, ‘sticks’ additionally include fern sections and branched pieces of plant for ‘Alalā (see objects lying around the platform in Scene B of Supplementary Video 3), given that: these were common objects in the housing aviaries; birds inserted them into baited platform tasks; and another study used a similarly inclusive object class ‘twigs’ for other corvid species<sup>17</sup>.

§‘Other natural object’ includes fern sections, branched pieces of plant, larger branches, leaves, grass blades, bark pieces, wooden splinters and stones (but not food objects) that do not fulfil the definition of ‘stick-type object’. Note that, in Fig. 3a, ‘other objects’ also include toys and other enrichment items, and ‘stones’ are shown separately.

||‘Combining’ is any manipulation in which an object is placed in contact with another object or substrate, but not including ‘insertions’ (compare with ref. 17). Combinations include attempted insertions with stick-type objects oriented at the wrong angle, as well as the placement and movement of objects.

¶‘Within the platform area’ was scored when a bird was on the platform itself, or its bill tip or any object held in its bill was within *ca.* 10 cm of the platform (*ca.* one quarter of a bird’s body length).

#While cases were omitted where a bird’s bait acquisition was immediately preceded by tool movements by another subject, it is possible that tool-bait interactions earlier during the trial were responsible for bringing bait within bill reach.

**Extended Data Table 2 | Observation rates of tool behaviour for three naturally tool-using bird species.** The most detailed study on the foraging behaviour of free-ranging ‘Alalā accumulated about 17.5 hours of focal observations for eight pairs in montane rainforest<sup>21</sup>, and although a sample like this would almost certainly yield conclusive tool-use observations in some habitual avian tool users (New Caledonian crow<sup>23</sup>; woodpecker finch<sup>52</sup>), it would not necessarily be sufficient for others (brown-headed nuthatch<sup>53</sup>). For comparison, orang-utans *Pongo* spp. and capuchin monkeys *Cebus/Sapajus* spp. were long thought to use tools exclusively in captivity, and it took decades of high-effort fieldwork to uncover the diverse tool behaviours of wild populations<sup>1,54</sup>.

## SI GUIDE (6 Videos)

**Supplementary Video 1 | Spontaneous tool behaviour by an ‘Alalā.** This unedited scene shows the first presentation of the log set-up to adult male #134 (21 January 2013). Note that the log is a prototype that, compared to the final design later used for the species-wide behavioural assay, contained two additional holes.

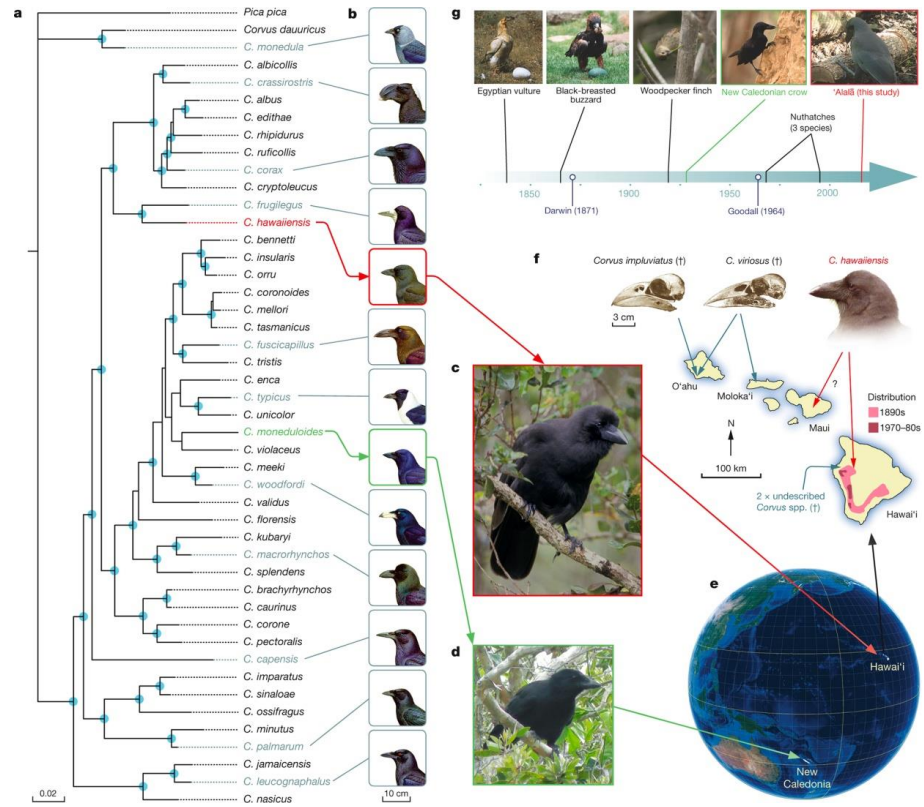
**Supplementary Video 2 | Tool selectivity, modification and manufacture in ‘Alalā.** During experimental trials, many ‘Alalā were observed: **a**, to choose tools of appropriate dimensions; **b**, to replace tools that were not suitable; **c**, to transport non-supplied sticks to the set-up to be used as tools; to modify tools **d**, before or **e**, during deployment; or **f**, to handle, try and modify several different sticks during an extraction attempt. Tool manufacture behaviour included: **g**, snipping-off twigs from supplied dead branches; the production of **h**, bark flakes and **i**, wood splinters; and **j**, successive subtraction of material from non-supplied live plant material.

**Supplementary Video 3 | Ontogeny of tool-related behaviour in naïve juvenile ‘Alalā.** Functional tool behaviour can result from (a combination of) genetic predispositions, social learning, and individual learning. To investigate the relative importance of different processes, ‘naïve’ juveniles can be reared in captivity without opportunities to observe tool-use behaviour in proficient adult conspecifics, or even in humans. Under such controlled conditions, ‘Alalā chicks develop functional tool use over the first few months of life: **a**, first handling and carrying objects, including sticks, stones and other items; before **b**, inserting them into holes and crevices with gradually increasing proficiency (here, during a probe trial with several baited extraction tasks presented on a ‘platform’).

**Supplementary Video 4 | Historical recordings of ‘Alalā using tools.** Before the commencement of systematic behavioural experiments, staff at the KBCC and MBCC facilities had regularly observed ‘Alalā using tools. Following these opportunistic observations, on the 28 July 2011, four different birds were filmed using tools to reach for bait placed in a water bath (#114, #118, #135), or behind wire mesh (#146).

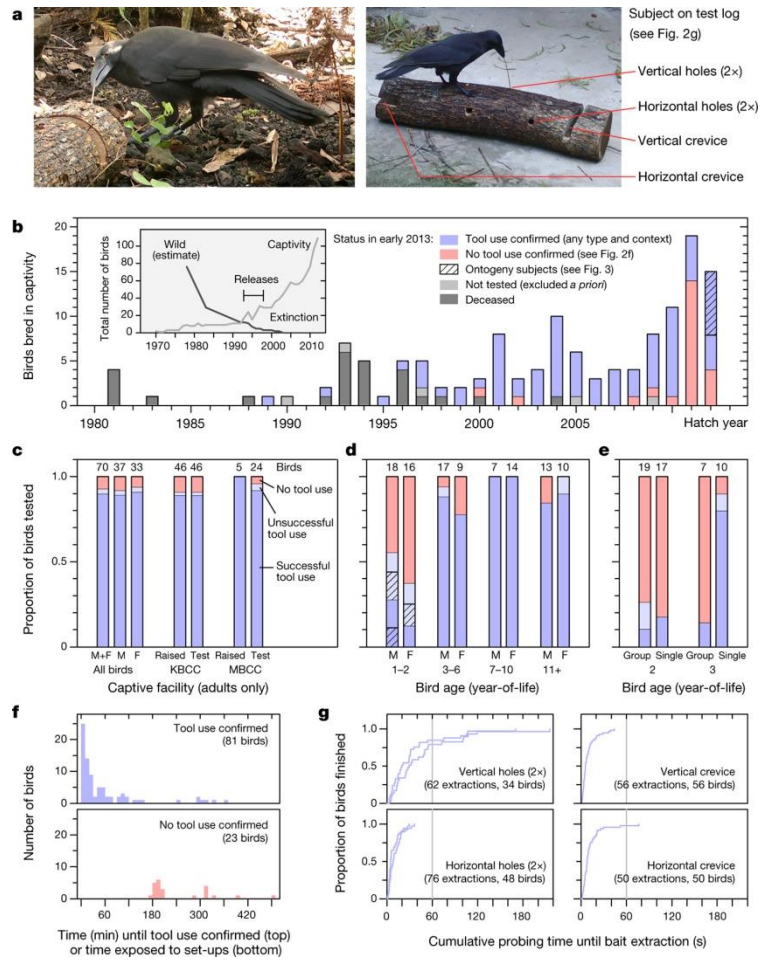
**Supplementary Video 5 | Eye movements in an ‘Alalā.** Like New Caledonian crows, ‘Alalā have unusually large eye-movement amplitudes. This video was taken when adult male #121 was trapped for a routine pre-breeding health check (19 March 2015) and presented with a neonate mouse to attract its attention.

**Supplementary Video 6 | Tool-use behaviour in crows.** Tool use of an adult male **a**, 'Alalā and **b**, New Caledonian crow. 'Alalā tend to hold stick tools in a frontal grip whereas New Caledonian crows prefer a transverse grip. **c**, Naturally non-tool-using rooks can be trained to use tools, but compared to most 'Alalā and New Caledonian crows, they appear to handle sticks less dexterously (but note difference in extraction tasks provided).



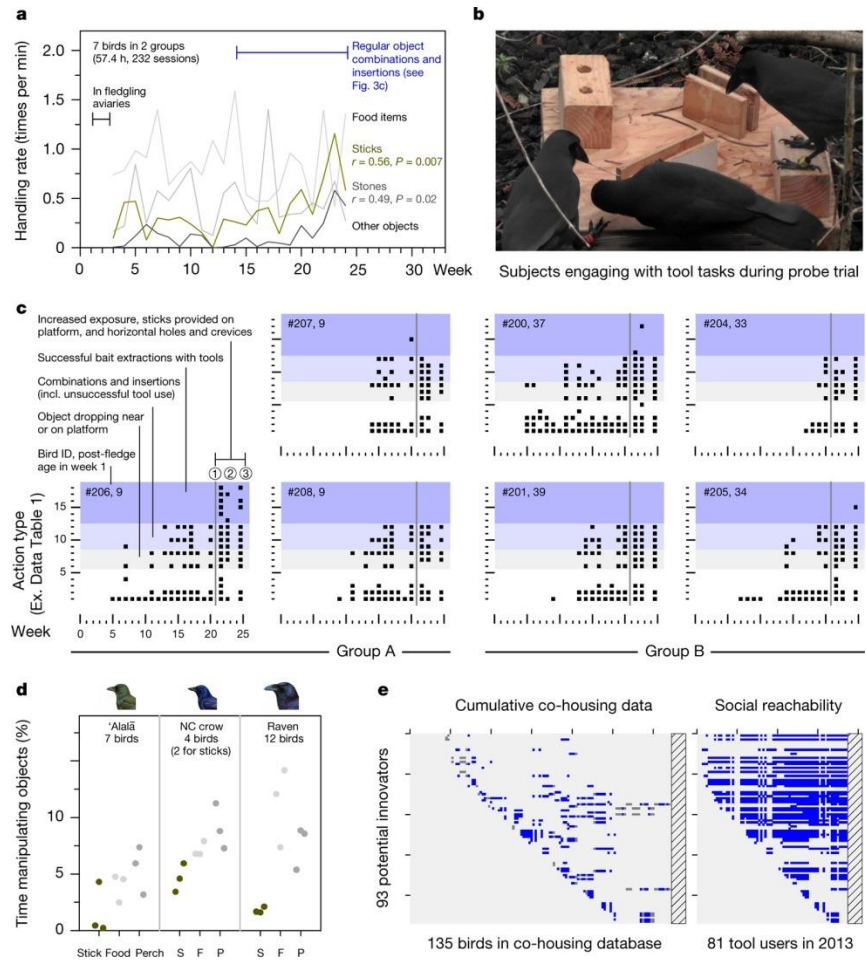
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Figure 1



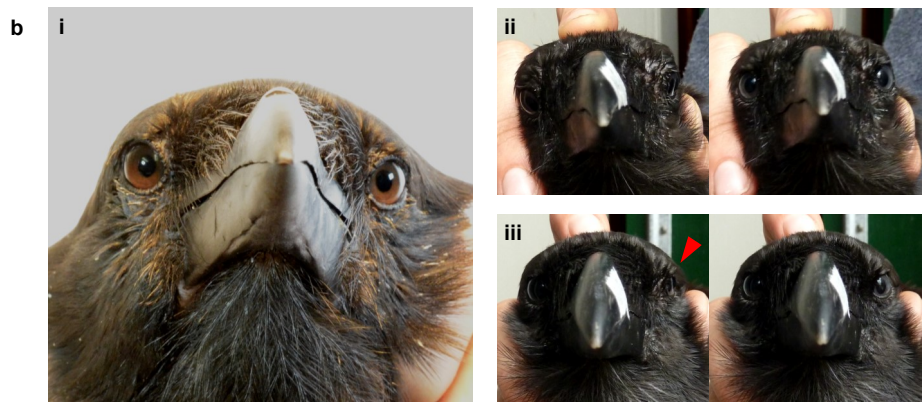
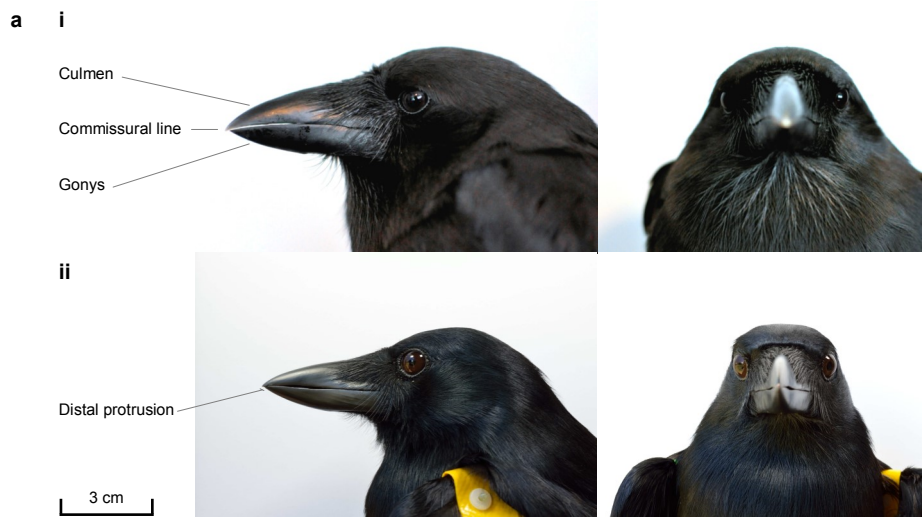
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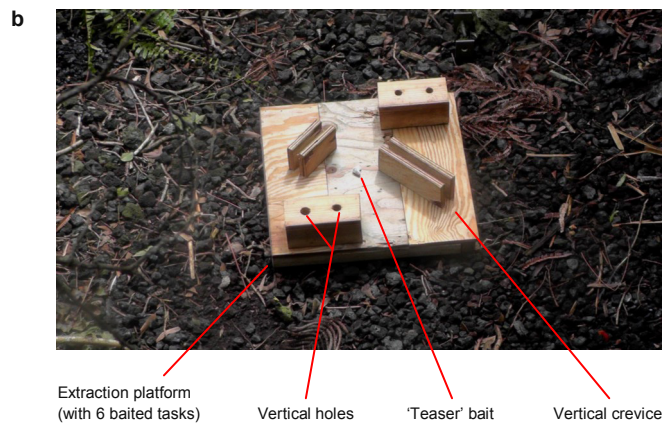
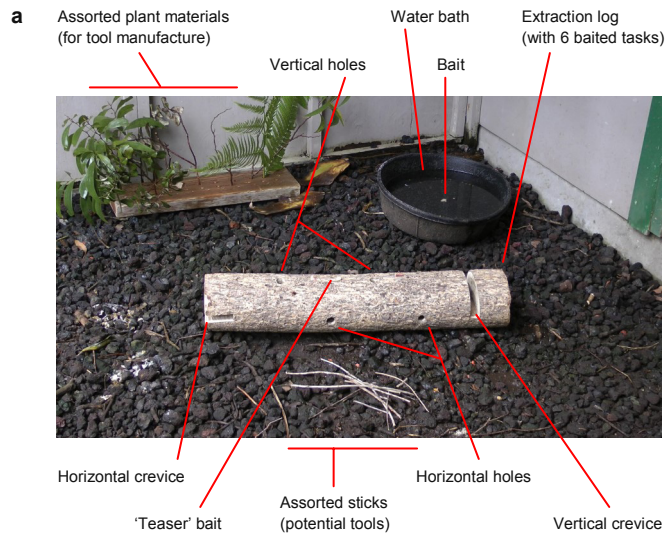
Figure 2



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Figure 3







Action type	Description
18*	Tool-assisted bait extraction from horizontal crevice (insert → move → acquire) <sup>†</sup>
17	Tool-assisted bait extraction from vertical crevice (insert → move → acquire) <sup>†</sup>
16*	Tool-assisted bait extraction from horizontal crevice (insert → move) <sup>†</sup>
15	Tool-assisted bait extraction from vertical crevice (insert → move) <sup>†</sup>
14*	Tool-assisted bait extraction from horizontal crevice (move → acquire) <sup>†</sup>
13	Tool-assisted bait extraction from vertical crevice (move → acquire) <sup>†</sup>
12	Inserting bill-held other natural object <sup>§</sup> into hole or crevice
11	Inserting bill-held stick-type object <sup>‡</sup> into hole or crevice
10	Combining <sup>  </sup> bill-held other natural object <sup>§</sup> within the platform area <sup>¶</sup>
9	Combining <sup>  </sup> bill-held stick-type object <sup>‡</sup> within the platform area <sup>¶</sup>
8	Dropping other natural object <sup>§</sup> (picked up within the platform area <sup>¶</sup> ), within the platform area <sup>¶</sup>
7*	Dropping provided stick <sup>‡</sup> within the platform area <sup>¶</sup>
6	Dropping non-provided stick-type object <sup>‡</sup> (picked up within the platform area <sup>¶</sup> ), within the platform area <sup>¶</sup>
5*	Extraction from horizontal crevice without tool <sup>#</sup>
4	Extraction from vertical crevice without tool <sup>#</sup>
3	Extraction from hole without tool <sup>#</sup>
2	Chiselling at hole or crevice
1	Within the platform area <sup>¶</sup>

Study species	Habitat (conditions)	Observation time (h)	Tool-use observations	Tool-use observations h <sup>-1</sup>
New Caledonian crow	Coastal dry forest	9.2	8	0.9
Woodpecker finch	Humid <i>Scalesia</i> zone	7.2	6	0.8
	Arid zone	14.1	134	9.5
Brown-headed nuthatch	Pine forest (few seeds)	150	10	0.07
	Pine forest (abundant seeds)	75	1	0.01