Wild Goffin’s cockatoos flexibly manufacture and use tool sets

Graphical abstract

Manufacture: Severing Splitting

Tools: Sturdy Fine Medium

Tool use: Wedging Vertical motion Horizontal motion & Extraction

Highlights

- Wild Goffin’s cockatoos use a tool set to access seed matter of a tropical fruit
- Only few individuals engage in the behavioral sequence required for tool use
- Up to three tool types are employed, differing in manufacture, size, and function
- Flexible manufacture and use of tool sets is no longer restricted to primates

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In brief

O’Hara, Mioduszewska et al. show how wild Goffin’s cockatoos craft and use different tools to access seed matter of a tropical fruit during a capture-release study. This finding extends the presence of tool sets beyond the primate lineage and highlights the convergent evolution of advanced tool use in species without hands.
Wild Goffin’s cockatoos flexibly manufacture and use tool sets

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SUMMARY

The use of different tools to achieve a single goal is considered unique to human and primate technology. To unravel the origins of such complex behaviors, it is crucial to investigate tool use that is not necessary for a species’ survival. These cases can be assumed to have emerged innovatively and be applied flexibly, thus emphasizing creativity and intelligence. However, it is intrinsically challenging to record tool innovations in natural settings that do not occur species-wide. Here, we report the discovery of two distinct tool manufacture methods and the use of tool sets in wild Goffin’s cockatoos (Cacatua goffiniana). Up to three types of wooden tools, differing in their physical properties and each serving a different function, were manufactured and employed to extract embedded seed matter of Cerbera manghas. While Goffin’s cockatoos do not depend on tool-obtained resources, repeated observations of two temporarily captive wild birds and indications from free-ranging individuals suggest this behavior occurs in the wild, albeit not species-wide. The use of a tool set in a non-primate implies convergent evolution of advanced tool use. Furthermore, these observations demonstrate how a species without hands can achieve dexterity in a high-precision task. The presence of flexible use and manufacture of tool sets in animals distantly related to humans significantly diversifies the phylogenetic landscape of technology and opens multiple avenues for future research.

INTRODUCTION

Observing animals using tools is always appealing, as it places our capacities into context. Nevertheless, not all tool use requires intelligence. When studying tool use, it is crucial to distinguish innovative (spontaneously acquired, learned individually, or spread socially) from specialized (inflexible, species-wide) tool behavior.1,11 Regarding the definition of tool use, a recent “tooling” framework provides a comprehensive description of tool use as a body-plus-object system that creates a biomechanical interface between a held object and the target.3 It is a coherent ecological approach, where the presence of tool use is determined based on observable spatial relations between organisms and their physical surroundings. Thus, this approach has recently been proposed as suitable for comparing species abilities by providing a rigorous and objective framework.3

To make meaningful assumptions about the evolution of technology and cognition, it is important to consider how wild, non-human animals acquire such skills. Comparative studies of distantly related species allow triangulating the socio-ecological factors underlying the evolution of behaviors. In turn, these factors can help to identify the precursors of a behavior on a proximate level. In birds, the evolutionary onset of tool use has been attributed to modifying pre-existing, ecologically relevant behaviors, such as food caching.5

Parrots are among the few species that possess traits shared with tool-using primate lineages despite being distantly related. They have a large relative brain size, complex sociality, and prolonged parental care.6,7 They are, however, unlikely candidates to develop tool use from necessity, as their grasping zygodactyl feet and versatile, sharp beaks make them highly adapted to their environment.8,9
Goffin’s cockatoos (Cacatua goffiniana; alternative common name: Tanimbar Corella; indigenous Tanimbarese name: Manik Tilro; hereafter: Goffins) are medium-sized parrots endemic to the Tanimbar Islands, Indonesia. Like all parrots, they lack food caching or nest building ancestry. Nevertheless, they have a strong, playful urge to combine objects and are opportunistic extractive foragers, which are characteristics associated with tool innovations. In a laboratory setting, Goffins innovate sophisticated tool use and even tool manufacture. Nevertheless, as a strong captivity bias on tool use has been proposed, it remains an open question whether these capacities are a product of being raised within an artificial captive environment. Even among non-human apes, observations of only two species (chimpanzees and orangutans) provide compelling evidence of innovative tool use in the wild.

In their natural habitat, Goffins were observed to forage on various food sources, including some that require extraction (such as young coconuts or papayas). However, wild Goffins have not been observed to use tools in their native environment despite extensive research effort invested over two recent field projects (total scanning time: 884 h 42 min) organized in close collaboration with local indigenous communities. Here, we report the discovery of tool manufacture and use to extract seed matter of a tropical fruit in two wild Goffins. These individuals were kept temporarily in a field aviary together with 13 other wild-caught conspecifics as part of a capture-release project. This study was triggered by an opportunistic observation and aimed at a thorough description and analysis of the exhibited behavior and involved objects.

Our investigation was guided by the following questions: how common is tool use within the group, how complex and flexible is the behavior, and which properties of the fruit predict tool use? If successful extraction required tool use, the seed matter should not be accessible without tools. Hence, seed-matter extraction would be limited if tool use is based on individual innovation but common if it were a species-wide trait. The complexity of the behavior could be assumed to increase with the number of required actions and the number of distinct types of tools. Consistent differences in the physical properties of tools would imply that more than one type of tool was used. Furthermore, differences in corresponding behaviors and the hierarchical order of their application would suggest distinct functions. Finally, flexible application of tools would manifest in the use of different types of tools depending on the fruit characteristics. The resulting detailed account of dexterous, dynamic, and flexible tool behaviors, along with comprehensive measures of the involved objects, shows that wild Goffins use a set of up to three different types of tools to achieve a single goal.

RESULTS

Tool use is limited within the group
Upon being presented with a Cerbera manghas fruit (indigenous Tanimbarese name: Wawai; common names: Sea mango, Pink-eyed Cerbera, and Bintaro; hereafter: Wawai), one individual (ring identification: left black [LB]) within the group of 15 Goffins immediately and repeatedly detached, modified, and used branch fragments to extract seed matter from the lignified endocarp of a Wawai fruit (Video S1). In a further two presentations in a group setting, only one additional individual processed the fruit with crafted tools (ring identification: no ring [NR]). Thereafter, we repeatedly provided both birds (LB and NR; individuals were treated as fixed factors in all analyses to account for individual differences) with fruit in a controlled setting (Table S1), which enabled us to track the sequence and number of manufactured tools, as well as to collect dropped and discarded tools. We conducted a frame-by-frame behavioral analysis (Figure 1A; Table S2) of 11 sessions in which tools were successfully traced (LB: n = 6; NR: n = 5; Figure S1). While other individuals were observed interacting with the fruit (n = 6) and combining various vegetation (wood pieces, liana pieces, and long dry beans) with the endocarp (n = 3), none of them manufactured or used tools.

The behavioral sequence to extract seed matter
Typically, tool users held the fruit in their left foot and balanced on the right foot while removing the pericarp with repeated parallel bites ($M_{duration} = 133.36 s$; $SD_{duration} = 68.68$; n = 11; Figure 1BII). Once the endocarp was exposed, individuals either dropped the fruit or proceeded with tool-assisted extraction (Table S1; Video S2). They detached wooden fragments from a suitable branch (Figure 1BII) and modified them ($M_{duration} = 54.62 s$; $SD_{duration} = 61.54$; n = 11) by turning the fragments with the tongue inside the beak, removing the outer bark, and performing selective cuts (Figure 1BIII). The resulting tool was held at its distal end between the upper mandible and the muscular tongue and pushed vertically into the exposed fissure (total duration: $M = 81.59 s$, SD = 55.59, n = 11; Figure 1BIV). Tools inserted into the fissure were then moved horizontally (Figure 1BV) by titling the head to lever seed matter out of the endocarp (total duration: $M = 81.56 s$, SD = 51.22, n = 11; Figure 1BVI). Once the distal end of the tool would reappear through the fissure, it would immediately be probed with the tongue. Any extracted seed matter would be ingested before repeating this sequence. On average, eight tools (SD = 7.14) were used per fruit, and each tool was inserted 8.25 times (SD = 9.85) before producing a new tool or dropping the endocarp. During extraction, the endocarp and the tools were dynamically and concurrently aligned (Video S2).

Different tool types with different functions
From 11 sessions, we recovered 50/77 tools (Figure S2) and created 3D models of all tools to measure their size, volume, and shape. A cluster analysis by partitioning around medoids of physical tool properties revealed three distinct “tool types” (Figure 2A; Video S2): “fine tools” (thin, sharp, and low volume), “medium tools” (medium-thick, medium-sharp, and medium volume), and a single “sturdy tool” (thick, blunt, and high volume), which was used for wedging (see below). An additional linear discriminant function based on the physical properties revealed that two tools that were dropped before being inserted (tool ID: LB_3_3 and LB_4_5) exhibited high probabilities to cluster within one of the tool types (LB_3_3: 96.5% fine tool, 93.5% medium tool, and 0% sturdy tool; LB_4_5: 98.3% fine tool, 1.7% medium tool, and 0% sturdy tool; Figure S2).

The probability to use a medium tool was significantly influenced by the normalized sequence position within each session (full null model comparison: $\chi^2_{(1)} = 11.85$; p < 0.001). In all sessions in which two tool types were used, medium tools were...
more likely to be used after fine tools ($\beta = 3.44$; SE = 1.41; $p = 0.015$; Figure S3). Individuals did not differ in the sequential use of medium and fine tools ($\beta = 0.55$; SE = 0.95; $p = 0.56$).

Overall, behavior proportions were affected by tool type (full null model comparison; likelihood ratio test: $\chi^2(4) = 38.977$, $p < 0.001$), and the interaction between tool type and “behavior” was also significant ($\chi^2(3) = 38.977$; $p < 0.001$; Figure 2 B; for model results for fixed and random effects, see Tables 1 and 2). There were significantly more horizontal motions with medium tools ($\beta = 1.42$; SE = 0.25; $p < 0.0001$), whereas more time was spent on manufacture ($\beta = 0.72$; SE = 0.29; $p = 0.013$) and modification ($\beta = 0.77$; SE = 0.30; $p < 0.01$) of fine tools (Figure 2 C). Tool type also significantly affected seed matter extraction ($\chi^2(9) = 11.85$; $p < 0.001$), with medium tools being more efficient than fine tools ($\beta = 2.06$; SE = 0.56; $p < 0.001$; Figure 2 C). “Individual” as a fixed factor was retained to control for individual differences, but no significant differences between individuals could be detected ($\beta = 1.11$; SE = 0.80; $p = 0.17$).

**Wedging**

One individual (LB) occasionally used distinctly sturdier wooden fragments wedged into the corner of the fissure while employing subsequent tools to extract seed matter. Unfortunately, due to practical constraints, only one such wedge could be retrieved for detailed 3D reconstruction. Based on a suggestion by an anonymous reviewer, we additionally analyzed video footage from five sessions in which wedging (having a wooden fragment wedged into the fissure before using a subsequent tool) occurred. Based on a discriminant function analysis, two out of eight tools used for wedging grouped as sturdy tools (Figure 3 A; Table S3). Moreover, we observed a distinct difference in the manufacturing process for several tools (Table S3; Video S3). Instead of splitting a fragment from a branch, a whole branch was severed at the base and a tool was crafted from the remaining branch stump. This manufacture method was employed to produce three tools used for wedging (session 1, tool 2; session W1, tool 16; session W5, tool 7; Table S3) and several wooden fragments that preceded these wedges but were lost (stolen by a conspecific or dropped during agonistic interactions) before or during initial insertion (four tools in session W1 and two tools in session W5; Table S3). Except for one tool, all tools with the distinct manufacturing process (7/8) were classified as sturdy tools by the discriminant function (Figure 3 B; Table S3).

**The fruit properties predicting tool use**

The Wawai fruit have a fibrous outer layer ($M = 13$ mm; SD = 2.4; $n = 51$) and seeds ($M = 1.2$ g; SD = 0.7; $n = 51$) that are embedded in a lignified endocarp (thickness: $M = 6.1$ mm, SD = 1.6, $n = 51$) and enclosed by a thin parchment-like coating (Figure 4). A narrow (width: $M = 2.2$ mm, SD = 0.6, $n = 50$) longitudinal fissure, which is very hard to force open due to the lignification of the endocarp, provides access to the seed locules. The force needed to open the endocarp was negatively correlated with the width of the fissure ($r(41) = -0.65$; $p < 0.0001$; Figure 5 A).

It is unlikely that the width of the fissure was influenced by the use of tools due to the rigidity of the endocarp and the fact that some of the discarded or not provided fruit also had fissures with larger widths (Figure 5). However, we cannot fully exclude the possibility that tool application widened the fissure, as the majority of tool use occurred on fruit with larger widths of the fissure.
and endocarp characteristics of these fruit (width of the fissure and the corresponding force required to open the endocarp) could only be measured after providing the respective fruit to the subjects. We analyzed the behavior of the two subjects (LB and NR), which used tools on 22/41 provided fruit (Table S1). A logistic generalized linear model (GLM) on fruit properties predicting tool use differed significantly from the respective null model ($\chi^2_{(4)} = 31.35; p < 0.0001$). While total weight did not obviously influence the probability to use tools ($\beta = -0.04; SE = 0.03; z = -1.57; p = 0.12$), nor could any differences be found with regard to fruit state (ripe versus spots: $\beta = -0.67, SE = 1.19, z = -0.54, p = 0.52$; ripe versus unripe: $\beta = 1.11, SE = 1.35, z = 0.83, p = 0.40$), the probability of using tools significantly increased with the width of the fissure ($\beta = 4.97; SE = 1.60; z = 3.12; p = 0.002$; Figure 5B). Individual differences bordered a significant effect, with subject LB tending to engage more in tool use ($\beta = 2.66; SE = 1.50; z = 1.81; p = 0.07$).

DISCUSSION

Two out of 15 Goffins instantly and repeatedly exhibited the complete behavioral sequence required to extract seed matter with manufactured tools upon the first provision of Wawai fruit within the capture-release aviary. The limited occurrence of such a complex skill implies that it is not a species-wide trait but had been acquired in the natural environment. Based on laboratory studies, the transmission of tool use could be propagated through affordance learning or goal emulation in Goffins, with the resulting technique being invented by the observers.20,21 The relative rarity of the observed tool use behavior...
Table 1. Results of the compositional mixed model on the proportion of time spent on different tool-related behaviors

| Term                          | Estimate | SE      | Lower CI | Upper CI | Min  | Max  |
|-------------------------------|----------|---------|----------|----------|------|------|
| (Intercept)                   | −0.714   | 0.222   | −3.448   | 1.945    | −1.056| −0.346|
| Behavior (manufacture)        | 1.098    | 0.344   | −2.568   | 4.964    | 0.537| 1.714|
| Behavior (modification)       | 0.746    | 0.388   | −3.031   | 4.430    | 0.041| 1.375|
| Behavior (vertical motion)    | 1.011    | 0.260   | −2.731   | 4.450    | 0.697| 1.288|
| Tool type (medium)            | 1.419    | 0.242   | −1.982   | 4.925    | 1.003| 1.734|
| Individual (LB)               | 0.000    | 0.138   | −2.106   | 2.032    | 0.000| 0.000|
| Behavior (manufacture): tool type (medium) | −2.137 | 0.373 | −7.013 | 2.456 | −2.706 | −1.487 |
| Behavior (modification): tool type (medium) | −2.186 | 0.389 | −6.845 | 2.906 | −2.727 | −1.501 |
| Behavior (vertical motion): tool type (medium) | −1.354 | 0.317 | −6.061 | 3.618 | −1.631 | −1.024 |

Fixed effects estimates presented together with standard errors, confidence limits, and range of estimates obtained when excluding levels of random effects one at a time.

within the population suggests that this skill may have emerged as a result of opportunity and innovation. 22–24

Three distinct tool types were identified based on their physical properties. A combination of qualitative observations on how subjects manufactured and manipulated the different tools, as well as quantitative measures of tool sequences and motion directions, indicates that at least two of three tool types served different purposes. Fine tools seemed to be used to pierce the parchment-like coating encapsulating the seed as they were sharp and required more elaborate manufacture. Medium tools were typically used for extracting seed matter and were applied after fine tools. For extraction, horizontal motions (in addition to vertical motions) were necessary and were performed more often with medium tools than with fine tools. The collected sturdy tool seemed to serve as a wedge, widening the fissure to allow easier access for the following tools. Although only one wedge could be retrieved, further wedging instances were video recorded and analyzed (Tables S1 and S3). During 35 sessions, ten instances of wedging were recorded. Three of the used tools were classified as sturdy tools, six as medium tools, and one as a fine tool. Notably, tools that were not classified as sturdy tools were removed while a subsequent tool was used, whereas sturdy tools remained inserted for the whole duration of using at least one subsequent tool.

In terms of tool manufacture, two distinct methods were observed. Fine and medium tools were produced by splitting a slim wooden fragment from a branch and modifying it in the beak, whereas sturdy tools were produced by severing a branch at its base, removing the remaining branch stump, and modifying the thick wooden fragment in the beak. Fragments crafted in the latter way, which immediately preceded the use of a sturdy tool but were lost (due to agonistic interactions or stolen by conspecifics), were also grouped as sturdy tools. However, tools manufactured immediately after a wedge (subsequent tools) were never classified as sturdy tools. Hence, the manufacture of sturdy tools did not seem to be accidental and likely served a different function (wedges) than fine and medium tools (perforators and probes).

The order of used tool types was flexibly adjusted to the depth and extraction difficulty of the encountered seed matter. Notably, two tools that were accidentally dropped before use already had distinct forms after manufacture (Figure S2), suggesting that their shape was determined before use rather than through the use on the fruit (e.g., by pushing a tool through the fissure or against the endocarp). Hence, it seems that the tools were not shaped by but rather according to the affordances of the fruit.

These behaviors fall within the definition of “tool sets,” where multiple tools with different functions are used sequentially to reach a single goal. 19,25 The use of tool sets is rare in the animal kingdom, as most instances of tool use involve employing a single type of tool for a single task, and has so far only been observed in tool-using primates. 19,26 Using more than one tool type for a single task has been suggested to demonstrate advanced causal understanding of object relations and elaborate motor control. 26,27 Additionally, tool sets can be flexibly implemented or hierarchically structured depending on the encountered characteristics of the target,28 as was observed in the current study. In terms of emergence, tool sets were suggested to arise from technical innovation and cumulation based on the ability to use a single tool.28,29 Our observations resemble previous reports of wild chimpanzees using tool sets to access bee or termite nests.19,30 While chimpanzees used between two and five types of objects, the core functions seem to parallel

Table 2. Results of the compositional mixed model on the proportion of time spent on different tool-related behaviors

| Term                          | SD  | Min  | Max  |
|-------------------------------|-----|------|------|
| Tool ID (intercept)           | 0.000 | 0.000 | 0.000 |
| Fruit (intercept)             | 0.000 | 0.000 | 0.000 |
| Fruit: behavior (manufacture) | 0.480 | 0.000 | 0.633 |
| Fruit: behavior (modification)| 0.662 | 0.000 | 0.795 |
| Fruit: behavior (vertical motion) | 0.000 | 0.000 | 0.129 |
| Residual SD                   | 4.232 | 3.603 | 4.377 |

Random effects estimates presented together with their range as obtained when excluding levels of random effects one at a time.

aThe first term indicates the grouping variable; brackets indicate whether the term is a random intercept or slope.
our findings in that they contained at least one object to perforate the embedded food source and another to probe and access the contents.

Wild Goffins were already observed to feed on Wawai fruit, and three lines of evidence suggest that their tool behavior is not an artifact of temporary captivity but had been acquired in the wild prior to capture. First, the highly proficient manner in which both subjects made and used tools in successive steps immediately after being provided with Wawai fruit strongly suggests they possessed the skill before capture. Second, on our outdoor feeding platforms, we managed to obtain close-up video footage of a free-ranging Goffin combining a wooden fragment with a Wawai fruit (Video S4) and several individuals skinning fruit in the same distinct way as the tool users. Third, we encountered fruit underneath Wawai trees that appeared to have been foraged on with tools, one still containing a wooden fragment inserted into the fissure (Figure S4).

The technique used by Goffins to extract seed matter embedded within the endocarp is particularly complex, requiring manufacturing a specific type of tool and involving high-precision actions. It required considering two different concurrent spatial relations: holding the fruit in the foot while orienting the fissure for tool insertion and holding the tool between the tongue and the beak while applying varying force and position. Moreover, it also required sequential spatial relations: applying the different tools in several consecutive steps. The actions were allocentric (not self-directed), dynamic, and highly specific in placement, orientation, and alignment. We thus believe that this discovery represents one of the most complex examples of tool use so far recorded in any species without hands.

As a starting point, this finding opens multiple directions for future research on flexible tool use in wild Goffins. To determine the extent to which the tool use behavior is present in the wild and how it is maintained in a population, it is necessary to study multiple groups across the Tanimbar Islands. In order to assess its ecological significance, a nutritional analysis of the Wawai plant will provide information on the value of this food source and an isotope analysis will indicate the degree to which it is part of the wild Goffins’ diet. Additionally, comparative studies with hand-raised laboratory individuals will provide information on whether the captivity effect may have an influence on the propensity for flexible tool use.

Our study provides evidence that wild Goffins have the capacity to innovate complex and flexible tool use and manufacture...
while seemingly lacking species-wide tool behavior. Similar to tool-using primates, this ability may be driven by opportunism and extractive foraging while being facilitated by persistence, sensorimotor control, a strong motivation to combine objects, and the capability to instantly memorize and repeat complex yet efficient behavioral sequences. The presence of flexible tool use in wild parrots strongly suggests a case of convergent emergence of sophisticated tool behavior and refines the phylogenetic landscape of technological evolution.

**STAR METHODS**

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**SUPPLEMENTAL INFORMATION**

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.08.009.

A video abstract is available at https://doi.org/10.1016/j.cub.2021.08.009#mmc8.

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AUTHOR CONTRIBUTIONS
Conceptualization, M.O. and B.M.; methodology, M.O. and B.M.; investigation, M.O. and B.M.; formal analysis, M.O., R.M., B.M., Y., R.R., and T.H.; funding acquisition, M.O., A.M.I.A., and L.H.; project administration, M.O., B.M., and D.M.P.; supervision, M.O. and B.M.; visualization, M.O. and R.M.; writing – original draft, M.O., B.M., and A.M.I.A.; writing – review & editing, M.O., B.M., A.M.I.A., R.M., L.H., D.M.P., Y., R.R., and T.H.

DECLARATION OF INTERESTS
The authors declare no competing interests.

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STAR METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---------------------|--------|------------|
| Deposited data      |        |            |
| Raw and analyzed data | This manuscript; Dryad | https://doi.org/10.5061/dryad.bzhk18979 |
| Goffin’s cockatoo (Cacatua goffiniana) | Tanimbar Islands | N/A |
| Wawai (Cerbera manghas) | Tanimbar Islands | N/A |
| Software and algorithms |        |            |
| BORIS v.7.9.8 | Friard and Gamba | https://www.boris.unito.it; RRID: SCR_021434 |
| CloudCompare v.2.9.1 | GPL, Software | https://www.danielgm.net/cc/ |
| Meshlab v.2016.12 | Cignoni et al. | https://www.meshlab.net |
| R v.4.0.2 | R Development Core Team | https://www.r-project.org; RRID: SCR_001905 |
| Regard3D v.x64 1.0.0 | Hiestand | https://www.regard3d.org |
| Custom code for analyses | This manuscript; Dryad | https://doi.org/10.5061/dryad.bzhk18979 |
| Other |        |            |
| 3D tool models | This manuscript; Dryad | https://doi.org/10.5061/dryad.bzhk18979 |
| GoPro Hero7 | GoPro | https://gopro.com/en/us/shop/switch?currency=USD&countryCode=US&pipeline=Product-Show&qstring=pid%3DCHDHX-701-master |
| Canon XA40 camcorder | Canon | https://global.canon/en/c-museum/product/dhc882.html |
| Canon EOS 7D Mark II | Canon | https://global.canon/en/c-museum/product/dslr819.html |
| Canon EF-S 35mm f2.8 Macro IS STM | Canon | https://global.canon/en/c-museum/product/ef460.html |

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Mark O’Hara (mark.ohara@vetmeduni.ac.at).

Materials availability
This study did not generate new unique reagents.

Data and code availability
- All datasets used for analysis in this study, along with 3D models of all collected tools, have been deposited at Dryad (files: Behaviors.txt, Tools.txt, FruitMeasures.txt, Extra tooimeasures.txt, LB_S2_BM.txt, LB_S2_MO.txt, LB_S5_BM.txt, LB_S5_MO.txt, and All_tools.zip) and are publicly available as of the date of publication (Dryad: https://doi.org/10.5061/dryad.bzhk18979).
- All code generated during this study has been deposited at Dryad (files: R-Code.R and Functions.r) and is publically available as of the date of publication (Dryad: https://doi.org/10.5061/dryad.bzhk18979).
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subjects
The Goffin’s cockatoo is a relatively small cockatoo species belonging to the Corella (Licmetis) subgenus. It is endemic to the Tanimbar Islands in Southeast Moluccas, Indonesia, where it is a feeding opportunist-generalist inhabiting tropical dry and moist deciduous forest. We observed 15 wild-caught Goffins temporarily group-housed in a field aviary at the Goffin Lab Tanimbar research...
field station located on Yamdena island. The aviary allowed controlled behavioral studies otherwise impossible to conduct on free-ranging individuals. The group was gradually habituated to human presence inside the aviary in order to eliminate any potential discomfort during observations. All training and test procedures were based on voluntary participation of subjects.

Two individuals (LB and NR) were identified as tool users and their behavior was studied in more detail. The first tool use observation occurred upon the first provision of Wawai fruit in the field aviary, 3 months after capture. In terms of prior experience, the subjects were wild-caught and therefore their history involving manipulation of objects and tool use is not known. Age of the subjects could not be reliably assessed in the field, however they were likely not juveniles (based on their tongue coloration and behavior). Morphological features (such as eye color and overall size) indicated that both individuals were males, which was confirmed for subject NR through DNA sexing (results for LB were inconclusive).

Capture-release procedure
Individus were captured using a nylon leg noose mounted on crops during corn harvest near the capture-release aviary. Active traps were monitored from a nearby hidden location. Trapped birds were immediately collected and brought to the aviary where morphometric measurements (beak length, wing length, body weight, etc.) were taken and health status was checked (all individuals were in good health). For individual identification, a metal ring was attached on each leg: a LIPI ID number ring and a color ring. One individual (NR) managed to open and remove both rings. Once testing was concluded, all birds were given a pre-release health check and their colored rings were removed (numbered rings were not removed to allow long-term monitoring).

During release, we followed a “soft release” procedure during which birds were free to leave at their own volition, without any handling in order to minimize stress (as directed by the International Union for Conservation of Nature guidelines; IUCN/SSC). Post-release support consisted of food and water provided on top of the aviary for a week (none of the released birds returned to feed). Post-release monitoring lasted one week during which none of the released birds was observed in the aviary area.

Housing
Goffins were group-housed in a large outdoor aviary (50 m², 2–3 m high) that featured an occluded test room (12.5 m²). Both the aviary and the test room were enriched with perches, natural vegetation, dry tree trunks, daily fresh jungle foliage, as well as fresh fruit and vegetables placed at various locations. Bathing opportunities, water, and food (fruit, vegetables, dry oats) were provided ad libitum. Additionally, dry mixture meals (corn, green beans, red beans, oats, and peanuts) were provided twice a day and local forest fruit were supplied at regular intervals. Subjects could be visually isolated from the group in the test room in order to avoid social interference during testing. The aviary was cleaned every morning and afternoon and all water and feeding plates were regularly disinfected. Their health and wellbeing were continuously monitored through weight and droppings checks as well as behavioral indicators of stress or illness.

Ethical statement
Fieldwork was conducted on the Tanimbar Islands, Indonesia, under the research permit 309/SIP/FRP/E5/Dit.KI/X/2018 and 398/E5/E5.4/SIP/2019 granted to MOH and 310/SIP/FRP/E5/Dit.KI/X/2018 and 399/E5/E5.4/SIP/2019 granted to BM by the Ministry for Research and Technology (RISTEK). Capture, maintenance, testing, and release of subjects was conducted with the authorization (PADIA No. S.823/K19/TU/KSA/09/2019) and under the supervision of the Department for the Conservation of Natural Resources (BKSDA Maluku) and the Research Centre for Biology–Indonesian Institute of Sciences (RCB–LIPI). The housing conditions complied with Austrian Animal Protection act and husbandry guidelines for Cacatua spp. Additionally, guidelines and ethical considerations for housing and management of Psittacine study subjects were followed. In accordance with local indigenous traditions, the purpose of the research project was communicated to and approved by the Lorulun village elders.

METHOD DETAILS

Wawai fruit
*Cerbera manghas* (indigenous Tanimbarese name: Wawai; common names: Sea Mango, Pink-eyed Cerbera, Bintaro; hereafter: Wawai) of the Apocynaceae family is an evergreen plant that varies in size from shrubs to small or medium-sized trees (4–40 m tall). Widespread in Southeast Asia, it is generally found in mangrove or coastal environments, but also inland in lowland dry deciduous forest and in secondary forest edges. The fruit is smooth, ovoid-globose with fleshy exocarp, green when young and ripening red. The endocarp (commonly known as fruit stone or pit) is lignified (rigid and woody) and externally rugose with one seed per locule (up to two locules/seeds). The seed is white, compressed, and ellipsoid. All parts of the plant contain toxic cardenolides, such as cerberin, neriferiol, and cerberoside.

Fruit measurements
To identify fruit properties that would potentially promote tool use, we sampled and measured intact fruit, as well as fruit that were provided to the individuals. A total of 68 Wawai fruit were collected with the condition of the fruit (unripe, ripe, bitten, spoilt) and the location (tree or ground) being noted. Fruit measurements consisted of the total weight of the fruit (before provision), weight of the endocarp, weight of the fruit flesh (total weight minus endocarp weight), and the seed weight (after provision). Further, we measured the length, width, breadth, and the thickness of the fruit flesh (exocarp and mesocarp) of intact fruit (before provision), as well as size...
and thickness of the endocarp, width of the fissure, and depth of the seed locule (after provision). Weights were assessed using a commercial precision scale (PSF-200, 200 g x 0.01 g) and size measurements were taken with a caliper (precision: 0.02 mm).

To measure the force required to break the endocarp open along the fissure (for intact fruit and fruit after provision), we constructed a Wawai breaking device by combining a bench vise and a commercial luggage scale (Passport; Figure S5). The endocarp was attached to the static jaw of the vise with a metal band pushed into the fissure. Another metal band pushed into the fissure was attached to the luggage scale mounted on the sliding jaw of the vise. We gradually increased the force by widening the gap between the jaws and monitored the applied kilogram-force by using a GoPro Hero7 at 4K/60FPS. The maximum kilogram-force displayed on the scale was considered as the breaking point and was converted to newton (N) through multiplication by standard gravity (9.80665). As the scale load was limited to 50 kg, any endocarps resisting the maximum force were noted as “> 50 kg” and opened by using a chisel for subsequent seed weight measurement.

**Behavioral recording**

We documented Goffins’ tool-use behaviors via direct observation. A group of 15 wild-caught temporarily-captive Goffins was presented with two fully intact ripe Wawai fruit as part of an ongoing research project on the foraging ecology of this species. After the first tool use observation upon this first provision (Video S1), we conducted two more sessions in a group setting, each time providing two Wawai fruit. A total of 63 fruit (for an overview, see Table S1) was provided to the two tool-using individuals (LB and NR) in a controlled setting at times during which Goffins displayed most activity (between 7:00–10:00 and 16:00–18:30, when temperatures ranged between 22–32 °C). For these sessions, the two subjects were separated individually or with a small number of conspecifics (maximum of 5) when individual separation was not possible (due to Goffins not willing to enter the test room). Every Wawai fruit provision was video recorded with a Canon XA40 camcorder. Focal observations were conducted for the entire time of fruit manipulation and the two subjects did not seem to differ in the proficiency of tool-related behaviors.

**Tool tracing**

Tools dropped after use were traced with an action camera (GoPro Hero7), either on a grid (test room) or on a cleaned sand patch underneath the usual tool use location (aviary), to recreate the exact sequence of tool use. Synchronized behavioral recordings and tool tracking footage were cross-validated in BORIS (v.7.9.8; 31). The analysis was conducted on 50 tools for which the sequence could be confirmed. We omitted tools that could not be found or for which the order of use remained uncertain.

**Feeding platforms**

Observations of free-ranging individuals were conducted on three outdoor feeding platforms placed within the focal area of the Goffin Lab Tanimbar (for details about the scanning area, see O’Hara et al.13). The platforms were elevated to approx. 1–3 m above the ground. The structure design featured upper and side branches to allow Goffins gradually approach the platform baited with dry corn (high value food). A camera trap (SECACAM Wild-Vision Full HD 5.0) was attached above the platform to monitor Goffins’ presence. A camouflaged action camera (GoPro Hero7) attached to a sturdy branch was positioned approx. 50 cm away from the platform to allow detailed behavioral recordings. Additional to the corn bait, a couple of ripe and unripe Wawai fruit were placed on the platforms. Each platform attracted small to medium-sized groups of Goffins (2–10 individuals). Total direct observation time from the platforms baited with Wawai fruit amounted to approximately 85 h. Additionally, while collecting data on wild Goffins’ behavior in the forest, we opportunistically encountered a skinned Wawai endocarp containing an inserted wooden fragment (Figure S4).

**QUANTIFICATION AND STATISTICAL ANALYSIS**

**Behavioral coding**

Subjects were included in this study based on their proficiency in using tools. Relevant behaviors related to tool use (for a detailed ethogram, see Table S2) were coded from video recordings in a frame-by-frame mode in BORIS (v.7.9.8; 31). Inter-rater reliability was assessed by double-coding two sessions representing 15% of all scored behaviors (see below). Due to the limited possibility of tool tracing and lesser quality of the initial videos, only fully controlled subsequent sessions featuring the two tool-using individuals (LB and NR) were analyzed (Table S3).

**3D modeling**

To digitally reconstruct tools for detailed analysis of their physical properties, we used a Structure-From-Motion (SFM) method. Tools were positioned on a syringe tip attached to an aluminum architectural scale ruler placed on a rotating cake plate with lines marking every 10°. For each tool, 108 high-resolution macro images were taken at 10° intervals orbiting three horizontal levels using a digital camera (Canon EOS 7D Mark II) with a mounted macro lens including an integrated LED light ring (Canon EF-S 35mm f/2.8 Macro IS STM). Additional light required for high-resolution macro photography was provided by a foldable photo studio (Orangemonkie Foldio2). Images were taken with an aperture of f/18 and ISO 100 to achieve an optimal depth of field.

Tools were reconstructed in three dimensions using Regard3D (v.x64 1.0.0; 35). Raw files were converted into high-resolution .jpeg format and matches between images were computed using the classic “A-KAZE” keypoint detector with the second keypoint detector “TBMR” (Tree-Based Morse Regions) enabled. Keypoint sensitivity was set to 0.0005–0.0001 (depending on the image features), the matching ratio was set to 0.7, and the used matching algorithm was “FLANN.” Triangulation to assess the 3D position...
of keypoints was achieved with the “New Incremental” algorithm with stellar initialization for structure-from-motion. For densification of the resulting point cloud, the “CMVS/PMVS” (Clustering Views for Multi-view Stereo/Patch-based Multi-View Stereo) algorithm was used. Clustering was not necessary as each tool comprised only 108 images. Therefore, the “visibility information” option, used to check if clustering during the densification process would be necessary, was deactivated. The “level” option was set to 0 to achieve accurate 3D models and high-resolution images. Cell size was set to 2 to recreate at least one patch reconstruction within every 2x2 px. The threshold to accept reconstruction was set to 0.7 and the minimum number of images for each 3D point to be visible was set to 4.

The resulting densified point clouds were saved as .ply files and further processed in Meshlab (v.2016.12;30) for rescaling models to life-size, removing artifacts (such as light glare, dust particles) and the scale ruler and syringe tip from the model. For estimating each tool’s volume, a 3D mesh was reconstructed from scaled and cleaned point clouds using a screened Poisson surface reconstruction.50 For batch-export of accurate measurements, CloudCompare (v.2.9.1;28) was used.

**Wedging coding**

We analyzed five additional sessions in which wedging occurred (Table S3). Due to logistic constraints, no tools were physically collected in these session (e.g., a tool was dropped beyond the tracking area or a tool was stolen and carried away by a conspecific). For data collection in these instances, we assessed basic tool properties (length, width, and thickness) from video recordings using the geometric measurement function in BORIS (v.7.9.8;31). Single video frames showing lateral and frontal views of the beak and tools were selected for analysis. The beak length, measured upon capture, was used as reference to allow calculation of the basic tool properties.

To increase accuracy and control for image distortion, we assessed each basic tool property from five different frames and used the average as the final measure. Method validation analysis, including measurements of nine tools for which exact properties were also available from the 3D models, provided moderate to excellent agreement (thickness: ICC2 = 0.55; width: ICC2 = 0.74; length: ICC2 = 0.92). Furthermore, using the same procedure, we measured: (1) wooden fragments wedged into the fissure before using a subsequent tool (wedging); (2) used subsequent tools (to ensure tools employed in earlier sessions were not generally larger); and (3) tools that had a distinct manufacture process of removing a full branch and manufacturing a tool from the remaining branch stump (severing).

**Statistical analysis**

All statistical analyses were carried out in R (v.4.0.2;24). Generalized linear models (GLM) were fitted using the function “glm”, whereas general and generalized linear mixed models (LMM and GLM) employed the “lmer” or “glmer” function of the package “lme4” (v.1.1-25;35). We included Individual as a fixed factor in all models. We retained this factor in all null-models to control for inter-individual differences, as the low number of individuals using tools prevented us from including Individual as a random effect. For an overall analysis of the effect of tested variables and their interactions, as well as to avoid cryptic multiple-testing,52 we compared the full models with null models lacking terms in the fixed effects part of the model using a likelihood ratio test.53 For LMM and GLM we assessed the stability of models based on estimated coefficients and standard deviations by excluding within every 2x2 px. The threshold to accept reconstruction was set to 0.7 and the minimum number of images for each 3D point to be visible was set to 4.

To analyze whether fruit properties (total weight, width of the fissure) or the state of the fruit influenced the probability of using tools, we fitted a generalized linear model (GLM) with binomial error structure and logit link function.68 To account for complete separation,55 which occurred as no tools were used if the fissure was narrower than 2 mm, we randomly set one tool use occurrence to “No Tool Use” and one observation without tool use occurrence to “Tool Use”69. This procedure was repeated 1000 times. Its averaged results rendered a slightly more conservative response, thus yielding more realistic estimates. The null model included only Individual. We used Wald’s z-approximation59 to infer the significance of individual effects. Variance Inflation Factors (max = 1.06)

**Inter-rater reliability**

Agreement between raters for behavioral categories was estimated as Cohen’s kappa using the “psych” package,66 which indicated almost perfect agreement (κ = 0.83; with 86.4% reliable scores in 331 events;37). To assess the temporal reliability of scored behaviors, we computed the mean absolute difference of mid-times (calculated as half the duration of a given behavior added to the time of its onset) between raters. We calculated the differences between the primary rater and 9999 random permutations of mid-times with given intervals between behaviors, as coded by the primary rater. Based on the means of these differences, we calculated the probability of finding lower differences between coded mid-times compared to differences that would be predicted by random permutations. This analysis yielded highly significant temporal reliability of scored behaviors (p < 0.001 for each session).

**Fruit properties predicting tool use**

To increase accuracy and control for image distortion, we assessed each basic tool property from five different frames and used the average as the final measure. Method validation analysis, including measurements of nine tools for which exact properties were also available from the 3D models, provided moderate to excellent agreement (thickness: ICC2 = 0.55; width: ICC 2 = 0.74; length: ICC2 = 0.92). Furthermore, using the same procedure, we measured: (1) wooden fragments wedged into the fissure before using a subsequent tool (wedging); (2) used subsequent tools (to ensure tools employed in earlier sessions were not generally larger); and (3) tools that had a distinct manufacture process of removing a full branch and manufacturing a tool from the remaining branch stump (severing).
Cluster analysis to identify tool types
A cluster analysis was performed by partitioning around medoids based on the physical properties of tools (size, volume, and normal change rate as a measure of "roundness/sharpness"). The appropriate number of clusters was assessed without priori assumptions based on the optimal average silhouette width using the "pamk" function of the "fpc" package. To illustrate the resulting clusters, we created a dendrogram employing the "hclust" function with the calculated distances of the "pamk" analysis and "ward.D" as the agglomeration method. The number of clusters was set to the suggested number based on the optimal average silhouette width. To predict group membership of two discarded tools, we performed a linear discriminant function employing the "lda" function of the package "MASS". The results of the cluster analysis were used as training data, which allowed us to assess the probability of each tool to be classified within either group.

Discriminant analysis to classify wedging tools
To predict group membership of tools measured from video recordings, we performed a linear discriminant function employing the "lda" function of the package "MASS". As training set for the discriminant function, we used the basic tool properties (length, width, and thickness) of collected tools and classification according to Tool Types as predicted by the cluster analysis. For assessing group membership of additional tools with basic measurements acquired from video recordings, we applied a discriminant function by employing the "predict" function.

Effect of Tool Types on behaviors
To investigate the extent to which the proportion of time spent on manufacture, modification, and tool motions (vertical and horizontal) depended on Tool Type, we used a compositional linear mixed model (LMM) with Tool Type, Behavior, and their interaction included as fixed effects. To control for potential differences between the two subjects (LB and NR), we included Individual as a further fixed effect. The response was measured as the proportion of time the subject spent performing a given behavior with a given tool in a given session. We used a model with a Gaussian error distribution and identity link to meet the assumptions of normally distributed and homogeneous residuals. To account for the fact that the proportions sum up to one per Tool ID and Individual, we first transformed the proportions such that no values of exactly zero or one occurred anymore as recommended for fitting a model with beta error distribution. We then used a centered log-ratio transformation (applied separately to each combination of Tool ID and Individual) which transforms the response to a space that is not constrained by any boundaries.

To investigate the effect of Tool Type on tool efficiency, we employed a logistic generalized linear mixed model with Fruit and Tool ID (as an implicit hierarchical variable composed of Individual, Session, and Sequential Tool Number) included as random factors. Tool efficiency was analyzed by comparing the number of extractions and the number of insertions without extractions per tool, tabulated as the response in a two-column matrix. Variance Inflation Factors (max = 1.11) indicated no signs of collinearity and no considerable overdispersion could be detected (dispersion parameter = 0.55). Model stability was good except for the intercept and the effect of Individual. The sample consisted of 47 tools inserted 395 times in total (1 to 41 times per fruit, median = 3) with a total of 193 successful extractions (0 to 24 extractions, median = 0).

Tool efficiency
To investigate the effect of Tool Type on tool efficiency, we employed a logistic generalized linear mixed model (GLMM) on all fruit where both Tool Types were employed. As the response variable, Tool
Type was encoded 0 for Fine Tools and 1 for Medium Tools. The sequence of used tools was normalized within each fruit, in order for the first tool in sequence to have a value of 0 and the last tool a value of 1. Fruit was included as a random factor. Variance inflation (max = 1.00; 78) indicated no collinearity. Model stability analysis revealed the model to be generally of good stability but relatively unstable concerning the effect of Individual (which most likely resulted from the low sample size of fruit on which both Tool Types were used). The sample consisted of 32 tools, of which 10 were Medium Tools used on 5 different fruit.