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Adjusting tool functionality in Goffin's cockatoos (*Cacatua goffiniana*)

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1. Acknowledgements

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2. Abstract

The ability to flexibly adjust manufactured tools to the task at hand can be seen in habitually tool using bird species like New Caledonian crows or Woodpecker finches. Since the Goffin's cockatoo, a non-habitually tool using bird, has also shown the capacity to use and manufacture complex tools in captivity, I was interested to explore if it has the capacity to flexibly adjust its tools upon task modification. Here I examined if Goffin's cockatoos are capable of flexibly adapting their manufactured tools relative to varying distances (between the goal and the tool opening) and varying widths of the tool opening in order to access an out of reach food reward. To investigate this topic an apparatus with exchangeable front plates (differing in hole size) and reward platforms (differing in reward distance) was presented to the birds. For tool manufacture cardboard sheets were provided. Based on the results, I argue that Goffin's cockatoos are able to flexibly adjust the length but not the width of their manufactured tools according to the respective task. They used two strategies to achieve this tasks: Either making tools with the full length of the cardboard sheets originally offered or flexibly adjusting the lengths of their tools to different goal distances. The context-dependent variability with which manufactured tools were discarded prior to insertion into the apparatus, points out the Goffin's ability to assess tool size relative to food reward distance. However, presumably due to constraints in their beak morphology, the birds failed to adjust the widths of their tools depending on the diameter of the tool opening. Altogether these findings provide evidence that a bird species, which is not specialized in tool use or manufacture, has the ability to flexibly adjust some of its tool's properties to function, suggesting that a specialization to tool use is not a precondition for flexible tool modification.

3. Zusammenfassung

Die Fähigkeit, Werkzeuge herzustellen und dabei flexibel an eine spezifische Aufgabe anzupassen, ist von habituellen Werkzeug gebrauchenden Vogelarten wie Neukaledonischen Krähen oder Spechtfinken bekannt. Da der Goffini-Kakadu, ein nicht auf Werkzeuggebrauch spezialisierter Vogel, gezeigt hat, dass er in Gefangenschaft komplexe Werkzeuge verwenden und sogar herstellen kann, war ich daran interessant zu erforschen, ob er auch über die Fähigkeit verfügt seine Werkzeuge flexibel an eine sich verändernde Aufgabe anzupassen. Hier untersuchte ich, ob Goffini-Kakadus in der Lage sind, ihre hergestellten Werkzeuge flexibel an variierende Distanzen (zwischen Ziel und Lochöffnung für das Werkzeug) und variierenden Weiten (der Lochöffnung für das Werkzeug) anzupassen um an eine nicht erreichbare Belohnung zu gelangen. Um dies zu erforschen, wurde eine Apparatur mit austauschbaren Plexiglas-Frontplatten (mit unterschiedlichem Lochdurchmesser) und Futterplattformen (mit unterschiedlichen Distanzen) verwendet. Für die Herstellung von Werkzeugen wurden Kartonstücke zur Verfügung gestellt. Basierend auf den Ergebnissen argumentiere ich, dass Goffini-Kakadus über die Fähigkeit verfügen die Länge, jedoch nicht die Breite ihrer hergestellten Werkzeuge flexibel an eine spezifische Aufgabe anzupassen. Sie verwendeten zwei Strategien um hierbei erfolgreich zu sein: Entweder stellten sie Werkzeuge mit der vollen Länge des zur Verfügung gestellten Kartonblocks her, oder sie passten die Länge ihrer Werkzeuge flexibel an die unterschiedlichen Zieldistanzen an. Die kontext-abhängige Variabilität mit der hergestellte Werkzeuge vor dem Gebrauch verworfen wurden zeigt, dass Goffin’s die Größe ihrer Werkzeuge relativ zur Futterdistanz abschätzen können. Dennoch schafften die Vögel es nicht die Weite ihrer Werkzeuge an den Lochdurchmesser der Werkzeugöffnung anzupassen, was vermutlich auf eine Einschränkung bedingt durch ihre Schnabelmorphologie zurückzuführen ist. Insgesamt liefern diese Ergebnisse den Beweis, dass eine Vogelart, die nicht auf Werkzeuggebrauch oder -herstellung spezialisiert ist, trotzdem die Fähigkeit hat, spezifische Eigenschaften ihres Werkzeuges flexibel an die jeweilige Funktion anzupassen. Dies deutet darauf hin, dass eine Spezialisierung auf Werkzeuggebrauch keine Voraussetzung für eine flexible Modifikation des Werkzeugs ist.

4. Introduction

The ability to use or even manufacture objects as tools to reach an otherwise unobtainable goal is frequently linked to advanced cognition. This association is not necessarily true as tool related behaviors can often originate from inherent behavioral routines that do not require cognitive investment such as stereotyped behaviors that can replace costly morphological adaptions (see summary in Shumaker et al., 2011). Tool behavior only requires cognitive effort if it is flexible. Such flexible tool use/manufacture is often associated with creativity and innovation (Call et al., 2013; Hunt et al., 2013). Flexible animals respond quickly to changes in their environment, create new solutions to unpredictable problems and usually employ several cognitive abilities in the process (Emery & Clayton, 2004).

In this thesis, I used the following definition of tool use: 'The exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment.' (St Amant & Horton, 2008), and the following definition of tool manufacture: 'Any structural modification of an object or existing tool so that the object serves, or serves more effectively, as a tool' (Shumaker et al., 2011).

Various previous studies suggest a correlation between enlarged brain sizes and technical innovations including tool use (for example see Cnotka et al. 2008; Lefebvre et al. 2002; Overington et al., 2009; Reader & Laland, 2002). In addition, the ability of some tool-using animals to perform flexibly in technical tasks hints at the existence of an elementary understanding of some of the physical features underlying the respective challenges (see Sanz et al., 2013 or Shumaker et al., 2011 for summaries).

Within birds, flexible tool use and manufacture has mainly been studied in corvids: For instance, in an experiment by Bird and Emery (2009) four non-habitually tool using rooks (*Corvus frugilegus*) were trained to insert stones as tools into an apparatus bearing a collapsible platform. A food reward was only released by dropping an object (with enough weight) into a tube opening above the platform. To make sure that the subjects understood the task requirements, the authors investigated the following three parameters: First, if the rooks would drop other objects of a similar weight into the tube, second, if they would only choose objects of a sufficient weight for the platform to collapse, and lastly, if they would be able to choose suitable objects to fit into the tube when the diameter of the opening was reduced. They were tested with various sizes of stones as well as sticks of different lengths, widths and weights, that could be employed as tools. The birds demonstrated their flexibility by selecting the appropriate tool depending on the diameter of the tube opening (Bird & Emery, 2009, see Sanz et al., 2013 for summaries).

Flexible tool use has also been studied extensively in the New Caledonian crow (*Corvus moneduloides*) which is perhaps one of the most skilled avian tool users (Hunt et al., 1996). In a study by Chappell and Kacelnik (2002) two crows were presented with a choice task. To successfully retrieve an out-of-reach food reward positioned at different distances from the opening of a horizontal tube, they had to choose between sticks of different lengths. In fact, the subjects were able to select tools matching the distance to the food significantly more often than would be expected by chance. In addition, the crows often simply selected the longest tool (which was always functional) (Chappell & Kacelnik, 2002).

The woodpecker finch (*Cactospiza pallida*), another avian tool specialist, was faced with a similar tool-length-decision task. While the majority of subjects managed to reach the food reward with their first selected tools, they did not match the tools to the given distance – other than the crows in the previously mentioned study (Tebbich & Bshary, 2004). Similar to the New Caledonian crows, the woodpecker finches tended to select longer tools than necessary. Nevertheless, they showed no distinct preference for the longest ones.

A comparative study by Silva et al. (2010) on adult humans (*Homo sapiens*), confronted with the same setups as used by Chappell and Kacelnik (2002), resulted in different outcomes to the bird studies: Surprisingly, humans neither adapted their tool choices to the exact distance of their goal object, nor did they consistently select the longest stick. Even though there was a correlation between the lengths of the stick and the position of the food, they tended to select relative to the lengths of the alternative tools (Silva et al., 2010).

As the previous studies indicate, trying to test the animal's understanding of the functional relationship between food distance and tool lengths by tool selection tasks can be difficult due to the fact that a selection between several tools could be also quickly achieved by employing associative rules. This can make the detection of mental processes underlying animal's performances more difficult. In the previous example animals could for instance avoid this issue by constantly choosing the longest tool (which is always functional) without suffering any noteworthy costs.

Tool manufacture is seen rarely, even in habitually tool using animal species (Shumaker et al., 2011). However, for examining tool-related flexibility, structural modifications prior to tool use can represent a powerful instrument, since they can help to uncover the subjects' perception of how the tool works. Additionally, failing to manufacture a functional tool can be expected to be more expensive (in terms of effort and time) than simply choosing a non-functional tool. Therefore, the prior example suggests that manufacturing a longer tool could represent more effort since a longer twig may have a naturally thicker stem base, which can be harder to break (Knaebe et al., 2016). Another factor here could be the fact that the production of a longer tool may entail a longer sequence of behaviors to obtain the desired tool (Auersperg et al., 2016). Looking at differing numbers and/or types of steps used in between the manufacturing processes and the appearances of the tools necessary for different tasks can therefore be highly informative to see how the animals perceive the problem.

Outside primates, studies on flexible tool manufacture mainly concentrated on New Caledonian crows (except for recent research on the Goffin's cockatoo). In an experiment, the crows were offered three sticks (Chappell & Kacelnik, 2004). One of the latter was loose and the other two were locked in a bundle. Subjects only opened the bundle when it contained the required tool. Furthermore, depending on the diameter of the tool opening, the crows broke different tools from natural twigs. They mainly used tools that were slim enough to fit through the tool opening. Finally, the authors detected an increase in the diameter of the distal end of the tools that were used by the birds.

Weir et al. (2002) were also able to show that New Caledonian crows could flexibly manufacture two entirely different tools by bending/unbending flexible material (depending on which task was presented).

Another study focused on the manufacture of tools that could be used to retrieve food from vertical holes (with different depths) by two New Caledonian crows (Hunt et al., 2006). The authors initial assumption that the crows were able to flexibly adjust the lengths of their first tools to directly match hole depth, could not be confirmed. Nevertheless, while the first employed tools had a similar length regardless of hole depth, whenever the food distance was far the next tool was slightly longer. At the time, Hunt et al. (2006) implied that the corvids may be applying a two-stage heuristic strategy to accomplish tool manufacturing tasks: They rule out learning by trial and error since the second tools did not variate randomly around the mean length of the first tools, however they significantly increased in length. They also exclude insight as there was no instant success. Instead they argue, that the first tool appears to illustrate a type of ‘default behavior’ whereas the second tool is either a delayed inference to the causal characteristics of the given problems or the effect of an associative learning rule which is based on the result of the ‘default behavior’.

In 2016, Knaebe et al. confronted wild-caught New Caledonian crows to a similar task. However, due to the fact that the effort between manufacturing long and short tools was still low, they added a physical barrier on the opposite of the tool opening (only when the food reward distance was small). Thereby they attempted to prevent the corvids from just consistently making long tools regardless of how far the reward was from the opening. The authors discovered that their subjects actually did built shorter tools when the food reward was close and longer ones when the food reward was far. Nevertheless, they often did not manage to adjust the length of the tool adequately to retrieve the food. The authors conclude that the birds may have pursued a relative rule, rather than an absolute one. An example for a relative rule would be to build longer or shorter tools, or to consistently manufacture shorter tools when the physical barrier is present. An absolute rule would be to match the precise lengths of the tools to the distance of the food reward. Since learning seemed to play a role in this task, the crows may also have experienced some negative reinforcement (often it was not effective to assume that the apparatus only required short tools) (Knaebe et al., 2016).

Goffin’s cockatoos (*Cacatua goffiniana*) are generalists and highly opportunistic parrots in terms of their foraging techniques (Mioduszewska, O’Hara, unpublished data). They are neither specialized tool users nor are they likely to be using tools, at least not on a population wide level in their natural habitat such as New Caledonian crows (Hunt et al., 1996). They exhibit none of the requirements that are supposed to be of importance for the development of avian tool use such as building nests or caching food (Kenward et al., 2011). However, they frequently alter and combine objects in their environment during exploration and play (Auersperg et al., 2015). These factors can induce individual tool innovations in captive and potentially also in feral individuals

(Auersperg et al., 2012; Osuna-Mascaro & Auersperg, 2018**).** The ability to socially transmit tool use across individuals has been shown only in captive Goffin's cockatoos (Auersperg et al., 2014). Moreover, these parrots demonstrate great flexibility in decision-making tasks involving choices between different food reward quality and tool functionality. Decisions were met relative to the gain in quality versus the working effort and if the respective tool was functional in combination with the present apparatus (Habl et al., 2017; Laumer et al., 2016).

Recent studies illustrate that Goffin's cockatoos show innovation in building the same stick-type tool out of diverse material sources (Auersperg et al., 2012; 2014; 2016). Two male individuals even managed to manufacture such tools from materials that had to be shaped actively, such as cardboard (Auersperg et al., 2016). To achieve this, they had to place a large amount of parallel bite marks into the edge of a cardboard sheet until it was long enough to curve the tool off from the initial sheet. Due to the amount of bite-marks, tool manufacture out of cardboard could be assumed to be energetically expensive (presumably more expensive than only breaking off a twig). However, the curving-off technique makes it possible to achieve a relatively precise length adjustment. It has to be noted, that the cardboard tools in the previous studies were on average only approximately one centimeter above the minimum length (6 cm) which was necessary to obtain the food reward. On the contrary, the length of wooden tools (that broke along the age lines of the tree and did not need active shaping) was significantly longer. To be specific, a wooden tool generally consisted of the entire length of the material provided (Auersperg et al., 2016).

Although the previous data indicate that subjects may pay attention to tool length while manufacturing them, this could not be confirmed at the time since the distance between tool opening and food reward remained unchanged across conditions (Auersperg et al., 2016).

With this study, I wanted to focus on two main research questions: Are Goffin's cockatoos able to demonstrate flexibility in tool manufacture to save effort? How accurately do they focus on the properties of their tools relative to their function during tool manufacture?

The use of cardboard material to examine flexible manufacture of stick tools presents an interesting instrument: It makes it possible to measure the working effort relatively precisely, as the energy required to build a stick-type cardboard tool increases with the length of the material in a gradual manner. In addition, it allows not only to manipulate the length but also the width of the stick-type tool.

Similar to previous studies on flexible tool use/manufacture in habitually tool using birds (Knaebe et al., 2017; Chappell & Kacelnik, 2004; Hunt et al., 2006), I thus aimed to manipulate the distance of the food reward and the diameter of the tool-opening but provided cardboard blocks for tool manufacture.

The ability of making flexible decisions in tool selection tasks has been already demonstrated by all of my focal subjects (Habl et al., 2017; Laumer et al., 2016). Moreover, at least one individual appeared to be capable of flexibly changing between the manufacture of either hooked or straight tools depending on task requirement by bending elastic materials (Laumer et al., 2017).

Based on these observations as well as suggestive evidence from a prior experiment (Auersperg et al., 2016), I predicted that the birds have the ability to save effort by flexibly adjusting the length of cardboard tools during manufacture depending on food reward distance, at least to some extent. Another assumption was that tools used in combination with the apparatus were primarily above the minimum length to obtain the food reward (for each condition). Moreover, I expected our subjects to discard deficient tools (too short or too wide) before using them in the task.

Nonetheless, I considered that several (not mutually exclusive) alternative strategies might apply as well. To achieve a successful outcome, associative learning or maybe a two-stage heuristic strategy as seen in New Caledonian crows (Hunt et al., 2006) might be required. A general preference for longer tools – as in New Caledonian crows (Chappell & Kacelnik, 2002) or woodpecker finches (Tebbich & Bshary, 2004) – could be an additional basic strategy, if the trade-off for building larger tools was not high enough.

I also considered two further points regarding the adjustment of tool width, depending on the diameter of the tool opening in the apparatus: First, making broader tools might favor the integrity of a tool. Second, it might be possible that the width of cardboard tools could be constrained by the depth of the birds' beak, given that in the previous experiment the subjects applied their sharp lower mandible as a cutting edge against their strong upper mandible which played the role of an anvil. To manufacture a cardboard tool, the birds positioned their head approximately at a 90° angle toward the cardboard's side, taking the edge of the material into their beak. Therefore, cutting deeper into the cardboard might generate ergonomical difficulties.

5. Material and Methods

5.1. Subjects

Six adult Goffin's cockatoos (consisting of 5 males and 1 female) participated in this study (table 1). They are housed together in a group aviary at the Goffin Lab in Lower Austria (an outpost of the Messerli Research Institute of the University of Veterinary Medicine Vienna). The group consists of 16 birds in total. They had been hand-raised and were marked individually with colored aluminum bands (acquired from the website www.vogelringe.de). The large group aviary, in which the birds lived, was partitioned into an indoor (45 m^2 ground space, 3 – 6 m high wall to gable) and an outdoor section (150 m^2 ground space; 3 - 4.5 m high; see Figure 1). The indoor space was enriched with branches, large bathing bowls, hiding places and wooden toys. It had an electronic timer to facilitate a 12-hour light cycle per day (from 7 am to 19 pm) and it was heated at 20° C during the winter (from October until May). The access to the outdoor aviary was dependent on the outside temperatures. The temperature limit was -5° C. When temperatures were higher the animals had access at least one and a half hours during animal care and the whole day if it was above 15° C.

Figure 1: The aviary of the Goffin's cockatoos. Photos: Alice Auersperg.

The animals received the following food sources: Two sources of fresh fruits, soy-yoghurt, cooked grains, noodles, vegetables and eggs fried in red palm oil in the morning. A basic food mixture (Austrian "Qualitäts-Mischfutter" ® from Josef Leimüller GmbH supplemented with dried fruits, fennel seeds, milk thistle seeds, Korvimin®, milk thistle seed powder and spirulina) and fresh drinking water were available ad libitum (certain treats such as nuts were only used as food rewards during experimental routines).

All birds were adapted to a daily experimental routine and observation. Each bird was tested individually in an adjacent indoor testing compartment (7.5 m^2, 3 m high) in visual isolation from the rest of the group. Since the birds are not clipped, participation in the experiment was on voluntary basis. Either the experimenter entered the group aviary and asked the subject to step up on the hand in order to bring it into the experimental compartment, or the door to the testing compartment was opened and the respective bird was called in by name. Each subject was tested two or three sessions per week with a maximum of one session per day.

5.1.1. Pre-experience

All birds had previous experience in diverse tool using tasks, including the use of stick-type tools (Auersperg et al., 2012; 2014; 2016; 2017; Habl et al., 2017, Laumer et al., 2016; 2017). Additionally, the subjects were also tested in a number of technical tasks that did not involve the use of tools (object play experiments (Auersperg et al., 2015; Szabo et a., 2016), a delay of gratification task (Auersperg, Laumer et al., 2013) and an inference by exclusion task (O'Hara et al., 2015).

Every subject that was tested in this experiment had already experience with tool manufacture. However, neither the position of the reward nor the diameter of the tool opening had been altered in the previous study (Auersperg et al., 2016).

Two subjects (Dolittle and Figaro) had previously made tools out of carboard but the position of the food reward and the diameter of the tool opening had not been altered at the time (Auersperg et al., 2016).

Table 1: List of all subjects participating in the study.

name	sex	hatched	group
Dolittle	male	2011	B
Figaro	male	2007	A
Fini	female	2007	A
Kiwi	male	2010	B
Konrad	male	2010	B
Pipin	male	2008	A

5.2. Ethical statement

The animal keeping conditions comply with the species-specific guidelines for parrots provided by the Austrian Animal Protection act. Furthermore, the keeping facility and the animals are registered at the local Animal Welfare Bureau (Bezirkshauptmannschaft St. Pölten, NÖ). All subjects were acquired from European breeders in compliance with CITES regulations.

This study was discussed with and approved by the institutional (University of Veterinary Medicine Vienna) ethics and animal welfare committee in accordance with good scientific practice guidelines and national legislation. As our experiments were purely appetitive and strictly noninvasive, they were classified as non-animal experiments in accordance with the Austrian Animal Experiments Act (TVG 2012). Since the animals' wings are not clipped, they participate in experiments voluntarily: They are called into the experimental compartment by name. If subjects were unmotivated to take part in training or testing, they were released back into the group aviary.

5.3. Apparatus

The apparatus was a long rectangular and transparent box (22 cm long, 13 cm wide, 16,2 cm high) bearing a reward platform fixated on a slanted sliding plate (see Figure 2). The sliding plate, as well as the Plexiglas front plate were exchangeable. The reward platforms could be positioned at three different distances (4, 10 and 16 cm) from the frontal hole in the box. The frontal hole came in three different diameters (1; 1,5 and 2 cm ∅). The apparatus was attached to a heavy wooden board (35 x 35 cm) to prevent the birds from tilting it over. The reward platform with different distances, and accordingly the Plexiglas panel with different frontal holes, were offered in a semi-random order (each 5 times within one session of 10 trials in random order), together with cardboard sheets (training: "Bristolkarton", 15 x 6 cm, thickness: 1,0 mm; testing: "Finnpappe", 20 x 6 cm, thickness: 1,0 mm) for manufacturing.

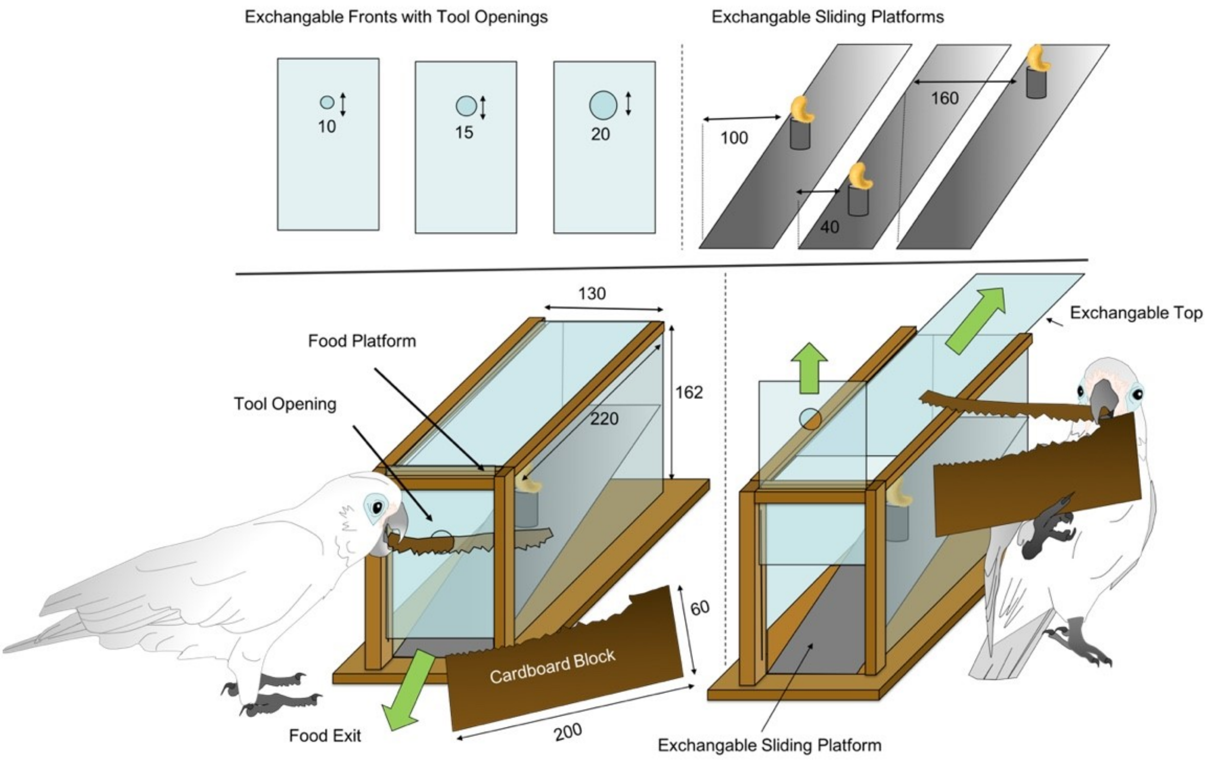

Figure 2: Basic apparatus with exchangeable fronts and platforms (dimensions in mm).

5.4. Training procedure

All of my subjects were proficient stick tool users at the beginning of this experiment. Nevertheless, only two subjects (Dolittle and Figaro) had previously manufactured cardboard tools before the testing started (Auersperg et al., 2016). In order to increase the sample size, four additional birds received training.

The training procedure was as following: At first the naïve subjects were habituated to the cardboard (first in the group and afterwards alone), by petting them, as well as feeding them with nuts while standing on the cardboard. After being allowed to retrieve food from the apparatus using a ready-made wooden tool, the four subjects previously naïve in cardboard tool manufacture (Fini, Kiwi, Konrad and Pipin) were offered a cardboard block (15 x 6 cm) in front of the baited apparatus from the previous study (Auersperg et al., 2016). If subjects successfully made cardboard tools they received up to nine additional trials within the same session (with the same procedure). If they failed to do so within 10 minutes of the same trial they received another session on the next testing day. If a bird was not able to successfully manufacture a cardboard tool within five sessions, a demonstrator bird (Dolittle or Figaro) made and used three tools in succession while the observer watched from inside an adjacent parrot cage (social learning). They both got rewarded when the demonstrator bird was effective. Afterwards each naïve bird was given the opportunity to make cardboard tools themselves (once again for 10 minutes) for a maximum of five demonstrator sessions. In case the subjects were still not able to manufacture cardboard tools, the next step in the training was to give them perforated cardboard sheets (with perforations along the longer edge of the cardboard, in a 1 cm interval) prior to being retested with the original cardboard material (until they became continuously successful).

Fini was successful for a single time in session five (before demos or perforated cardboard sheets). Subsequently she received demonstrations. After succeeding to make a functional tool each for a single time after demonstrator sessions one and two she became continuously successful (10 consecutive trials) after demo session three. Kiwi, Pipin and Konrad did not succeed before receiving perforated cardboard sheets. All made functional tools from regular cardboard sheets from session one after experiencing perforated sheets, Kiwi became continuously successful at doing so from session three (S1: 1 tool; S2: 1 tool; S3: 10 tools), Pipin from session 6 (S1: 2 tools; S2: 1

tool; S3: 1 tool; S4: 3 tools; S5: 3 tools; S6: 10 tools) and Konrad from session 7 (S1: 1 tool; S2: 1 tool; S3: 1 tool; S4: 1 tool; S5: 1 tool, S6: 4 tools; S7: 10 tools).

The training was conducted by Isabelle Laumer and it was documented by using a Lab journal as well as a camcorder.

5.4.1. Reminder trials

Subjects that already had experience with cardboard tool manufacture were given two sessions of reminder trials (1 session consisted of 10 trials) to test whether they still made tools out of cardboard after a testing pause of several months (Auersperg et al., 2016). First the respective bird had to sit on a chair beside the testing table (1 x 1 m) where he was offered a ready-made wooden stick tool and the baited apparatus that was used in the previous study (Auersperg et al., 2016). After a successful food retrieval, the subject was provided with a cardboard sheet (15 x 6 cm) as well as the apparatus (as mentioned before). If the bird did not manage to retrieve the food reward, the experimenter offered assistance: Either a perforated cardboard (with perforations along the longer edge of the cardboard, in a 1 cm interval) was given or the experimenter bent the cardboard. A reminder trial was finished when the bird had successfully manufactured a cardboard tool and had retrieved the reward. If the subject didn't manufacture any cardboard tools, the trial was stopped after 10 minutes.

5.5. Testing procedure

Prior to testing, each subject received one habituation session (consisting of 10 trials) to the new, unfamiliar apparatus, alongside a cardboard block (15 x 6 cm) for tool manufacture. For the habituation, the food platform and the frontal tool opening were set at a baseline arrangement (baseline distance of food platform: 10 cm, baseline frontal hole opening size: 1,5 cm ∅). For all testing sessions the subjects were offered slightly longer cardboard blocks made out of a tighter material (20 x 6 cm).

I used two subtasks in this experiment: A distance task (DT) and a width task (WT). In the DT the diameter of the Plexiglas hole stayed at the baseline (1,5 cm ∅), while the distance of the food platform varied (two conditions: near: 4 cm or far: 16 cm). Whereas it was the other way around in the WT: the distance of the food platform remained at the baseline (10 cm) and the diameter of the frontal hole varied (small: 1 cm or large: 2 cm ∅).

Each bird had to complete both tasks. Subjects received 6 sessions each, composed of 10 trials each. Within a session each condition (near/ far or small/ large) was offered 5 times in random order. Subjects were divided into two groups of three birds each. Group A received the distance task (DT) first followed by the width task (WT) and group B vice versa.

Similar as in the training, the birds were given up to 10 testing trials per session and a period of 15 minutes per trial to manufacture a tool out of cardboard and get the reward out of the apparatus. If a bird did touch neither the apparatus, nor the cardboard for a time span of 5 minutes, the trial was stopped. In the case one trial was not successful, the remaining trials were randomized again, and the subject received one motivation trial (a ready-made wooden stick tool; the 1,5 cm ∅ Plexiglas hole, as well as the 10 cm food platform was used) in between the testing trials. If a bird failed to retrieve the food reward during the motivation trial it received a new session on the next testing day. After a motivation trial was finished, the testing session continued. Successful cardboard tool manufacture and use was rewarded with a sixth of a cashew nut.

In between the testing trials the subjects had to sit on the backrest of a chair in the experimental room to make sure they were not able to see the experimenter baiting the apparatus for the next trial in the adjacent room. During the test, the experimenter sat on a chair near the testing table, wore mirrored sunglasses, avoided lateral head movements and did neither speak nor touch the animals until the trial was over.
All cardboard tools manufactured while testing – successful used tools as well as discarded tools – were stored in a lab book and the testing was documented by using a camcorder.

5.6. Statistical analysis

All trials were videotaped (Panasonic Camcorder Model No.: HC-V160) and coded directly from the videos. Due to methodological issues, exact measurements of discarded and unsuccessful tools are lacking in 5.5 % of all trials (the information on successful tools is complete for all trials; see appendix for further information). All other cardboard tools manufactured while testing – the successful tools, the pieces of material that were unsuccessfully inserted into the box as well as the first pieces of material that were manufactured but discarded before establishing contact with the box were measured, labelled and stored. I measured the length from the two farthest spots as well as the width at the distal end, the proximal end and at the center of the tool. In addition, I counted all discarded tools per trial. The website ‘www.random.org’ was used to randomize the test-combinations (assignment of subjects into two groups; order of conditions within a trial).

To investigate success-rate of first employed tools, a binomial mixed model with logit link function was used. Condition (near/far reward, large/small opening), session, as well as group (testing an effect of task order) were included as fixed effects and we accounted for repeated measures by considering subjects as a random effect. In order to test to what extent individuals adjust the length of manufactured tools to the distance of the food reward, a linear mixed model was fitted on the square root transformed length of first pieces of material that were inserted into the tool opening (successful or unsuccessful tools) and discarded tools (immediately discarded before getting in contact with the apparatus), smaller than the maximum length (200 mm). Group, session, as well as an interaction term for condition and tool application (used or discarded) were included as fixed factors whereas subjects were considered as a random effect.

A generalized linear mixed model was fitted (following a Poisson distribution), to examine the number of tools with a maximum length (200 mm) used in the distance conditions. Distance to food, group and session were introduced as fixed effects and subject as random effect.

To draw a comparison if overall used tools on average exceeded the required length to reach the reward was tested for in each condition using Wilcoxon 1-sample signed ranks tests with mu set to the respective reward distance. Kendall’s Tau correlation was used for testing the relation between session and tool length.

To identify potential underlying cognitive strategies (Hunt et al., 2006), the length of first and second applied tools was analyzed with a further linear mixed model including group, session and interaction of condition and tool order as fixed factors. To account for repeated measures, subjects was included as a random factor in both models.

For the subject Fini, who successfully solved the small opening condition, only a descriptive comparison of tool width was made between conditions and tool application (discarded or used). In order to explore a possible influence of morphological restrains (e.g. beak length determining the maximum width of created tools) on the width of created tools, the width to beak measurements of tested subjects were compared by using Wilcoxon 1-sample signed ranks tests with mu set to the respective beak length.

The selection of a model was based on stepwise backward model refinement from a full model using the Akaike Information Criterion (AIC) and likelihood ratio testing (Bolker et al., 2009). Model assumptions were checked visually, and the applicable normality of residuals was tested using the Shapiro-Wilk test, while the assumption of homoscedasticity was tested for using Levene's test for each factor, or interaction of factors. Alpha levels were set to 0.05, factor level contrasts were set manually, and p-values were adjusted for multiple testing employing the false discovery rate correction (Benjamnini & Hochberg, 1995; Benjamini & Yekutieli, 2001).

The statistical analysis was conducted in R version 3.4.3 (R Core Team, 2017). Models were calculated using the lme4-package (Bates et al., 2015) and graphical representation of results employed ggplot2 (Wickham, 2009).

6. Results

6.1. Analysis of performance in different conditions

Overall, we found no effect of group (GLMM: $\chi^2(1) = 0.32$, $p = 0.571$), but the success rate was influenced by session (GLMM: $\chi^2(1) = 35.43$, $p < 0.001$; see Figure A1) and differed significantly between conditions (GLMM: $\chi^2(3) = 425.38$, $p < 0.001$; see Figure 3). Every condition differed significantly from each other (see Table A1 for detailed contrast results). Within the subtest for distances the 'near' condition (M= 81.11 % ± 3.73 SE) was solved more readily than the 'far' condition (M= 67.78 % ± 4.38 SE). In the ‘large opening’ condition subjects were most successful (M= 96.67 % ± 1.26 SE), whereas only one individual (Fini) was able to succeed in the ‘small opening’ condition (M= 6.67 % ± 2.87 SE).

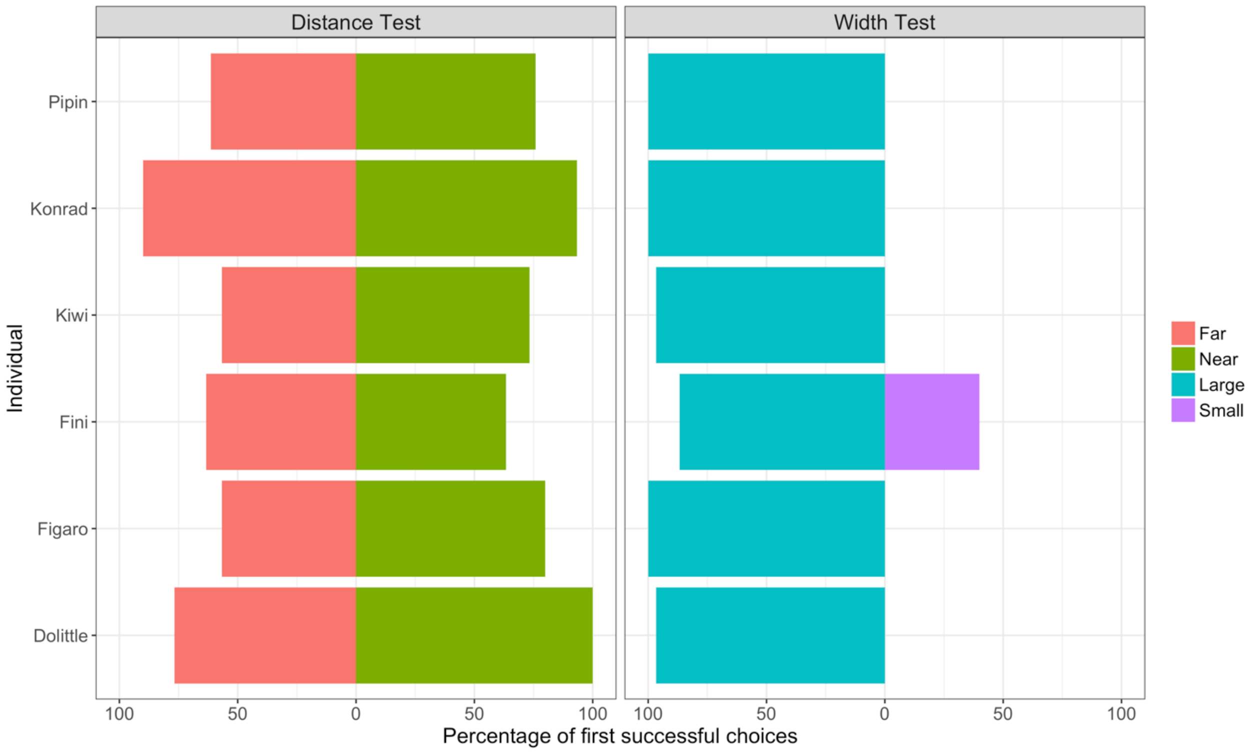

Figure 3: Percentage of successfully retrieving the reward with the first tool in different conditions and for each individual.

6.2. Tool length

Due to methodological issues measurements of discarded and unsuccessful tools are lacking for some trials. For Fini measurements in 14.6 % (17 trials) are missing, for Figaro 13.33 % (16 trials), for Kiwi 2.5 % (3 trials), for Konrad and Pipin each 1.67 % (2 trials) are unaccounted for. In total these make up 5.56 % of all trials in which full data was not available. We omitted these trials from the analysis.

The model revealed no significant effect of group (LMM: $\chi^2(1) = 0.34$, $p = 0.56$), concerning the lengths of tools applied in the distance task. Therefore, the final model which had the best fit, included session as a fixed factor and tool use nested in condition. The influence of session was only marginally (LMM: $\chi^2(11) = 18.85$, $p = 0.064$), whereas a significant effect of use nested in condition (LMM: $\chi^2(11) = 103.57$, $p < 0.001$) was found. Especially, when the reward distance was 160 mm away from the opening (M = 133.5 mm ± 4.88 SE; LMM: $\beta = 0.72$, SE = 0.26, $p = 0.0269$) the employed tools (first objects successfully and unsuccessfully inserted into the apparatus) were significantly longer than when the reward was at 40 mm (M = 118.8 mm ± 4.36 SE) from the opening (see Figure 4). Furthermore, we found a significant variation of discarded tools (tools that were dropped before inserting them) between conditions (LMM: $\beta = 1.09$, SE = 0.38, $p = 0.019$). Shorter pieces (M = 57.8 mm ± 3.87 SE) were discarded when the reward was closer, while longer pieces (M = 75.5 mm ± 4.7 SE) were discarded in the far condition (see Figure A3).

All other combinations between discarded and used tools in the different distance conditions showed significant differences (see Table A2 for detailed contrast results and compare Figure A2). Nevertheless, considerable variation respective to quality between and within subjects could be detected with peak densities of applied tools towards the margins of the functional size, in general around the 'baseline'-length of 100 mm as well as at larger (towards maximum) tool sizes. Discarded tools generally occurred in the 160 mm distance condition around 100 mm, however in the ‘near’ condition they shifted towards the borders of the functional length for three individuals (Fini, Kiwi and Pipin) which discarded the majority of tools.

In this respect, it is important to note that tools of an absolute correct length (bridging the distance from hole to reward) did not necessarily have to be of functional length (since a part of the tool must be maintained in the beak to be handled; the difference between absolute and functional length is indicated by grey shading in Figure 4). Peak densities of tool lengths in the 'far' condition (160 mm) were mainly located within the functional length for three individuals (Figaro, Dolittle and Fini). In contrast, the subject Konrad made only a small number of tools shorter than the maximum length of 200 mm that fell between baseline (100 mm) and functional length. Only one bird (Kiwi), demonstrated a distribution of tool-length around the baseline distance (100 mm), whereas Pipin showed two main density peaks, manufacturing tools either below 100 mm or within the functional length. In regard to the 'near' condition Figaro and Dolittle mostly produced tools at the baseline length or above it, while three subjects (Fini, Kiwi and Pipin) exhibited a shift in peak densities below 100 mm. In this condition, Konrad only produced and discarded each one used tool that was not 200 mm long (within the functional length).

By following up the marginal effect of session on overall tool lengths a significant positive correlation ($\tau = 0.15$, $p < 0.001$) was uncovered, which suggests increasing tool length in successive sessions (see Figure A3).

The analysis of the number of tools that were not adapted in length (using maximum length tools) in different distance conditions uncovered a significant effect of distance to the reward (GLMM: $\chi^2(1) = 8.1$, $p = 0.004$). In the near condition, significantly fewer 200 mm tools were used (M = 2.9 ± 0.27 SE) than compared to the far condition (M = 4.2 ± 0.28 SE; GLMM: $\beta = -0.38$, SE = 0.13, $p = 0.005$; see Figure A4). In group and session no significant effects were found.

On average, compared to reward distance, significantly longer tools were applied in each condition (near: M = 163.7 mm ± 3.9 SE, $p < 0.001$; width: M = 177.3 mm ± 2.3 SE, $p < 0.001$, far: M = 181.7 mm ± 3.1 SE, $p < 0.001$).

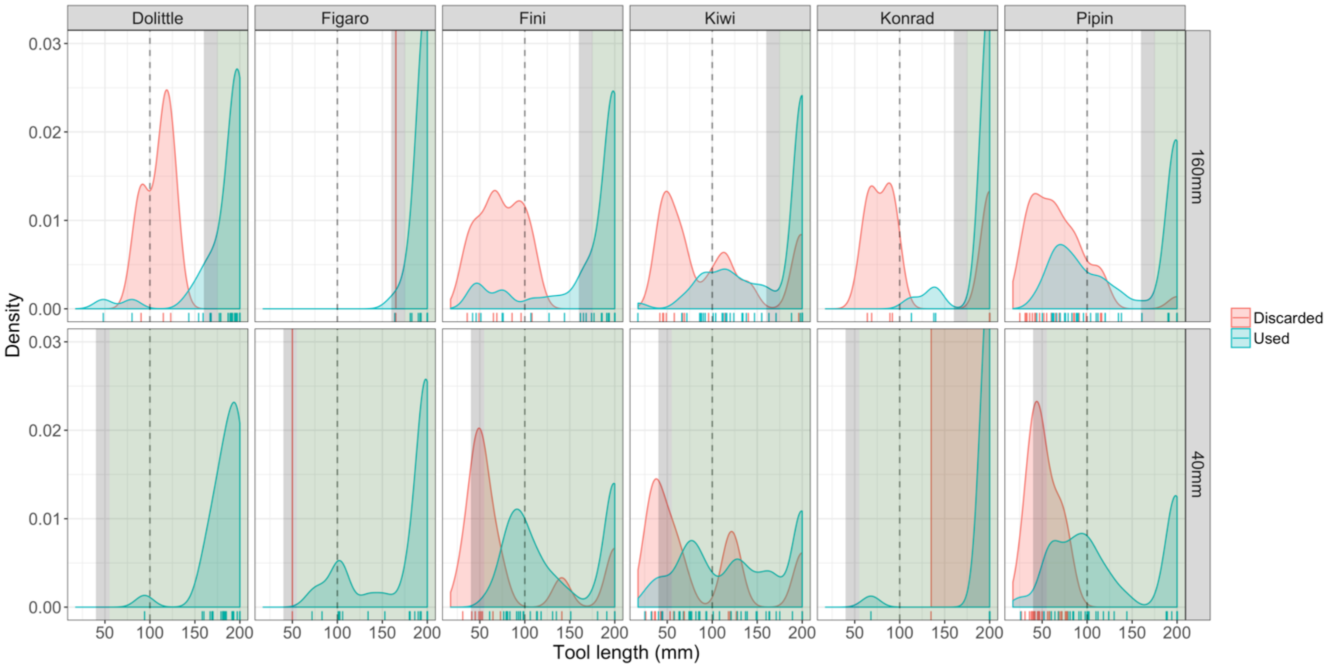

Figure 4: Density plots of all used (green) and discarded (red) tools; green areas indicate potentially functional length; the grey area indicates a 15 mm margin that might be required to maintain manipulability of the tool; the grey dashed line represents distance to the reward in the baseline and the 'width'-test; the jitter below the density plot provides information about number and exact length of tools.

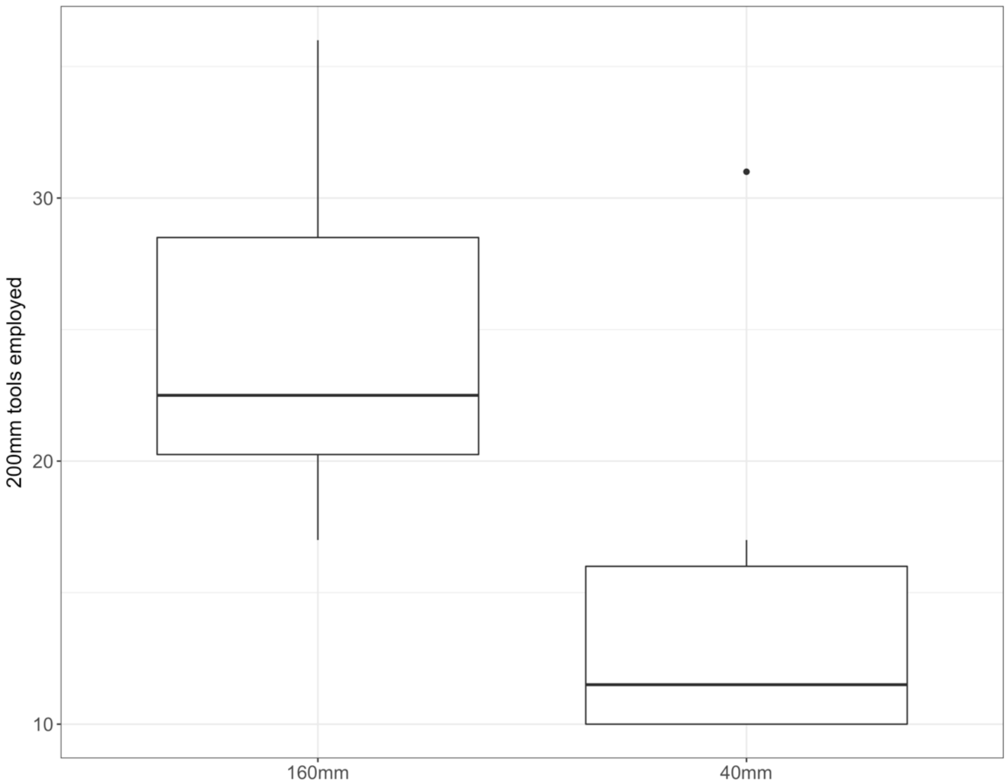

Figure 5: Average number of tools with maximum size (200 mm) employed in the far condition (food distance: 160 mm) and the near condition (food distance: 40 mm); bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

6.3. Relation between first and second tools

A significant sequential effect (LMM: χ^2 (1) = 4.58, p = 0.032) was revealed by linear mixed models concerning the length of first and second used tools (including maximal size tools) in only unsuccessful first attempts. Secondary applied tools were longer than tools used in first (unsuccessful) attempts (LMM: β = 20.79, SE = 9.61, p = 0.033; see Figure A5). We found no significant effect of distance (LMM: χ^2(1) = 2.50, p = 0.114) or session (LMM: χ^2(1) = 2.03, p = 0.155).

6.4. Tool width

The only individual succeeding in the ‘small’-condition, called Fini, potentially differentiated between tool width respective to the tools she discarded. In the large condition discarded tools were on average slimmer than in the small condition (large: M = 9.43 mm ± 0.55 SE; small: M = 11.02 mm ± 0.14 SE). While the distinctions between inserted tools seem only marginal (large: M =9.98 mm ± 0.20 SE; small: M =10.52 mm ± 0.17 SE, see Figure A6), overall it seems to be the case that tool width is restricted by beak morphology (see below). The examination of a potentially limiting effect of beak length on the width of created tools (see Figure 5) pointed out that two individuals produced significantly wider tools in relation to their beak size (Kiwi: beak = 14 mm, Mtool = 14.3 ± 0.16, p < 0.001; Konrad: beak = 14 mm, Mtool = 14.6 ± 0.09, p < 0.001).

Note: We measured only the edge of the upper mandible from the tip to the curving point into the horizontal part of the beak as it seemed to be most likely to limit tool width from our videos (see Figure 5). The subject Fini showed no significant difference (beak = 10.5 mm, Mtool = 10.5 ± 0.1 SE, p = 0.34) and three individuals manufactured significantly slimmer tools (Dolittle: beak = 14 mm, Mtool = 12.9 ± 0.07, p < 0.001; Figaro: beak = 14 mm, Mtool = 11.9 ± 0.09, p < 0.001; Pipin: beak = 13 mm, Mtool = 11.7 ± 0.09, p < 0.001; see Figure A7).

Figure 6: A morphological feature that is likely involved in restricting the width of a cardboard tool is the distance between the tip of the beak and the edge of the horizontal part of the upper mandible (left: Dolittle; photo by Bene Croy; right; Figaro; photo by Solvin Zankl): Birds used their sharp lower mandible like a cutting edge against their strong upper mandible. They placed their head approximately at a 90° angle towards the cardboard’s side, taking the edge of the material into their beak. Cutting deeper into the material may thus cause ergonomical difficulties.

7. Discussion

In this experiment, I discovered that the tested subjects apparently switched back and forth between two major types of strategies: The first strategy would implicate adjusting the tool length according to the condition by curving it out of the cardboard material with a swift lateral cut of the upper mandible, often while creating a curved shape in the cardboard block (cut-out tool). The second strategy would simply be to chew through the entire length of the material (full-length tool) using both mandibles against one another like blade and anvil. These two parallel strategies most likely developed from a trade-off between two distinct types of costs that were involved in this specific type of tool manufacture: On the one hand, the cognitive costs involved in attending to the reward distance relative to the tool length during tool making, and on the other hand, the physical costs involved in the manufacture of a longer tool. Simply blindly biting along the edge of the material until running out of cardboard represents low cognitive costs but high physical costs since a separate bitemark has to be placed every few millimeters in order to fabricate the full-length cardboard stripe. The physical costs of not having to make full-length tools could be saved by taking into account the distance to the food reward. Nonetheless, this is likely to come with a cognitive burden due to an increased investment in attention and working memory load. The latter strategy is also likely to be riskier (as the tools might end up being too short after all and new ones need to be built).

However, in compliance with my original predictions, I did indeed detect flexibility in cut-out tool manufacture: The first self-manufactured pieces that were inserted into the apparatus (on each trial) were considerably longer in the far distance as compared to the near distance condition, indicating that in these cases the birds did in fact pay attention to tool length respective to food reward distance while subsequently saving unnecessary effort. In addition, I could confirm my assumption that the animals showed sensitivity to the distance of the food reward to the tool opening, since the applied tools reached their maximum length more frequently when the reward distance was further away.

In contrast to prior research results on New Caledonian crows (Knaebe et al., 2017; Hunt et al., 2006), and in accordance with a previous study at my own lab (Auersperg et al., 2016), the first produced tools that were applied to the apparatus (on each trial) were substantially above the minimum length necessary to achieve the food reward (for each condition). Additionally, in trials in which the first inserted cardboard piece was ineffective, the length of the second tool was consistently larger. This hints at the possibility that a two-stage heuristic strategy, as found in the New Caledonian crows in the form of adapting an initial default behavior, may also play a restricted role but only in a specific context (Hunt et al., 2006): Since the reward distance had no significant effect on the size of the second tool, I suspect that a default behavior was corrected relative to the previous tool rather than relative to the distance between the tool opening and the food reward in those cases. Although the animals appear to actually take the food reward distance into account in most trials, and flexibly match their tools' length respectively, as soon as an object-task combination was unsuccessful, they seem to go back to an earlier developed associative learning mechanism. The rule seems to be as follows: 'If a tool is not functional, the next tool has to be longer than the one before'. This might thus represent a risk avoidance strategy: To retreat from tool manufacture based on distance to tool manufacture based on default in a trial where the production of a tool already caused unrewarded effort.

As in the habitually tool making birds, the cut-out tools that were applied first tended to be larger than necessary to reach the food reward in all distance conditions. This indicates that our subjects may use a similar strategy as New Caledonian crows and woodpecker finches, namely to primarily build large or even full-length tools (Chappell & Kacelnik, 2002; Tebbich & Bshary, 2004). However, the interpretation of this finding needs to be handled with some caution since the cut-out tools of the Goffins' were close to or slightly above the length necessary for passing the baseline (10 cm) in the close condition (4 cm) and actually around the margin of the adequate size in the long condition (16 cm). This implies that, while some subjects demonstrated flexibility between the two conditions (which were offered in random order) and even though this flexibility did save some effort, a more accurate adjustment to the actual food distance could only be accomplished in the far condition. I assume that the oversizing of tools in the near condition may derive from a 'leftover' tool-manufacturing pattern, in this case the subjects are focused on a specific minimum size for their tools. This resulted presumably from the baseline training at least in some of the birds. Due to the training criterion it may have become manifested as a fixed routine briefly before the birds were permitted to enter the test. This fact facilitates the assumption that an associative rule was formed in this connection.

It should be mentioned that the manufactured tools tended to gain in length across sessions. This phenomenon can be seen as an updated associative rule that may have developed during the test to produce larger tools and in that way to gradually enhance the subjects' success.

As an alternative, I propose that the birds may acquire more proficiency in making cardboard tools with sufficient practice. In addition, the physical cost involved in tool production may consequently decrease, which can eventually lead to an acquisition of a similar strategy as in New Caledonian crows and woodpecker finches (Chappell & Kacelnik, 2002; Tebbich & Bshary, 2004). The latter species are both specialized tool users and were tested with manufacture material they already applied in their daily tool using routine. An interesting approach would be to supply them with novel materials that demand more effort in terms of tool production than simply cutting off a twig in order to test for a modification in their original strategy.

The ability of my subjects to evaluate the size of their tools relative to the reward distance is underpinned by the context-dependent variability with which already produced cardboard pieces were discarded prior to insertion into the tool opening. Often the birds approached the apparatus with a manufactured piece of cardboard, then dropped it briefly before inserting it into the tool opening and started to build a new one. The discarded cardboard pieces in the respective condition were significantly shorter than the required distance to obtain the reward. Longer pieces were discarded when the reward was further away, whereas shorter pieces were discarded when the reward was closer. This indicates that the birds seem to match the reward distance relative to the size of the cardboard piece in two ways: Once mentally before and once visually after the tool making process, shortly before the tool is inserted into the apparatus.

In the diameter test, most of our subjects were unsuccessful even at inserting a manufactured tool into the narrow tool opening. Only the female bird Fini accomplished this task. There is a possibility that she was sensitive to tool width, at least in regard to discarded tools.

Nevertheless, we have to submit to the fact that single subject designs have to be carefully controlled and since there is only a small number of discarded tools in the large condition (N = 5), we withhold from drawing any conclusions on the basis of these data.

Another factor is that there seemed to be a constraint to the width of the cardboard tool due to beak morphology. In Goffin's cockatoos the lower edge of the upper mandible has an almost 90° sharp curved angle from the tip of the beak to the corner of the mouth. During the tool making process, the edge of the cardboard block is pushed into the deepest possible point of the beak curve. In the meantime, the tip of the beak acts as an anvil whereas the cutting edge at the front of the lower mandible carves through the cardboard. This shows that the width of the cardboard tools is mainly defined by the distance between the tip of the subjects' beak and the deepest part of the curve on the lower edge of the upper mandible. Similar to many other parrot species, Goffin's cockatoos have a tendency to exhibit a slight gender dimorphism respective to body weight and beak size in particular: Males are normally slightly heavier and have larger beaks whereas for females it is the other way around (Forshaw, 2001). While measuring the above-mentioned beak distance in our birds, I actually found that this part of the beak was several millimetres larger in all males we tested in contrast to the female Fini. The manufactured tools of two males were generally slightly larger (by less than a millimetre) than their beak size, whereas the female Fini made tools that were almost just as wide as her beak size. The three other male subjects produced slightly smaller tools (up to 2 mm) compared to their beak, however they were still too wide to fit through the small tool opening in the diameter condition. Since the curve of the subjects' upper mandible defines the maximum tool width, the birds were incapable to manufacture a tool that is wider than their beak, at least when this specific tool manufacturing technique is used. Nonetheless, while it should be ergonomically possible for the birds to make their tools thinner, it is presumably not very practical given that the deepest point of the beak's curve can therefore not serve as support to hold the cardboard block in place while biting it off at the front of the beak.

Goffin's cockatoos, as well as rooks have been shown to be able to choose the appropriate forms (in terms of length and width) in tool selection tasks (Habl et al., 2017; Bird & Emery, 2009), however they are both not specialized in tool manufacture. My test subjects thus seem to be able to attend to width properties during tool use but do not seem to be able to flexibly produce those properties with tool manufacture. This further supports the assumption that their failure in the width test is ergonomical rather than cognitive.

In conclusion, my results support prior studies on Goffin’s cockatoos illustrating that they can not only select (Habl et al., 2017; Laumer et al., 2016), but also manufacture different tools depending on the task at hand (Laumer et al., 2017). When making cut-out tools, the birds display flexibility across conditions and they demonstrate very high success rates when using them. Furthermore, they seem to be capable of assessing when a manufactured tool is too short for success by comparing the length of their tool relative to the condition. This happens not necessarily during the manufacture process but briefly before bringing the tool in contact with the apparatus. However, there seems to be a restriction to their sensitivity to exact goal distances. It remains subject to future research whether this is a consequence of a manifested routine from the training procedure.

In addition, the fact that the birds don’t adjust the width of their tools to function could be a sign for a cognitive limit within their tool innovation abilities. However, the Goffin’s beak morphology as well as its technique to build cardboard tools suggests an ergonomical reason. Upcoming studies providing different types of materials that need less restrictive handling should be able to follow this up.

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9. Appendix

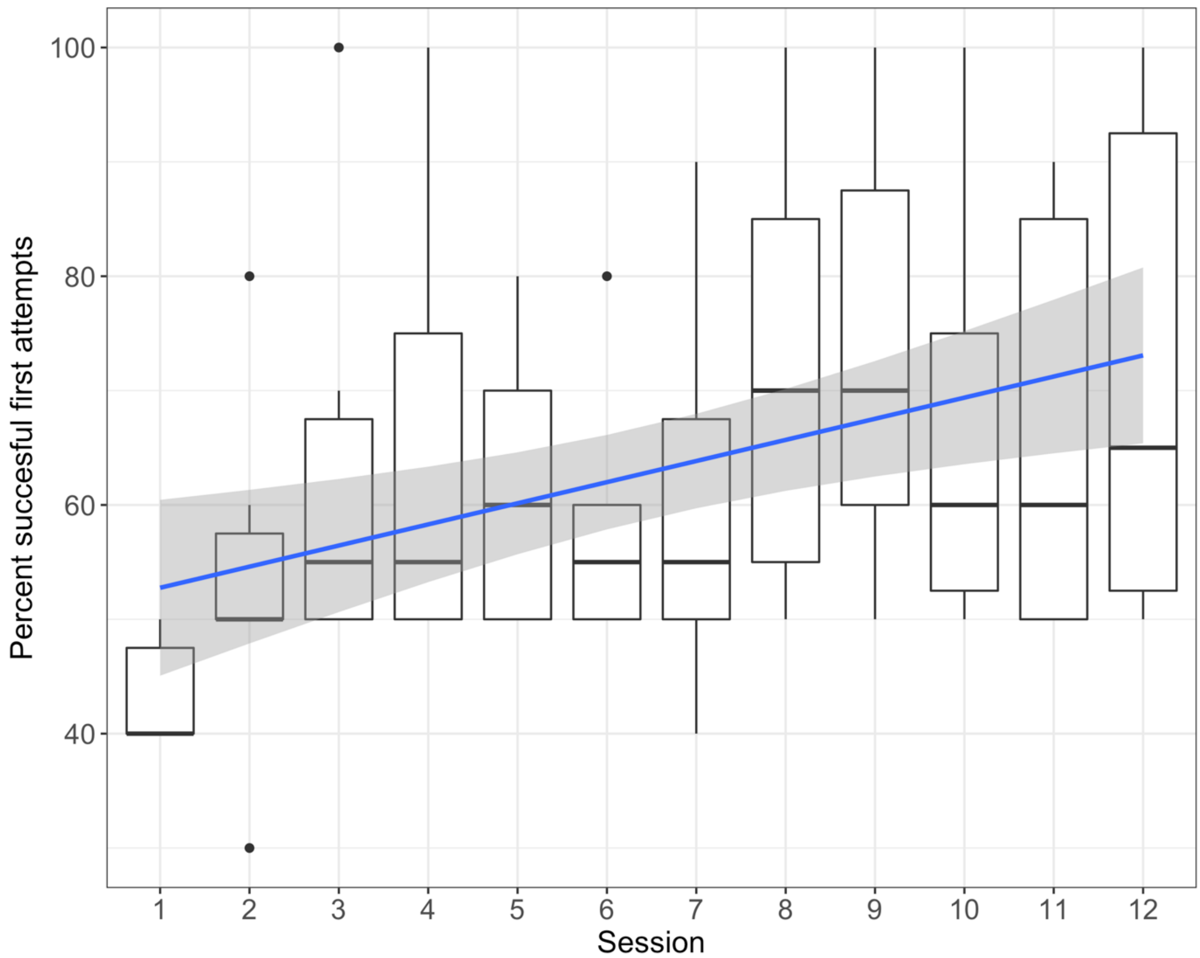

Figure A1: Percent of successful first attempts over sessions; blue line represents the fitted regression line; shaded area represents 95% confidence region; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

Table A1: Multiple comparisons of overall success rates in different conditions. P-values are adjusted for multiple comparisons.

Model: *first correct choices ~ Condition + Session + (1|Subject)*

Significance codes: *'***' for p < 0.001; '**' for p < 0.01; '*' for p < 0.05; '.' for p < 0.1*

	β	**Std. Error**	**z**	**p**	**Sig.**
Large vs. Far	28.91	0.476	6.071	<0.001	***
Near vs. Far	0.783	0.261	2.997	0.013	*
Small vs. Far	-37.33	0.375	-9.945	<0.001	***
Near vs. Large	-21.08	0.485	-4.344	<0.001	***
Small vs. Large	-66.25	0.588	-11.261	<0.001	***
Small vs. Near	-45.17	0.396	-11.412	<0.001	***

Table A2: Detailed contrast results for levels of tool application and distance to reward. P-values are adjusted for multiple comparisons.

Model: $\sqrt{Length}$ ~ *Distance/Use + Session + (1|Subject)*

Significance codes: *'***' for p < 0.001; '**' for p < 0.01; '*' for p < 0.05; '.' for p < 0.1*

	β	**Std. Error**	**z**	**p**	**Sig.**
40mm Discarded vs. 160mm Discarded	-10.885	0.3750	-2.903	0.0191	*
160mm Used vs. 160mm Discarded	22.852	0.3171	7.207	<0.001	***
40mm Used vs. 160mm Discarded	15.618	0.3225	4.843	<0.001	***
160mm Used vs. 40mm Discarded	33.737	0.3391	9.949	<0.001	***
40mm Used vs. 40mm Discarded	26.503	0.3324	7.973	<0.001	***
40mm Used vs. 160mm Used	-0.7234	0.2588	-2.796	0.0261	*

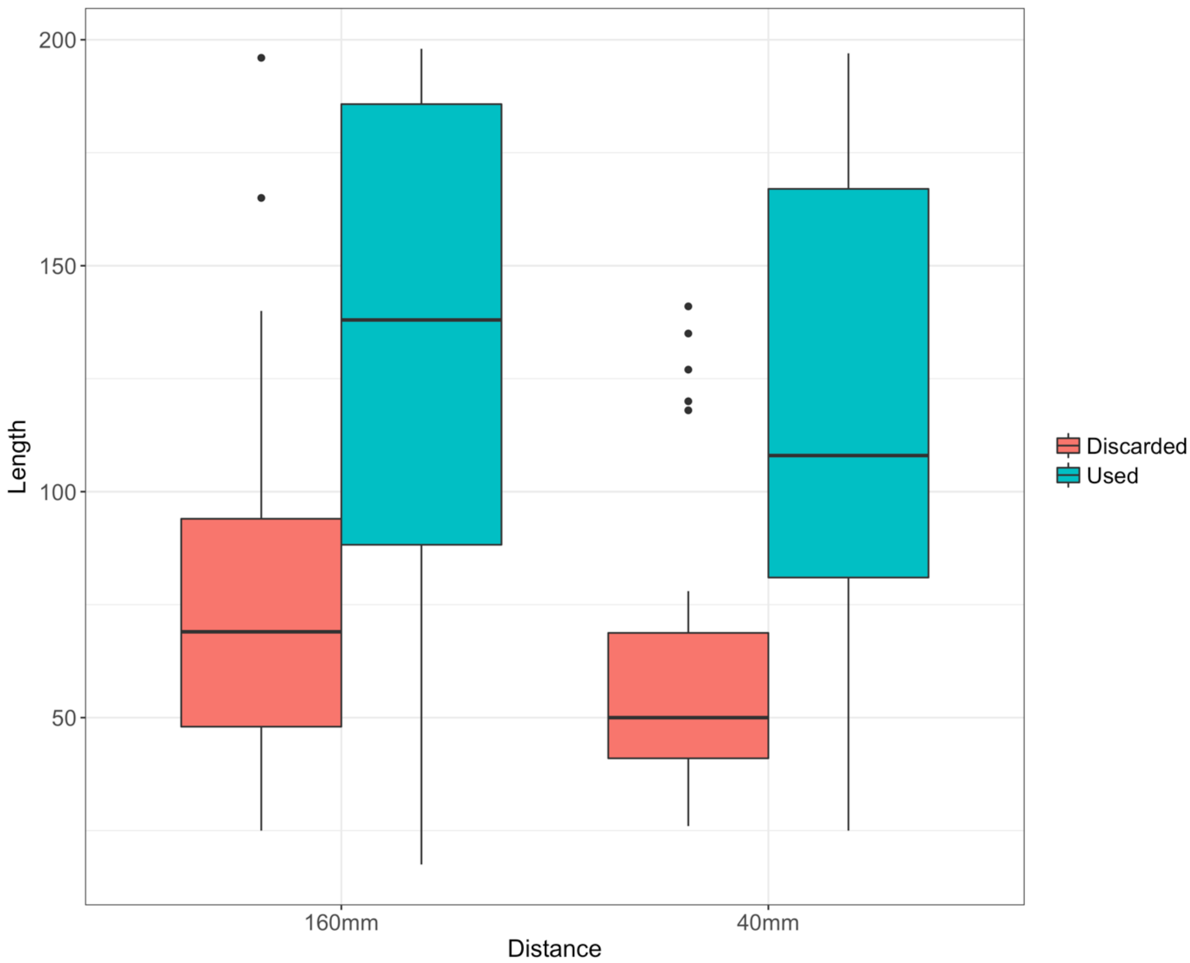

Figure A2: Length of employed and discarded tools in different distance conditions; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

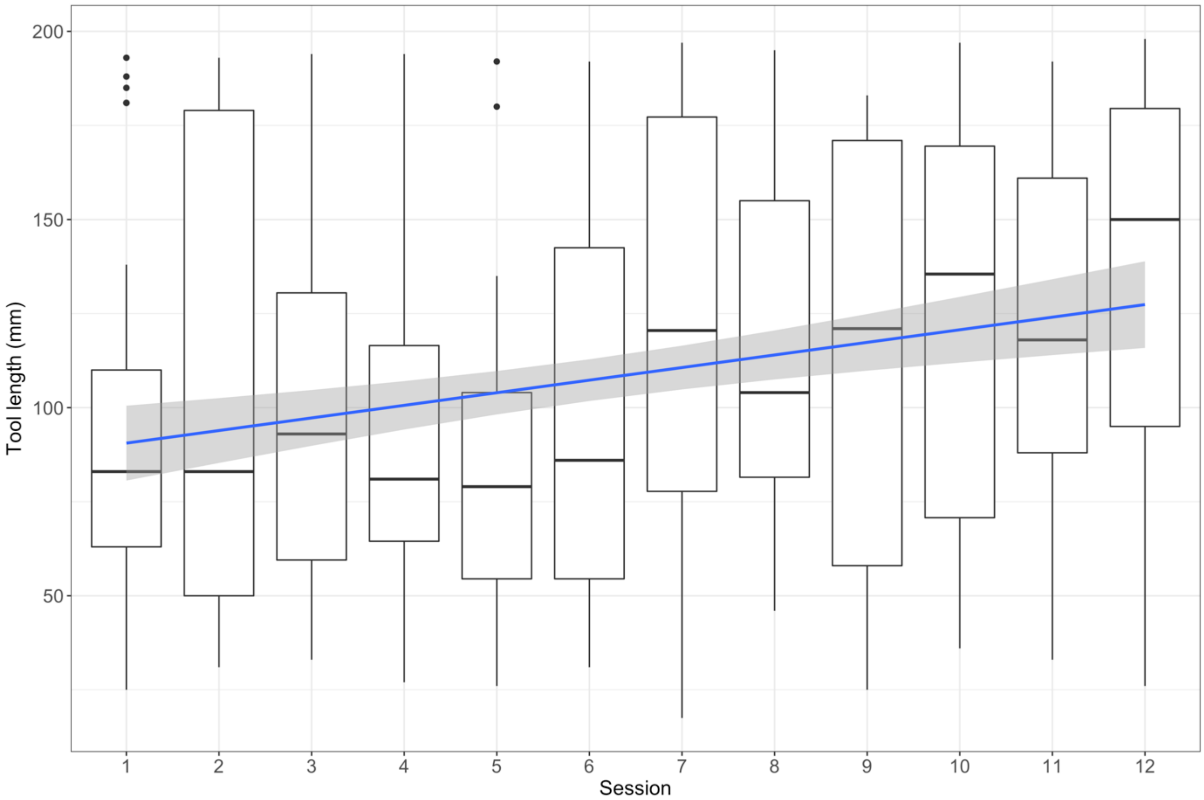

Figure A3: Length of tools in mm (discarded and used, smaller than 200 mm) in the distance test over sessions; blue line represents the fitted regression line; shaded area represent 95% confidence region; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

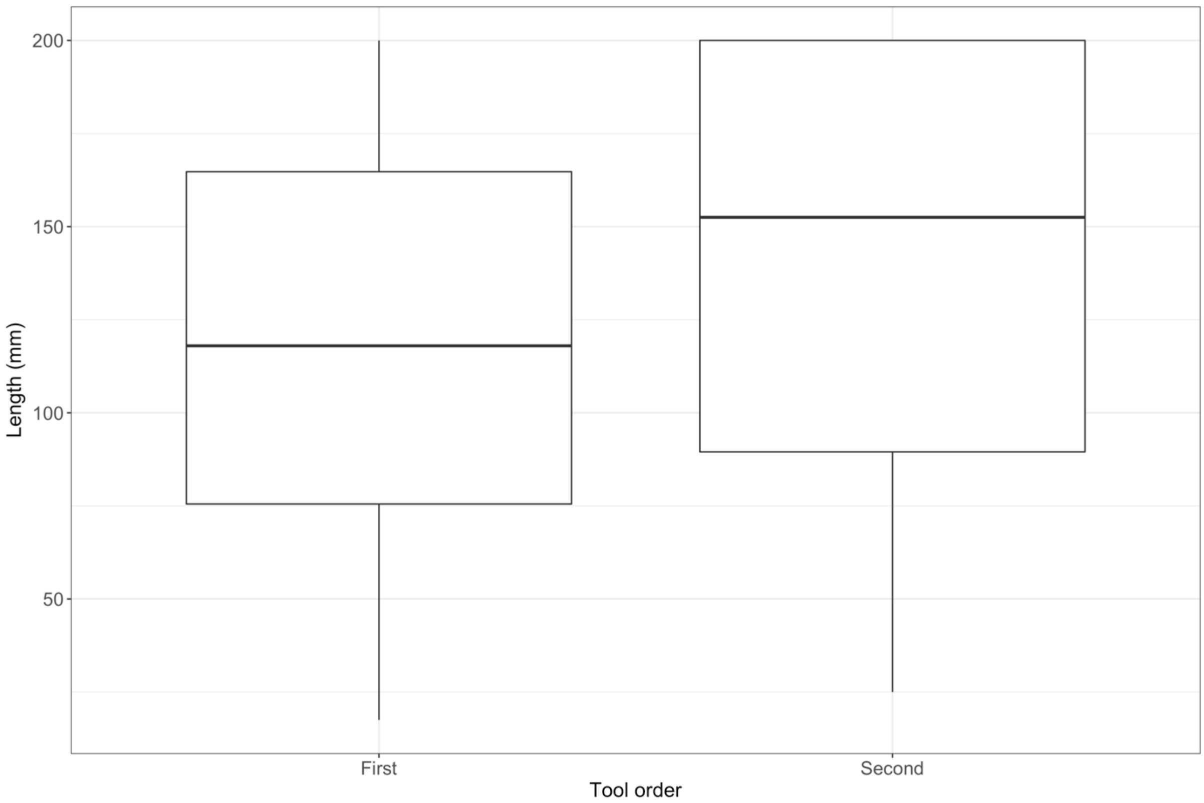

Figure A4: Differences in tool length between unsuccessful first tools and second employed tools (in mm); bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

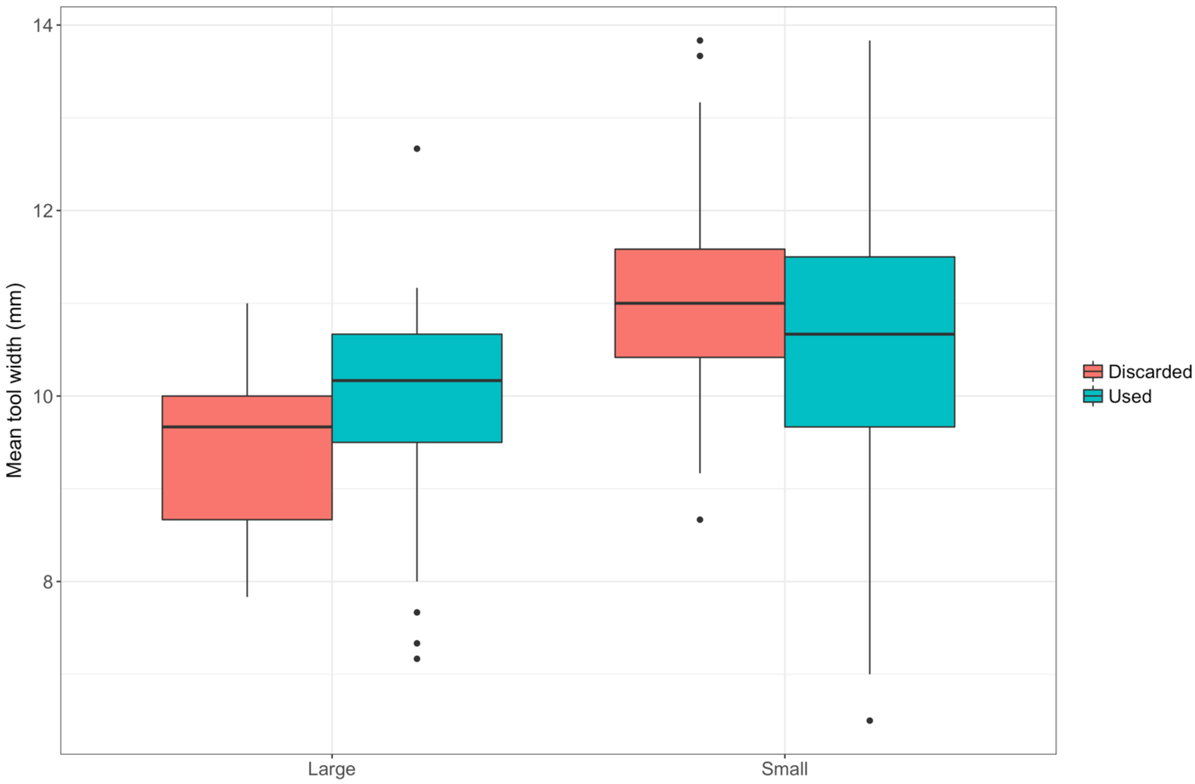

Figure A5: Mean width of discarded and used tools of Fini with large and small holes; bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

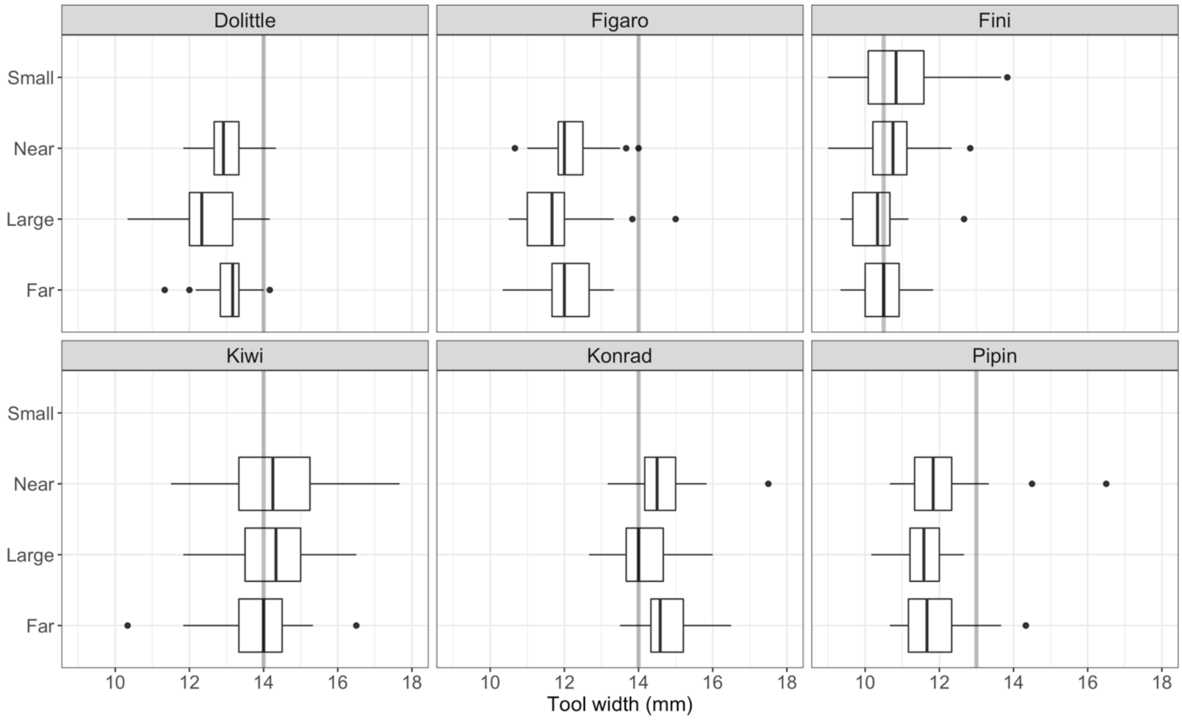

Figure A6: Width of tools (in mm) in different conditions for each subject compared to the distance between the tip of the beak and the horizontal part of the upper mandible (grey vertical line); bold horizontal lines indicate median values, boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

Figure A7: Photographs of the basic apparatus with exchangeable fronts and platforms. Photos by: Carina Köck