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The Role of Experience and Social Learning in the Tool Use and Tool Making of the New Caledonian Crow (*Corvus moneduloides*)

Review

Tool use and manufacture are central points in the development of human culture and certain sophisticated aspects of it are believed to be uniquely human. Studies of New Caledonian crows present findings that question this uniqueness by attributing highly sophisticated tool behavior to these crows. The purpose of this paper is to discuss this behavior and to present different theories on how this behavior is obtained. Recurring evidence supports the view that inheritance interacts with experience and social learning over the course of the development of tool use and tool manufacture, but further research is required to identify the extent to which each aspect contributes to it. Nevertheless, the behavior of the New Caledonian crow may offer a new perspective on animal cognition.

Keywords: social learning, development, tool manufacture

INTRODUCTION

Tool use and tool making in non-human animals have been studied intensely, but those non-human animals were mostly close relatives to humans, such as primates. In the past two decades researchers started to further investigate tool use in animals which are not related to humans, mainly a variety of bird species. Birds are frequent tool users, but due to the definition of 'true' tool use, which states that an object has to be held discretely in the hands or mouth to be considered a tool, many actions taken by birds do not classify as tool use (Lefebvre, 2002). However, a variety of bird species have shown extraordinary skills in the manufacturing and the use of tools classified as 'true'. Research on these bird species could help establish models of animal cognition and give a new perspective on human cognition. It is therefore of interest how these behaviors arise in these animals. Early research was conducted on woodpecker finches (Eibl-Eibesfeldt, 1961), but recent studies have focused on the abilities of the New Caledonian crow (Corvus moneduloides) specifically (e.g. Taylor, Hunt, Holzhaider & Gray, 2007).

The New Caledonian crow falls within the class of Corvidae, a class of birds encompassing, amongst others, crows, ravens, and jays. Most animals that fall within the Corvus family have displayed the use of tools in the wild (Beck, 1980), but so far only the New Caledonian crow has been observed to do so habitually, i.e. with frequent repetition (Hunt, 1996; Hunt & Gray, 2003). Hunt (2000, 2002, 2003, 2007) has spent a significant amount of time researching the New Caledonian crows and his findings propose new assumptions about aspects of tool use and manufacture in not human-related animals, such as using tools for the acquisition of more proficient tools (termed metatool use), human-like specializations, rule systems and underlying cognitive mechanisms.

Despite the amount of research done on this bird species and its tool behavior over the past decades, a number of questions still remain. One of the main questions regarding this behavior is its development. How does the New Caledonian crow realize a tool behavior that, as it seems, exceeds that of nearly every other non-human species? It is not yet clear on which mechanisms New Caledonian crows rely to acquire certain skills that are necessary to accurately make and handle tools. Some researchers support the view that the use and manufacture of tools is entirely inherent (Kenward, Rutz, Weir & Kacelnik, 2006), while others propose an interplay of possible inherent factors and experience or some form of social transmission (e.g. Hunt & Gray, 2013). This paper gathers early assumptions about the role of tools in the life of birds, as well as further investigations, new theories and, most importantly, recent studies on New Caledonian crows to get a better perspective on the role of social learning and experience in the manufacturing and use of tools within this species.

Pandanus tool use and goal-directed behavior

In humans, the use and the manufacture of tools is a common phenomenon with a high degree of diversification and the early stages of manufacture were defined by the alteration of what could be found in our environment (Hunt & Gray, 2004a). This process is characterized by appropriate material selection, preparational manufacture and sculpting (Oakley, 1967). The latter, fine sculpting, is believed to be a uniquely human skill, while material selection and preparations, such as trimming, are more frequent in non-human species including the woodpecker finch (Cactospiza pallid) and chimpanzees (Pan troglodytes) (Beck, 1980). However, the New Caledonian crow (hereafter mainly referred to as NC-crow) shows tool manufacture skills that can be described as sculpting (Hunt, 2004b). These animals are stick-tool users and either shape hook tools from sticks (Hunt, 1996; Weir, Chappell & Kacelnik, 2002) or, a more frequent phenomenon in wild NC-crows, manufacture tools from the blade-like leaves of the Pandanus, Pandanus spp., tree (Hunt & Gray, 2004a).

The wild NC-crows manufacture their Pandanus tools by ripping off the hooked edges with their beak (Hunt, 1996; Hunt & Gray, 2004a), but do not alter the acquired tools afterwards (Hunt, 1996). This way of tool acquisition leads to leftovers which work as artefactual evidence of the tool manufacture process. These leftovers are leaves which are still attached to the tree and form nearly perfect counterparts to the tools used by the crows (Hunt, 2000). Evidence for diversification (Hunt & Gray, 2004a), the non-random use of the leaf's hooks in foraging (Hunt, 1996) and the stepped process of manufacture (Hunt & Gray, 2003) contrast with contemporary beliefs of non-human tool manufacture which tend to exclude goal-directed, specialized sculpturing (Hunt & Gray, 2004b).

Further evidence for goal-directed tool behavior that includes sculpting and tool selectivity comes from laboratory studies about NC-crow's hook shaping. Weir et al. (2002) studied two New Caledonian crows, one female and one male, by placing a food reward into a transparent vertical tube and leaving the crows only a straight piece of garden wire for assistance. The female crow repeatedly bent the wire and retrieved the food, thereby expressing the ability of modifying tools specialized for a certain task, but the male refused to participate in the task and resorted to stealing the female's food reward. However, with only one individual per sex, behavioral differences cannot be attributed to sex differences without additional testing with a bigger sample size. In general, conclusions based on the behavior of a single individual should be viewed with caution. Further, while the female crow had never witnessed the bending of wire, she did observe goal-directed use of hooked wires on at least one occasion (Weir et al, 2002) and therefore it cannot be concluded that this process of tool manufacture was not influenced by social transmission. Nevertheless, these observations are evidence for purposeful tool manufacture that goes beyond simple selection and trimming (Weir et al., 2002).

The acquisition of tools made from Pandanus leaves can either be a result of trial-and-error, a process that does not involve predetermination of a certain goal design, or of a rule system which includes specific rules to achieve a certain goal (Hunt, 2000), in this case that of a certain design. Recurring evidence supports the presence of a rule system rather than trial-and-error to be involved in the tool manufacture of NC-crows (Hunt, 2000). Chappell & Kacelnik (2002) showed that NC-crows are capable of selecting appropriate tools without the need of trial-and-error and therefore give evidence for the NC-crows' ability to at least partly understand functional attributes of objects. At that time, only two other studies that presented evidence for non-primate tool selectivity existed, one with black-breasted buzzards (Aumann, 1990) and the other with Egyptian vultures (Thouless, Fanshawe & Bertram, 1989), but the study by Chappell & Kacelnik (2002) differs from these studies in that they changed the task and the required tool with each trial. The main task for the NC-crows was to choose from an array of differently long sticks and use one to acquire a food reward within a transparent horizontal pipe. The birds seemed to execute two different strategies during the trials and either chose the longest stick or the matching stick. However, if they chose an unfitting stick from those given, they discarded it immediately. This type of behavior is evidence for tool selectivity in terms of the tool's length (Chappell & Kacelnik, 2002).

Acquisition and development of tool use and manufacture

Generally, the discussion of causal factors in the use and manufacture of tools by the New Caledonian crow revolves around the nature-nurture debate, that is, how much causation can be attributed to external factors, such as experience, and how much to inherent factors, such as genetic make-up. Hunt & Gray (2003) studied tool manufacturing from Pandanus leaves by the wild crows in New Caledonia based on artefactual evidence, i.e. the leaves themselves and their counterparts. They concluded that a possible external factor could be cultural transmission. Supporting evidence for a significant role of cultural transmission lies in the geographical distribution of differently shaped stick tools used by NC-crows, whereby three different styles of tools geographically overlap at one location and seem to have developed from one original, simpler tool (Hunt & Gray, 2003). This finding supports a cumulative evolution of tools within the species, a phenomenon that to that time had only been observed in humans (Hunt & Gray, 2003).

Cumulative evolution requires three distinct characteristics to be identified as such: diversification within the design of a tool; original and simpler tools from which modern tools developed; and a transmission by means of social learning (Tomasello et al., 1993; Foley & Lahr, 1997). Hunt & Gray (2003) investigated the three characteristics within the tool behavior of New Caledonian crows and found an indication of rudimentary cumulative evolution. Their study was based on the sampling of leaves from which NC-crows had already obtained tools and comparing them based on their geographical location, shape and the technique of manufacture. Leaves where sampled at 21 locations in New Caledonia and from those the presence of three designs, three types of manufacture and a differentiated distribution across the locations became apparent (Hunt & Gray, 2003). Hunt & Gray (2003) proposed a chronological evolution starting with a wider tool without any stepping, i.e. a simple strip of the leaf's edge, that evolved into a narrow, multi-stepped tool. The narrower, multi-stepped tool has a functional advantage in handling and precision and is more widespread than the simpler tool, thereby showing characteristics of cumulative evolution of its manufacture (Hunt & Gray, 2003).

Another approach to the underlying mechanisms of the skill acquisition is based on a number of learning paradigms of which two are noteworthy: operant conditioning and perception-action development. The two paradigms differ in their source of reinforcement during the act of tool use. Operant conditioning explains the NC-crow's behavior only in the presence of a food reward or thereafter (Kenward et al., 2006) and the paradigm of perception-action development explains active tool use based on reinforcement lying within the act itself (Gibson & Pick, 2000). According to Kenward et al. (2006) it is possible that these animals possess an innate tendency for object exploration which develops into functional tool use and tool manufacturing when being coupled with a form of learning.

Furthermore, the evidence of spontaneous metatool use by the NC-crows suggests that analogical reasoning could function as an explanation for their higher physical cognition (Taylor et al., 2007). Metatool use, the use of tools to create more proficient tools, poses a number of requirements, including the recognition of the capability of using tools in relation to objects that are not food, the inhibition of animalistic instincts and the ability to use behaviors that are organized in a hierarchical fashion (Byrne & Byrne, 1993; Byrne & Russo, 1998). The first requirement is said to be based on the ability to reason analogically (de Beaune, 2004). Analogical reasoning describes the mental process of using the experience of a prior task and applying it onto a similar novel task. Taylor et al. (2007) proposed that analogical reasoning may have been the means by which NC-crows managed to solve the metatool task and additionally presented again that NC-crows do not solve problems with the trial-and-error strategy.

The quick and successful solving of novel problems (Weir et al., 2002) and the discarding of insufficient tools before a trial-and-error phase (Chappell & Kacelnik, 2002) could be explained by insight. Insight is the concept of a sudden, rather than a gradual acquiring of a solution for a problem and this concept is rarely observed in non-humans (Kenward et al., 2006). It would account for certain aspects in the tool behavior of New Caledonian crows, but considering its ambiguity in overt behavior and its inability to explain the emergence of tool use in children (Lockman, 2000), it cannot be concluded that tool use in New Caledonian crows is based only on insight. Nevertheless, continuous experience of tool use could lead to the emergence and use of insight in adult NC-crows (Kenward et al. 2006).

Additionally, some researchers believe in a strong genetic component underlying the actions of New Caledonian crows and some hypotheses go as far as stating that the tool behavior is entirely under genetic control (Kenward et al., 2006). However, it is difficult to conclude the causal properties of inheritance based on direct observations and both, genetic control and learning theories, do not exclude each other (Kenward et al., 2006).

The development of tool use and tool manufacture may give an account on which of these approaches to underlying mechanisms may be the most likely and how great the influence of experience is. Auersperg et al. (2014) observed object play in crows and other birds and noted that juvenile crows show a high degree of playful manipulation, while adult crows show no playful engagement with inedible objects at all. This finding supports a combined role of inherited curiosity and experience and the possibility that tool use emerges spontaneously during the period of object play and then diminishes after crows acquire a functional understanding of objects (Kenward, Schloegl, Rutz, Weir, Bugnyar, & Kacelnik, 2011).

DISCUSSION

The tool use and tool manufacture as observed in New Caledonian crows exceeds the early beliefs on non-human tool behavior. The NC-crows' behavior as observed over the past decade raises new questions regarding the cognitive capabilities of non-primate animals. How do these crows realize a behavior that we long believed to be dependent on human-like cognitive capacities? It is not yet clear which exact mechanisms underlie their behavior, but a combination of inheritance and experience is likely. The engagement in tool behavior without prior observations of such (e.g. Kenward et al., 2005) excludes social learning as a necessary factor for the emergence of tool use. However, social and cultural transmission are likely to shape later tool use as well as tool manufacture (Hunt & Gray, 2003). This is also supported by studies that included human demonstrations of tool use to the NC-crows (Kenward et al., 2005). Furthermore, the act of engaging in playful behavior that does not involve a food reward (Auersperg et al., 2014) suggests that the possible learning aspect involved is based on perspective-action mechanisms. In contrast to operant conditioning, these mechanisms propose the act of discovering as a reward itself (Gibson & Pick, 2000).

It is important to note that there have not been any findings to support the role of direct imitation in the acquisition as well as the development of tool use and tool manufacture in this animal. New Caledonian crows are capable of using and manufacturing tools without having observed these actions by another member of their species (Weir et al., 2002; Kenward et al., 2005). The crows do pay close attention to demonstrations by humans, but there is no apparent difference between the behaviors of tutored and untutored crows (Weir et al., 2002).

So far it can be concluded that the tool use and manufacture is at least partly innate, meaning that those traits are present even in those individuals not exposed to any display of tool use or manufacture, and partly shaped by experience, whereby the latter may account for individual differences that can be observed in tool designs (Kenward et al., 2006). But while there is no doubt that tool use and tool manufacture in New Caledonian crows is highly sophisticated, there is still the need for further research on the exact mechanisms underlying the behavior. Especially the extent to which such abilities are inherited or learned requires further examination and may shed a new light on how we view the human's uniqueness as well as our view of animal cognition. Since a lot of research is based on animal models, a full understanding of animal cognition may advance the development of such models and the ability to translate them into human models. Additionally, further research is needed to conclude which higher-cognitive functions are necessary and present in the NC-crow.

Hunt (2000) proposed the possibility of a left hemisphere specialization in New Caledonian crows which gives rise to tool use in a fashion similar to handedness as observed in humans. Replication of these findings is required to infer such a human-like specialization, but it is a first look at the cerebral level which generally needs further investigation in relation to tool use and tool manufacture in this species. The studies reviewed in this article base their conclusions mainly on observational data and no studies on possible genetic components have been reviewed. The lack of data on an inherited factor in tool behavior does not equal its absence. The current state of research does not allow a conclusion of definite factors that play a role in the crow's tool behavior or of how much they play a role. It is therefore necessary to further investigate the role of external and inherent factors.

However, the findings show that the New Caledonian crow might be a good model in relation to mechanisms that underlie the development of sophisticated tool behavior and their interactions. Due to the important role of tool technology in human culture this poses a central issue in understanding it (Kenward et al., 2005) and further findings related to the New Caledonian crows' tool behavior development could also contribute to our knowledge and understanding of the development of tool behavior in other animals.

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